I. Plenary Lectures

Comparative Vertebrate Neuroanatomy: Diversity in Brain Evolution Across the Taxon

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The extensive data now available on brain anatomy in all of the major vertebrate radiations—cyclostomes, cartilaginous fishes, ray-finned fishes, and tetrapods—are of interest not only for understanding the diverse lines of brain evolution but also for their more general implications, including theoretical aspects of how and what homology is and bioethical issues ranging from animal welfare considerations to how consciousness evolved and what its neural substrate consists of. To address these issues, the breadth of diversity in brain evolution will be surveyed first. From comparative studies, models of the earliest vertebrate brains and how brain evolution has proceeded within each radiation can be constructed. Common features of vertebrate brains will be considered first, including postulated features in the earliest vertebrates, and then some of the specializations that have evolved in various groups. These findings and hypotheses of homology are based on cladistic analyses of data mostly derived from extant species, since most neural features are not preserved in the fossil record. The methodology will be considered in the context of the current views of homology and the implications of new findings of shared gene-expression patterns that are more widely based than all instances of consistent phenotypic expression of particular traits. Finally, the findings of different degrees of elaboration and expansion of various brain regions in different vertebrate radiations has profound bioethical implications, including the questions of how consciousness—from basic sensory awareness to very high levels—is generated by neurons and in which groups of animals it is present. The comparative method may have the highest potential for yielding insight into these tantalizing questions. Common features of the brain across all vertebrates (the term vertebrates used here as synonymous to the term craniates, i.e., to include cyclostomes as monophyletic and as the outgroup to jawed vertebrates) include the three major brain divisions of forebrain, midbrain, and hindbrain. The forebrain consists of a telencephalon rostrally, which includes a dorsal portion, the pallium, and a ventral portion, the subpallium, and the diencephalon caudally with its four main divisions, one of which is the dorsal thalamus, which relays ascending sensory inputs to the telencephalon. The midbrain roof is involved in spatially mapping sensory inputs, while the ventral part of the midbrain and the hindbrain are the site of multiple cranial nerve sensory and motor nuclei, as well as the reticular formation, which has diverse motor and integrative functions, and the cerebellum, which is involved in motor control. In contradiction to the now out-dated but persistent notion of a *Scala Naturae*, brain evolution has proceeded independently within each major radiation. Two groups across the radiations can be recognized based on the degree of brain elaboration, i.e., neuronal proliferation and migration and thus the degree of enlargement and complexity of brain structure. Group I consists of those species with relatively little elaboration and includes lampreys, some sharks, non-teleost ray-finned fishes, and amphibians (as well as lungfishes and crossopterygians). Group II, whose members have relatively elaborated brains, include hagfishes, other sharks and skates and rays, teleosts, and amniotes. Thus, it is clear that brain elaboration has occurred independently at least four times across the vertebrate spectrum. Further, different parts of the brain are differentially elaborated in various groups, from the huge cerebellum of mormyrid fishes, to the taste lobes in the hindbrain of some other teleosts, to the large telencephalic pallium of Group II cartilaginous fishes and, independently, in mammals and birds. In evaluating homologies, multiple neural criteria are used, including relative topographic (or topologic) position of a given neuronal cell group, its afferent and efferent connections, morphological and histochemical similarities of the neurons, and embryological origin. These criteria are usually used to assess historical, or phylogenetic homology, noting the distribution of the neural character across a phylogeny generated from non-neural traits. Recent examples of neural characters with multiple and minute similarities but with sporadic, non-congruent phylogenetic occurrence, which might be regarded as distant parallelism, and also cases of reversal, might now be considered to be syngeny, or generatively homologous, i.e., based on the inheritance of their patterning genes from a common ancestor. Most instances of historical homology are also cases of syngeny, the opposite condition being allogeny, which essentially equals convergence. Likewise, the concept of field homology has been bolstered by illumination of developmental events. Functional characteristics, including neuronal physiology and correlated behavioral outcomes, are not appropriate criteria for any kind of homology, however, but rather indicate similar function, i.e., analogy.

Comparison of the telencephalic pallium (and some other elaborated dorsal neural derivatives) across Group II vertebrates implies that both shared patterning genes for elaboration plus unique gene expression patterns and/or timing differences contribute to substantial diversity of neural architectures, and controversy persists over possible homological relationships of some pallial areas, particularly between mammals and sauropsids. Both the pallium—specifically mammalian neocortex—and dorsal thalamus have been hypothesized to be involved in the generation of consciousness, including the higher-order consciousness of humans. However, while much of the research on cognitive abilities has focused on mammals, and on humans in particular, recent studies on birds have revealed cognitive abilities in some species of a surprisingly high degree. Since higher-order consciousness is correlated with high levels of cognitive abilities in humans, it is parsimonious to hypothesize that this correlation holds for other vertebrate species as well, with the important caveat that absence of cognitive ability does not guarantee absence of consciousness. Nonetheless, the strategy of comparing the behavioral abilities of birds and mammals, including humans, and comparing their neural circuitry and related features may contribute to elucidating the neural basis of consciousness. Similarities do not include some specific architectural features of mammalian neocortex, which birds lack, but do include circuitry that operates by inhibition of inhibition mechanisms, allowing for the generation of synchronous activity by pallial neurons.

Understanding Muscle Performance: The Structural and Molecular Basis of Function

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When animals move they make use of a multitude of specific design features of their muscular system which characterize muscle on different levels of structural organization as well as with regard to particular functional properties of muscle tissue components. On the macroscopic level it is found that parallel fibered muscles and pinnate muscles perform differently with regard to speed of contraction, excursion and force per muscle cross-sectional area. Looking at the microscopic composition of muscle cells, we find that muscles that are active most of the time such as the heart and the diaphragm contain many more mitochondria and capillaries than locomotor muscles that are used only occasionally. Speed of contraction of muscle is further regulated by particular characteristics of the myosin molecule and associated proteins which come in several molecular configurations. Of particular interest is the malleability of skeletal muscle tissue. Massive changes in muscle structure and function can be induced rapidly using specific exercise regimes. The advent of appropriate molecular tools has enabled us to begin to study the mechanisms of muscle plasticity. Muscle cells rely on external mechanical, metabolic, neuronal and metabolic signals which are sensed and transduced over multiple pathways to the muscle genome. In exercise many of these sensory and stimuli dependent signaling cascades are activated, the individual characteristic of the stress leading to a specific response of a network of signaling pathways. Signaling typically results in the transcription of multiple early genes among those of the well known *fos* and *jun* family as well as many other transcription factors. These bind to the promoter regions of downstream genes initiating the structural response of muscle tissue. While signaling is a matter of minutes, early genes are activated over hours leading to expressional modifications of structure genes that can then be effective over days. The multiplicity of the signaling pathway and of the early gene activation leads to a bewildering number of possible genomic responses. The response is tailored by "structural" genes having promoter regions capable of recognizing a host of activators and depressors. The current molecular techniques are in principle capable of dealing with the task of unraveling the

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enormous complexity of genomic response to external stimuli. Changes over the entire transcriptome can be assessed with appropriate array technologies and proteomic approaches are rapidly developed. The current molecular techniques paint a fine picture of the modulatory events involved in muscle malleability. This will potentially enable scientists to demonstrate adaptive patterns long before structural, let alone functional tests discern the changes orchestrated by the underlying genomic phenomena. The challenge that molecular exercise scientists face currently and in the near future is to extract the biologically relevant information from the sheer mass of data generated by the available technology and to integrate this information into models of system physiologic relevance.

Odd Morphologies in Early Fossil Vertebrates: The Limits of the "Anatomically Possible"

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Living and fossil jawed vertebrates (gnathostomes in the classical sense) display a wide range of morphological disparity, like skates, seahorses, snakes, birds, or whales, compared to generalized representatives of their respective groups. However, their anatomy is amenable to a small number of constant structures that compose what is generally referred to as a "Baublan", often erroneously referred to as the "vertebrate Bauplan" (and abusively exemplified by shark anatomy). Each of the two living groups of jawless vertebrates, hagfishes and lampreys, display a remarkably homogeneous morphology, respectively, but differ from jawed vertebrates by a number of fundamental characters, in addition to the lack of vertically biting jaws and paired fins. Whether these jawless vertebrates provide any information on the 'vertebrate Bauplan', or not, largely depends on whether they are a clade (the cyclostomes), as suggested by current molecular phylogenies, or a grade (hagfishes being the sister group of lampreys and jawed vertebrates), as suggested by morphology- and physiology-based phylogenies. Palaeontological data show that the morphology of these living jawless vertebrate taxa has been remarkably stable for at least 310 million years (Myr) for hagfish and 360 Myr for lampreys. However, the morphological disparity of jawless vertebrates is documented by major extinct taxa, notably the armoured jawless vertebrates, or 'ostracoderms', which lived 470–360 Myr ago, and are currently considered as stem gnathostomes, although they lack jaws. These taxa generally possess a mineralized skeleton and, therefore, part of their anatomy can be assessed on objective grounds. Each of them, such as osteostracans, galeaspids, or heterostracans, respectively, show a relative morphological homogeneity, but display particular characters that are strongly at odds with their homologues in either cyclostomes or jawed vertebrates, and somewhat defy current conceptions about the 'vertebrate Bauplan.' An example is the branchial apparatus of osteostracans, which is almost incapsulated in the braincase and shoulder girdle, and lies far more anteriorly, relative to the brain, than in any other vertebrate group. The most spectacular anatomical oddity of these forms is polybranchy; that is, the considerable increase of the number of gill arches, up to about 45 in the Devonian galeaspids and 33 in the Silurian-Devonian euphaneropids. In the latter, the branchial apparatus extends posteriorly to the anal region, thereby imposing an unusually dorsal position to the digestive tract. Hagfishes, which possess 5 to 15 gill pouches, are the only instance of living vertebrates in which the number of gills exceeds 7 and is inter- and intraspecifically variable, but this feature has rarely raised interest, possibly because hagfish development was almost unknown until recently. Classical model vertebrates for developmental studies are lampreys (7 gill arches) and jawed vertebrates (7–5 gill arches or less). It is surprising that the number of gill arches in a small group of about 60 known galeaspid species ranges from eight to 45; that is, at the limit of the "anatomically possible", whereas it is never more that five to seven in the 24500 species of living piscine gnathostomes. The anatomy of the major fossil jawless vertebrate taxa known to date suggests a much greater morphological disparity, and perhaps developmental plasticity, than that of living vertebrates (in particular crown-group gnathostomes), as to certain reputedly fundamental vertebrate structures, such as the branchial apparatus, the extension of the paired fins relative to the body axis, or the histological structure of hard tissues. Before the rise of mineralized hard tissue (bone, teeth, calcified cartilage), the information provided by early fossil vertebrates preserved as soft-tissue imprints are scarce. However, thanks to recent advances in understanding the process of exceptional soft-tissue preservation, a number of these forms now yield anatomical information that is relevant to their position in the vertebrate tree. Some of these partly or entirely soft-bodied forms, such as euphaneropids or euconodonts, are probably stem gnathostomes, stem hagfishes and lampreys, but others, such as the early Cambrian myllokunmingiids and yunnanozoans are likely to be stem vertebrates, somehow "filling" the morphological gap between cephalochordates and vertebrates. However tenuous may seem the anatomical information these fossils provide, such as myomere shape, or presence of sensory capsules, heart and gonads, they are the only data one can expect for this basal segment of vertebrate phylogeny. Admittedly, some of these anatomical features could be theoretically predicted by the current living vertebrate tree, as component characters of hypothetical ancestral morphotypes at nodes, but being able to provide their actual minimum age is, after all, a remarkable piece of luck that should not be regarded as merely anecdotal.

New Insight Into the Morphology of the Cardiac Outflow Tract in Chondrichthyans and Actinopterygians: Implications for Heart Evolution

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The heart of chondrichthyans and actinopterygians is considered to be formed by four chambers, with blood flowing through the sinus venosus (inflow tract), atrium, ventricle, and outflow tract. It is widely reported that the cardiac outflow tract of the chondrichthyans consists of the conus arteriosus, a contractile chamber whose walls are composed of cardiac muscle overlying an elastic fibrous coat; it connects the ventricle with the ventral aorta. A well-developed conus also exists in basal actinopterygian taxa such as the polypteriformes and lepisosteiformes. In the acipenseriformes, amiiformes, and in some basal teleosts, an intrapericardial, nonmyocardial chamber, the bulbus arteriosus, is interposed between the conus and the ventral aorta. It is generally assumed that in most teleosts, the conus arteriosus is vestigial or even absent, a fact which is concomitant with the remarkable development of the bulbus arteriosus. Recent work has contradicted the classical viewpoint that in teleosts, the conus arteriosus has been lost throughout evolution. The data reported prove that a distinct conus arteriosus lies between the ventricle and the bulbus arteriosus in phylogenetically advanced teleosts. The morphology of the teleostean conus varies according to the structure of the ventricular myocardium. Nonetheless, the conus displays specific anatomic, histochemical, and immunohistochemical characteristics that distinguish it from the ventricle. Embryonically, the conus arteriosus appears earlier than the bulbus arteriosus, yet it shows a negative allometric growth with regard to the bulbus. The embryonic conus forms the mesenchymal cushions from which the conal (not bulbo-ventricular) valves develop. The spatial arrangement of the conal myocytes suggests that the conus is implicated in the mechanical performance of the valves.

The actinopterygian bulbus arteriosus is an elastic chamber, whose walls usually contain smooth musculature. In phylogenetically basal taxa, the bulbus displays a tubular shape, but in most teleosts, it is swollen proximally and tapers distally into the ventral aorta, though a large variety of shapes occur within these parameters. Despite the wide range of structural variants, the bulbus seems to perform the same function in all species, namely, it acts as an elastic reservoir or 'Windkessel' during cardiac cycle, thereby protecting the gill vasculature.

A comparative study still in progress on the cardiac outflow tract morphology has corroborated the former, hitherto neglected observation that in chondrichtyians, a distinct, nonmyocardial segment connects the conus arteriosus with the ventral aorta. This segment, located within the pericardial cavity, is almost tubular in shape, showing arterial characteristics. However, its walls, which are crossed by the coronary artery trunks, differ histologically from those of the ventral aorta. Embryological data indicate that this intermediate segment is morphogenetically equivalent to the bulbus arteriosus of sturgeons and teleosts. Therefore, the bulbus arteriosus cannot be furthermore regarded as an apomorphy of the actinopterygians; it probably appeared in a yet undetermined, early period of the craniata (vertebrate) evolutionary story.

The chondrichtyian bulbus largely varies in size and structure between species. Preliminary data point to the possibility that this variation is related to the biology of species. The bulbus seems to be more developed in speedy swimmers than in slow and sluggish animals.

The embryonic origin and morphologic significance of the bulbus arteriosus have been a matter of controversy. Several authors have considered that the bulbus is a backward extension of the ventral aorta into the pericardial cavity: it cannot be a cardiac chamber, because it lacks cardiac muscle. The observations of other authors have led to the assumption that

the bulbus originates as a modification of the anterior part of the conus arteriosus, i.e., that the bulbus is of cardiac origin.

Recently, it has been shown that the teleost bulbus becomes specifically labelled by the fluorescent nitric oxide indicator 4,5 diaminofluorescein diacetate (DAF-2DA) throughout development. This is also the case for the chondrichthyan bulbus, a fact which supports the assumption that this chamber and the actinopterygian bulbus are homologous. DAF-2DA also marks the arterial pole of the chick heart, i.e., the base of the aorta and pulmonary artery. Taking into account that this region in the chick is not considered to be part of any heart chamber, it has been concluded that the bulbus cannot be regarded as a genuine cardiac component.

Most information on "fish" heart development comes from studies carried out in actinopterygian representatives. Currently, it has been assumed that in this group, the myocardium of the developed heart originates from bilateral primary heart fields located in the lateral plate mesoderm. However, data from zebrafish indicate that in contrast to other vertebrates, cardiac neural crest cells migrate into most embryonic segments of the teleost heart, contributing to cardiomyogenesis. It is well known that in birds and mammals, new cardiac segments are added to the embryonic straight heart tube during looping. The definitive inflow tract myocardium is generated from a caudal continuation of the primary heart fields, whereas the outflow tract myocardium derives from a population of cells which reside in the splanchnic and pharyngeal mesoderm, constituting the so-called anterior or second heart field. The smooth muscle tunics of the aorta and pulmonary artery are neural crest-derivatives. However, the prospective smooth muscle cells that form the proximal walls of both arterial trunks are derived from the secondary heart field. This fact, together with the results of bulbus labelling mentioned above suggests that a second heart field might exist in chondrichthyans and actinopterygians. This opens a wide field for further investigation that should throw new light on the morphogenesis of the bulbus arteriosus and conus arteriosus. In addition, it should contribute to the establishment of homologies between these cardiac structures and the components of the arterial pole of the tetrapod heart, a crucial aspect to reach a more accurate morphologic definition of the vertebrate heart and a better understanding of its evolution.

"Form and Function" 200 Years Ago: A Tribute to Georges Cuvier for his Contribution to the Understanding of Animal Morphology

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Two hundred years ago, after the French Revolution, the Museum d'Histoire naturelle in Paris became a world center for the study of the life sciences. In the Jardin des Plantes, Georges Cuvier, Etienne Geoffroy Saint-Hilaire and Jean-Baptiste Lamarck worked with passion and emulation on the anatomy of living and extinct animals. The first one had just published his *Leçons d'Anatomie comparée* forwarding a functional approach of the study of the living beings. He had just finished a fruitful study of the *Elephans vivans et fosssiles* and he had started new researches on the fossil bones from the gypsum of the Montmartre hill. The second was publishing notes on the anatomy of the pectoral fin of fishes and on the skull of crocodiles and birds with a structural approach of the unity of plan among vertebrates. The third had just read his public lectures *Les animaux sans vertèbres* and was writing his famous book, *La Philosophie Zoologique*. The history of the youth of Cuvier and of his early works allows us to have a better understanding of the scientific program and of the strategy of the talented naturalist who wanted to improve the status of natural history "which can only reach its perfection when completed by the specific history of all living beings." It also helps to see how Cuvier participated with or against his colleagues of the Museum to the theorical discussions and debates on the study and the organization of the animal reign.

II. Abstracts

Gait Analysis During Unsteady Locomotion

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The analysis of gaits in the framework of antero-posterior sequences of movements (APS) breaks the stride paradigm in the study of interlimb coordination in quadrupeds. It considers that gaits depended from a common basic pattern controlling the coordination of the forelimbs (forelag, FL), the coordination of the hindlimbs (hindlag, HL) and a relationship between these two pairs of limbs (pairlag, PL), in an APS movement. During locomotion, the limbs are coordinated in time and space, thus three analogous space parameters (fore gap, FG; hind gap, HG and pair gap, PG) are associated to the three time parameters. We studied interlimb coordination during unsteady locomotion in dogs and cats moving on a trackway. In the middle of the trackway, the gait was perturbated by an obstacle, and the animal had to change from a symmetrical to an asymmetrical coordination to clear it. The results demonstrated that the APS method permits to quantify the interlimb coordination during the symmetrical, asymmetrical phases and the transition between them in both dogs and cats. The space and time parameters allowed to quantify the spatio-temporal dimension of gaits in different mammals. The slight differences observed between dogs and cats can reflect the morphological differences. The APS could thus be used to understand the implication of morphology in interlimb coordination. All the results were coherent with the current knowledge in biomechanics and neurobiology, so that the APS may reflect the actual biological functioning of quadrupedal interlimb coordination.

Asymmetric Defects of the Inner Ear in Mice Heterozygous for a chd7 Loss of Function Mutation

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Heterozygous mutations in the chromodomain gene CHD7 underlie 60 to 80% of cases of CHARGE syndrome, a multiple congenital anomaly condition that includes defects of the inner ear, impairing hearing and balance. We generated a novel Chd7 deficient, gene trapped lacZ reporter allele, Chd7 Gt. Homozygous mice have an embryonic lethal phenotype. Heterozygotes are viable and display circling and head bobbing behaviors consistent with dysfunction of the vestibular (balance) organs of the inner ear. Examination of heterozygous embryos (e16.5) revealed defects in the semicircular canals. The goal of this study was to characterize the defects in the vestibular organs of early postnatal and adult Chd7 Gt/+ mice. Gross morphologic assessment revealed that the lateral and posterior semicircular canals were absent or truncated in all Chd7 Gt/+ ears. The extent of canal dysgenesis varied between mice and between right and left ears of the same mouse. Staining for actin and 200 kD neurofilament showed that the posterior ampullary sensory epithelium contained stereocilia but lacked normal innervation, regardless of canal morphology. When the lateral ampulla was present, the epithelium and innervation pattern appeared to be normal. The remaining labyrinthine sensory epithelia appeared normal. These results are consistent with the highly variable and incompletely penetrant phenotype of CHARGE patients and suggest that Chd7 plays an important role in the development and innervation of the labyrinthine sensory epithelium. Supported by NOHR, the Williams Professorship, and NIH grants DC01634, DC05188 and HD40188.

Extreme Trophic Specializations in Catfishes: It's All in the Jaws

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Teleost fishes, not only comprising by far the most diverse group of vertebrates, also explore an extremely broad spectrum of feeding specializations. One group, the catfishes or Siluriformes, is generally considered as having a more conserved morphology and functioning of the trophic apparatus, even though it comprises a very diverse group of more than 2500 species. However, this may be the case for some groups but certainly is not the case for others that concern the morphology. Knowledge on the function, based on experimental evidence, is almost completely lacking with only a few recent studies giving some insight in catfish feeding functionality. This paper attempts to give an overview of some

highly specialized morphologies in relation to feeding adaptations in some catfish lineages, based on data from the literature. Some new evidence is provided, focusing on two extreme cases of feeding specializations in catfishes: functional morphology of the trophic system in a haematophagous candiru catfish and kinematic analysis of feeding with a reverted lower jaw in a Neotropical suckermouth catfish. Trophic evolution in loricariids has been considered as the result of a sequence of decoupling events, resulting in mobile upper and lower jaws. The functional analysis now also shows that the decoupling is not only at a structural level, but also at a functional and even neurological level. Decoupling even appears to have occurred on a contralateral level.

Integration of the Cichlid Mandible and the Evolution of Alternate Feeding Strategies

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The cichlid feeding apparatus is a classic example of adaptive radiation. A fundamental divergence among cichlids occurs between species that exploit hard and/or attached prey items, and species that feed on highly mobile prey. This divergence is concomitant with the evolution of stereotypical mandibular morphologies that reflect the mechanical properties of the feeding apparatus. Species that prey on hard food evolve short, stout jaws efficient for biting, whereas those that feed on mobile prey often evolve elongate, gracile jaws for suction feeding. Working within this functional paradigm, we explore patterns of integration of the cichlid lower jaw in a laboratory cross, among natural populations, and in the context of experimental embryology. Quantitative genetic analyses demonstrate that the opening and closing lever mechanisms are genetically modular, and therefore free to evolve independently. Patterns of phenotypic variation and covariation in our F2 mapping population are similar to those observed among natural populations, consistent with selection acting on a common genetic mechanism. Finally, we demonstrate that distinct patterns of bmp4 expression are associated with alternate feeding morphologies, and sufficient to modify mandibular morphology in a way that mimics adaptive variation among cichlid species. We conclude that patterns of morphological integration of the cichlid jaw reflect a balance among conflicting functional demands, and posit bmp4 as an important target for natural selection.

Evolution of Scales and Their Hard Proteins in Reptiles in Relation to Cornification of Skin Appendages in the Amniote Integument

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Skin appendages characteristic of amniotes include scales, feathers, claws and hairs. The cellular organization of these appendages is likely the result of specific dermal-epidermal interactions. Horny scales form from dermal-epidermal interactions over large areas of the body, whereas hairs, feathers, claws, hooves, horns, beaks, and nails may have arisen by more localized interactions. Appendage evolution is characterized by the production of specific keratins and associated proteins in the inter-filament matrix: beta-keratins in reptiles-birds (sauropsids); high-glycine-tyrosine/high-sulfur proteins in mammals. The accumulation and composition of corneous materials in scales, feathers, and hairs are presented, with emphasis on beta-keratins and matrix proteins. Unlike mammalian keratin-associated-proteins, all beta-keratins contain a beta-folded region of 20–25 amino acids, the core-box. This region shows 70-90% homology among reptilian and avian beta-keratins, and determines the polymerization of beta-keratin molecules into beta-keratin-filaments. The evolution of these sequences and genes for beta-keratins are presented for sauropsids, and are compared with mammalian keratin-associated proteins. It is hypothesized that genes coding for glycine-serine-rich sequences of alpha-keratins produced a new class of small matrix proteins. In sauropsids, matrix proteins originated after mutation and enrichment of proline, giving rise to the core-box and beta-keratins. In the therapsid-mammalian lineage, mutations in matrix proteins formed tyrosine or cysteine but no core-box.

Homology of the Proximal Femoral Trochanters of Reptilia

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Palaeontological and phylogenetic studies have shown the ancestral reptilian proximal femoral region to exhibit only two major processes: A caudolateral 'external trochanter', and a medial 'internal trochanter.' This arrangement has been retained with little modification by most members of the Eureptilia excepting some of the more derived Archosauriformes, which are unique in the shared absence of the internal trochanter and the presence of a more distal, caudally-directed 'fourth trochanter' on the femoral shaft. The archosaurian fourth trochanter has been interpreted as a novel structure characterising a major clade, but this currently orthodox conclusion has been based on osteology, without a detailed consideration of musculature—which suggests instead that the fourth trochanter is at least partly homologous to the internal trochanter. Based on new anatomical work, our study is testing hypotheses about the evolution of proximal femoral trochanters by integrating osteological (recent and fossil taxa) and myological data for diapsids, and interpreting them within an explicit phylogenetic framework. The results have implications for understanding the definition, homology, evolution and phylogenetic utility of femoral trochanters.

A New Stem Batrachian (Temnospondyli: Amphibamidae) from the Lower Permian of Texas

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The on-going controversy over lissamphiban origins is fueled by their highly derived morphology with respect to archaic fossil "amphibians." Here we report a significant new specimen that bridges the morphological gap between amphibamids and frogs and salamanders (Batrachia). The specimen is nearly complete. The broadly rounded skull has a light, strut-like construction. The pterygoid just fails to reach the lateral skull margin, except perhaps dorsally. The rostrocaudally narrow vomer bears only denticles arranged in three rows on a ridge. Marginal teeth are tiny, monocuspid, pedicellate cones. A very large otic notch, with articulation scars for the tympanic cartilage, closely approaches the orbital margin. There are 17 presacral vertebrae, and a short stretch of poorly ossified caudal vertebrae. Ribs are short, laterally-projecting elements with spatulate distal tips, especially broad cranially. The olecranon is ossified. A basale commune is present in the pes, which has a phalangeal formula of "?-2-3-4-3." This specimen has a mosaic of amphibamid characters and synapomorphies of both frogs and salamanders. The overall impression of the skull is frog-like. Pedicellate teeth are known only from lissamphibians, amphibamids, and possibly one branchiosaur. The vomers are especially batrachian. The vertebral count is transitional between *Amphibamus* (21) and *Triadobatrachus* (14). The phalangeal count is identical to frogs. However, the basale commune is unique to salamanders. The basale commune has recently been described in branchiosaurs, so its presence in an amphibamid suggests that the preaxial digital development pattern was more widespread than currently appreciated, and may have been primitively present in frogs.

The Morphology and Genetics of the Developing Mammalian Jaw Joint: The Role of the tgf-ß Superfamily of Signalling Molecules in Pattering the Mammalian Jaw Articulation

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The evolution of the novel mammalian jaw articulation, the squamosal-dentary or temporomandibular joint, has resulted in an increased complexity and modularity of the dentary bone, reflecting the multiple roles it now fulfils as the primary bone of the mandible. Our study hopes to address some of the questions concerning the role of molecular signals and mechanical forces in the pattering of the dentary, and in particular the processes of the proximal articular portion, an important growth centre and muscle attachment site. Mouse genetic studies indicate that a range of secreted proteins, including members of the Tgf-ß superfamily, and transcription factors, such as Pax9 and the Dlx family, are important

in the pattering of the mandible. We show here the association of the expression the mRNA of one such molecule, Tgf-ß2, with one of the mandibular elements lost in the corresponding knockout mouse, and the conditional knock out of the type 2 Tgf-ß receptor (Tgfbr2) in Wnt1 expressing neural crest cells. We also compare the expression of the connective tissue marker Scleraxis (Scx) and the muscle marker Myf5 in the developing mandible of both wild type and Tgfbr2 wnt1-cre flox/flox mice, since it has been suggested that mechanical force is essential for normal mandibular development. Finally, we demonstrate that mouse dentary explant cultures at E13.5 and E14.5 can successfully be made to induce secondary cartilage in the absence of any ossification and mechanical action, and this cartilage is abolished by pharmacological inhibition of signalling via Tgfbr2.

Determination of Bile Acid Patterns in Feces of Different Xenarthra Species

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Seventy five feces from different Xenarthra species were analyzed by Thin Layer Chromatography (TLC), to determine the bile acid pattern. The species were: *Zaedyus pichiy* (n = 6), *Chaetophractus vellerosus* (n = 5), *Chaetophractus villosus* (n = 53), *Dasypus hybridus* (n = 4), *Priodontes maximus* (n = 1), *Tamandua tetradactyla* (n = 2) and *Myrmecophaga tridactyla* (n = 4). Twenty two chromatographic plates were analyzed and different eluents were tested. The best eluent was toluene: acetic acid:water (5:5:1.5 v/v). There were differences between the bile acid patterns of all the species, but not between males and females, nor between wild and captive animals of the same species. We found seven unidentified bile acids (X1 to X7). All the species have lithocholic acid (Rf: 0.517 ± 0.035) and cholesterol (Rf: 0.549 ± 0.033). Only *Chaetophractus villosus* has glicocholic acid (Rf: 0.22 ± 0.009). *Zaedyus* and *Chaetophractus vellerosus* have 2 or 3 bands of dehydrocholic acid, while the other species have 1 or 2. *Zaedyus* has two unidentified bile acids, X6 (Rf: 0.915 ± 0.019) and X7 (Rf: 0.851 ± 0.06), that are almost indistinguishable in the other species. *Dasypus hybridus* differs from *Z. pichiy, Ch. vellerosus* and *Ch. villosus* because it has no X2. *Priodontes* is the unique species without deoxicolic acid and differs from *Tamandua* and *Myrmecophaga* because it has an unknown acid X1 (Rf: 0.37 ± 0.014). *Tamandua tetradactyla* is the species which has the lowest number of acids (nine), and differs from the others because it has no chenodeoxycholic, cholic and dehydrocholic acids. These results are the first for Xenarthrans and may have impact on future studies about the conservation and the ecophysiology of the group. This study was supported by SGCyT-UNS, PGI 24/B122, ANPCyT-BID 1728/OC-AR-PICTR 074/03 and CIUNSa, 1475.

Dolphin Dental Development: Morphology and Developmental Mechanisms

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Research on dental development has flourished in the last 10 years with studies on tooth identity and cusp formation. With the knowledge of underlying genetic mechanism, this research has allowed better interpretations of morphological characters. However, most developmental biological research has been limited to a few taxa which prevents these studies from applying to all mammals. We have chosen to look at cetacean dental development because of their unique tooth morphology. Cetaceans have dramatically altered their dentition from the typical mammalian condition. Specifically, odontocetes have increased their tooth number, lost their deciduous dentition and reduced all their teeth to a single cusp. Even though there is a detailed paleontological record of dental evolution among cetacean fossils, there are many unanswered questions of how and why early cetaceans changed their feeding mechanisms. The answers to these questions could play a large role in understanding how a land mammal evolved to an aquatic lifestyle. We looked at several possible developmental pathways that may have been disrupted in cetaceans using embryos of the dolphin, *Stenella attenuata*. The embryos show a unique pattern of dental development. Using immunohistochemistry we determined the expression patterns of several of the signaling molecules (Fgf8, Bmp4, Shh, Msx1 and Barx1) that have been shown to play a role in establishing tooth identity. By gaining an understanding of tooth development in cetaceans we will better be able to assess their evolution and the possible selective pressures that influenced their tooth morphology.

Innervation and Activation Pattern of Trunk Muscles in Mammals

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Among vertebrates locomotion evolved from lateral undulation of the body axis in fishes up to the axial and leg movements in tetrapods and mammals. Major reorganizations of the trunk's musculature are involved in these evolutionary changes. In primarily aquatic vertebrates, the axial musculature is organized in serial, segmental units, i.e., myomeres. These myomeres are innervated segmentally and separated into epaxial and hypaxial parts. In tetrapods this segmental organization was reorganized. Epaxial and hypaxial muscles fused to form polysegmental and multiinnervated muscle tracts. The current study was undertaken: (1) to test whether epaxial muscle tracts are partitioned into morpho-functional subunits, (2) to determine the activation pattern of the multifidus and rotatores muscles during locomotion, (3) to compare their intramuscular innervation and the spatio-temporal activation pattern with other vertebrates. Two adult laboratory rats were dissected scrupulously in order to determine the intramuscular innervation pattern of the epaxial musculature. In the multifidus and the longissimus muscle numerous morphological subunits along the cranio-caudal axis could be identified. The spatio-temporal activation pattern of the multifidus and rotatores muscles (both body sides) was determined in seven adult laboratory rats during trotting on a treadmill. Therefore, multichannel surface EMG electrodes (16 and 32 channels) were chronically implanted. The activity was recorded between L3 and L6. Afterwards the EMG was combined with gait characteristics to calculate RMS (Root Means Square) profiles. The detected biphasic activation pattern of the multifidus and rotatores muscles seems to be conservative in consideration of the similarities with that of Lissamphibia, Squamata and humans.

Ecological Implications of Ear Morphology in Semiaquatic and Subterranean Insectivoran-grade Afrotherians

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The golden mole *Eremitalpa* is a successful insect-predator in the extremely arid environment of southern Namibia and northwestern South Africa. Many aspects of its ecology and locomotor habits have been well-documented over the past two decades, establishing, for example, that the animal does not construct permanent burrows but rather 'swims' through poorly indurated sands and uses its sensitivity to low-frequency sound to locate prey at a distance. In this presentation, I investigate the applicability of the swimming-analogy in *Eremitalpa* by comparing its skeletal anatomy, particularly that of the auditory region, to that of other afrotherians that are semiaquatic (e.g., potamogalines), terrestrial (e.g., *Tenrec*), and semi-arboreal (*Echinops*). Skeletal adaptations that may correlate with 'sand-swimming' are investigated both in extant and fossil groups of insectivoran-grade afrotherians. The ecologically less-well known marsupial mole *Notoryctes* lives in a somewhat similar environment as *Eremitalpa*, but major anatomical differences separate the two arid-adapted, subterranean taxa.

Reconstruction of Ancestral Scapular Size and Shape and Hypotheses for Early Locomotion in Didelphidae, Marsupialia

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Didelphid opossums (a monophyletic group of about 90 species), though usually considered morphologically conservative, present considerable variation in substrate use and scapula size and shape. Scapulae size and shape for 31 representative Didelphidae taxa were captured using a landmark-based geometric morphometrics approach, and mean shapes were plotted on a phylogenetic tree based on IRBP nuclear gene sequences. Size and shape estimates were then reconstructed for all internal nodes using squared-changed parsimony, in order to infer on the evolution of their locomotor adaptations. Using Procrustes Distances as a measure of shape similarity, closest living models for specific nodes were chosen. The hypothetical reconstructed basal scapula for Didelphidae is similar in size to Micoureus and in shape to Micoureus and Gracilinanus. Reconstructed scapulae at several internal nodes are similar to most medium-sized marmosines, and major scapular shape modifications appear to be associated not only to specific locomotor habits, but also with increase in body size, reflecting stronger mechanical demands on the scapula for both larger terrestrial (*Metachirus*) or arboreal (larger *Caluromyines*) taxa. The strikingly different scapular shape observed in *Chironectes* (closer to several mouse opossums than to the remaining Didelphini) could thus be more related to lower mechanical demands, as a consequence of a semi-aquatic life, than to specific adaptation to this habit. These data suggest scansorial habits for a small- to medium-bodied Didelphidae to be ancestral, for which terrestrial and understory locomotion represent similar challenges, with less constrains than larger taxa.

Morphometric Diversification in the Scapula of New World Opossums: A Relative Warp Analysis

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Most species of living New World marsupials (Didelphimorphia, Paucituberculata and Microbiotheria) are traditionally considered morphologically conservative. In spite of strong developmental constraints on their anterior limbs and shoulder girdles, they present considerable variation in body size and locomotor habits, with terrestrial, scansorial, arboreal and semi-aquatic species. This study explores shape variation in the scapula of New World opossums in order to evaluate the existing variability, and its possible relation to locomotion, phylogeny or body-size. Landmarks were established in 1172 scapulae, representing 19 genera and 61 species, and patterns of shape variation were analyzed through relative warp analyses. First relative warp is related to an increase in the infraspinous fossa associated with an enlargement of the cranial border, and distinguishes most big-bodied Didelphidae taxa (except *Chironectes*) for having a more oval-shaped or rectangular scapula, with the remaining Didelphidae in an intermediate position and Microbiotheriidae and Caenolestidae on the opposite end. Second relative warp distinguishes more arboreal taxa, with increased caudal angles and cranially dislocated acromia (Caluromyinae, *Dromiciops*), from terrestrial species, with caudally dislocated acromia and enhanced supraspinous fossae (Caenolestidae, *Metachirus*, some *Monodelphis*). Within Didelphidae, relative warps separate Caluromyines, Didelphini and smaller taxa, except for *Chironectes* scapulae, being more similar to marmosines. Patterns of shape variation seem to carry strong phylogenetic signals when the three orders are compared, but within the more diverse Didelphimorphia, variation is related to a combination of locomotion, body size and phylogeny, with most smaller species presenting similarly shaped scapulae regardless of locomotor preferences.

Intrafollicular Atresia in Amphibian Ovary (Anura: Ranidae)

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Atresia is a specific kind of physiological intraovarian degeneration that affects germ cells at all stages of oogenesis. We studied morphology of atrectic ovarian vesicles in three European frog species *Rana temporaria, R. lessonae,* and *R. ridibunda.* Three types (I—III) of atresia were identified. In type I the oocyte is digested by its own follicle cells, which proliferate, hypertrophy, and become phagocytic. Connective tissue of the theca does not invade the follicle, but becomes thicker as a result of the follicle shrinkage. The follicular cells eventually disappear, and only remnants of the theca are still recognizable as a group of cells that accumulate black pigment. Type I, characteristic of vitellogenic oocytes, is subdivided into four stages: A—the germinal vesicle shrinks, nucleoli fuse, oocytes envelope interrupts at several sites, and follicular cells hypertrophy; B—after disintegration of the oocyte envelope, the follicular cells multiply and invade the vesicle, thus becoming phagocytic; the nucleus in not visible; C—the entire vesicle is filled by phagocytic and degenerating follicle cells; D—degenerating phagocytic cells accumulate black pigment. Type II is rare and resembles histolysis of the oocyte; its cytoplasm is spread in the space between adjacent vesicles. In type III the ooplasm and germinal vesicle shrink and become denser; the follicle cells do not invade the follicle, and finally the vesicle collapses. Types II and III were observed mostly in previtellogenic oocytes.

Aerodynamic Importance of Variation in Aspect Ratio of Bat Wings

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Bat wing morphology varies greatly among species. Traditionally, the function and relative performance of these morphologies has been inferred using aerodynamic theory originally developed for fixed-wing aircraft. For such aircraft, as wing aspect ratio (AR) increases, the lift slope (lift force vs. angle of attack) becomes steeper, while the angle at which stall is observed decreases. However, flapping bats differ from human-engineered aircraft in several respects, including: 1) they operate at much lower Reynolds numbers (103-5 vs. 106-9); 2) their wings are composed of compliant skin membranes rather than rigid structural materials; 3) they have more complex wing planforms than typical engineered aircraft. In this study, we use bat-like, physical models to test the theory that bat wings behave like engineered aircraft wings, with respect to AR. Six model bats were built out of steel wire and latex membrane, holding surface area constant and varying AR from 4.8 to 11.5. The details of wing planform shape are based on wing traces of 6 species from varying families and ecological niches. The models were mounted in a wind tunnel instrumented to measure lift and drag at Reynolds numbers relevant to bat flight. Our results show that lift production does not increase with aspect ratio as was expected. Additionally, the models did not follow the expected trend for stall, nor did their lift slopes decrease. We propose that these results are likely due to the properties of compliant membrane wings increasing camber, and the wing planform shape giving a greater Oswald's Efficiency.

3D Alligator Shoulder Kinematics

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Efforts to reconstruct aspects of extinct dinosaur forelimb anatomy and function often rely on comparison to extant archosaurs, crocodilians and birds. Although several studies have elucidated key aspects of avian shoulder morphology associated with flight, comparably little is known about crocodilian forelimbs during locomotion. I employed a recently developed method, "scientific rotoscoping", to collect detailed 3-D shoulder and forelimb skeletal kinematics of three alligators (*Alligator mississippiensis*) walking on a treadmill. Digital bone models with intact articular cartilages were created using a 3-D laser scanner. In the animation program, Maya, models were articulated and aligned to simultaneously record x-ray and light videos to reconstruct motion during "high walks". Major results show the following: (1) Lateral bending of the vertebral column and large excursions of the coracosternal joint contribute the majority (63%) of fore-aft movement; the glenohumeral joint provides only 34%. (2) General kinematic patterns of the coracosternal and glenohumeral joints are similar to those described in the literature for varanid lizards, with the exception of an increased shoulder adduction reflecting the difference between the sprawling posture of lizards and the high walk of the alligator. (3) Complex articular cartilage morphology is not well reflected in bony specimens, indicating a need for caution in studies attempting to use articular geometry to assess joint ranges of motion in extinct archosaurs.

Testing Hypotheses of Functional Morphology: A Dental Microwear Investigation into Feeding Mechanisms of Pycnodont Fishes

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Aspects of the ecology of extinct species are often inferred from an analysis of functional morphology, but this type of analysis can provide us with only indirect evidence of what an animal was actually doing while alive. Tooth microwear can provide direct evidence, but until recently the technique had been applied only to tetrapods. Work on extant fishes, however, has shown that dental microwear varies according to how and where individuals fed (Purnell et al. 2006; J. Animal Ecol., 75:967). This breakthrough now allows us to rigorously investigate trophic resource use and jaw movement in fishes by application of quantitative dental microwear techniques. We present an investigation of tooth microwear in the pycnodonts, principally of the Jurassic Solnhofen Limestone, Germany. Tooth microwear offers a unique opportunity for us to test hypotheses of feeding mechanisms derived by more conventional means. Previously these fishes have been interpreted as durophagous crushing feeders based on their functional morphology and limited evidence of stomach contents (Kriwet 2001; Geowiss. Reihe 4: 139). Our findings show that this may not have been the case and that a far more complex feeding behavior was being employed, with implications for the early evolution of novel feeding strategies.

An Ontology for Handling Knowledge About Extinct Organisms

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While much is known about extinct organisms from fossil analysis, this knowledge has not been formalized to make it computationally accessible. Indeed, it has proven difficult to compile databases of extinct organisms because it is hard to articulate what is known in a computational format. We suggest that one way of solving this problem is to produce a database in which each organism has its own page that will include (1) knowledge about that organism (in a searchable format) and (2) a link to a sub-database which includes information about the fossil material in a relational format. The key to making the database useful is to formalize our knowledge about each organism in a way that is intuitively understandable. Such a formalism is known as an ontology and is used for annotating and searching data. This approach has already proven successful for handling knowledge about anatomy, genes, cell types and other areas that can be structured hierarchically (see obo.sourceforge.net/ and www.geneontology.org/). Because each term in an ontology carries a unique ID, the ontology can also be used to search remotely any database where the data has been appropriately annotated. As a first step, we have assembled a simple ontology (*fossil.owl*) that allows organisms to be annotated with terms and FOS IDs that cover: time period, location, habitat, basic taxonomy, life events and behaviour, each of which can be structured herarchically. This ontology is written in OWL (the web standard) and can be visualized in standard browsers (e.g., oboedit, Protégé, COBrA).

Feeding Mechanism in Fruit-Eating Birds: Toucans and Hornbills

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Lingual food transport and swallowing has been largely described in terrestrial and aquatic neognath birds. Eating whole fruits in Toucan (*Ramphastos toco*) and hornbills (*Buceros hydrocorax*) is based on another mechanism called ballistic feeding. These birds took and positioned the food by the tip of the beak, and placed the food at the same place in the beak before rapidly tilting the head backwards to impose a ballistic curve to the food. The upper beak was suddenly opened and the food continued its ballistic curve freely inside the beak. In the toucan, as the food reached the level of attachment of the beak on the skull, the tip of the tongue moved upward from its resting position on the lower jaw to open the pharyngeal cavity by depression of the hyoid apparatus. The tongue of the hornbill was never visible. The ballistically projected food entered directly into the pharynx. Our findings show a unique mode of feeding in birds with the tongue never playing any role for food intra-oral manipulating and transporting. A mechanical hypothesis is suggested to show the action of the hyobranchium and the long and thin tongue in toucans. Our data show that toucans and hornbills are unique in their feeding mechanism without intra-oral transport.

The Mechanism of Drinking in Lizards

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In this paper, we present a comparative analysis of the drinking mechanism in two gekkotan lizards that have very similar tongue surface, tongue action in feeding (used for transporting and swallowing prey) and tongue-based vomerolfactory behaviors (used for collecting chemicals): *Eublepharis macularius* (terrestrial) and *Phesuma madagascariensis* (arboreal). These gekkotans occupy very different ecological environments, in which water may be either very abundant (rain forest—*Phelsuma*) or exceedingly scarce (semi-arid—*Eublepharis*). We selected the Gekkota because the tongue does not play any role in food capture, but is known to play a major role in collecting liquid and chemicals. Light and X-ray filming revealed that both species use similar mechanisms to collect and introduce water into the buccal cavity (immersion phase). Kinematics of jaws, tongue and hyobranchium are quantified to illustrate the complexity of drinking behavior. Water displacement through successive oro-pharyngeal compartments is strongly related.

Functional Morphology of Avian Pedal Claws in Non-Passerines: Correlations Between Claw Form and Foraging Behaviour

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Analysis of the pelvic limb claw of digit III in the Cuculiformes, Columbiformes Picinae and a disparate group of ground birds clearly shows that the radius of curvature scales allometrically ($\approx$ proportional to $M0.3$) and displays no correlation to foraging mode. In contrast, the angle describing the dorsal arc of the claw is highly correlated with where species' actively forage (six categories spanning ground to vertical surface foragers). A claw angle of about 100o effectively divides those species that forage predominately or exclusively on the ground from those that forage arboreally. This approach, with its finer scale of resolution than previous studies, when applied to fossil non-avian theropod and Mesozoic bird material suggest that most species were adapted for ground foraging. — Preliminary analysis of the pedal claws of Falconiformes and Strigiformes also shows claw allometry, however, the scaling exponent differs between claws of the different digits, reflecting predatory specialisations. A correlation between claw morphology and foraging behavior is observed, with the type of prey and its mode of capture reflected in the observed claw angles. The dorsum of the claw in raptors commonly deviates from the circular arc seen in other avian orders, suggesting that the material characteristics, growth and wear patterns of the keratin are substantially different to those of other birds.

The *Australopithecus* Pelvic Morphology (stw 431 and sts 14): The Taxonomic Evidence

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It is classically said that the fossils which were found in Sterkfontein (Member 4), Makapansgat (Member 3), and Taung, belong to a single species, *Australopitheus africanus* (South Africa, 3 MYA). However, Clarke (1988, New York: Aldine de Gruyter, pp. 285–292; 1994, Advances in Human Evolution series, Prentice Hall, Englewood Cliffs, New Jersey, pp. 205–222) described cranial and dental remains suggesting that a robust species coexisted with *A. africanus* in Sterkfontein. Digital models created from CT-images of original fossils allowed us to obtain

the complete pelves of Stw 431 and Sts 14. The material for comparison comprised the original pelvic bones of Sterkfontein (Sts 65), Makapansgat (MLD 7, MLD 25), Kromdraai (TM 1605), Swartkrans (SK 50, SK 3155), and the pelvic bones of 160 *Homo sapiens*, 143 *Pan troglodytes*, 27 *Pan paniscus*, and 29 *Gorilla gorilla*. Procrustes analyses demonstrated that Stw 431 shared the majority of ilium traits with the *A. robustus* specimens of Swartkrans and Kromdraai. The results confirmed the hypothesis of a robust species, represented by the Stw 431 skeleton, which was contemporaneous with *A. africanus* (3 MYA), and probably at the origin of *A. robustus* (1 MYA).

Computer-assisted 3D-reconstruction of the Skull of *Siphonops annulatus* (Lissamphiba: Gymnophiona) From Serial Section Digitized Images with Special Reference to the Ear Region

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The mainly subterranean gymnophione amphibians show highly derived conditions in the skull characters related to their burrowing way of life. In consequence of their adaptations to this lifestyle they have lost the middle ear, the ear drum and the operculum with the opercularis muscle, prominent in urodeles and anurans. Most of them have retained, however, the sense organs of the inner ear as the basilar and amphibian papillae or the macula neglecta. The mechanisms for sound transfer to the inner ear and the relationships between the skeletal parts and the soft-tissued inner ear labyrinth in the gymnophionans are not completely understood. In previous studies clearing and staining methods, sectioned series and CT-scans were used in morphological examination of the skull bones and the membranous labyrinth. While each of these methods has its advantages, a combined approach of some classical and modern methods seems to be very useful in analyzing the cranial and soft tissue morphology. Computer-assisted x-ray tomography produces high-quality three-dimensional reconstructions, mainly of skeletal elements, whereas the classical sectioned series allows a thorough examination of the soft parts, lacking, however, the three-dimensional aspect. Here, a sectioned series of the skull of the gymnophione *Siphonops annulatus* is used as the basis for a very detailed computer-assisted three-dimensional reconstruction allowing investigation of both the cranio-skeletal elements and the membranous labyrinth with the endorgans in high detail. The observed anatomical characters are compared to the results of earlier studies with an evaluation of the qualitative possibilities of the different methods.

Span-wise Flow and Lift in the Hammerhead Shark at Slow Swimming Speeds: A New Explanation for the Cephalofoil?

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The function of the laterally expanded head of hammerhead sharks (Family Sphyrnidae) is not currently understood. Although some differences exist between turns of hammerhead sharks and those with conventional head form, studies have shown no convincing advantage for hammerheads that accounts for the striking divergence in head shape. The expanded head increases the area of electro-sensors, but this comes at the expense of substantial potential hydrodynamic consequence because the cephalofoil is located anterior to the center of mass and could generate pitching moments. Many hammerhead species are predators of benthic prey in shallow coastal regions and slow swimming would be advantageous when using their electro-sensors to search for prey concealed in the substrate. However, as negatively buoyant animals it is necessary to generate lift to maintain position in the water column. We propose that the cephalofoil of hammerhead sharks works with the spontaneously occurring yaw of the head while swimming to generate lift by span-wise flow across the width of the foil (i.e., from the laterally placed eye toward the midline). This provides lift to the anterior portion of the body at lower swimming speeds. As a preliminary test of this hypothesis we evaluate the forward and lateral velocity of the head of the scalloped hammerhead (*Sphyrna lewini*) and compare this with conventionally shaped sharks (sandbar and lemon sharks). We demonstrate that substantial lift can be generated by the lateral motion of the hammerhead cephalofoil that is unavailable to conventionally shaped sharks.

Developmental and Evolutionary Insights from the Anatomy of *Anolis carolinensis* and Other Squamata: Membranes and Muscles, Tracking the Neural Crest, and the Presence of the Superficial Rectus Lateralis in Iguania

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The anatomy of the connective tissue and musculature of *Anolis carolinensis* and other Squamata is rich with ontogenetic and phylogenetic information. Fibroblast-containing membranes, the fascia and septa derived from mesoderm and neural crest, are organizing structures, together an "extended skeleton" forming a connective network that provides pathways for other structures during development. For example, the posteriorly extended endolymphatic sac, an apomorphy of Squamata undescribed in relation to other structures of the neck, passes within the septal membrane deep to the transversospinalis and longissimus bundles of primaxial cervical muscles. Connective tissue in *A. carolinensis* contains concentrations of neural-crest-derived pigment cells in regions where neural crest embryonically contributes heavily to connective tissue (e.g., the attachment of the cucullaris group to the pectoral girdle); concentrations elsewhere may predict embryologically unidentified neural crest contributions. The topology of the lateral plate-derived abaxial membranes containing the body wall musculature elucidates the nature of the rectus lateralis muscle, previously considered synapomorphic for Autarchoglossa. A division of the rectus abdominis into medialis and lateralis portions by the deep attachment of the obliquus internus fascial membrane is shown here to be plesiomorphic within Squamata. Several parts of Iguania apomorphically share with Autarchoglossa a portion of the lateralis superficial to the obliquus externus membrane, to the possible exclusion of Gekkota (rare macroanatomical support for the phylogenetic position of Gekkota suggested by DNA sequence data). Autarchoglossa further shows a derived intimacy of the lateralis with the dermis, a condition, associated with the characteristic large, platelike ventral scales of Autarchoglossa, that deserves developmental study.

Interpreting the Significance of Whole Body Mechanics in Primitive Mammals

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Common among most primitive mammals are an unspecialized locomotor apparatus and a crouched posture. We explored the effects of these locomotor characteristics on walking and running dynamics in a series of small (<1 kg) marsupials and eutherian mammals. Whole body ground reaction forces and simultaneous videography were obtained and then converted to reflect center of mass mechanics. Calculated fluctuations in gravitational potential and kinetic energies are consistent with pendulum-like mechanics during walking. Compliant leg behavior, enabled in part by the flexed limb posture during stance phase, limited the vertical oscillations in the center of mass during walking. At higher speeds, spring-mass mechanics rule the trotting gait. The physiological benefit of these patterns of whole body mechanics is questionable, as pendulum-like and spring-mass mechanics are estimated to provide trivial savings to the overall metabolic costs of locomotion in small, crouched mammals. This implies that the high cost of locomotion in small mammals is due in part to the absence of energy-saving mechanisms.

Were Notoungulates (Mammalia) the Oldest Grazers?

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Considering extinct taxa, the Oligocene South American notoungulates are frequently evoked as the oldest grazers. This hypothesis is only based on the statement that the abrasion of their hypsodont cheek teeth might have been caused by a rich-in-grass diet. However, high hypsodonty levels are not necessarily synonyms of grazing habits. Actually,

some arguments do not support the hypothesis that Oligocene hypsodont notoungulates were grazers. There is no evidence of grass-dominated ecosystems in South America before the Middle Miocene, and the potential abrasiveness of grass silica phytoliths has been challenged recently. The dental microwear of notoungulates from the Late Oligocene Salla Beds of Bolivia was digitized using an optical stereomicroscope connected to a tri-CCD camera (Merceron, 2003, Palaeo3 207:143–163) to yield information on paleodiet. The microwear pattern thus detected on notoungulates cheek teeth mainly presents a high number of thin parallel striations. A partly similar pattern with more striations than pits is retrieved in modern grazers but also in mammals having a gritty diet. Furthermore, our study of premaxillaries points out that a majority of hypsodont notoungulates do not present a grazing morphotype (except hypsodonty). Actually, the hypothesis of an early grazing diet in notoungulates is currently far from being supported. Alternative hypotheses for their teeth abrasion such as a higher ingestion of exogenous grit adhering to food items must be explored. This particularly implies that more direct investigations of the potential effect of grass and dust on the teeth of extant mammals must be undertaken to go further these hypotheses.

Growth of Discrete Processes Within the Weberian Apparatus: The Role of Positive and Negative Allometry in the Origin of This Evolutionary Novelty

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The Weberian apparatus, a complex assemblage of vertebral modifications, significantly enhances hearing within Otophysi. Ultimately we are interested in the genetic mechanisms responsible for the origin, development and morphological diversification of these vertebral elements within the Weberian apparatus of cypriniform fishes. However, a necessary first step involves identifying changes in growth of this region as compared with the thoracic vertebrae from which these modified elements purportedly derive. Using an ontogenetic series of the zebrafish, *Danio rerio*, we collected growth data for specific elements within the Weberian apparatus, including neural arches, ribs, and parapophyses. These data are compared to both serially homologous structures in posterior thoracic vertebrae (which act as internal controls), as well as to vertebral elements from the same axial levels in two other non-Otophysan teleosts. Significant differences in growth rate were found among serially homologous structures at different vertebral levels. Global changes in growth rates (in which all structures derived from a specific somite were equally affected) were not found, indicating precise targeting of morphological change to specific structures. Such patterns of growth help illuminate the specific heterochronic mechanisms required for the origin and subsequent morphological diversification of the Weberian apparatus. This morphological diversity is exemplified by the multitude of forms seen in the cypriniform Weberian apparatus. Understanding the patterns of growth within elements of the Weberian apparatus allows us to hypothesize as to the specific developmental changes, likely constituting differences in gene expression, responsible for this morphological diversity.

Pendular Walking Mechanics in Domestic Cats

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Many quadrupedal animals use pendulum-like mechanics to exchange kinetic energy (KE) and potential energy (PE), thereby reducing muscular work required for walking. Pendular mechanics are well characterized for cursorial specialists, but are poorly understood for less cursorial animals. The "stealthy" walking style of cats provides a good contrast to cursorial specialists, yet their gait mechanics have not been documented in detail. We tested the hypotheses that cats have low and in-phase fluctuations of PE and KE compared to cursors. We collected kinematic and force plate data for five adult cats. Using these data, we computed the PE and KE fluctuations throughout individual strides and calculated the phase relationship of peaks in PE and KE, percent recovery of mechanical energy, and percent congruence of change in PE and KE. Phase shift and percent recovery were low in cats relative to cursors and were highly variable. In addition, all three measures revealed an abrupt shift in mechanics at a threshold speed. At this speed (around 0.95 m/s) variability in the indicators decreased dramatically and tended toward higher recovery and phase shift and lower congruence. This abrupt shift with speed is suggestive of a change in mechanical gait from one that is not well characterized by energy recovery, congruence, or energy phase to one with consistently higher pendular energy recovery. Low phase shifts, low energy recovery, and high congruence in cats support the hypothesis that cats recover less mechanical energy through pendular mechanisms than cursorial specialists, favoring stealth over efficiency.

Frogs with Claws: Diversity, Morphology, and Function of Pedal Unguals in the Astylosternidae

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Claws, or ungual phalanges, are ubiquitous in amniote vertebrates. Within extant amphibians, only a single lineage, the Astylosternidae (sensu Dubois, 1992, Bull. Mens. Soc. linn. Lyon 61: 305–352), contains species with bony pedal claws. However, there have been no studies of the diversity of this character within this lineage or of the morphology and function of these pedal claws. We present a survey of pedal claw morphology in all five genera and discuss the morphology and function of these unique claws. Recurved pedal claws are found in three of the five genera: *Astylosternus, Scotobleps, Trichobatrachus*. These claws are used in defense; when live specimens are handled, they kick wildly and rake the pedal claws across the handler's skin. In larger species, especially *T. robustus*, this defensive behavior often results in bloody scratches. Unique among tetrapods, when the claws, which normally are contained within the fleshy digit tip, are exposed for defense, they tear through the ventral surface of the digit tip. The pedal unguals are sharp and recurved, and each exhibits a large flexor tubercle near its proximal base. A cartilaginous sheath, imbedded within the fleshy digit tip, attaches to the dorsal base of the ungual and covers its dorsal surface. This sheath terminates in a small bony nodule that is weakly fused to the ungual tip in specimens in which the claws are not exposed; this fusion is apparently broken when the flexor musculature acts to expose the ungual. We provide further discussion of the functional morphology and discuss the retraction of the claws.

Evolution of Fetal Membranes and Placentation in Reptiles

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Squamate reptiles have evolved viviparity and placentation convergently on more than 100 separate occasions. Consequently, these animals are ideal for studies of placental structure, function, and evolution. In recent years, placental morphology and physiology in reptiles have been analyzed with a battery of contemporary techniques, including light microscopy, electron microscopy, histochemistry, and quantitative analysis of nutrient provision. Squamate placentas accomplish gas exchange, and provide at least small quantities of nutrients. However, in four unrelated clades of lizards, placentas provide most of the nutrients for embryonic development. One of these clades is represented by New World lizards of the genus *Mabuya*, which ovulate tiny eggs and provide nutrients via a highly specialized chorioallantoic placenta similar in many respects to those of eutherians. An allied African form (*Trachylepis*) is also highly placentotrophic, and shows invasive implantation. Evidence from morphology, biogeography, and evolution indicates that these placentotrophic forms are closely related. We offer a scenario in which placentotrophy originated in African skinks, and spread to South America during the Cenozoic via a trans-Atlantic route. This reptilian clade shows how reproductive specializations once thought to be confined to therian mammals have originated through evolutionary convergence. Ongoing analysis of this clade illustrates how integration of multiple lines of evidence can provide insight into the evolution of developmental and reproductive specializations.

Experimental and Modeling Approaches to Studying the Evolution of Bone Function

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Many aspects of bone function have the potential to change through evolution. I will outline several recent studies showing the diverse approaches available to gain insight into these changes. First, studies of

fossils can provide critical insights into evolutionary patterns, and models of bone function in fossil taxa can be constructed based on experimental data from extant species. For example, we have used bone loading data from living iguanas and alligators as a basis for modeling changes in bone loading through the evolution of mammals from mammal-like reptiles, and found that a wide range of limb postures were viable through this transition. Second, explicitly phylogenetic comparative methods can be used to test hypotheses about the significance of variation in bone function across species. For example, in comparisons of antler Young's modulus among deer species, we predicted that moose might show stiffer antlers than other deer to help accommodate the weight of their broad antler palms. We found that moose antlers are distinctively stiff only among their close odocoileine relatives, and generalized least squares reconstructions of ancestral antler modulus show that moose have diverged significantly from their ancestors. Finally, experimental comparisons of functionally and phylogenetically diverse species can give insight into the evolution of bone design. Our comparisons of bone loading and safety factors across amphibians and reptiles provide a critical evolutionary context for understanding the similarity of patterns previously observed in birds and mammals. Together, such approaches can clarify the origins of functional diversity in bone. Supported by NSF I0B-0517340.

Are Digits Neomorphic Structures? Some Palaeontological and Genetic Arguments

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The evolution of the digited limbs is one of the most important events in tetrapod evolution and, despite the great amount of research done on the developmental genetics involved in the patterning of the tetrapod hands and feet (autopods), much remains to be discovered to elucidate their origins. The pectoral fin of the late Devonian (365-360 million years old) fish-tetrapod intermediate *Panderichthys* has been CT-scanned and modeled in 3D to reveal that, contrary to what had previously been described, the distal part of the fin is composed of small separate elements (distal radials) similar to those of the closely related Tiktaalik. This suggests that fingers are not neomorphic structures in tetrapods but would have been derived from sarcopterygian (lobe-finned fishes) distal radials. Clearing and staining of the developing fin of *Neoceratodus forsteri*, our closest living fish relative, shows a developmental discontinuity between the central fin elements and the distal radials, a pattern observed in urodeles, where the digits develop prior to the elements of the palm (mesopodium) and in the earliest tetrapods like *Acanthostega* and *Ichthyostega*, having fully developed fingers but lacking wrists and most of the mesopodium. Hoxd13 is a gene involved in polarizing the anterior to posterior (thumb to little finger) axis of the developing hand and in digital arch formation. Because its expression differs between actinopterygians, chondrichthyans and tetrapods, In situ hybridizations of Hoxd13 were performed on the developing fins of *Neoceratodus* to gain information on the change of gene expression between non-tetrapodomorph fishes and tetrapods.

A Combined Linear and Geometric Morphometric Analysis of the Effect of Epiphyseal Cartilage Loss in *Alligator mississippiensis* on Humerus and Femur Joint Shape: Implications for Fossil Archosaurs

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Epiphyseal cartilage loss in fossil archosaur long bones has significant implications for inferring locomotor scope: both absolute length and epiphyseal shape are affected, but how much joint shape information is lost has been difficult to determine. Although a previous analysis of extant archosaurs showed significant differences in long bone length, shape differences were reported qualtitatively. To quantify size and shape differences, we dissected and macerated the humeri and femora of approximately 30 wild *Alligator mississippiensis* individuals ranging in size from small juveniles (< 1 meter snout-vent length) to large adults (> 2 meters snout-vent length). Specimens were measured and photographed for geometric morphometric analysis. We show, as in previous analyses, that there is a statistically significant difference in several linear dimensions of *A. mississippiensis* humeri and femora when epiphyseal cartilage is lost. However, the geometric morphometric analyses of the humerus and femur show little or no significant difference in shape with epiphyseal cartilage removal. These data suggest that whereas epiphyseal thickness is significantly truncated after maceration, the underlying calcified cartilage more faithfully reflects the shape of the overlying cartilage that previously suspected. Our results further suggest that whereas a significant percentage of overall size is lost in fossil archosaur humeri and femora, the preserved calcified cartilage on the articular ends retains much of the shape of the epiphysis. Preliminary data from sectioned articular surfaces indicates that most of the variation between the joint surface and the underlying bone is related to variations in the thickness of the distal articular cartilage.

Correlation of Snout Morphology and Life Style in Lampropeltinine Snakes (Serpentes: Colubrinidae)

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Shifts in the diet are believed to be among the most important factors driving snake evolution. Lampropeltiini inhabit very diverse habitats, from dry semi-deserts to tropical forests in Eurasia and North and Middle America, and feed on wide variety of prey, ranging in adults from fishes, frogs, reptiles to birds and mammals. In addition, their prey is encountered on the trees, in the water, on the ground or under the ground—in holes and burrows of small vertebrates. Dissection and examination of several snake species revealed some morphological convergences, that evolved independently in different lampropeltinine lineages. Snakes, that hunt their prey in holes or actively burrow for prey have wide dorsal margin of nasal process of prefrontal, deeper medial lamina of nasals and shorter vomers and spetomaxillares. As a whole, the snout unit is deeper and wider but shorter as compared to above-ground hunters. Such construction provides more efficient force transmission during digging and makes the snout more stress-resistant. Members of *Eupreciophis, Oreocryptophis* and *Lampropeltis* are examples of species adapted to digging and burrowing, whereas *Orthriophis* are well suited for aboveground hunting. *Elaphe, Pantherophis* and *Zamenis* seem to be intermediate, and particular species show different degree of specialization. The relatively firm snout construction in the above genera may also reflect their origin from ancestor adapted for digging and burrowing. Adaptive and functional meaning of this variation are discussed.

The Role of the Rigid Cephalic Shield of Pteraspidiformes During Active Swimming

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We have studied the flow pattern around the rigid cephalic shield of the Devonian agnathan *Erriwaspis waynensis* (Pteraspidiformes: Heterostraci). Flow visualization along a generic 23-cm, anatomically exact model of the fish was made in a wind tunnel, taping colored gas (propilenglycol vapour) emitted from a point close to the anteriormost part of the model that was cut by successive planes of transversally oriented light beams. Those planes were geometrically integrated to reconstruct the behavior of the flow along the body. The body-induced vortical flow observed around our model is very similar to the vortical flow over a delta wing, dominated by paired, nearly symmetrical, counter-rotating vortices, which are created at the leading edge and grow downstream attached to the upper surface. This strategy generates lift forces through vortex generation (vortex lift). Since *Erriwaspis* lack pectoral fins and other obvious control surfaces, vortex lift forces added by this mechanism during locomotion may have played a major role not only to counteract the negative buoyancy of the fish, but also as a source of mano-

euvring. The present work constitutes a preliminary part of a more extensive ongoing project to study hydrodynamic and manoeuvrability in Pteraspidiformes.

A New Phylogeny of Extant Ratite Birds

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Although living ratites have been studied in considerable detail, avian systematists have been unable to resolve conflicts between morphological and molecular studies. In most recent morphological phylogenetic analyses including the higher-order phylogeny of modern birds by Livezey and Zusi (2007, Zool. J. Lin Soc 149:1–94), the Apterygidae (kiwis) are sister to all other extant ratites. This clade splits into two sister taxa, Dromaiidae (emu) plus Casuariidae (cassowaries) and Rheidae (rheas) plus Struthionidae (ostrich). In most molecular works the Apterygidae group with the Dromaiidae plus Casuariidae, and the Rheidae and Struthionidae diverge independently at the base of the tree. A new pattern of diversification of extant ratites is presented herein. The phylogenetic analysis is based on more than one hundred morphological characters and includes all living ratite species plus two outgroups, the palaeognathous Tinamidae (tinamous) and the neognathous Galliformes (fowls). In the single most parsimonious tree obtained, the Apterygidae are sister to all other living Ratites. Within this clade, the Struthionidae are sister to a clade comprising the Rheidae and the Dromaiidae plus Casuariidae. Monophyly of the new taxon Rheidae-Dromaiidae-Casuariidae is based on 20 strict synapomorphies. This novel topology is confronted against the vicariance biogeography hypothesis, which proposes that ratites achieved their current distribution pattern via the breakup of Gondwana.

The Development and Vascularization of the Bony Core (Third Phalanx) of the Cat Claw

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The retractable claws of cats have generally been analyzed as isotropic entities in biomechanical studies, but the musculo-tendinous retraction mechanism acts only on the bony core formed by the third phalanx of the digits. In adult cats, this bony core consists of a proximal articular base for the attachments of tendons and ligaments, a distal unguicular process supporting the cornified sheath of the claw, and a hood cupping the proximal part of the unguicular process. The development and blood supply of the third phalanx were explored with light microscopy, SEM, and synchrotron x-ray microcomputed tomography (μCT with a resolution of 9 μm, i.e., roughly the diameter of a capillary). Virtual 3D-reconstructions of the tomography data were performed using the OsiriX and Amira software. In fetal and perinatal cats, the third phalanx resembles that of most mammals, consisting only of an articular base with a single growth plate and an unguicular process. During the first postnatal 24 months, the growth plate and the cartilaginous processes of the articular base ossify, the hood ossifies starting on both sides of the unguicular process, and the unguicular process develops a dorsal ridge under the bony hood. The blood supply enabling these growth, differentiation, and remodeling processes is provided by vascular branches entering and leaving the bone through numerous Foramina nutricia. The superficial blood vessels may serve as a framework for appositional bone formation as they are walled in by successive layers of bone. (Supported by a Faculty Research Grant from Louisiana State University).

Development and Resorption of Deciduous Teeth in the Bowhead Whale Fetus (*Balaena mysticetus*; Mysticeti: Balaenidae)

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Baleen whales (Mysticeti) lack teeth as adults, but bear plates of baleen with brushlike oral surfaces on their palates. Baleen plates consist of tubular horn supported by a complex connective tissue papillary body and start to form in the late fetal stages. In fetal minke whales *(Balaenoptera acutorostrata,* Mysticeti: Balaenopteridae), deciduous teeth develop and are resorbed before they erupt and before the onset of baleen development. To elucidate the tooth and baleen development in the bowhead whale, the jaws and palate of six fetuses ranging from 300 mm body length (about the end of the first trimester of gestation) to 3.5 m body length (near term) were studied by dissection, light microscopy, SEM, CT, and MRI. The dental lamina, an ectodermal thickening, forms on the upper and lower jaws at the end of the first trimester and contributes to the formation of tooth germs in the second and early third trimester. The tooth germs consist of enameloblasts and odontoblasts enclosing the pulp cavity filled with vascularized mesenchymal tissue. The tooth germs are bunodont and vary in size and shape and in the timing of their resorption depending on their position on the dental arches. In the third trimester, the tooth germs are completely resorbed prior to the onset of baleen development. The tooth germs on the upper dental arches and their vascular supply may induce and influence the patterning of the complex connective tissue papillary body in preparation for the development of the cornified baleen plates.

Review: Keratins and Keratinization in the Common Integument and Other Epithelia

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Keratins are structural proteins with a molecular weight ranging roughly from 15 kDa to 70 kDa. Several genes decoding for various keratins have been analyzed. The amino acid sequences of keratins in ectodermal, endodermal, and mesenchymal epithelia are similar. The main function of keratins is the formation of tonofilament bundles of the cytoskeleton in combination with other microfilaments and filament-associated proteins. The keratin filaments bundles are attached to cell adhesion complexes via special proteins anchoring the cytoskeleton to the cell membrane. The thickness and orientation of the keratin filament bundles depend on the mechanical forces exerted on the individual cells or epithelial tissues. In general, alpha-keratins (i.e., coiled fibrils forming filaments in the soft skin of land tetrapods and hard cornified structures of mammals) are distinguished from beta-keratins (i.e., leaf-like proteins in reptilian and avian scales and claws and avian beaks and feathers). Both alpha- and beta-keratins occur as acid and alkaline keratins depending on the isoelectric point. In mammalian skin, keratins of type A (suprabasal) and of type B (basal) as well as keratins low in sulfur versus keratins rich in sulfur are distinguished. Keratins can be produced in almost all cells but the layers of stratified epithelia are characterized by specific keratins, and regenerating or proliferating epithelia also produce specific keratins.

4D-imaging Methods in Vertebrate Morphology

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These are exciting times in the field of vertebrate morphology. Imaging technologies such as CT-scanning, MRI, ultrasound, and laser scanning confocal microscopy are opening up vast worlds of cross-sectional and three-dimensional anatomy. Studies of functional morphology, paleontology, and development are poised at the edge of a revolution in our ability to capture and quantify complex morphology and function in 4D (three spatial dimensions plus time), and to integrate our understandings of function, development, and evolution. In this workshop I shall give a general overview of 3D-imaging methods, with particular attention to current limits in spatial and temporal resolution and suitability for in vivo imaging. Recent developments in microsource CT, high-field MRI, and high-frequency ultrasound have greatly increased the spatial resolution of these methods and made them suitable for use with developing embryos as well as larger specimens. Improvements in labeling techniques and contrast media are making it possible to tag specific tissues or gene expression in the context of the full 3D-morphology, thereby inte-

grating developmental, genetic, and comparative approaches to the study of evolutionary morphology. Advances have been made in image acquisition speed, but the temporal resolution of true 3D-methods remains fairly poor (generally not more than 1 Hz), so 4D-imaging that could capture locomotion and other natural movements is currently unavailable. At the end of the presentation, I will discuss "CTX Imaging", a method we are developing at Brown University for visualizing and measuring 4-D skeletal motion at up to 1000 Hz.

Accurate 3D-reconstruction of Skeletal Morphology and Movement with CTX-imaging

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Accurate 3D skeletal movement data would be valuable for many areas of biomechanics research, but such data are hard to collect from external views because loose skin introduces artifacts and many bones are too deep in the body to be tracked externally. We are developing a method "CTX-imaging" for visualizing skeletal position during rapid movement. This method is based on a single-beam fluoroscope animation method ('scientific rotoscoping'), with the addition of dual-beam biplanar fluoroscopy and a more automated workflow. Here, we describe our work on a marker-based CTX-method. Two OEC 9400 C-arm cinefluoroscopes were retrofitted with high-speed video cameras and arranged such that the intersection of the x-ray beams covers a basketball-sized volume. The steps in marker-based CTX are: 1) at least three radiopaque spheres (1 mm) are surgically implanted into each bone of interest; 2) biplanar x-ray movies of animal movement are collected; 3) distortions introduced by fluoroscope and camera are removed from the movies and XYZ coordinates of the markers are measured; 4) the animal is CT scanned and digital 3-D bone models are made with the markers in still place; 5) the data from marker motion capture (steps 1-3) are used to position and orient the 3-D bone models (from step 4), resulting in an accurate reconstruction of bone position over time. The result is an accurate movie of 3D-bones moving in 3D-space. We are also working on a markerless CTX-method that will not require surgical implantation of radiopaque spheres.

Phylogenetic Analysis of Extant Armadillos (Xenarthra: Dasypodidae) Based on Postcranial Data

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Living armadillos are the only armored mammals and are the most speciose group in the order Xenarthra. The twenty-one living species are distributed within eight genera in the single family Dasypodidae. Despite several recent morphological and molecular phylogenetic analyses, the relationships among living armadillo genera remain unclear. The relationships among *Chaetophractus, Euphractus* and *Zaedyus* have proven particularly difficult to resolve. A better understanding of the phylogenetic relationships among the living genera of armadillos will provide valuable information for the study of the evolutionary history of this distinctive mammalian lineage. The postcranial skeletons of seven (*Cabassous, Chaetophractus, Dasypus, Euphractus, Priodontes, Tolypeutes, Zaedyus*) of the eight living genera of armadillos were examined and fifty-four discrete osteological characters were employed in a cladistic analysis using PAUP 4.0Beta. The North American opossum *Didelphis virginiana* was designated as the outgroup. An exhaustive search with equally weighted and unordered character states resulted in three most parsimonious trees (TL = 113; CI = 0.573; RI = 0.474). A strict consensus tree left *Chaetophractus, Euphractus* and *Zaedyus* as an unresolved trichotomy, grouped *Cabassous* and *Priodontes* together in a monophyletic Tribe Priodontini which in turn was the sister taxon to the Euphractines. This larger clade then formed an unresolved basal trichotomy with *Dasypus* and *Tolypeutes*.

Integrating Signaling Theory and Whole-organism Performance into a Functional Understanding of Threat Displays

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Threat displays are signals that function to intimidate rivals in contests, in part by advertising individual differences in fighting prowess. How do we account for the diversity of these behaviors and for the specialized structures that support them? Game theory models suggest that evolutionarily stable signals can be categorized based on the factors maintaining variation in signal use. Signal categories that can advertise prowess include indices and quality handicaps. Indices are signals in which individuals are physically constrained to produce a certain signal variant. Variation in quality handicaps is maintained by variation in signal production costs; quality handicaps "use up" the attribute that is being signaled. To generate specific hypotheses for the function of a given threat display, one must first recognize the structures and behaviors utilized in contests and then select corresponding measures of whole-organism performance. Next, performance traits that are statistically robust predictors of success in dyadic contests and that co-vary with signal attributes should be identified. We can then formulate hypotheses of the form: "performance trait X is advertised by display attribute Y," testable by manipulating X and examining the effect on Y, as well as by manipulating Y and testing for variation in rival responses and success in dyadic contests. Threat display components that do not co-vary with performance traits may relate to resource value rather than prowess or may function as amplifiers, signals that augment a rival's ability to assess preexisting signals.

More Than Meets the Eye: A Cineradiographical Analysis of Egg Eating in the Snake Genus *Dasypeltis*

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Despite being one of the best known cases of extreme morphological specialization with far reaching ecological consequences, relatively little is known about the mechanics of egg eating in snakes of the genus *Dasypeltis*. Most of our knowledge on the system stems from a groundbreaking set of papers by Gans and co-workers from the last century (see summary in Gans, 1974). Here we revisit several hypothesis proposed by Gans and co-workers using high-resolution digital videofluoroscopy. Our data for three specimens of two species of *Dasypeltis*, feeding on eggs varying widely in size, confirm predictions by Gans (1974) that the egg shell is broken before coming into contact with the modified and enlarged hypapophyses of the 29th through the 38th vertebrae. Moreover, our data show that these enlarged hypapophyses do indeed function to rupture the egg membrane as suggested previously. Finally we address mechanisms of egg ingestion and the packing of the egg shell for regurgitation. Gans, C. (1974) Biomechanics. Ann Arbor: University of Michigan Press.

Mathematical Modelling of Breathing Parameters in Birds and Sauropod Dinosaurs

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The dorsal ribs of birds attach to the vertebral column by two-headed articulations. Thus, their movement is confined to an axis defined by the articulation sites. The appendicocostal muscles, attaching to hook-like structures (uncinate processes) on the caudal margins of the ribs play a central role in inspiration (Codd et al. 2005. JEB 208.849-857). This hypothesis is also supported by a 2-dimensional model (Zimmer, 1935. Zoologica 88:1-66). We scanned ribcages of various birds to obtain 3-dimensional coordinates representing their mechanical configuration and developed a vectorial model of rib cages in order to calculate the resulting forces exerted by the appendicocostal muscles. The model uses standard vectorial calculations to determine the resulting forces pulling the ribs cranially during inspiration. The existing model serves as a basis to model breathing mechanics in dinosaurs: despite the fact that sauropod dinosaurs lack ossified ventral ribs and sternum, our present model represents the general ribcage morphology of sauropod dinosaurs if the length of the uncinate processes is reduced to zero. We are currently developing a model of the mechanical configuration of the ribcages of sauropod dinosaurs based on 3-dimensional scan data of separate fossilized bones. Sauropod vertebrae are separately scanned and digitally retrodeformed. After computerized "mounting" of the vertebral column and ribs, the model will be used to examine the forces associated with breathing as well as other parameters like tidal volume and air distribution during respiration.

Ontogeny and Homology in Fishes

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Ontogeny is a powerful tool to test hypotheses of homology, but has only rarely been utilized in fishes. The present contribution highlights this approach with examples from different teleost groups and stresses the great potential of this aspect of ontogenetic research. The first example deals with the enigmatic little teleost *Indostomus*, the phylogenetic position of which depended largely on the correct interpretation of its body armor formed by bony plates. Ontogeny reveals that this armor is formed from two different ontogenetic sources, endoskeleton and exoskeleton, and thus resembles that of gasterosteoids, and not syngnathoids with which it was previously thought to be closely related. The second example investigates the homology of the "tail" of the Ocean sunfishes of the family Molidae. Two competing hypotheses exist: (1) it is a highly modified caudal fin and (2) it is formed by the dorsal and anal fin that have grown together. Ontogenetic studies show unequivocally that the second hypothesis is correct. The third example concerns the Weberian apparatus, a highly complex sound conducting apparatus, with several skeletal components, the homology of which has been debated controversially for almost 190 years. Again ontogenetic studies help to resolve the homology of the different parts and I will focus on one of them, the neural complex.

Nutritional Endoderm in a Direct Developing Frog: Was Nutritional Endoderm a Step in the Evolution of the Amniote Egg?

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The egg of the direct-developing frog, *Eleutherodactylus coqui*, has 20x the volume as that of the model amphibian, *Xenopus laevis*. We hypothesize that increased egg size led to the origin of nutritional endoderm, a novel cell type which provides nutrition but does not differentiate into digestive tract tissues. As the *E. coqui* endoderm develops, there are two cell types: differentiated intestinal cells and large yolky cells. A distinct boundary exists between them, which persists even when yolk platelets are depleted. The yolky cells do not become tissues of the digestive tract and are eventually lost, as shown by lineage tracing with FDA. We attempted to distinguish the two cell types by the expression of EcSox17, the *E. coqui* orthologue of a key endodermal transcription factor. Expression of EcSox17 throughout the endoderm indicated that it cannot be used as a molecular marker for this purpose. To test the necessity for cell division of the yolk mass in *E. coqui*, c-mos RNA, an inhibitor of cell division, was injected into the large vegetal blastomeres of the cleaving embryo. Some embryos excluded the uncleaved yolk and became smaller froglets. Others incorporated the large uncleaved cells into the body, indicating that some degree of incomplete cleavage can be tolerated. A large endogenous food supply to support direct development may limit signaling to cells, near prospective mesoderm, leading to the presence of nutritional endoderm. This change may parallel a step in the evolution from the holoblastic amphibian egg to the yolk-rich, meroblastic amniote egg.

Molecular Control of Successional Tooth Formation in Snake

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The rodent is the main model for tooth development but there is a major shortcoming, the absence of generational teeth. We chose to study snake dentition since there are many generations of teeth. We show that in *Python sebae*, the initiation phase, as was described in mouse, is only evident for the first generation teeth while subsequent generations arise from the invaginating dental lamina. Proliferation studies show that the dental lamina extends by relatively higher proliferation at the tip than at the base (oral side). Apoptosis is present in the dental mesenchyme adjacent to the generational teeth, perhaps helping to create a path of decreased cell density for the extending dental lamina. We investigated expression of a gene involved in human succedaneous tooth formation, Runx2, and the secreted signal Shh, shown to be regulated by Runx2. Python Runx2 is completely mesenchymal and is localized mainly around the tooth forming side of the lamina. Shh transcripts do not overlap with areas of Runx2 signal. Instead, Shh is expressed in the enamel organ and on one side of the base of the dental lamina (an area with low proliferation). These Shh-expressing epithelial cells may be involved in maintaining a connection between the dental lamina and the oral cavity. Once this connection is lost, the dental lamina is degraded and no additional teeth form. The expression of Runx2 is inconsistent with a proposed role as a repressor of tooth formation. Instead, Runx2 is more likely to be mediating differentiation of ameloblasts and bone. This work is supported by CIHR grants to JMR.

An Endogenous Retinoic Acid Gradient is Used to Set up Rostrocaudal Upper Beak Pattern

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Skeletogenic cranial neural crest cells gradually become committed to a specific fate both during migration and once they reach their final destinations. Only recently has a surprising degree of plasticity been demonstrated in post-migratory neural crest. Previously, we discovered that by changing the levels of two signaling molecules (retinoic acid and BMPs) in the first pharyngeal arch, a homeotic transformation was induced within the face. The duplicated elements replaced many of the maxillary derivatives. In addition, the supernumerary interorbital septum and prenasal cartilage always pointed in the same direction as the normal beak, with the tip of the prenasal cartilage terminating in the transformed maxillary bone (changed into a premaxilla). We wondered if it was the position of the RA bead relative to the epithelium that contributed to the direction of the duplicated elements. Unexpectedly, we find that when the Noggin bead is closest to the epithelium, two sets of duplicated elements form instead of the usual single set (n = 9/17). This second set occurs less frequently when the retinoic acid bead was closest to the epithelium (n = 3/22). The caudal duplication arises mainly through transformation of the quadrate to a prenasal cartilage. We conclude that RA and Noggin are key signals used to pattern the facial midline since together they can induce several competent regions of the head to make midline structures. In addition we suggest that patterning of the upper beak is influenced by a rostral to caudal RA gradient. This work was funded by CIHR grants to JMR.

Bridging the Axial and Appendicular Systems

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The body plan of vertebrates comprises an axial system of a cranium and segmental vertebrae. In jawed vertebrates the axial system is integrated with an appendicular system, the paired fins or limbs and their girdles. The two systems have become highly integrated during the evolution of diverse vertebrate locomotor adaptations. In a developmental sense, however, the body plan is highly conserved throughout the lineage. The appendicular skeletal elements arise from the lateral plate mesoderm (LP) and the axial skeleton arises from the paraxial somites. All of the striated muscles for both systems arise from the somitic myotomes. We have explored the integration of the somitic and lateral plate mesoderm in a variety of tetrapods and define distinct primaxial and abaxial domains in the developing body wall. The dynamic interface between these domains we call the Lateral Somitic Frontier. Certain muscles serve to bridge the axial and appendicular systems, and some of these muscles also bridge the frontier. Experimental evidence from chick and mouse suggests that patterning information changes when somitic cells cross the frontier. I will present a hypothesis whereby primaxial and abaxial domains behave as independently patterned modules facilitating morphological evolution within the vertebrate body plan.

Functional Morphology of the Paravertebral Musculature of Saltatorial Small Mammals

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Different modes of locomotion have evolved in mammals. Whereas most mammals are quadrupedal, some developed a saltatorial mode of

locomotion such as the jerboa. Despite the different demands onto the trunk, the macroscopic topography of the paravertebral musculature is comparable between quadrupedal and those saltatorial mammals. Therefore, the question arose whether other muscular parameters differ between quadrupedal and saltatorial small mammals such as the fiber type distribution or the cross-sectional area of the back muscles. For this, serial cross sections of the back of two representatives of the Dipodidae (Rodentia) were investigated using enzyme histochemical methods and thereby identifying different muscles fiber types. Surprisingly, the three-dimensional fiber type distribution showed no major differences compared to quadrupedal species. Thus, the fiber type composition per se does not indicate differences in the functional demands onto the respective back muscles. In order to test whether the anatomical cross-sectional areas of the back muscles reveal any adaptation in the Dipodidae facilitating this saltatorial mode of locomotion, selected cranio-caudal levels along cross-sectional series were measured for both quadrupedal and saltatorial small mammals. At several presacral levels, the epaxial muscles (Mm. transversospinales, M. sacrospinalis) were significantly larger in the Dipodidae than the quadrupedal ones. But at 6th and 7th presacral level, the M. quadratus lumborum was significantly smaller in the dipodoids than in the quadrupedal mammals. Therefore, the altered functional demands onto the paravertebral muscles due to the saltatorial mode of locomotion were only reflected by the size of the muscles but not their metabolic profile.

Mechanics of Limb Bone Loading During Terrestrial Locomotion in River Cooter Turtles *(Pseudemys concinna)*

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Studies of limb bone loading during terrestrial locomotion have focused primarily on birds and mammals. However, data from a broader functional and phylogenetic range of species are critical for understanding the evolution of limb bone function and design. Turtles are an interesting lineage in this context: although their slow walking speed might lower limb bone loads relative to mammals and birds, the weight of the bony shell carried by turtles might counterbalance slow speeds and lead loads similar to those of similarly sized mammals and birds. Our measurements of in vivo strains from femora of turtles (river cooters, *Pseudemys concinna*) have shown moderately high strain magnitudes. To help understand the mechanics underlying loading patterns identified during strain recordings, we synchronized measurements of 3D ground reaction force (GRF) components acting on a single hindlimb with measurements of hindlimb kinematics. Net GRF magnitude was approximately 0.5 BW and directed nearly vertically for the middle 75% of the contact interval, nearly orthogonal to the femur. Peak bending stresses were low (< 10 MPa) similar to other reptiles, with moderate torsional shear stresses. These loading patterns may relate to several factors including short femoral length and limited active force production by hip retractor and adductor muscles spanning the length of the femur. Together with data from other lineages, these results indicate that low limb bone loading may be a primitive feature of limb bone design. Supported by NSF I0B-0517340.

An Ecological Twist on the Morphology-Performance-Fitness Axis

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Understanding the ties that bind performance, morphology, and fitness remains one of the central goals of evolutionary ecology. Though numerous studies have linked either performance and morphology or morphology and fitness, relatively few have illustrated the full causal pathways that connect variation in morphology with variation in performance and also show how these interact to influence fitness. Here, I incorporate data from a field study of natural selection into a path-analytic model to elucidate morphology-performance-fitness relationships in the brown anole, *Anolis sagrei*. Locomotor performance among species of anoles is correlated with limb length and body size and is thought to have played a key role in the habitat-based diversification of ecomorphs in the Greater Antilles. I show that the same ecology-morphology-performance correlations that characterize species of Anolis lizards (e.g., ecomorphs), also exist within a single species of anole. Interactions between locomotor performance and habitat use had significant effects on survival, despite relatively weak natural selection on limb morphology per se. Results indicate that natural selection may act on correlations between performance and habitat use without affecting the morphological variation underlying variation in performance. Thus, while this study demonstrates a link between morphology performance and fitness, that link depends strongly on the ecological context in which performance is both measured and expressed.

The Automated Balance System of Birds

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Birds maintain balance during bipedal terrestrial locomotion through a heretofore undescribed automated system involving the pelvic girdle and hindlimb, the center of which is the knee joint. As the knee begins to flex in early stance phase of a stride, the proximal end of the femur begins to experience yaw mediad relative to the proximal end of the tibiotarsus. The yaw is produced by the combination of a tightly bound articulation between the femur, tibia, and fibula and a sliding motion involving the menisci of the knee joint, facilitated by several muscles. With the ankle joint limited to fore and aft movement, the hip joint transfers the yaw generated by the knee to the body. The yaw brings the bird's center of mass over the planted foot, which allows the bird to maintain its balance. Slight, long-axis femoral rotation exerts lift on the pelvis, resulting in body roll toward the planted foot. As the knee joint begins to extend in late stance phase the direction of yaw is reversed and the bird's center of mass is swung over the opposite foot as it is planted and that knee flexes and exerts control over the yaw of the bird. At initiation of the swing phase the knee and ankle joints rapidly flex to raise the foot, and prior to initiation of the next stance phase the extension of the knee joint completes the reversal of the yaw movement and returns the tibiotarsus and foot to a forward position, completing the cycle.

How to Produce Phenotypic Variation in Limb Bone Length by Tinkering with Growth Plates: A Case Study Using Rodents

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Mammals are incredibly diverse in the lengths and proportions of their appendicular skeleton. The size and shape of individual limb bones are thought to evolve primarily in response to selective pressures associated with specific locomotor behaviors. However, the number and nature of the developmental mechanisms that selection acts upon to generate variation in limb bone length are poorly understood. For example, intra- and interspecific differences in bone size could result from differences in rates of chondrocyte proliferation, from variation in the size and number of chondrocytes, or a combination of these mechanisms. To address these hypotheses, this study compared postnatal development in the growth plates of the limb bones of two rodent species that differ in absolute size: the mouse (*Mus musculus*) and Mongolian gerbil (*Meriones unguiculatus*). Results indicate that size and shape in the proximal (stylopod, zeugopod) and distal (autopod) limb elements within a species are regulated by separate growth plate mechanisms, which are themselves distinct from the developmental mechanisms that underlie differences in absolute limb bone size between species. These findings show that phenotypic variation in limb bone size is regulated by multiple independent developmental processes within and between species. This suggests that natural selection does not favor one developmental mechanism over others, and that there may actually be advantages to maintaining a plurality of developmental processes for generating phenotypic diversity in limb size and shape in mammals.

Morphofunctional Analysis of the Postcranial Skeleton of *Neoreomys australis* (Rodentia, Caviomorpha, Dasyproctidae) from the Miocene of Patagonia

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The postcranial skeleton of the extinct Dasyproctidae has not been evaluated from a functional-adaptative perspective. Morphofunctional analy-

sis of the well-preserved postcranial bones of *Neoreomys australis*, one of the most abundant Miocene dasyproctids from Patagonia, provides evidence to infer its locomotor behavior. Osteological and myologycal features of the extant species were used as a model to interpret the functional significance of the postcranium of *N. australis*. Several postcranial features of this species are functionally compatible with cursorial habits: the humeral tuberosities, specially the greater tuberosity, are higher with respect to the humeral head, restricting the mobility of the gleno-humeral joint; the humero-ulnar and humero-radial joints limit pronation/supination movements at the elbow joint and increase the stability during flexion/extension (e.g., the capitular tail and capitular eminence are well developed, in congruence with the enlargement of the subrectangular radial head, which is anterior with respect to the ulna). The shape of the hip, knee, and cruro-astragalar, calcaneo-astragalar, and astragalo-navicular joints would have limited the rotational movements, improving the flexion/extension (e.g., the greater trochanter is proximally projected, increasing the mechanical advantage of the glutei; the tibial tuberosity is anteriorly projected, improving the mechanical advantage of quadriceps femoris; the intercondylar tubercles enhance the stability; the internally concave posterior process offers a stop at the upper ankle joint; the anterior distal tibial spine acts as a stop to lateral movements; the distal portion of the calcaneus is elongated).

The Evolution of Weapons in Hartebeest

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The horns of bovids are used in male intrasexual competition and evolved under sexual selection; however, recent studies of developmental variation within populations showed that reduced nutrient availability limits the investment in horns by males. This suggests that selection for larger horns may be opposed by food constraints but, to date, no study has tested how sexual and natural selection interact in the evolution of fighting structures in ungulates. I used variation within the hartebeest clade (Alcelaphus) to test the hypothesis that dimorphism in horns, the pedicel (a bony structure that bears the horns) and skull weight increase when the potential reproductive benefits for males are greater, and in more productive and less seasonal habitats. Dimorphism in horn circumference and length, pedicel height and skull weight, was quantified using 382 museum specimens for eight hartebeest sub-species and regressed against independent variables while controlling for phylogenetic similarity. The length of the breeding season, a surrogate measure of the potential for polygyny in time, predicted dimorphism in pedicel height and skull weight, while habitat productivity predicted horn length dimorphism. The length of the breeding season was also the best, albeit non significant, predictor for horn circumference dimorphism. These results suggest that taller pedicels and heavier skulls are under sexual selection, and that natural selection affects the evolution of fighting structures by limiting investment in longer horns. I argue that the pedicel, by increasing the defence to the head during clashes, might reduce the selective pressures on horns as protective structures.

The Evolution of the Reproductive Anatomy of Talpid Moles (Mammalia)

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In previous studies of the reproductive biology and genetics of European moles (*Talpa* spp.), some of us showed that all female moles have ovotestes (gonads with testicular and ovarian tissue) instead of normal ovaries, a unique case among mammals. Females are fertile as their ovarian tissue is fully functional. Testicular tissue is abnormal and sterile, but produces testosterone. This phenomenon was later reported in a few other talpid species from Europe and North America. To examine the evolution of reproductive features in talpids, a group comprising 17 living genera with diverse life history features, we examined histologically the gonads of several female specimens belonging to the Asian genera *Mogera* and *Urotrichus* from Japan. Whereas *Mogera wogura* has ovotestes, *Urotrichus talpoides* is characterized by normal ovaries. As not all American mole species have ovotestes, the results fit parsimoniously with recent morphological and molecular studies of talpid phylogeny. A clade of strictly fossorial moles shows conservation of the generalized XX true hermaphroditism. Shrew moles (e.g., *Urotrichus*) lack ovotestis and are more basal than desmans, which have them. Mapping of this singular reproductive trait provides clues about the evolution of territoriality among talpids.

Fossil Evidence (Pisces; Placodermi) for the Paired Origin of Basibranchials and Their Derivation from Neural Crest

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Goodrich proposed a paired origin and derivation from neural crest (NC) for basibranchials in gnathostomes based on their assumed origin from paired streams of NC and on documentation of a NC origin for dorsal elements in the branchial arch. However, later studies of branchial arch development usually did not extend ventrally to establish the definitive origin of basibranchials. Discovery that the median basihyoid and basibranchial in *Bombina* (flame toad) are not derived from primary NC calls Goodrich's hypothesis into question. A strict specificity was demonstrated between the hypobranchial and branchial muscles and their connective tissues and entheses (attachment sites)—the latter two are NC in origin, independent of the attachment site. Thus, indirect evidence for a NC origin would include documentation of a dual or paired origin and attachment of hypobranchial or branchial musculature. Some chondrichthyans demonstrate the first criterion as transitory paired mesenchymal condensations in ontogeny. However, the common pattern of muscle attachment is for the hypobranchial muscles to be connected laterally to the hypobranchial elements or ceratobranchials, rather than these paired (later fusing) condensations representing the basibranchials. In the extinct placoderms, paired median elements are preserved in several taxa. New evidence from *Cowralepis mclachlani* (based on a well preserved ontogenetic sequence) clearly demonstrates both the presence of paired medial elements in the adult and entheses for hypobranchial muscles. Thus, placoderms meet both criteria for a NC interpretation. The presence of unpaired elements in extant gnathostomes represents a peramorphic shift from a paired primitive state to a fused medial element.

Morphology and Function of the Feeding Apparatus in Suction-feeding Pipid Frogs

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The morphology of the feeding apparatus was examined in five species of frogs representing each genus in the family Pipidae (*Xenopus laevis, Pipa pipa, Silurana tropicalis, Pseudhymenochirus merlini, Hymenochirus curtipes*). Pipid frogs are fully aquatic and use suction during prey capture, a method unusual for anurans but common to other aquatic vertebrates. Using silicone molds of the buccal cavity, the buccal volume was found to be up to 8 times greater in pipids than in other anurans. A large buccal cavity is commonly seen in other suction feeding vertebrates. The hyoid is thought to be primarily responsible for movement and support of the buccal cavity in pipid frogs. Using measurements of cleared and stained specimens, the hyoid was found to have a large surface area in all pipids examined and is highly ossified in a few species. The hyoid is positioned farther posteriorly in pipids than is typical for anurans, but maintains the same spatial relationship with the posterior buccal extension. The insertions of the muscles associated with expansion of the buccal cavity were found to have shifted posteriorly, both relative to the body as well as the hyoid itself. Some derivatives of the m. rectus abdominis have insertions that appear to be unique to pipid frogs. A model of buccal expansion for suction feeding in pipids illustrates that expansion occurs primarily through retraction and depression of the hyoid, but is also affected by flexion of the pectoral girdle.

Maximum Running Speed in Mammals is Inversely Correlated with a Proxy for Male-male Competition

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The physical demands of rapid and economical locomotion differ from the demands of aggressive behavior in ways that may prevent simultane-

ous evolution of optimal performance in both behaviors. In this analysis, I used body size sexual dimorphism as a proxy for male-male aggression to test the hypothesis that species of mammals that are specialized for fighting tend to be slow runners. Species values of male and female body mass, and maximum running speed were collected from the literature for 28 species of mammals (18 artiodactyls, 1 perrisodactyl, 8 carnivores, and 1 lagomorph) that inhabit open country habitats, such as savannas or deserts. Scaling effects were removed by calculating body mass residuals of size sexual dimorphism and maximum running speed. Regression of residuals of maximum running speed against residuals of size sexual dimorphism demonstrated a significant negative correlation ($R2 = 0.468$, P-value < 0.0001). Hence, in this sample, species that have relatively high levels of size sexual dimorphism tend to be slow runners. This observation is consistent with the hypothesis that specialization for aggressive behavior is incompatible with simultaneous specialization for high-speed running. Musculoskeletal characters that may enhance fighting performance but limit maximum running speed include relatively short limbs, a limited capacity to store and recover elastic strain energy, relatively massive forelimbs, and relatively massive distal limbs.

The Ancestry of Modern Amphibians

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The interrelationships of frogs, salamanders, and caecilians and their ancestry from among Paleozoic amphibians are among the major unresolved problems in vertebrate phylogeny. An integrated investigation involving understanding of the functional anatomy of feeding and locomotion, modes of reproduction, development, and ways of life of the modern taxa, broad comparison with all Paleozoic lineages, and molecular systematics provides a strong basis for answering these question. Use of functional complexes rather than individual osteological characters and extensive evidence from the polarity and sequences of bone ossification in fossil and living groups documents the origin of many divergent characteristics of the three living orders from among Permo-Carboniferous tetrapods. Recently discovered fossils of anurans and caecilians from the Lower Jurassic of Arizona and salamanders from the Middle Jurassic of China as well as putative antecedents of salamanders and anurans from the Permo-Carboniferous document the progressive evolution of anatomical characters leading to each of the modern orders from Carboniferous precursors. The degree of divergence of the modern orders is also documented by their very different larval anatomy and modes of development, which can also be determine among Paleozoic and early Mesozoic fossils. Evidence of the patterns and rates of evolution as well as their initial biogeographical origins are further supported by molecular analysis of the timing and sequence of divergence of the three groups within the Paleozoic.

Mechanisms of Blood Coagulation and Fibrinolysis in Xenarthra

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Blood coagulation is an important process regulated by a large number of proteins that transform fibrinogen into fibrin. The blood coagulation network is probably present in all jawed vertebrates and possibly evolved before the divergence of tetrapods and teleosts. Among Xenarthra, nothing is known for sloths and anteaters, but we demonstrated that the armadillo has a haemostatic system similar to that of humans and other mammals. We identified the basic mammalian coagulation system, with two activation pathways, contact coagulation system and tissular factor coagulation system, and a common pathway, that leads to fibrin clot formation. We also demonstrated the presence of the coagulation factors and that of natural anticoagulation systems (antithrombin, protein C and protein S), with functional analogy to the human counterpart. Based on these facts, the armadillo has a haemostatic system similar to the one of the human being and other mammals. However, in this species the contact system pathway seems to play a greater role in the activation of the coagulation system than it does in humans, and the common pathway appears to limit the velocity of the system. We also demonstrated the presence of a fibrinolytic system, similar to that of other mammals, through the measurement of the degradation products of fibrinogen and fibrin, with activity of alpha-2-antiplasmin. Essentially, the results suggest that armadillos have a hypercoagulable and hypofibrinolytic profile. Our findings constitute the only contribution on the physiology of the haemostatic and fibrinolytic system in Xenarthra. This study was supported by SGCyT-UNS, PGI 24/B122 and ANPCyT-BID PICTR 074/03.

Cuvier, Hegel, and Naturphilosophie

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Cuvier's and Hegel's lives show important coincidences in time and space. Both were born as subjects of the same old regime state of Württemberg, with only a year of difference (23rd August 1769 G.C. 27th August 1770 G.W.F.H.) and they died during the first epidemic of cholera that struck Europe (G.W.F.H. on 14th November 1831; G.C. on 13th May 1832). Probably they met in Stuttgart, during Cuvier's studies at the Carolinum. They had some common friends (Ferdinand von Authenrieth, for example). Besides the rather anecdotic interest of these biographic coincidences, there is another point of larger transcendence for the history of science, on which the parallelism between both men deserves to be reviewed, i.e., is their basically shared feelings against Naturphilosophie and Naturphilosophen. Those feelings were based on their particular points of view about their respective disciplines, natural history and philosophy. The three basic ideas of transcendental anatomy, namely, the structural unity of plan, the scale of beings, and the parallelism between the development of the individual and the evolution of the group, which Naturphilosophie assumed, were for Cuvier unacceptable. On another hand, for Naturphilosophen (Schelling, for example) nature was previous to idea, an assumption that Hegel's extreme idealism could not admit. I am trying to show that although these aspects are frequently forgiven, their knowledge can help a lot in the correct understanding of Cuvier's attitudes on morphology. Moreover, it is impossible to separate those attitudes from the current criticisms that Cuvier's work receives.

Ontogeny of Muscle Fiber Type Distribution in Climbing Hawaiian Gobioid Fishes: Muscle and Locomotor Correlation

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Three species of Hawaiian amphidromous gobies are remarkable in their ability to climb waterfalls up to several hundred meters tall. Juveniles of *Lentipes concolor* and *Awaous guamensis* climb by rapid bursts of axial undulation with long rest periods during which the animal is attached to the waterfall with its pelvic sucking disk. Juveniles of *Sicyopterus stimpsoni* alternately attach the pelvic disk and their sucking mouth to the waterfall and climb using prolonged bouts. Based on these differing climbing styles, we hypothesized that propulsive musculature in juvenile *L. concolor* and *A. guamensis* would be dominated by fast, white muscle fibers whereas *S. stimpsoni* would exhibit more, slow red muscle fibers. We further predicted that, because adults of these species shift to burst swimming, rather than climbing, as their main locomotor behavior, muscle from adult fish of all three species would be dominated by white muscle. Fish were collected in several Hawaiian streams, sectioned, and frozen at -80° C in isopentane. Serial sections were made and ATPase activity in transverse sections of muscle was evaluated. Juvenile *L. concolor* and *A. guamensis* tail musculature was dominated by white fibers while juvenile *S. stimpsoni* showed a higher proportion of red fibers. White fibers predominated in adults of all species. Thus, the proportions in which different muscle fiber types occur in these species through ontogeny appear to help accommodate differences in their locomotor demands. These results indicate that these species overcome the common challenge of waterfall climbing through both diverse behaviors and physiological features.

Early Developmental Morphogenesis of Visceral Elements in Axolotl: 110 Years from an Eminent Work of Julia B. Platt

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Endoskeletal cartilages of the anterior neurocranium and pharyngeal arches form a base of the developing vertebrate head. To investigate how individual cartilage elements develop, how they specify and later

organize to form one structural coherent unit, we have examined their early differentiation using a combination of histological sectioning and reconstructions, vital dye analysis, immunohistochemical and molecular markers. We studied embryos and larvae of the Mexican axolotl (*Ambystoma mexicanum*), for which early morphogenesis of neural crest cells, the source of these elements, has been already described in details (Cerny et al., Dev. Biol. 276, 2004). Here, we have analyzed morphogenetic stages from late migration of cranial neural crest cells up to a phase of well established cartilages. We conclude that all endoskeletal cartilages arise solely from cranial neural crest cells; moreover, that all cartilages that belong to one cranial segment or pharyngeal arch develop from a single ventral condensation. Ventral (and medial) neural crest cell condensations next grow up and become subdivided into individual elements of a series. Detailed morphogenesis dealing with precartilage and cartilage development is described and discussed, especially in the context of the eminent work of Julia B. Platt (1857–1935).

An Approximation to Multivariate Ontogenetic Allometry in Birds

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Morphometric approaches are seldom used when describing morphological change during ontogeny despite their usefulness in handling large amounts of data at once, and in providing unambiguous readings from instantly recognizable graphic descriptions of the data. We are presenting a morphometric study of embryonic phenotypic change in birds. Ten traits were characterised with longitudinal measurements of the head (e.g., eyes and beak), body, and limbs, of alcohol-preserved specimens, and data was treated using multivariate exploratory procedures (PCA). The sample comprises embryos of five species from four different Orders: *Gallus gallus, Somateria mollissima, Passer domesticus, Larus ridibundus,* and *Sterna paradisaea.* The developmental stages of each taxon were categorized following the Hamburger and Hamilton standard series. The analysis revealed that ontogenetic trajectories were characterized by two expected factors, size and proportional growth (i.e., ontogenetic allometry). Size was noticeably the predominant factor, and subsequently, more pronounced proportional change was found to take place between elements of the CNS (eyes) as opposed to hindlimb proportion. All taxa were found to share nearly-equivalent allometric trajectories (i.e., their trajectories overlap) along earlier developmental stages, except for *Passer domesticus.* We interpret this size shift as a possible taxonomic factor. Equivalently to what other qualitative studies have suggested elsewhere, differences in the ontogenetic trajectories among the remainder taxa begin around H-H 33 and beyond. At such time, more pronounced differences among multivariate trajectories depend upon shifts towards differential growth of the hindlimbs. These match locomotion preferences observed in their adults (e.g., cursoriality vs. noncursoriality), and maturity patterns within the altricial-precocial spectrum.

Rhythm Generating Neuronal Circuits: From Hindbrain Segmentation to Breathing After Birth

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The functional scaffold of brainstem neuronal circuits is first set in the embryonic neural tube, when the hindbrain is partitioned along the anterior-posterior axis into polyclonal developmental compartments called rhombomeres (r). Analysis of loss- and gain-of-function mutations in mouse and chick embryos revealed an important role for Hox genes in the establishment of rhombomeric territories, the assignment of segmental identities, and rhombomere-specific neuronal patterns eventually required for a normal breathing behavior at birth. An "anti-apneic" neuronal system has been located in the r4-derived ("para-facial") caudal pontine reticular formation, ventral to the facial motor nucleus (another r4-derived structure). In vivo, neonatal mice with impaired anti-apneic (para-facial) function show an abnormally low respiratory frequency and apnoeas lasting 10-times longer than normal. Most of the animals die during the first two days after birth. Rhombomere r3 is important as a source of Krox20, that is crucial to initiate parafacial development. Current studies with calcium imaging of rhythm generators in mice also show that the parafacial control is embryologically distinct from the post-otic (pre-Bötzinger) respiratory generator originating caudal to r5. Finally, genetic abnormalities affecting rhombomeres rostral to r3 can lead to pontine defects, in which the respiratory frequency is not significantly affected. Altogether, data in mutant mice therefore identify a dual (parafacial and post-otic) brainstem control of the breathing rhythm.

Experimental Anatomical Imaging in Osteichthyan Fishes

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Ever since the birth of comparative anatomy, osteichthyan fishes were mainly explored on the basis of dissections and, later, of radiographs. The development of aquaculture of many actinopterygian species (e.g., trout, sturgeon, turbot, bass), the survey of wild populations, and the studies of rare species and specimens nowadays appeals for non-invasive and non-destructive investigations of the anatomy of these animals (Chanet et al., 2007. Cybium, 31(suppl.) in press). Consequently, we have experimented using different modern techniques of medical imaging of osteichthyan fishes and we will present the advantages and applications of these approaches. Previous data have been presented with these imagery techniques (Guintard et al., 2006. 27th Congr. Europ. Assoc. Vet. Anat. 77.). The anatomy and physiology of anaesthetized or freshly dead animals can be investigated via echography and Doppler ultrasonography. Detailed anatomy of alcohol-or formalin-preserved specimens can be explored with Nuclear Magnetic Resonance and High Resolution Tomography (Brito et al., 2006. Mém. Inst. Océanogr. Paul Ricard: 44.). Different examples of such works on live trout, freshly dead and preserved flatfishes, and preserved coelacanths will be presented.

Phenotypic Plasticity and the Possible Role of Genetic Assimilation in an African Cichlid Fish

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The role of phenotypic plasticity in evolution is highly controversial, even though models have shown rather convincingly that plasticity will sometimes facilitate and sometimes constrain evolutionary changes, depending on the shape of the fitness landscape. In our study we have investigated the possible role of phenotypic plasticity and genetic assimilation in the process of adaptation and evolutionary change in the cichlid *Pseudocrenilabrus multicolor*. We examined the plasticity in response to alternative oxygen environments for fishes from three habitats in Uganda that differed widely in stability and dissolved oxygen (DO) availability. One population occurs in a stable hypoxic environment, a swamp, the second in a stable well-oxygenated environment, a lake and the third population in an environment that fluctuates seasonally from almost as hypoxic as the swamp to almost as well-oxygenated as the lake, a river. Broods were split and each half was grown under hypoxic or well-oxygenated conditions. We measured morphological parameters of three categories: (a) the gill apparatus, (b) the surrounding structural elements, i.e., the feeding apparatus, the eye and the brain and (c) the outer shape of the fish. The amount of phenotypic plasticity varied for the different morphological parameters and the different populations. We discuss the results in the light of the costs and benefits of plasticity. Furthermore, we discuss the absence and presence of indications for genetic assimilation.

Genetics of Morphological Integration in the Mammalian Skull

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Studies of nonhuman primate cranial morphology have indicated that developmentally-related features of the skull tend to be inherited as relatively independent modules allowing for somewhat independent evolution of different regions of the cranium. The co-inheritance of develop-

mentally-related groups of traits can alter short-term response to selection and result in considerable divergence between observed species differences and the selection required to produce them. Illustrations of this point are provided from various primate clades. The genetics underlying morphological integration can be investigated by quantitative trait locus studies in model organisms, such as the mouse. We have found that developmentally distinct portions of the skull are modular in their genetic basis, with relatively independent inheritance of modules being due to the restriction of gene effects to developmentally-related traits, rather than to a balance between positive and negative pleiotropy. Furthermore, these developmental modules show considerable variation in levels of dominance across the range of pleiotropic effects, resulting in multivariate single locus overdominance for cranial shape factors with important consequences for maintaining genetic variability for morphological traits within populations. The range and strength of pleiotropic effects is itself genetically variable, in part, due to epistatic interactions that vary in their pattern among traits affected by the interacting loci. Selection for modularity then can produce a change in the range of pleiotropic effects displayed by individual loci.

Phylogeny and Ecology Shape the Mandible of Murine Rodents

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The respective role of the phylogenetic and ecological components in an adaptive radiation is tested on a sample of Old World rats and mice (Muridae, Murinae). Phylogeny was established on nuclear and mitochondrial genes and reconstructed by maximum likelihood and Bayesian methods. The radiation of the murine rodents included an ecological diversification, particularly of the diet. The mandible outline, quantified using Fourier analyses, provided a morphological marker related to this ecological factor. The pattern of morphological diversification reflects both, ecology and phylogeny. Omnivorous groups tend to display a slender mandible while herbivorous ones are characterised by more robust mandibles. Differences in functional demand related to different foods can explain the difference in mandible shape: consumption of abrasive and resistant herbs requires more strength during occlusion, favouring larger zones of insertion for the masticatory muscles. A phylogenetic component further interferes and causes the differentiation of several groups (*Praomys, Arvicanthini, Rattus, Apodemus*). Comparison of genetic and morphological (based on mandible shape) distances evidenced a correlation of both for omnivorous taxa, whereas ecological specialisation triggers a deviation from this trend of phenotypic drift.

Variation in Neck Posture and Feeding Strategy Among Sauropod Dinosaurs

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A robust and reliable mechanical method for the reconstruction of the habitual posture of a long neck in a terrestrial vertebrate is based on the comparison of the distribution of compressive forces along the neck with the distribution of the cross-sectional areas of the intervertebral joints. In habitual postures compressive forces tend to be proportional to the cross-sectional areas of the intervertebral joints resulting in nearly uniform stresses in the joint cartilage along the neck. This method has been successfully tested on recent vertebrates with long necks. Applied to sauropods, it reveals a considerable variation in neck posture and feeding strategy among different species. Comparative studies on neck movements, vertebral joints and soft tissues in recent vertebrates with long necks indicate, that at least in some sauropods like *Diplodocus*, the neck could have been more mobile than often assumed. Estimates of energetic costs of vertical neck movements reveal physiological and ecological constraints for neck movements. Frequent changes of the height of the head during feeding are only likely under certain conditions concerning the distribution of food. For sauropods, the results corroborate the assumption of very lightly built necks with large air-sacs. It appears that the considerable reduction of neck mass due to the air-sacs was a prerequisite for the evolution of the unique feeding strategy of using a very long neck that made sauropod gigantism possible.

Convergent Evolution of the Sabertooth Craniodental Morphology: The Clouded Leopard *(Neofelis nebulosa)* and *Paramachairodus ogygia* Compared

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The sabertooth cats (Machairodontinae) were characterized by a large number of unusual skull and mandibular adaptations for attaining a large gape and efficient biting with hypertrophied upper canines. Homologous regions of the skull and mandible among extant felids are morphologically and mechanically different. However, the term sabertooth is historically tied to advanced forms such as *Megantereon* or *Smilodon*, which were among the first sabertoothed predators described. Primitive sabercats were unquestionably very different, probably approaching extant great cats to a large extent. However, prior to the discovery of the Late Miocene carnivore trap at Cerro Batallones-1 near Madrid, Spain, primitive sabercats were very poorly known, and evolutionary scenarios regarding the development of the extreme morphology of several derived sabercats were largely speculative. Today, the primitive sabercat *Paramachairodus* is well-known, and does indeed approach a pantherine skull morphology in a number of respects. However, it also differs in several key issues, most notably in having large, somewhat blade-like upper canines; a verticalized lower jaw symphysis, where the symphysis forms a much less inclined angle to the mandibular ramus than among extant felids, a slightly ventrally enlarged mastoid process, and a reduced paroccipital process, and proportionally reduced lower canines. In all those respects *Paramachairodus* bears a closer resemblance to other sabercats than to extant pantherines. However, the extant clouded leopard possesses these traits also, often to an extent as to make to two species near identical. The clouded leopard thus appears to be a primitive sabercat belonging to the Felinae lineage.

Feeding Ecology, Bite Mechanics, and Canine Morphology in Extant Bears (Carnivora: Ursidae)

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Despite comprising only eight extant species, the bear family spans the entire ecological spectrum, from the virtually exclusively herbivorous giant panda, the almost equally herbivorous spectacled bear, the frugivorous and insectivorous sloth bear, four omnivorous species (Eurasian brown bear, Asiatic and American black bears, Malayan sun bear), to the largely carnivorous polar bear. This diversity in feeding ecology is, however, not mirrored in differences in the bite mechanics and upper canine morphology, and with the exception of the giant panda, and to a certain degree the sloth bear, the other bears are mechanically largely similar. The polar and brown bear are particularly similar, reflecting their close phylogenetic relationship and a very short evolutionary lineage leading to the modern polar bear, during which other factors than craniodental adaptations for hypercarnivory were prevalent. The reasons for the lack of a derived anatomy accompanying the large ecological diversity appear to be a combination of a rather short phylogenetic history, since the Ursine bears probably did begin their evolutionary radiation until the Pliocene; omnivory being the plesiomorphic stem state for the extant ursids, with the possible exception of the giant panda; and sheer size and strength. Ursids appear to have been ecologically and evolutionarily successful in no small measure simply owing to their physical size and power.

Stealing Phenomenon Caused by Anomalous Origin of the Right Coronary Artery from the Truncus Pulmonalis: A Rare Congenital Anatomical Anomaly

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We present a 71 year-old male with an anomalous right coronary artery originating from the pulmonary artery which is a rare congenital coro-

nary abnormality. The patient had prolonged exertional chest pain probably related to myocardial ischaemia. The ECG revealed anterolateral dynamic T-wave changes and echocardiographic examination showed segmential wall motion abnormalities. Because of reversible perfusion defects showed on myocardial perfusion scintigraphy coronary angiography was performed. Coronary angiography revealed large, ectasic left main, LAD and CX arising from the left sinus of Valsalva and LAD giving off extensive collateral vessels to the right coronary artery that was drained into the truncus pulmonalis. There was no significant stenosis. The diagnosis of anomalous origin of the right coronary artery from the pulmonary artery, an anomaly that has been associated with angina, myocardial infarction, heart failure and sudden cardiac death was confirmed. The ischemic symptoms and findings were thought to be due to coronary stealing phenomenon which was caused by preferential blood flow into the low-pressure pulmonary artery. The patient underwent successful surgical treatment with double ligation of the right coronary artery from the proximal segment. After surgical treatment, the patient's symptoms and the findings of ischaemia were relieved. Afterward the patient was discharged on medication.

Comparative Scanning Electron Microscopie Study of the Lingual Dorsal Surface in Dasypodidae

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Filiform, fungiform, foliated and circumvallated papillae are distributed over the dorsal mucosa surface of the tongue of mammals. They differ in shape, size, number, distribution and development degree between species. That variability could be related with food habits. We compared the morphological characteristics of the lingual dorsal surface of three armadillo species *Zaedyus pichiy, Chaetophractus vellerosus* and *C. villosus*, using scanning electron microscopy. The pieces of lingual tissue were fixed in diluted Karnovsky solution and processed with routine histological techniques. Observations of tongue surface were made using an Evo 40 XVP (Cambridge, England) scanning electron microscope at 7 kV. Filiform, fungiform, and circumvallated papillae were identified. In the anterior third of the tongue prominent conical filiform papillae and fungiform papillae, in less proportion, were observed. Fungiform papillae have visible taste pores on surface. Filiform branched papillae are numerous in the middle third of the tongue. The number of branches varies considering the species, finding between 3 and 5 in *Z. pichiy* and *C. vellerosus*, and between 3 and 9 in *C. villosus*. The posterior third of the tongue shows two circumvallated papillae surrounded by a groove, placed at both sides of the midline of the tongue. Posterior to circumvallated papillae, the filiform papillae are smaller and scarce. At high magnification, a network of microridges was observed. Filiform papillae and microridges may function as a supporting structure for food-uptake, mastication and swallowing. The presence and distribution of filiform, fungiform and circumvallated papillae are basically comparable among the studied armadillo species.

The Relationship Between Skeletal Constraint and Pulmonary Complexity in Archosaurs

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The clade Archosauria presents an unparalleled opportunity to examine evolutionary pathways in respiratory design and function. Birds and crocodylians are the only living representatives of the Archosauria, a once-diverse group that includes dinosaurs, pterosaurs and other fossil forms exhibiting an enormous range of anatomical diversity. Crown-group archosaurs offer examples of highly specialized respiratory systems serving both cold-blooded (ectothermic) and warm-blooded (endothermic) metabolic physiologies. Important transformations that may serve to enhance our understanding of the evolution, structure and function of the tetrapod respiratory system are likely documented in the archosaur fossil record. The avian thorax exhibits fewer degrees of freedom of movement than the crocodylian thorax. For example, birds lack the intermediate ribs and lumbar region characteristic of crocodylians and have fully ossified rather than cartilaginous sternal ribs. The relatively highly constrained trunk skeleton of birds ventilates a highly efficient, extremely heterogeneous pulmonary air-sac system. The evolution of higher levels of pulmonary heterogeneity in the archosaur fossil record (indicated by increased levels of postcranial skeletal pneumaticity) is associated with a decrease in the degrees of freedom of movement of the thorax and increased control over displacement of the abdominal body wall. I hypothesize that increased levels of constraint on thoracic mobility function to exert greater control over the timing, location and amount of trunk expansion in progressively more heterogeneous pulmonary systems. Increased control over skeletal aspiration breathing may be a prerequisite for the generation and maintenance of precise and complex airflow patterns in structurally complex and highly efficient pulmonary systems.

Jawless Feeding in Hagfish

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We examined feeding morphology and kinematics in two hagfish species, *Eptatretus stoutii* and *Myxine glutinosa*. Hagfish ingest and transport food with a pair of cartilaginous dental plates that exit and enter the mouth via protractor and retractor muscles, respectively. As in gnathostomes, the hagfish feeding apparatus (HFA) includes skeletal, dental, and muscular constituents. Dental elements, skeletal elements, and whole samples of the HFA are larger in *E. stoutii*. The clavatus muscle, a major retractor muscle, is larger and generates more force in *E. stoutii* than in *M. glutinosa*. Maximum force production in the clavatus ranges from 5N to 16N, exceeding the bite forces generated by some gnathostome species. We filmed feeding behaviors in a glass aquarium for kinematic analyses. Despite some differences in feeding morphology, feeding kinematic profiles are similar in both *E. stoutii* and *M. glutinosa*. In lateral view, dental plate protraction and retraction resembles a pulley system and lacks the leverage in gnathostome jaws. With gape cycle times (GCT) averaging 995ms, hagfish require more time to complete a gape cycle than gnathostomes. This result suggests that a functional advantage to jaws is speed-modified leverage to reduce GCT, which in turn allows gnathostomes to exploit elusive prey. In addition to producing high magnitudes of force in the feeding muscles, hagfish can evert their dental plates to 180 degrees, exceeding the gape angles attained in virtually all gnathostomes, suggesting neither force generation nor gape were selective forces imposed on the common ancestor to gnathostomes.

Genomic Coadaptation and Integration Stability in the Skull of the House Mouse

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The comparison of developmental instability levels, usually measured by fluctuating asymmetry (FA), between hybrids and parental groups has been used for inferring incompatibilities between divergent genetic systems. Whether level of fluctuating asymmetry can appraise perturbation between homologous parts of a biological structure, it does not consider perturbations occuring on the morphological integration between different characters. As a consequence, it is not well known whether breakdown of genomic co-adaptation found in hybrids between genetically differentiated entities can also result in perturbations in phenotypic integration. This has, however, broader implications if morphological innovations are regarded as arising from changes in phenotypic integration. We predict that the patterns of integration in hybrids should be more disturbed between populations that have accumulated significant genetic changes in systems controlling character development. We studied patterns of skull integrations in hybrids (F1 and backcross) and their parental groups in two distinct laboratory crosses of house mice (between subspecies and between chromosomal races). For both crosses it has been previously shown that the amount of FA levels in hybrids differed from those of parental groups suggesting that new genes association influence developmental stability. Here we explore the divergence in integration patterns between parental populations. The difference in strength of

phenotypic integration between parents and hybrids is analyzed in regard to genetic and chromosomal imbalance.

Evolutionary Mechanics of Unguligrady in Artiodactyls

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Forefeet in terrestrial artiodactyls show remarkable anatomical specialization and evolutionary convergence. The ancestral condition for all artiodactyls is a 5-toed manus with a reduced pollex, similar to many extant long-legged, digitigrade placentals. In each of three major lineages (Suina, Tylopoda, Ruminantia), 4-toed descendants adopted an unguligrade posture. Here called "primary unguligrade," these groups, including living suids and tragulids, have lost the pollex and have modified interosseus muscles of the manus into stiff ligaments which maintain an elevated metacarpophalangeal (MCP) joint. In tylopods and ruminants, descendants of 4-toed primary unguligrades have lost lateral digits, often fusing bones of the manus and giving rise to morphology here termed "secondary unguligrade." Secondary unguligrade forefeet are modifications of less specialized primary unguligrade ones. Previous explanations of these specializations, especially in secondary unguligrades, have focused on reduced costs of locomotion by lightening limbs and/or increasing step length. I hypothesize that primary unguligrades reduce locomotion costs both by replacing muscle tissue with ligaments and by storing elastic energy in these ligaments during stance. Further, I hypothesize that reduction of bony elements and elongation of ligaments will provide greater energy savings in secondary unguligrades. To test these hypotheses, I am using the CTX imaging system developed at Brown University. CT-generated models animated using 3-D coordinates calculated from digitized bone markers yield accurate representations of in vivo kinematics. Preliminary kinematic results in minipig locomotion show the MCP joint undergoes hyperextension during stance, indicating that the interosseus ligament is a potential site of elastic energy storage.

Morphology and Variation of Cranial Endocasts in the True Porpoises (Cetacea: Phocoenidae)

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Cetacean cranial endocasts generally show a close correspondence to the external morphology of the brain. Indeed, the endocast may more accurately reflect the hydrostatic shape of the brain in life than do brains that have been removed from the cranium. Features of the circulatory system that are represented by bony indicators such as canals or grooves are also often preserved in endocasts. We present a series of HRXCT-derived endocasts from all six extant species of the Phocoenidae, a monophyletic group of odontocetes that includes the smallest known cetaceans. Systematic patterns of endocast variation are inferred by optimization onto published phylogenies, using an endocast of a bottlenose dolphin (*Tursiops truncatus*) for outgroup comparison. Intraspecific variation is assessed using endocasts derived from six harbor porpoise (*Phocoena phocoena*) skulls. Investigated features include both linear and volumetric measurements (e.g., volumes of whole endocasts and of components of the endocasts), and identified anatomical features (e.g., features of the circulatory system such as canals and grooves for the meningeal arteries, rostral rete mirabile impressions, etc.). Among the features seen to vary between species include the prominence of particular vascular channels (e.g., the spinal meningeal canal is poorly developed in the early-diverging *Neophocena* compared to other phocoenids), the extent to which gyri are visible, the degree of flattening of the dorsal anterior telencephalon, and various other features related to shape and proportions. These results reveal a potential for phylogenetic signal in cranial endocast data, although there is a significant amount of intraspecific variation.

Comparative Anatomy in Exhibitions

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Comparative anatomy was created by Georges Cuvier in the Natural History Museum in Paris. The collections of the first Gallery of Comparative Anatomy have been transferred in the actual building more than a century ago. The advent in Paris of the ICVM, which gathers the international community of vertebrate anatomists, is a unique opportunity to organize a reflection on the discipline's evolution, its place in the future and the ways of mediation. The Gallery of Comparative Anatomy shows not only osteology but also splanchnology. What is the present meaning of such an exhibition, based on preserved biological objects, when today science is made through technology? What message can be transmited through thematic collections of organs (teratology and splanchnology)? The place of human beings in a comparative anatomy exhibition can also be discussed: is it a reference or a mammal among others? How can we transmit an evolutionist message when the public's reference is their own body? In systematics, phylogeny and comparative anatomy: How to use biological objects within the evolutionary framework? After a presentation and a visit of the gallery, we propose to provoke a reflection on each aspect of comparative anatomy and others. Exhibitions are a medium between scientists and the public. Moreover, the role of permanent exhibitions is crucial as far as education is concerned: its purpose being to be both time current and everlasting.

Sound Production Mechanism in the Clownfish *Amphiprion clarkii* (Amphiprioninae, Pomacentridae)

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Clownfishes live in social group within sea anemones. They are prolific "singers" that produce a wide variety of sounds, described as "pops" and "chirps", involved in both reproductive and agonistic interactions. Although clownfish sounds were recorded since 1930, the mechanism of sound production has remained unresolved. The sounds used to describe the sonic mechanism were directed towards hetero- and conspecifics that approach their sea anemone host. Sound recordings were synchronized using a high speed video (500 fps) coupled or not with an X-ray system. These systems allowed quantifying the movements of external and internal bones during sound production. Sounds were typically accompanied by rapid ($<$ 30 ms) head movements such as elevation of the skull, lowering of the hyoid bar and the anterior part of the branchial basket, retraction of the pectoral girdle, and, finally, closing of the mouth. Synchronization of sound pulses with X-ray images indicates that sound is produced when the hyoid apparatus is completely lowered and the mouth closed by a previously unknown mechanism. Dissections of freshly dead specimens reveal an unusual ligament responsible for the rapid mouth closing. This ligament joins the hyoid bar to the internal part of the mandible. Acting as a cord, it forces the mandible to turn around its articulation during the lowering of the anterior part of the branchial basket, forcing the mouth to close. Sounds result from the collision of the jaw teeth, transferring energy to the jaws that are presumably the sound radiator.

Primate Skull Adaptations to Fracture Resistant Foods

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Previous work by Lucas and others has investigated the relationship between food mechanical properties and tooth form. Less has been done to examine how these same properties affect skull shape. This project investigates whether, and in what way, the fracture resistance of foods influences the hard tissues of the anthropoid masticatory system. A comparative study of four primate groups was designed to test the hypothesis that fracture resistant foods affect primate skull shape in a consistent and predictable way. The face and jaws of Cebus monkeys, macaques, baboons, and apes were compared in three dimensions using geometric morphometrics (5–7 taxa per clade, 63–73 landmarks per skull). The taxa from each clade that are reported to eat the most fracture resistant foods all showed similar morphological trends in their masticatory systems relative to the other members of their clade. These trends include a taller mandibular corpus and symphysis, a taller mandibular ramus, and a more orthognathic face. The fact that these trends exist in New World monkeys, Old World monkeys, and apes suggests that the influence of food mechanical properties on masticatory form is widespread in living anthropoids. This observation not only has the potential to increase our

understanding of primate dietary adaptation, but could also be valuable in interpreting homoplasy in both living and fossil primates.

Gene Heterochrony in the Development of Cetacean Hyperphalangy

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Most mammals have a generalized phalangeal formula with two phalanges in the thumb and three in the remaining digits. Cetaceans are the only mammals that have more than three phalanges per digit (hyperphalangy). The function of hyperphalangy is probably unrelated to simple digit elongation as bats have greatly elongated fingers caused by prolonged expression of bone morphogenic proteins but are not hyperphalangeous. Cetacean hyperphalangy has been linked to the role of forelimbs in steering and balance, as opposed to propulsion. Developmental mechanisms generating hyperphalangy are unknown. We test the hypothesis that dolphins exhibit greater expression of the genes controlling development of limb growth from the body wall, and joint formation. The generalized mammalian pattern is to express the protein Fgf-8 while the limb is growing out from the body wall and the protein Wnt-9a while joints develop in the digits. Our studies of gene expression during dolphin ontogeny indicate that the protein Fgf-8 is active while the forelimb is projecting from the body wall from at least day 24 to day 30 of gestation. After 30 days Fgf-8 expression stops but the forelimb continues to grow out from the body wall, and also begins patterning of the digital rays. The cessation of Fgf-8, at day 30 is unlike the generalized mammalian pattern, suggesting that heterochronic changes of expression took place. Ongoing research will focus on elucidating the temporal and spatial expression patterns of Wnt-9a and hedgehog morphogens.

Morphology of the Mammalian Vestibulo-ocular Reflex: The Spatial Arrangement of the Human Fetal Semicircular Canals and Extraocular Muscles

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The vestibulo-ocular reflex (VOR) is the system of compensatory ocular movements in response to stimulation of the kinetic labyrinth seen in all vertebrates. It allows maintenance of a stable gaze even when the head is moving. Perhaps the simplest influence on the VOR is the spatial orientation of the planes of the semicircular canals relative to the extraocular muscles. It is hypothesized that the muscles are in parallel alignment with their corresponding canals in order to reduce the amount of neural processing needed and hence keep reflex times to a minimum. However, despite its obvious importance, little is known of this spatial arrangement, nor of any ontogenetic changes in the relative orientations of the muscles and canals. As part of a broader project encompassing a wide variety of mammals, the morphologies of fetal and adult specimens of *Homo sapiens* were examined using magnetic resonance (MR) images. Using three-dimensional co-ordinate data taken from the images, vector equations of the extraocular muscles and planes of best fit for the semicircular canals were calculated in order to determine their relative orientations. Significant trends were seen between both the anterior and lateral semicircular canals and their corresponding extraocular muscles during ontogeny. Furthermore, it was noted that none of the six muscle-canal pairs is in perfect alignment, either during ontogeny or in adulthood. Overall, it was shown that there is significant reorientation of the extraocular muscles and semicircular canals during ontogeny, but that, in most cases, there is little realignment beyond the fetal period.

Masticatory Motor Patterns in Six Herbivorous Australian Marsupials

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Electomyograms of the adductor muscles of the hairy-nosed wombat (*Lasiorhinus latifrons*), red kangaroo (*Macropus rufus*), Tammar wallaby (*M. eugenii*), koala (*Phascolarctos cinereus*), potoroo (*Potorous tridactylus*) and the brush-tailed possum (*Trichosurus vulpecula*) were analyzed and compared with those of placental herbivores. Marsupials have developed several different and distinct masticatory motor patterns that are all fundamentally different from those of placental herbivores where jaw movements are controlled by a relatively conservative pattern of working and balancing side muscle pairs (Triplet I and II or Diagonals I and II). For example, in the three species of macropods, all regions of the balancing and working side temporalis are active synchronously and the power stroke is divided into two distinct shearing and grinding phases. In addition, force generated by the balancing side muscles exceeds that of the working and is transferred to the working side via a slender mobile unfused mandibular symphysis. In wombats only the working side adductors are active during the power stroke. Koalas have lost the ubiquitous inflected mandibular angle of marsupials and their motor pattern is convergent on that of placental herbivores. In ring-tailed possums the pattern is transitional between the "primitive pattern" of placentals and that of macropods. This greater variety of motor patterns reflects the independent acquisition of mammalian herbivory in Australasia when the continent was isolated during much of the Tertiary.

Resting Metabolic Rates, Bone Growth Rates and Bone Tissue Types in Amniotes

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There is an abundant literature dealing with the problem of estimating metabolic rates of extinct taxa, mainly archosaurs, using differences in bone tissue types. These paleobiological estimations are important to analyze the evolution of endothermy in synapsids and diapsids. However, the relationships between bone histodiversity and metabolic rate have never been tested in extant species. Here, we have measured a bone histological variable (density of primary osteons) and resting metabolic rate in a sample of 44 growing individuals belonging to 13 species of amniotes. In some species of our sample (Chelonia and Lacertidae), growth takes place only at the free external surface of the bone. In contrast, in mammals, varanids, crocodiles and birds, we have observed the formation of big cavities which are subsequently filled by a process of centripetal apposition of bone and form primary osteons. This last growth mode is linked to sustained high bone (and overall) growth rates, which require a fast metabolism because they involve high rates of protein synthesis and degradation. We hypothesize that resting metabolic rate may determine the maximum possible growth rate and, consequently, the density of primary osteons. We have found a positive linear relationship between density of primary osteons and resting metabolic rate in our sample, which does not contradict the above hypothesis. This relationship is a first step in the construction of a model of paleobiological inference of metabolic rate by using bone histodiversity.

Functional Benefits of Plantigrade Foot Posture

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It has long been thought that digitigrade and unguligrade foot posture increase locomotor efficiency in animals; however, little attention has been paid to the functional benefits of plantigrade foot posture. In this study, we used human subjects to test the hypothesis that greater torques can be applied to the ground with plantigrade rather than digitigrade foot posture. The application of ground torques is essential to sharp turning performance and physical aggression. Subjects performed maximum effort lateral pushes and 90 degree cutting turns on a Kistler force plate while maintaining plantigrade or digitigrade foot posture. The lateral pushes were performed while standing on a single limb to assure that the measured torques came from a single limb rather than from two limbs. We calculated the torque (i.e., free moment) applied to the ground following the method of Holden and Cavanagh (1991, J. Biomechanics 24:887–897). The average maximum torque generated by lateral pushes from a plantigrade stance was approximately 2-fold the average maximum torque generated from a digitigrade posture. The difference between plantigrade and digitigrade 90 degree cutting turns was less dramatic, but larger torques were produced during plantigrade turns then during digitigrade turns. Hence, plantigrade foot posture does appear to provide a performance advantage in the production of ground torques. Although humans are highly specialized for endurance walking and running, the retention of plantigrade foot posture is unlikely to improve

locomotor economy or speed. Rather, plantigrade foot posture in *Homo* may enhance agility and performance in aggressive encounters.

Finite Element Modelling of the Cat Skull

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A Finite Element model of a cat skull *(Felis sylvestric catus)* was loaded and constrained to replicate the classic experimental set-up used by Buckland-Wright in 1978. The FE analysis produced results broadly comparable with those of Buckland-Wright in terms of general patterns of strain, although the strain values predicted were usually lower. In the cat, as in many other mammals, the bony postorbital bar is incomplete and the frontal and zygomatic are linked by a postorbital ligament that represents a thickening in the anterior margin of the temporal fascia. Ligaments are effective in the transmission of tensile stress. The analysis was repeated with and without the addition of a postorbital ligament. Although stress levels remained high in the zygomatic arch and antorbital margin, peak stresses were less when the ligament was in place.

Multibody Dynamics Analysis of a Macaque Skull

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Evaluating the stress and strain fields in anatomical structures is a way for us to test the hypothesis that facial and skeletal morphology is related to mechanical loading. Engineering techniques such as finite element analysis are now commonly used to calculate the stress and strain fields, but if we are to fully accept these methods we must be confident that the applied loading regimens are reasonable. Multibody dynamics analysis (MDA) is a relatively new computer modelling technique that can be used to predict muscle, joint and bite forces during static and dynamic motions. MDA was used here to model a macaque (*Macaca fascicularis*) skull, where the geometry of the skull was obtained from microCT, and the model was constructed so that the temporomandibular joint (TMJ) could translate in the sagittal plane and rotate about the coronal axis. The muscles of mastication and the TMJ ligaments were included and defined with representative force-length relationships, but, for simplicity, constant muscle force-velocity relationships were assumed in this initial model. However, the model did include wrapping of the temporalis muscle groups about the skull and the fanning of the muscles into many segments over their origin/attachment sites. This paper will present preliminary results from the model, and demonstrate how muscle, bite and joint forces vary with different gape angles and bite points.

Shape, Arch Height and Plantar Pressure in the Biologically Representative Human Foot

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During hominin evolution, foot function evolved from primarily grasping into a complex lever mechanism for efficient bipedal locomotion. Initially in the supporting phase of a walking or running step, the foot structure must be flexible to maximize intimate ground contact, but it has then to become rigid to provide the leverage at push off. To date, insights in these functional changes are far from complete. Problematic in this respect is that most of our knowledge is based on habitually shod Western subjects. It has been shown that footwear effects foot shape (e.g., arch height) and thus most likely its function as well. Therefore, it is important to study habitually barefoot-walking people to establish form and function of the biologically representative foot. We collected morphometrics (toe spread, navicular height and anatomical foot type), dynamic plantar pressures and kinematics for barefoot walking of 40 habitual barefooted Indian adults (3 trials for both feet, at preferred velocity). Similar data were obtained from 40 habitually shod Indians. Barefooters had a larger toe spread and a slightly lower foot arch than habitually shod subjects. Interestingly, the variation in foot type is significantly higher in shod walkers (i.e., higher incidence of pes planus and pes cavus) than in barefoot walkers. Kinetically, subtle differences between the two groups were found as well. We conclude that, when studying the human foot from a biological or paleoanthropological perspective, habitually barefoot walking subjects should be preferred.

Prey Capture Behavior in Anolis Lizards: Testing the Effect of Surface Diameter (Branches Versus Flat Substratum)

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Feeding strategies in squamates involve a complex series of behavioral activities integrating trophic, appendicular and axial movements. To date, the trophic systems and the locomotor design have been studied separately and less often in the context of prey-predator relationship. This paper aims to present a first comparative kinematic study of the integration of locomotor and trophic systems in the iguanid lizard, *Anolis carolinensis*. Anolis lizards are considered as sit-and-wait predators using lingual prehension, in contrast to the majority of scleroglossan lizards that are often considered as active foragers mainly using jaw prehension. We analyze predator behavior in *A. carolinensis* during prey (living crickets) chasing on flat substratum and on narrow branches (18 mm diameter) to measure the potential effect of surface diameter on the kinematic variables of limbs and trophic system during this prey ingestion. A high-speed video system (250 Hz) was used to determine movements of the limbs, the head, the jaws and the tongue for five adult males. Various variables were recorded from analysis of the films (i.e., speed, acceleration, maximal angular movement of the limbs, tongue protraction and retraction), and kinematic curves were built to compare the coordination of movements of the different structural elements under both environmental constraints (flat surface versus narrow branch). Kinematic variables (timing of events and amplitudes) were extracted from curves and compared by using one two-way ANOVA testing the diameter of the surface (fixed effect) and the individuals (random effect) on the integration between locomotor and trophic system.

Tooth Attachment Complexity in a Cretaceous Mosasaur

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Vertebrate teeth are attached to jaws by a variety of mechanisms, including acrodont, pleurodont, and thecodont modes of attachment. Recent studies have suggested that several variations of modes of attachment exist within each sub-category. Especially squamates feature a broad diversity of modes of attachment. Here we have compared tooth attachment with modes of attachment found in recent reptiles. Using histologic analysis of ultrathin ground sections of mosasaur jaws, five attachment elements that anchor the tooth to the jaw were identified: (i) the compact tooth bearing element (TBE), (ii) the interdental ridges (IR) connecting adjacent teeth, (iii) the spongy pedestal (PD), (iv) a mineralized periodontal ligament ("bone of attachment"; BA), and a cementum layer (CEM) at the interface between root and periodontal ligament. Calcium/phosphate ratios were similar between all five attachment elements. The complex, multilayered attachment apparatus in mosasaurs was compared with the attachment in recent reptilians such as iguanas and crocodilians. We propose that the mineralization status of the periodontal ligament is a dynamic feature in vertebrate evolution subject to functional adaptation based on a light mineralization status of the ligament in crocodilians and its structural similarities with mosasaur bone of attachment. Based on structural differences between the bone of attachment of

replacement teeth compared to surrounding teeth, we also suggest that theca remodeling takes place during mosasaur tooth replacement. Funding by NIH grant DE15425 and NSF grant MCB-0236226 is gratefully acknowledged.

The Musculotendinous System of an Anguilliform Swimmer: Muscles, Myosepta, Dermis and Their Interconnections in *Anguilla rostrata*

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Eel locomotion is considered typical of the anguilliform swimming mode but little is known of the internal morphology that contributes to this function. We conducted a morphological analysis of the connective tissue system (myosepta and skin) and of red muscle in *Anguilla rostrata* focusing on the interconnections between these systems. Our aim is to identify the morphological features that distinguish this anguilliform swimmer from subcarangiform or carangiform swimmers, and to reveal possible pathways of muscular force transmission by the connective tissue. We investigate three body positions along the trunk using microdissections, histology and 3-dimensional reconstructions. We find that eel myosepta have a mediolaterally oriented tendon in each the epaxial and hypaxial regions (epineural or epipleural tendon) and two longitudinally oriented tendons (myorhabdoid and lateral tendon). Myosepta insert into the dermis via fiber bundles that pass through the stratum spongiosum of the dermis and either weave into the layers of the stratum compactum or traverse the stratum compactum perpendicularly. These fiber bundles are evenly distributed along the insertion line of the myoseptum. Red muscles insert into lateral and myorhabdoid myoseptal tendons but not into the horizontal septum or dermis. Thus, red muscle forces might be transmitted along these tendons but will only be delivered indirectly into the dermis and horizontal septum. We find that based on internal morphology eels are similar to subcarangiform swimmers but different from carangiform swimmers.

Enameloid/enamel Transition Through Successive Tooth Replacements in *Pleurodeles waltl* (Lissamphibia, Caudata)

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The study of the evolutionary enameloid/enamel transition suffers from discontinuous data in the fossil record, but a developmental enameloid/enamel transition exists in living caudates, salamanders and newts. Answering the question of when and how the enameloid/enamel transition is achieved during caudate ontogeny is of high interest because the caudate situation could reflect what has occurred during evolution. Using light and transmission electron microscopy, we monitored the formation of the upper tooth region in six successive teeth of a tooth family (position I), from late embryos to young adult *Pleurodeles waltl*. Enameloid was only identified in embryonic tooth I1 and in larval teeth I2 and I3. A thin layer of enamel is deposited lately by the ameloblasts on the enameloid surface of these teeth. From post-metamorphic juvenile onwards, teeth are covered with enamel only. The collagen-rich enameloid matrix is deposited by odontoblasts, which subsequently form dentin. Enameloid, like enamel, mineralizes and then matures, but ameloblast participation in enameloid matrix deposition is not proven. From tooth I1 to tooth I3 the enameloid matrix becomes denser, and resembles more and more the dentin matrix, although it is still subjected to maturation. Our data suggest that there is no enameloid/enamel transition but, rather, an enameloid/dentin transition, which seems to result from a progressive slowing down of odontoblast activity. As a consequence, the ameloblasts in post-metamorphic teeth appear to synthesize the enamel matrix earlier than in larval teeth.

Bone Vascular Supply in Monitor Lizards: Functional and Phylogenetic Considerations

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Bone vascular canals occur unevenly in tetrapods, and the meaning of this polymorphism remains obscure: is it primarily dependent on taxonomy, or on functional causes, especially the speed of cortical accretion? The Varanidae, a monophyletic clade (one genus, 9 subgenera, 53 species) gathering species with impressive size differences but very similar morphologically, is an excellent model for deciphering this question. Cortical vascularization was studied in 20 monitor species, on two bones (femur and fibula) differing by the absolute growth speed of their diaphyseal cortices. In all species less than 400 mm SVL, bone cortices are void of vascular canals, whereas all larger species display canals. This size is thus a threshold. The distribution of these two categories is not strictly related to taxonomy. When present, vascular canals always occur in the femur, but are less frequent, sparser and thinner in the fibula. A positive, linear relationship links vascular density to specific size. During individual growth, vascular density decreases exponentially in the femur. In most species, canal orientation (longitudinal, oblique, radial) varies between individuals and is diverse in a single section. There is no clear relationship between canal orientation and vascular density. These results suggest that: a) the occurrence of bone vascular canals is basically dependant on specific size, not on taxonomic frames; b) vascular density reflects the absolute growth rates of bone cortices; c) the orientation of vascular canals is neither related to taxonomy, nor a mere result of growth rate. The polymorphism of bone vascularization thus refers to morphological plasticity, not morphological diversity.

Body Mass Estimation in Xenarthra Through Stepwise Multiple Regression

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The Magnorder Xenarthra include strange extinct groups, like glyptodonts, similar to big armadillos, and ground sloths, terrestrial relatives of the extant tree sloths. Recently, palaeobiologists have paid special attention to their unusual traits. These odd features make it difficult to understand their ecology. The body mass estimation of extinct species is very important for palaeobiological reconstructions. The commonest way to estimate body mass from fossils is through linear regression. Troubles arise as the studied species have no similar extant relatives. Thus, regression allometric patterns for extant relatives could be different than those shown by the extinct group. This is the case for gliptodonts and ground sloths. Then, stepwise multiple regressions were developed including extant xenarthrans (their taxonomic relatives) and ungulates (their supposed ecological relatives). Weighting was applied in order to maximize the taxonomic evenness. Twentyeight equations were obtained. The distribution of the Percent of Prediction Error (% PE) was analyzed between taxonomic groups (Perissodactyla, Artiodactyla and Xenarthra) and size groups (0–20 kg, 20–300 kg and more than 300 kg). Only five equations have a homogeneous error among the aforementioned groups. These were applied to 6 extinct species. A body mass of 80 kg was estimated for *Propalaeohoplopharus australis* (Cingulata: Glyptodontidae); 594 kg, for *Scelidotherium leptocephalum* (Phyllophaga: Mylodontidae), and 3550.7 kg for *Lestodon armatus* (Phyllophaga: Mylodontidae). High scatter in body mass estimates is observed for the remaining species: *Catonyx tarijensis* (Phyllophaga: Mylodontidae), *Thalassocnus natans* (Phyllophaga: Megatheriidae) and *Pronothrotherium typicum* (Phyllophaga: Megatheriidae). This could be due to different specializations.

The Association Between Mandibular Shape and Habitat in Ungulates Analysed by Geometric Morphometrics Methods

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The presence of dust in open environments means an extra abrasive factor for teeth in the diet, independently of the foraging habits of the animal, and this factor could have an effect upon the shape of the cra-

niomandibular complex. In this work, we have explored this possibility in the ungulate mandible using geometric morphometric methods. We photographed 94 the mandibles in lateral view (each representing extant and different species) and digitized a configuration of eleven homologous landmarks that homogeneously capture their geometry. Landmark configurations were processed using common Procustes analysis, and shape differences were visualized with deformation grids based on the Thin Plate Spline interpolation function. Ordination methods (relative warps) were used to explore directions of greater shape variance. A canonical variates analysis (CVA) was also performed for testing the possible discrimination between habitat groups (open habitat, mixed habitat and closed habitat) in association with the shape of the mandible. The CVA shows that habitat discrimination can be solved as a function of shape variables. Thereafter, these functions were applied on a fossil lower jaw of *Megaloceros giganteum* in order to test whether we could infer its corresponding habitat. The shape of the mandible complex suggests that *M. giganteum* would have possibly inhabited open environments, though with some degree of cover.

Revision of the Scelidotheres of Brazil (Xenarthra: Scelidotheriinae)

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The history and anatomy of Brazilian scelidotheriine sloths have had a long and tortuous history. P.W. Lund concluded in the mid-1800s, after many years of researching in the Lagoa Santa region of Minas Gerais (Brazil), that two scelidotheriine species were present during the Pleistocene. Writing early in the 20th century, H. Winge agreed with Lund's conclusions. However, this view of scelidotheriine history was overturned by R. Hoffstetter during the 1950s. Of the material that Lund and Winge had assigned to these scelidotheres, Hoffstetter considered one to be a scelidotheriine and the other a peculiar megalonychid and he erected the new subfamily Ocnopodinae for this purported megalonychid. Hoffstetter also recognized a third species from Minas Gerais (near Lagoa Santa), erected by P. Gervais during the late 1800s on only a partial calcaneum, as having megalonychid affinities. Hoffstetter's views have since been followed by subsequent authors. Lastly, a new scelidotheriine species was erected on remains from Piaui, Brazi. However, adundant and well preserved material recovered over the past decade leads to a reassessment of Hoffstetter's opinion and the validity of the Piaui species. These new remains essentially corroborate the earlier views of Lund and Winge. All the specimens attributed by Hoffstetter to Megalonychidae, including Gervais'species, are scelidotheriine, and belong to one or the other of the scelidotheriine species originally recognized by Lund. The species recently described from Piau is, similarly, a synonym of one of Lund's species.

On the Status of *Megatherium (Pseudomegatherium) tarijense* (Xenarthra: Megatheriidae)

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Knowledge of the history and anatomy of megatheriine ground sloths has been based largely on material recovered from Brazil and Argentina. In recent years, however, much new material described from northwestern South America has altered our ideas of the evolution of this clade and has resulted both in the recognition of several new taxa and the validation of species named on sparse remains. Falling in the latter group is *Megatherium* (*Pseudomegatherium*) *tarijense* Gervais and Ameghino, 1880, which is based on a complete but eroded calcaneum from the Pleistocene of southern Bolivia. Most authors of the past century viewed this species as poorly defined and probably a synonym of *Megatherium* (*Megatherium*) *americanum*. Confusion over the status of *M. (P.) tarijense* was also caused in large part by the presence of *M. (M.) americanum* in the Bolivian Pleistocene. However, well preserved and nearly complete remains of several individuals suggest that *M. (P.) tarijense* is indeed valid. This material includes abundant remains from the Tarija Basin (Bolivia) housed in the Field Museum of Natural History (USA) and the Museo Nacional de Paleontología y Arqueología de Tarija (Bolivia); and from Yantac in the Peruvian Andes housed in Universidad Nacional de Ingeniería (Peru). *Megatherium (P.) tarijense* differs from *M. (M.) americanum* mainly in its smaller size, shallower mandibular ramus, reduced size of the humeral deltopectoral crest, and less twisted femur.

In Silico Adaptation of Bone Vascular Microstructure to Biomechanical Loading Mode

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Bird wing bones experience a special mechanical loading mode during flapping flight. Because the application center of lift forces is offset from long bone axis, humerus and ulna have to resist high torsional loading, unlike limb bones implied in terrestrial locomotion, which usually experience axial bending/compressive loads. Recent comparative microstructural studies have suggested that wing bones exhibit special micro-architectural adaptations that provide resistance to torsion: namely, laminar bone tissue (in which vascular canals are grouped in circumferential planes) appears preferentially in wing bones and is suspected to increase bone stiffness and strength under torsional loads. In order to go beyond the static observation of a correlation between extant structures and functions, I used FEM (finite element modelling) and an EA (evolutionary algorithm) to assess what bone 3D-micro-architectures can emerge from selective pressures on increased bone tissue mechanical stiffness, under several loading modes. Starting from initial random architectures, structured tissue patterns arose progressively in successive generations. After some thousands of generations of simulated Darwinian evolution, patterns strongly analogous to natural structures were obtained: laminar tissue-like architectures emerged when torsional stiffness was set as the fitness criterion. As Evolutionary Computation techniques (generally used in engineering) become more and more used in several fields of evolutionary biology, the aim of the present work is to illustrate the potential usefulness of evolution simulation approaches, combined with mechanical modelling tools (e.g., FEM), in order to address issues in evolutionary biomechanics.

Biomorphodynamics as a Framework for the Understanding of the Vertebrate Skeleton

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Biomorphodynamics (old constructional morphology, sensu Seilacher) discriminates the different factors contributing to mold the form of organisms, namely phylogenetic legacy, fabrication and function in an effective environment. However, the vertebrate skeleton has received little attention from this perspective. We shall deal mainly with the first two factors, since the remaining factors are the best known. The plan of the tetrapod skeleton (its historic legacy) shows minimal changes since its origin. Skeletal biomaterials are also part of this legacy. Therefore, this phylogenetic tradition strongly constrains the number and the nature of adaptive solutions. Heterochrony opens discrete fields for allowed variation; this narrows the domain of natural selection. Genome and development must be considered as the foundation of this heavy stability throughout the history of the groups. Fabrication is the second factor considered, which involves properties of biomaterials and self-organization processes, from biomineralization (involving purely physicochemical interactions between hydroxyapatite and collagen in bone and tooth) up to epigenetic interactions among gene products that confer emergent properties to cells or cell collectives, e.g., geometry. Since cell collectives interact among them, this determines the morphology of the different skeletal elements in a mechano-chemical way. Therefore, gradients in vertebrae in the backbone or in dentition are fabricational products. Patterns that are similar to those of phyllotaxis (with inhibiting factors) may be found in the distribution of scales of fishes. Other fabricational issues result from mechanical responses, e.g., pneu structures (globular skulls) or close packing (ichthyosaur fins). Again, all these mechanisms constrain new possibilities in adaptation.

Towards a Classificatory Scheme and Nomenclature ofc Bone Histology

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Current research in bone tissue biology still demonstrates a great diversity in the terminology used by various authors. This creates misunderstandings because a given word may carry different meanings (homonymy) and, conversely, a given structure (or concept) may be known under various terms (synonymy). A common language is a desirable goal. However, while classifications of bone as a tissue and related nomenclatorial systems have been in use for almost two centuries, it appears that incomplete progress has been made towards standardization. This suggests that bone tissue classification and nomenclature is a complex subject, replete with contradictory or even conflicting demands. Accordingly, before any new system of bone tissue classification and nomenclature can be proposed, it seems necessary to critically analyze the various aims and purposes it should fulfill, as well as the factors which necessarily will act as its major constructional constraints. We review these herewith: 1) history and stability. Names (and concepts) have been coined for bone tissue structures for centuries. Nomenclature implies stability over time. 2) Bone and bones. Tissue classification/terminology should address their proper hierarchic level of integration. 3) Why classify? Structural variability at the tissue level (histodiversity) should be recognized because it has biological significance. 4) Significance. Objective classification (tissue typology) as a basis for comparative descriptions should be able to express simultaneously several signals: structural, phylogenetic and functional. 5) Aim. A proper tissue classification/terminology should integrate all of the above points of view. 6) How to classify? Additive (open) versus subtractive (closed) schemes.

Ontogeny, Morphology and Mechanics of the Tessellated Skeleton of Cartilaginous Fishes

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The cyclic loading of the feeding and swimming modes of elasmobranch fishes (sharks, rays and relatives) is not compatible with the fact that cartilage cannot repair. Materials counteract the gradual build-up of fatigue damage through either being overbuilt (with an excessive safety factor) or resistant to fatigue. As the former is unlikely in active animals, I posit that elasmobranch skeletons are inherently fatigue-resistant and that this is a function of the calcification of the tissue. The uncalcified hyaline-like cartilage core of each element is overlain by a tessellated bark of abutting mineralized tiles (tesserae), adjoined by a fibrous phase. I employ a diversity of imaging techniques and ontogenetic tissue series to investigate the development, ultra-scale morphology and mechanics of the tessellated skeleton in a species of stingray. Tesserae form in histotroph embryos and gradually widen and thicken with ontogeny. Chondrocytes flatten and are engulfed by tesserae to form cell-rich laminae with communicating passageways between entombed lacunae. Elasmobranch chondrocytes decrease in size and density with age as in endochondral ossification, yet do not hypertrophy and die as in tetrapods. Nanoindentation tests show that the mineralized tissue behaves as a nearly elastic tissue and is an order of magnitude stiffer than the uncalcified layer, which is highly viscoelastic. Mathematical models suggest that, during skeletal bending, this layered biological composite acts to distribute damaging tensile stresses to the compressive portion of the mineralized phase where the elastic modulus is more than three times higher and therefore better able to resist applied forces.

Axial Muscle Function During Locomotion in the Salamander *Ambystoma maculatum*

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Trunk muscles were examined in the spotted salamander, *Ambystoma maculatum*, to determine the relationships between anatomical position, fiber type composition, and muscle activation pattern during swimming. All epaxial and hypaxial muscles examined are activated out of phase (180–270 degrees) with maximum bending, the exact phase relationship varying with undulation rate and segment number. Most muscles at a given body segment show simultaneous activity in a large burst associated with segment lengthening (i.e., bending to the contralateral side), and are electrically silent when bending to the ipsilateral side is greatest. Some muscles show a smaller secondary burst of activation when the segment is shortening. In the epaxial muscles, no effect of the fiber type composition or distance from the vertebral column is apparent in the activation patterns during swimming. Similar patterns of activation are seen in fast twitch muscles (m. dorsalis trunci profundus, m. rectus lateralis, and m. subvertebralis pars ventralis), slow twitch muscles (m. interspinalis, m. dorsalis trunci superficialis), and even regionalized muscles (m. subvertebralis pars transversalis). Differences in activation between fast and slow twitch muscles and among those with different mechanical advantages may become evident in slower and/or terrestrial locomotion.

Feeding Functional Morphology of Extant Amphibians

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Understanding the relationship between form and function is critical for correctly interpreting the fossilized remains of organisms and for assigning plausible evolutionary relationships and character transformations. The relationship between feeding function and cranial morphology in extant amphibians is useful in this regard because it is well studied and the anatomical correlates of feeding functions are relatively clear and generalizable. Living amphibians use their skull, jaws, and hyobranchial apparatus to feed using four modes: jaw prehension, tongue prehension, suction feeding, and suspension feeding. Jaw prehension can be used in combination with the others; however, suction/suspension feeding versus tongue prehension appear to be conflicting functions that require compromises in structure, most evident in extreme forms. Suction feeding taxa possess a robust, often mineralized or ossified hyobranchial apparatus whereas tongue prehension is associated with slender, cartilaginous hyobranchial elements. Jaw prehension taken to the extreme requires robust jaws and skull, and is observed in both suction feeding and tongue protracting species. The interplay of form and function in the feeding systems of living amphibians may provide insights that allow more confident assessments of lissamphibian ancestry among the tetrapod taxa of the late Paleozoic.

Advances in Molecular and Phylogenetic Studies of Xenarthra

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The introduction of molecular data has had profound effects on mammalian systematics and evolution. Living xenarthrans, that represent one of the four main placental lineages, have been no exception to this trend. Indeed, to early attempts based on morphological, cytological, immunological, and protein characters, have followed up more recent phylogenetic studies based on mitochondrial and nuclear genes. Reviewing the recent advances made in xenarthran molecular systematics, we show how molecular data allowed reconstructing the phylogeny of living xenarthrans at the genus level, but left uncertain the position of Xenarthra within placental mammals. Moreover, we present new results on the phylogenetic position of the enigmatic pink-fairy armadillos (genus *Chlamyphorus*) based on sequences of mitochondrial and nuclear genes obtained from museum specimens. The resulting phylogenetic framework is subsequently used to define a molecular timescale for the evolutionary history of extant xenarthrans. These molecular dating analyses reveal a striking synchronicity between some diversification events in xenarthran phylogeny and the major environmental changes that occurred in South America during the Tertiary.

Dental Microwear Methodology of Dietary Assesment for the Paleoecological Reconstruction of *Procervulus* (Artiodactyla, Cervidae)

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Attempts to reconstruct the diet from an incomplete and potentially biased record of teeth reveal insights of paleovegetation and the type of paleohabitat that a species occupied. They also provide useful data for the reconstruction of terrestrial mammalian paleoenvironments and the environmental changes that occurred through time. Because the analysis of microwear features on teeth is considered to be one of the most effective ways to infer the dietary behavior of fossil vertebrates, we use it to assign *Procervulus* samples from the intramountain basins of the Iberian Chain which cover a temporary interval between 19.3 to 13.75 million of years to the established feeding categories. As can be expected from its important brachydont cheek teeth and from being considered a stem group of the family Cervidae, *Procervulus* should be interpreted as a strict closed wood browser of an almost exclusively soft diet. However, data from dental microwear failed to support this hypothesis and suggest the occupation of a mixed niche. The evolutionary trend in *Procervulus* dietary preferences indicates the presence of more arid open habitats during the Early Aragonian that were supposed in previous paleoenvironmental reconstructions. These data furnish valuable information for comparisons with other taxa and facilitate precise insights concerning the evolution of paleoenvironmental conditions during the Miocene.

Vertebral Structure Modifications During Growth of Farming Rainbow Trout

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Severe vertebral body resorption was reported in farmed rainbow trout. This phenomenon was thought to be related to disturbances in phosphorus and calcium metabolism promoted by intensive growth. In order to test this hypothesis, we induced differential growth rates in trout by modulating temperature (7°C constant, seasonal T° and 17°C constant) and food intake (65%, 80% and 100% of satiety). For each trout, vertebrae 36–38 were embedded in resin and sectioned into 125 ± 10 μm transverse ground sections. The middle vertebra cross-section, where the notochordal canal is the narrowest and the bone tissue area the most spread, was microradiographed and digitized. Bone density profiles, from the center to the periphery of the vertebral body, were obtained using imaging software designed for bone tissue analysis (Bone Profiler 3.23). Modeling of each profile enabled statistical comparison, using six parameters that give precise information about the localization and extent of the resorption. Our results do not indicate a pathologic evidence of vertebral resorption, which is strongly linked to fish length, independent from growth rate. During growth, the remodeling processes increase bone density around the notochordal canal and at the periphery of the vertebra, while reducing bone density in the center of the vertebral body. This important remodeling phase results in that the initial "trabecular" structure is replaced by a "tubular" one. These structural modifications are interpreted as a compromise between the necessity to mobilize mineral stored in the vertebral bone for growth needs and to maintain vertebral biomechanical properties throughout muscular gains.

Color Pattern and Cleaning Behavior in Labridae (Teleostei): Correlated Evolution?

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The family Labridae contains numerous fishes known to act as cleaners in the wild. Previous studies suggested that a small body size and specific color patterns may be pre-requisites for cleaning. We investigated whether cleaning behavior is linked to particular fish phenotypes. We first present a phylogeny based on partial 12S rRNA gene sequences of thirty-two wrasses sampled from different localities in the Indo-Pacific and Atlantic oceans, and in the Mediterranean Sea. Secondly, descriptive data (fish body size, fish body shape, and fish body color patterns) were analyzed in a phylogenetic context using comparative methods. We found no relationship between fish cleaning behavior and fish body size and shape, but instead, a correlation between cleaning behavior and the presence of a dark lateral stripe within wrasses. Our results suggest that the evolution of cleaning depends upon the presence of a dark median lateral stripe on the fish body surface.

Spatiotemporal Similarities and Differences of Gene Expression During Tooth, Hair and Feather Morphogenesis

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Teeth, hairs, glands, and feathers, but also scales and claws develop as ectodermal appendages, resulting from a continuous dialogue with the underlying mesenchyme. Despite their differences in final architecture, epithelial appendages share one similar stage at the onset of their morphogenesis: the formation of a placode, i.e., a thickening of the epithelium, which is associated with a condensation of fibroblasts. Recombining an epidermis and dermis from different vertebrate classes have shown that dermal-epidermal interactions might be mediated by similar signal molecules as they can be understood at least at the early stages across tissues of different origins. Cells and tissues communicate via conserved signal molecules which are used reiteratively during more advanced morphogenesis, including several Wnts, FGFs, BMPs, Shh, Eda, and the Notch system. Studies of human genetic disorders, as well as knock-out mice emphasized defects both in hairs, teeth and sweat glands. However, feather and hair primordia morphogenesis are not identical: there are some spatiotemporal differences in gene expression which can lead to a lack of understanding between an early dermis and an epidermis from a glabrous area. Moreover, there is a basic genetic program in the integument, which leads to scale formation in reptiles, feather formation in birds and hair formation in mammals. In fact, it is more complicated for a bird to form a scale than a feather. Likewise, for a mammal it is more complicated to form a cornea than a hair.

Postnatal Physiology of Alveolar Myofibroblasts: Spatiotemporal Distribution and Quantity of α-SMA Contractile Elements and Functional Implication in the Developing Lung

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Alpha-smooth muscle actin (α-SMA)-positive myofibroblasts are contractile cells known to play a critical role in alveolarization of mammalian lungs. Recapitulation of the normal ontogeny of these cells has been speculated to underlie disease and repair in adult lungs. Here, we quantify the amount of α-SMA-expression within the alveolar interstitium and assess changes in its spatial and temporal distribution patterns through postnatal ontogeny. Using the antibody against α-SMA, we immunofluorescently labeled myofibroblasts in lung sections from a growth series of outbred Wistar rats. Confocal images were segmented using thresholded pixel intensities to determine α-SMA areal density in the alveolar parenchyma. Myofibroblast distribution and quantity paralleled major morphogenetic events in postnatal remodeling of the lung. In immature animals, α-SMA localized both at septal tips and within the interstitium. Adults lacked the interstitial population of α-SMA-positive cells, and a-SMA was found predominately in alveolar ducts, at alveolar ends and bends. The areal density of α-SMA doubled from neonates (2-day) to 21 days, from 4% to 8%, then decreased towards adulthood. The results are consistent with increasing α-SMA expression during the period of peak myofibroblast activity, corresponding to the phase of rapid alveolarization in the developing lung. Computational modeling indicates that changes in amount of α-SMA in the alveolar septa influence the mechanical behavior of the lung during breathing, contributing to hysteresis and altering acinar airflow. These age-dependent, α-SMA-mediated changes in lung functioning at the level of the acinus are an area of ongoing investigation.

The Amphibian Ancestors Came from Fresh Water – Considerations Based on Renal Development

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Among many other features, the performance of the kidney is of crucial importance when, even temporarily, invading terrestrial biotopes. Renal

anatomy in Caudata (Urodela) and Apoda (Gymnophiona) is probably less evolved than in Salientia (Anura). Accordingly, the renal morphology, e.g., of salamanders and newts, might resemble the ancestral pattern of renal tubules and vessels more closely than in the kidney of frogs. Comparison of the renal structure of aquatic (neotenous) axolotls (*Ambystoma mexicanum*), terrestrial salamanders (*Salamandra salamandra*) and experimentally thyroxine-metamorphosed axolotls indicate the hypothetical changes involved in terrestrial adaptation. The general structure of the kidney is quite similar in both species. Glomeruli are relatively large and strongly ovoid. Conversion of the kidney for living in a terrestrial habitat (metamorphosis) resulted in a decrease of the glomerular filtering surface by more than 1/3. In salamanders, the corresponding values are intermediate. No fossil remainders of the excretory organs of amphibian related crown vertebrates, e.g., *Tiktaalik, Gogonasus, Eusthenopteron* can be discerned. However, mechanisms must have evolved that allow short time response to variations in the hydration of the body, as well as long time adaptations to lower environmental water supply. Consequently, the morphological differences observed in this study might mimic some of the constructional achievements that were required for terrestriality.

Mechanical Properties of Hominoid Foods: Plant Underground Storage Organs and the Adaptive Significance of Molar Enamel Thickness

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Most models of hominin behavior include a discussion of molar enamel thickness and diet. The relatively thick enamel of some species—along with a variety of other craniodental traits, such as microwear—is most often associated with a diet of hard and/or abrasive foods, such as grass seeds or plant underground storage organs (USOs). Yet the concept of hardness is normally based on the subjective impressions of human observers. Here, we present the second in a series of studies on the mechanical properties of hominoid foods, all of which use standardized techniques. The aim of the present study is to compare the Young's modulus, E, and fracture toughness, R, of putative hominin foods with foods consumed by *Hylobates lar, Pan troglodytes,* and *Pongo pygmaeus*. We studied over 90 species of USO-bearing plants across sub-Saharan Africa. Our results show that USOs form discrete mechanical groupings; in general, raw tubers and rhizomes are implausible foods for precooking hominins. These results suggest that the current usage of the term USO is too broad—anthropologists may wish to emphasize bulbs and corms in future models. Importantly, the mechanical properties of bulbs and corms differed; corms were significantly more resistant to deformation than bulbs, as well as fruits consumed *Hylobates* and *Pan*, which have relatively thin molar enamel. The E- and R-values of corms resembled foods consumed by *Pongo*. These results are compatible with the hypothesis that bulbs and corms are relatively hard food objects, and that bulbs and corms were consumed to some extent by hominins. This research was funded by the A.H. Schultz Foundation, the American Philosophical Society, the Denver Zoological Society, the Leakey Foundation, the UC-Santa Cruz Committee on Research, and the Wenner- Gren Foundation.

Origin and Evolution of the Vertebrate Dermoskeleton: Integrating Bone and Stone

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The origin of a dermoskeleton has classically been considered on the basis of living representatives. Given that chondrichthyans are the most primitive living vertebrates with any vestige of a mineralized skeleton, hypotheses of skeletal evolution and models of skeletal patterning have been polarized assuming the chondrichthyan condition as primitive. This is as clear in the work of Williamson in 1840s as it is in Reif's Odontode Regulation Theory, which has been so influential in interpreting dermoskeletal and oral skeletons since it was codified in the 1980s. However, even a cursory consideration of fossil data reveals that living chondrichthyans are representative neither of the primitive condition of their own lineage, nor of vertebrates as a whole. To understand the origin and early evolutionary history of the vertebrate skeleton we have no recourse than to palaeontology. This is because the early episode of vertebrate evolution, prior to the diversification of living jawed vertebrates, let alone living chondrichthyans, is dominated a great diversity of jawless 'ostracoderms', so-called because they share the characteristic of an extensively developed dermoskeleton. In fact, although these various groups are united in armor, they turn out to be related in successive nested sets, to living jawed vertebrates. Within this evolutionary framework it is possible to organize the characteristics of their integument and infer its evolution through early vertebrate evolution. This analysis reveals that early tissues are little more than elaborations of a mineralized dermis. Through phylogeny, all classes of tissue exhibit increasing organisation and complexity, paralleling an episode in which genes implicated in the specification of matrix proteins are known to have diversified and to have been preferentially retained in the face of gene loss. In contrast to the traditional chondrichthyan model, the integument of the earliest skeletonizing vertebrates exhibited greater similarity to osteichthyans and it can be inferred that the dermoskeleton of chondrichthyans evolved from this condition, in contrast to the assumptions of classical models of skeletal developmental evolution such as the Odontode Regulation Theory.

Cranial Integration in Canids

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How constrained is the mammalian cranium by patterns of developmental integration? Is the face more plastic than the neuro- or basicranium and therefore more responsive to evolutionary pressures? The artificial selection and breeding of the domestic dog has produced an incredible range of forms with which to investigate these questions. Using morphometric analysis of three-dimensional landmark data we present an investigation of how patterns morphological integration have or have not been conserved in the various breeds of dogs by comparing them to the patterns of morphological integration present in their ancestor, the wolf.

Pharyngeal Dentition in Asp: From Harmless Asp's Baby to the Freshwater Beast

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Cyprinid fishes lack oral teeth; however, they possess pharyngeal dentition instead. We studied dental development of asp *(Aspius aspius)*, a carnivorous cyprinid fish with much prolonged early development what makes it possible to study particular steps of early odontogenesis into great details. Over 300 specimens were studied using wholemounts and serial sectioning followed by standard histological techniques. The first tooth is mineralized and attached to ceratobranchiale 5 (cb5; the first head element which ossifies) at 17 dPF which precedes the beginning of cb5 ossification. The larval dentition is the A-type (cf. Nakajima). The shape of larval teeth changed successively from a simple conical, through four further intershapes to a typical adult shape. The growth rate of the dentigerous surface of cb5 is much higher during the early larval period as compared to juvenile period, by which the next generation of teeth is attached at a certain distance medially to the teeth of previous generation that do not shed (in contrast to the juvenile and adult tooth replacement mode). Multi-rowed larval dentition, for which simultaneous shedding of the whole tooth rows is typical, is transformed into the transient dentition, in which all larval tooth rows are straightened to a single one that represents the main tooth row of the juvenile dentition. The lateral tooth row of juvenile (or adult) dentition appears then subsequently de novo. The chondrification of head skeleton proceeds in a cranio-caudal direction; however, ossification follows functional needs (i.e., food intake). In comparison to other structures, odontogenesis is highly accelerated.

The Functional Anatomy of the Hystricognath Rodent Feeding Apparatus

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Tullberg (1899) separated the rodents into two groups based on the morphology of the mandible. In sciurognaths, the ventral border of the mandible is continuous from the lower incisor to the distal end. In hystricognaths, the border is discontinuous: the anterior border is medial to the posterior border. The superficial masseter muscle, arising at the anterior root of the zygomatic arch and inserting on the ventro-lateral angle of the mandible, is a synapomorphy of the rodents. In hystricognaths, the separation between the anterior and posterior borders is a groove for the pars reflexa of the superficial masseter. The tendon of the pars reflexa in the naked mole rat (*Heterocephalus*) is flat and wide, as is the smooth groove in the ventral border of the mandible over which it glides. In the guinea pig (*Cavia*) and degu (*Octodon*) the tendon is accompanied by a dense connective tissue sesamoid that permits the tendon to glide through the groove. These South American hystricognaths are also hystricomorphs. The zygomatico-mandibularis muscle originates on the snout and converges on a tendon that runs posteriorly through the infraorbital foramen. The tendon runs over the bony root of the zygomatic arch and turns inferiorly, to insert at the anterior end of the masseteric groove. A second sesamoid is found in this tendon. Each of these elaborations of the masticatory muscles is a pinnate muscle that curves around a bony structure, permitting the muscle to be longer than similar muscles in other mammals.

3D-imaging and Biomechanics: Finite Element Modeling in Comparative Vertebrate Morphology

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The development of 3D-imaging techniques has given comparative morphologists the ability to visualize and compare structures in exciting new ways. Work in our lab focuses on taking 3D-data a step beyond imaging by transforming them into finite element models that serve as the basis of comparative biomechanical analyses. FEA is relatively new to functional morphology but clearly can provide a truly novel qualitative, as well as quantitative, perspective on form-function relationships. In the engineering world, engineers use powerful computer aided design (CAD) tools to rapidly create a mathematically geometric model of the product that is required for FEA. Unfortunately, the geometry of biological systems is highly irregular and not amenable to construction by CAD tools. Instead, the complex geometries of many biological structures must be digitally reconstructed from stacks of 2-D images. This digital reconstruction process from raw image data to 3-D mathematical geometric models is the most significant impediment to the widespread use of comparative FEA. Our lab has been working to simplify this process and make FEA more available to vertebrate morphologists. For example, we have created freely available software that applies muscle loads to FE models. We are also offering FEA workshops and developing a digital library of FE models and utility material properties data (www.biomesh.org). We present these resources and highlight the power of FEA to address problems in comparative biomechanics using examples from our research into the links among cranial morphology, bite force and biting behavior in mammalian evolution.

The Effects of Food Processing on Masticatory Performance and Its Implications for Hominid Cranio-dental Evolution

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A steady decrease in relative dental and facial size occurred during the evolution of the genus *Homo*. It is often hypothesized that this reduction was made possible by, or was an adaptation for chewing food that was cooked or otherwise processed. This study therefore tested experimentally the extent to which cooking and pounding influence masticatory performance capabilities. Fourteen subjects where asked to chew standardized samples of root vegetables and meat that were raw, roasted, or pounded (meat only). Masseter and temporalis EMG data were collected and calibrated to masticatory force using a force transducer. Comminution (fragmentation) performance was assessed using particle-size analysis of unswallowed boluses. Results from preliminary experiments indicate that processing affects masticatory performance differently depending on the food and the way it was processed. Roasting increases the amount of force recruited by the adductors when chewing meat (compared to raw and pounded samples), but tends to decrease force production when masticating root vegetables ($p = 0.07$). Roasting also affects the degree to which meat, but not vegetables, is broken-down in the oral cavity. The number of chews that a subject takes to swallow does not change as a result of processing yet meat is fragmented to a much greater extent when roasted. These results suggest that processing techniques do affect masticatory performance. The difference in food-type response to these techniques, however, highlights the complex nature of the relationship between diet and masticatory force production and cautions against a single causal explanation for reductions in hominid cranio-dental size.

The Arterial Pole of the Heart in the Carcharinoid Sharks *Galeus melastomus* and *G. atlanticus*

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It is generally accepted that the outflow tract of the chondrichthyan heart consists of the conus arteriosus, a myocardial chamber furnished by a variable number of valves; it connects the ventricle with the ventral aorta. However, former, hitherto neglected observations denoted that in several chondrichthyan species, a non-myocardial segment was interposed between the Conus arteriosus and the ventral aorta. On this basis, we studied the arterial pole of the heart in embryos and adults of *Galeus melastomus* and *G. atlanticus*. The specimens were examined by means of histochemical and immunohistochemical techniques. A morphometric analysis of the cardiac arterial pole components was also performed. Our observations confirmed the existence of a distinct, intermediate segment between the Conus arteriosus and the ventral aorta. This segment, located within the pericardial cavity, displays a tubular shape and is devoid of myocardial muscle; it shows arterial characteristics. Nonetheless, its walls, which are crossed by coronary arteries, diverge histologically from those of the ventral aorta. Embryological data, and especially the specific labelling by the fluorescent nitric oxide indicator 4,5 diaminofluorescein diacetate demonstrate that the intermediate segment found in the present species is morphologically equivalent to the Bulbus arteriosus of the actinopterygians. Therefore, the Bulbus arteriosus is not an apomorphy of this latter group. It probably appeared in an early period of the vertebrate story. In the *Galeus* species studied, the bulbus arteriosus is well-developed in size; its length is similar to that of the conus arteriosus. However, significant statistical differences exist between both species.

Head Morphology of a Duckbill Eel, *Hoplunnis punctata* (Nettastomatidae: Anguilliformes)

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This study was conducted to examine the morphological specialization of the head of a duckbill eel, *Hoplunnis punctata* (Nettastomatidae) and to compare of it with representatives of two other Anguilliformes, i.e., belonging to two subfamilies of congrid eels: Congrinae *(Conger conger)* and Heterocongrinae (*Heteroconger hassi*). These three lineages have been considered to comprise a monophyletic group. The Nettastomatidae is a family of long-snouted eels that are benthic inhabitants of the continental slope and tropical waters. The rostral region distinguishes *H. punctata* from most other Anguilliformes because of the deep and prolonged premaxillo-ethmovomerian complex, in contrast to the moderated rostrum of *C. conger* and the short rostrum of *H. hassi*. The adductor mandibulae complex of *H. punctata* is hypertrophied, as in *C. conger* but in contrast to the small jaw muscles of *H. hassi*. The lifestyles of the predators *H. punctata* and *C. conger* and the plankton feeder *H. hassi* clearly appear to be reflected in their jaws and relevant muscle structures. The cranial musculature of *H. punctata* shows a similar pattern in terms of presence with that of *C. conger* and *H. hassi*, except for A1 and Aω subsections of the adductor mandibulae complex which are respectively absent and present in *H. punctata*. However, some variation is observed in the insertion, subdivision and volume of the muscles. Most elements of the cephalic skeleton of this species were found to be

common for Anguilliformes, but with some specializations that are specific for Nettastomatid eels.

The Avian Femur: Evolution of Its Distal Features

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In contrast to the synapsids, the lateral condyle of the sauropsid femur tends to receive the fibular head in a fibular trochlea which, when well developed, defines the medial, condylar part, termed tibiofibular condyle. In non-avian theropods and other saurischians, the tibiofibular condyle is subdivided into two parts termed semicondyles: the ectocondylar tuber (proximal semicondyle) and distal semicondyle. In modern birds, the lateral condyle bears a single tibiofibular semicondyle (hitherto known as the tibiofibular crest), which was proposed by others to be homologous to the ectocondylar tuber. However, in the basal birds the parts corresponding to the ectocondylar tuber and distal semicondyle form a continuous condylar structure that must have arisen through the bridging of the distal groove. Subsequently, on the way to the modern birds, the part corresponding to the distal semicondyle has been reduced, leaving the tibiofibular semicondyle, which is in place of but did not evolve directly from the ectocondylar tuber. This two-stage model for the evolution of the lateral condyle in modern birds is consistent with the gradual change from the erect position of the femur in theropods to its subhorizontal position in modern birds (Gatesy, 1990; Paleobiology 16: 170-186).

Enhanced Sensory Systems in Small Sharks? Cephalic Pore Fields of Unknown Function in Pentanchine Catsharks (Scyliorhinidae)

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The heads of three Scyliorhinids (*Scyliorhinus canicula, Galeus melastomus, Apristurus aphyodes*) were investigated to clarify the anatomy of the electroreceptive system. Bundles of Lorenzinian ampullae in each species were digitally 3D-reconstructed according to section series and the superficial pore patterns were mapped. Neurocranial structures as a topographical reference were reconstructed by means of computertomography. These investigations revealed that not all pore fields in *G. melastomus* and *A. aphyodes* (Pentanchinae) are part of the electroreceptive system as previously assumed. Mediorostral, preorbital, and supralabial pore fields in both species are part of a subdermal system of grooves, surrounded by the same dense connective tissue as the canals of the mechanoreceptive lateral line. The preorbital and supralabial groove patches in particular are tightly bound to the lateral line canals, but the systems lack a canalicular connection. Histological sections show extraordinary digitiform protuberances and maculae similar to neuromast organs of the epithelia in the grooves in *Galeus melastomus*. Accordingly, histology rather indicates a mechanoreceptive function. The exact function or biological role of this elaborate system is by no means clear yet. A similar groove system was found in *Apristurus fedorovi, A. herklotsi* and *Galeus murinus*. In *Scyliorhinus canicula* (Scyliorhininae) no comparable grooves are found. In *Mustelus asterias* (Triakidae) the lateral line canals show branching with pore field formation in the same head areas where the groove patches were found in *Galeus* and *Apristurus*, a fact that might indicate that the pentanchine groove system derives from such branched, elaborate lateral-line systems phylogenetically.

Tyrannosaur Life Tables: An Example of Non-avian Dinosaur Population Biology

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Little is known about non-avian dinosaur population biology. Did these animals show survivorship patterns akin to extant living dinosaurs, the birds, like their cousins the crocodilians, or were they similar to more distantly related ecological analogs? We used the age and size distribution from four death assemblages of the North American tyrannosaurs: *Albertosaurus, Tyrannosaurus, Gorgosaurus,* and *Daspletosaurus* to produce the first age-standardized ecological life tables for non-avian dinosaur populations. The results revealed a pronounced, bootstrap-supported pattern of age-specific mortality characterized by relatively high juvenile survivorship, and increased mortality at mid-life and near maximum lifespan. Such patterns are common today in wild populations of long-lived birds and mammals. Factors such as predation and entrance into the breeding population may have influenced tyrannosaur survivorship. This survivorship pattern can explain the rarity of juvenile specimens in museum collections. It also reveals that the majority of tyrannosaur specimens in museums are young adults. The application of this methodology to other dinosaurian or other vertebrate fossil assemblages is strongly encouraged.

The Function of Sonic Hedgehog in the Development of the Pectoral Fin of the Australian Lungfish, *Neoceratodus forsteri*

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Sonic hedgehog has been shown to be expressed in a similar pattern in limb and fin buds from chondrichthyans to mammals and birds. In tetrapods, Shh is acting like a polarizing agent controlling the anterior to posterior identity of the digits. In Australian lungfish, *Neoceratodus forsteri*, a basal sarcopterygian, the pectoral fin has the stylopodium and zeugopodium components of a tetrapod; humerus, radius and ulna, but the autopodium is composed of a continuous array of axial elements with pre- and post-axial radials, rather than a digital arch. It has been hypothesized by Shubin and Alberch that the tetrapod autopodium is derived from mainly postaxial elements of a sarcopterygian ancestor. Studying the expression and function of Shh in Australian lungfish may therefore provide some clues to how the tetrapod autopodium and limb have evolved. To elucidate the function of Shh in Australian lungfish we have used cyclopamine, a downstream inhibitor of Shh pathway, applied at different stages and intervals during development.

Correlations of Limb Kinematics and Bone Strain in Frogs and Toads

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Experimental data have shown that the hind limb bones of frog experience variable magnitudes of strain even during jumps of similar performance. Studies of other species have shown that modifications of limb posture can influence the load magnitude and regime that bones experience. To test whether variations in limb kinematics might account for variation in bone loading during jumping in frogs, we collected high speed video of frogs *Rana catesbeiana* and toads *Bufo marinus* during jumps in which we simultaneously recorded bone strains, and regressed values of kinematic variables on strain magnitude. Despite a ten-fold range in strain magnitude in each species, no correlations were found between values of kinematic variables at peak strain (e.g., femur retraction, femur adduction, angles of the knee and ankle) and peak strain magnitude. This suggests that unlike other species previously examined (e.g., alligators), variation of strain magnitude is not influenced by limb position. Supported by NSF (IOB-0517340).

How Does Tooth Wear Affect Dental Complexity?

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Recent work has established that there is a relationship between tooth complexity and gross diet. Dental complexity tends to increase when there is an increasing requirement of mechanical processing, from hypercarnivores through omnivores to herbivores. These measurements of dental complexity were largely based on individuals at a similar wear stage. Any change in dental complexity with wear will affect the overall functional effectiveness of the tooth. For instance, as enamel is breached at the early stages of wear, dentine basins form which is likely to increase dental complexity. In several rodent species examined, where

there are enamel-free areas on the tooth at the time of eruption, it was found that dental complexity was relatively constant for much of the tooth wear that occurred. Only in the last stages of wear was dental complexity substantially decreased. A similar result was obtained for several carnivoran species with primary occlusal morphology: tooth wear does not greatly change dental complexity. This indicates the maintenance of tooth shape with wear in many species, which is a very important characteristic in retaining an effective tooth form despite substantial wear.

Shape-searching in Dental Morphology Using the Morphobrowser

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A number of challenges are faced when we try to make comparisons of 3D-morphology. First, it can be very difficult to make any meaningful comparison between two dissimilar 3D-shapes. This is certainly true in dental morphology, where the diversity of mammalian teeth mirrors that of ecology. Second, the problem is greatly compounded when a very large number of shapes are involved. This is becoming a common situation due to the explosion of 3D-data collection methods in recent years. We have addressed these issues by implementing shape descriptor and shape-searching algorithms in MorphoBrowser, an online database that contains a diverse range of 3D-tooth morphologies. Over 120 mammalian species are represented in the database, covering extant and extinct taxa. The shape descriptors represent automatically-calculated characteristics of the shape using mathematically-defined manipulations of the 3D-data. These include cusp angularity, tooth elongation, surface complexity and surface relief. A significant advantage of these descriptors is that they are user-independent, as they do not require interpretations of the morphology by the user. Comparisons between objects can then be based on the similarity of the shape descriptors. Likewise, a shape search can be carried out among a large number of teeth. These techniques have been found to be useful in reconstructing diets from dental morphology.

Investigating Cryptic Diversity and Convergences in Bats: A Geometric Morphometric Approach

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A traditional question in evolutionary biology is the relative roles of convergence and common history in shaping phenotype. Species complexes are particularly relevant to investigate this question, because morphological differentiation is weak and any differences in shape could be more easily linked to homology or convergence. Assemblages of such highly similar species are common in bats. Here, we studied two complexes: the long-eared bats complex (*Plecotus auritus-austriacus-macrobullaris*), and the mouse-eared bats complex (*Myotis myotis-blythii-punicus*). Geometric morphometric methods were used to investigate skull variations among species. The skull is a complex morphological structure involved in many functions (e.g., brain protection, smell, vision, breathing, mastication, echolocation, etc.), therefore providing the case for potential convergence. We took advantage of a robust phylogenetic framework based on molecular data to interpret phenotypic proximity as convergence vs. homology. Our results show that the skull shape, within the complexes studied, only partially reflects the phylogenetic relationships, therefore suggesting that selective pressures may override phylogenetic effects. We combined the visual inspection of shape variation with the knowledge of the species biology to suggest ad hoc functional hypotheses.

Sound Production by *Synodontis* (Mochokidae): A Morphological Study

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Mochokidae are benthopelagic freshwater catfishes living in Africa. These fishes are able to produce stridulatory sounds with their pectoral spines. This study examined the anatomical basis of the first pectoral spine in seven species of *Synodontis*. The aim is to seek the relation between spine morphology and produced sounds. Differences in stridulations among species were first investigated by comparing distress calls recorded in air. These sounds present groups of pulses that vary in temporal and spectral characteristics. The functional morphology of the mechanism was studied following two axes. First, pectoral spine movements were recorded with a high-speed camera (500 fps). Stridulatory sounds are produced during spine abduction and adduction, but amplitude and speed of movements are specific and could partially explain some temporal patterns of the sounds. Second, the spines were observed with a scanning electron microscope to compare the bony ridges or grits situated on their ventrolateral surface. These bony particularities are responsible for sound production when they rubbed against the rough ventrolateral wall of the spinal fossa. The spine morphology of the seven *Synodontis* species appears to reflect the differences observed in the sounds.

Voxel-based Finite Element Analysis—Working Directly with Microct Scan Data

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Finite element analysis (FEA) is an invaluable tool for investigating the biomechanical function of complex skeletal structures. The usual approach is for the 3D-geometry to be obtained by (micro)CT; these data are then processed to produce smooth interpolated triangular surfaces, from which a mesh of solid tetrahedral finite elements is created. Inevitably during that process, some details and fine structures are lost, but in addition commercial FE software has limitations on the shape and number of elements that can be analysed, so further simplification is often necessary. An alternative approach is to use a voxel-based FE mesh where each CT-voxel is converted directly into a finite element. This has a number of advantages, apart from its simplicity, but does require significantly more elements to adequately represent the surface geometry. We have developed our own voxel-based FE software (VOX-FE) that can comfortably analyze models with over 100 million elements (more than two orders of magnitude greater than most commercial software) allowing inclusion of very fine details in the models. We have also developed a sophisticated graphical user interface that allows the complex loading regimens that are inevitably present in biomechanical analyses to be readily applied to the model geometry, and the resultant 3D stress and strain patterns to be visualized easily. Detailed sensitivity and validation studies will be presented, comparing VOX-FE, commercial FE software and strain gauge experiments, demonstrating that voxel-based FE modelling does provide accurate results, and demonstrating its obvious potential in vertebrate biomechanics.

Revision, Osteology, and Locomotion of *Aphelosaurus*, an Enigmatic Reptile from the Lower Permian of France

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The radiation of early amniotes is a key episode in vertebrate evolution: the oldest amniote is Carboniferous in age, but discussions still remain about the morphological specializations within the clade from the Permian. How did so many terrestrial ecological niches become occupied so quickly by the amniotes? While Late Permian amniotes are relatively well known, this is not the case for the Early Permian amniotes because of the paucity of the fossil record. A few European localities yielded Lower Permian reptiles such as the enigmatic *Aphelosaurus lutevensis* Gervais, 1859 from Usclas, Lodeve basin, Southern Massif Central, Southern France. Erected by Gervais (1859) and briefly redescribed by Thevenin (1910), no one provided, up to now, either a systematic revision or a detailed redescription of this reptile which is, however,

commonly considered as an aeroscelid. *Aphelosaurus* is documented by a unique but well preserved postcranial skeleton housed in the MNHN collections, Paris. The holotype shows gracile (elongate and narrow) fore-and hindlimbs. The ribs are relatively short, slender and curved. The last phalanxes of the manus and the pes are elongate, slightly curved and sharply pointed at their extremities. This suggests relatively long and efficient claws. The stylopode/zeugopode ratios are equal to one, as is the case in the aeroscelids. A phylogenetic analysis of most of the representatives of the Permian amniotes, including *Aphelosaurus*, tests this hypothesis. Several reconstructions of this gracile skeleton are also proposed to test different scenarii about the locomotion of *Aphelosaurus*.

Molecular Insights into Evolution of the Gastrointestinal Tract

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Gastrulation in amniote embryos culminates in the formation of the primary germ layers: ectoderm, mesoderm and endoderm, which contain the progenitors of the tissues of the entire fetal body. The formation of the ectoderm and mesoderm have been well studied in many species but only in the last few years has the endoderm received much attention. The endoderm gives rise to the epithelium of the gut and associated organs such as the stomach and pancreas. The gut appears to be a simple endodermally-derived organ but it predates any mesodermally-derived organ and it has reached a level of complexity that is only starting to be appreciated. Studies in a number of vertebrate model systems have provided insights into the genes and cellular mechanisms regulating endoderm formation, revealing a high degree of conservation. For example, members of the TGF, GATA and forkhead factor families have been implicated in the specification of the endoderm across phyla, although formation of various organs appears to be more, divergent. Molecular aspects of the specification and regionalization of the gut tube and the morphogenesis and differentiation of the associated organs (stomach, pancreas and intestine) will be discussed.

Past and Current Trends in Reconstructing Xenarthran Palaeobiology

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Since the early description of the giant ground sloth *Megatherium americanum* by Cuvier at the end of the 18th century, reconstruction of xenarthran palaeobiology has reflected the importance given to this strange mammalian group and the predominant points of view and methods of the times. Over the past 210 years, extinct xenarthrans have been viewed, for example, as one of Nature's oddest anatomical experiments, as climatic proxies, as phylogenetic entities of uncertain affinities, as stratigraphically useful fossils, and as overly endemic beasts thriving in the isolation of South America and doomed to die when proper competitors arrived. Most, if not all, of these aspects are still actively researched, and several, more recent topics must be added to the list, including investigations into their trophic and locomotory habits, utilizing morphometric and biomechanical techniques, the synecology of selected communities to which they belong, their soft anatomy and appearance, thermodynamics, molecular makeup, proneness to extinction, and interaction with humans. Here, I give an overview of how extinct xenarthrans have been conceptualized and focus on recent research that has altered our interpretations of their palaeobiology. This historical parade passes from the Baron's hairy, lumbering quadrupedal creature, to the herbivore requiring a tree for extra support, to today's hairless biped of debated diet, and from the image of armored glyptodonts as clunking, tank-like dolts to that of fighting beasts of unlikely speed and agility, as well as the possible inclusion of giant sloths in palaeoindians' diet. Finally, I outline possible directions for our future endeavors.

The Right-to-left Shunt Serves to Supply the Gastrointestinal System with Carbon Dioxide

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A long standing and central problem of the study of the circulatory arrangement of vertebrates is understanding the factors leading to the fully divided circulatory systems of birds and mammals, and understanding the factors responsible for the evolution and retention of the incompletely divided systems of all other amniotes (e.g., turtles, snakes and lizards, crocodilians). Identifying these factors has proved very difficult. A primary function of the circulatory system is gas exchange with the environment, that is, the uptake of oxygen from the environment and the elimination of carbon dioxide from the body. From this perspective the undivided system of non-avian reptiles is puzzling because systemic venous blood can be shunted past the lungs, the site of gas exchange. This shunt is known as the right-to-left shunt or the pulmonary bypass shunt. We examined the importance of this blood flow pattern to gastrointestinal function in two groups of juvenile American alligators. In one group the ability to shunt was blocked by surgically sealing the left aortic orifice. The second group underwent a sham surgery. The effects of these procedures on digestive processes were then studied. Our results indicate that the right-to-left shunt functions to carry carbon dioxide to the gastrointestinal system to facilitate digestion.

Unidirectional Flow in the Lungs of Archosaurs

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Reptiles have one of the most diverse arrays of lung structures of any class of vertebrates in terms of the intrapulmonary arrangements of gas-exchange surfaces and supporting structures, yet the functional reasons for this diverse morphology are not understood. Lung complexity is not directly related to the gas-exchange demands of exercise, raising the possibility that other factors have contributed to lung design. Measurements of air flow within the lungs of American alligators during periods of eupnea and apnea show that with each beat of the heart there is a mechanical tugging on the lungs, which causes gases to move primarily in one direction. This cardiogenic, unidirectional flow appears important for convection of gases from sac-like ventrolateral regions of the lung, which contain little gas-exchange surfaces, into mediodorsal regions, where most of the gas exchange surfaces reside. Effective cardiogenic flow is a plausible selective pressure for an intrapulmonary morphology that favors movement of gases in one direction. Once a bias in direction was established for the purpose of enhancing convection during apnea, this bias may have become advantageous during eupnea for extraction of oxygen under conditions of hypoxia, thought to have been present during the Mesozoic.

How Many Coronary Arteries Are There in Mammals?

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It is commonly accepted that in mammals, the blood supply to the heart takes place through two coronary arteries, right and left, arising from the right and left aortic sinuses, respectively. This arrangement, which is regarded as the normal coronary artery pattern, is concomitant with the presence of two coronary ostia, right and left. Existence of a solitary coronary ostium in the aorta and ectopic location of one or both coronary ostia are considered to be coronary artery anomalies; they entail the risk of clinical complications. Supernumerary coronary ostia have received little attention due to their limited clinical relevance. However, knowledge about their frequency and morpho-physiological significance is suitable to obtain an accurate survey of the coronary artery pattern of each species. On this basis, we sought for supernumerary coronary ostia in a large series of Syrian hamsters and laboratory mice belonging to different strains. In addition, we undertook an extensive review of the literature, focusing on the number of coronary artery ostia in wild living mammals. Our findings indicate that the existence of two coronary artery ostia in the aorta is the most frequent condition, but not the rule in mammals. The number of coronary arteries is subject to a considerable intraspecific variation. The conal and septal arteries often originate from separate ostia located in the aortic root. In conclusion, occurrence of more than two coronary artery trunks arising from the aorta cannot be regarded as the product of a disorder in the normal coronariogenetic process.

A Peculiar Ossification of the Skull of *Neosclerocalyptus* Paula Couto, 1957 (Mammalia: Cingulata)

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In glyptodonts many sutures of the skull are obliterated during ontogenetic development, hindering the recognition of the different bony elements that compose it. A detailed revision of a number of skulls assigned to different glyptodontids brought to attention several skulls with precise bony limits that permit the identification of previously undescribed bony elements. In this communication we describe a peculiar bony element observed only in several adult individuals of the Pleistocene genus *Neosclerocalyptus* housed at Museo Argentino de Ciencias Naturales of Buenos Aires and Museo de La Plata (Argentina). The dorsal surface of the skull presents clear sutures for the parietal, frontal and nasal bones. The anterior margin of the latter partially overlaps a fourth bony element, the exposed surface of which represents, in dorsal view, nearly one quarter of total skull length. Laterally, this element is overlapped by the premaxillae. We interpret this structure as comprising the ossified nasal cartilages, separated internally by a triangular and ossified septum nasi. The following anatomical structures are identified: dorsally the tectum nasi extends anteriorly with the cartilago cupularis and laterally with the paries nasi. A longitudinal depression between the latter and the tectum nasi may represent an obliterated fenestra superioris nasi. The paries nasi projects medially into a fold that expands within the extensive turbinal (marginoturbinal?) and medioventrally as a plate that possibly represents the processus superioris alaris.

Walking and Climbing on Small Branches: Convergent Solutions in Chameleons, Marsupials, and Primates

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Many tetrapod vertebrates are able to move on trees so long as the support diameter is large, but only a few groups have developed the specialized adaptations to foraging on small branches. Quadrupeds that climb and walk on such narrow support face two key problems: controlling the gravity-induced momentum imposed on the body axis (balance) and reducing the gravity-induced forces imposed on the limbs (compliance). The combination of prehensile extremities and simultaneous footfalls of diagonally opposite limbs increases the balancing abilities of primates, arboreal marsupials, and chameleons over those of other arboreal vertebrates by allowing them to shift their weight dynamically sideward, or backward and forward. Chameleons, arboreal marsupials, and primates use a crouched limb posture, but only chameleons and primates possess relatively elongated limbs, which increase step lengths and contact times, and thus, reduce the peak substrate reaction forces. So, chameleons and primates display a highly compliant gait. Arboreal quadrupedalism does not necessarily demand three-dimensional limb excursions. Cineradiographic analyses show that forelimb abduction generally results from constraints in shoulder morphology. But, because the shoulder morphology differs in chameleons and mammals, each had to find different solutions to overcome these constraints. Chameleons support their parasagittal limb excursions by possessing the most mobile scapulocoracoid among reptiles. In primates, in contrast, the "emancipation" of the arm from the scapula was an important pre-requisite for developing locomotor modes reliant on shoulder joint mobility rather than on scapular excursions.

Morphological Variations and Dietary Adaptations Within the Anthropoid Masticatory Apparatus

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Comparative studies of primate craniofacial morphology have identified the masticatory apparatus as a key region of homoplasy. The most likely reason for the convergence of masticatory form is dietary adaptation. If shared characteristics are truly homoplastic responses to similar diets then these traits should also possess similar mechanical roles. The present study uses geometric morphometrics to investigate the craniofacial skeletons of 20 anthropoid species with varying diets and relatedness. More than 200 landmarks were chosen to represent craniofacial geometry. Key structural areas identified from the analyses indicated the occurrence of several homoplasies. To ascertain whether diet or some other factor underpinned the homoplasy, it was necessary to determine whether such regions had a similar mechanical function. As such, a three-dimensional computer model of symmetrical jaw opening was created using C++ and OpenGL. Jaw movement occurs by means of active (muscle force) and passive forces (gravity, bony constraints, ligaments and passive muscles). Using the model, aspects of skull morphology (i.e., coordinate data) were geometrically altered to determine the effects of a range of structural changes on overall masticatory performance. The results were examined in the context of species' phylogenetic, morphological, functional and environmental affinities. Such a study can provide an insight into possible evolutionary scenarios, adaptive opportunities and constraints within the anthropoid masticatory apparatus.

The Effect of Food Rheological Properties on Human Mastication

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Food is a complex stimulus which the masticatory process is known to adapt to throughout the chewing sequence. We explored correlations between masticatory parameters and food properties (varying hardness and rheological behavior) when chewing edible model foods of known and controlled properties. Two model foods were developed which presented predominately either elastic or plastic rheological behavior. Each food type consisted of 4 products of the same size and shape and of varying hardness. Fifteen male participants, with normal dentition aged 24.1 ± 1.9 years, were asked to chew 3 replicates of each elastic and plastic product during two sessions (3 x 4 = 12 samples per session). Jaw movements and activities of the masseter and temporal muscles were recorded simultaneously by electromagnetic induction and surface electromyography (EMG) respectively. Food hardness was shown to significantly influence the number of chewing cycles, sequence duration and EMG activity throughout a chewing sequence. Changes in the rheological behavior of the food (from elastic to plastic) were reflected in increased vertical and lateral jaw movements used to prepare the bolus for swallowing. Overall, masticatory frequency was found to be significantly dependent on the rheological properties of the food and relatively independent of the food hardness. This work shows that mastication is influenced by numerous food properties throughout the masticatory process and that strategies differ when adapting human masticatory behavior to changes in food hardness or to another rheological property.

Functional Morphology of Leporid Hind Limb—The Phylogenetic and Adaptational Implications

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Leporids, although not a particularly numerous and diverse mammalian group, show surprising environmental plasticity. Hares, cottontails, and rabbits inhabit almost every environment type and all regions of the world (except the Antarctic). The adaptations to extremely different habitats (such as deserts or tropical forests) are realized within the conservative body plan known already in the Eocene ancestors, which undergoes only subtle change due to adjustment to particular habitat. The hind limb structure of five genera (one representative of the Plio-Pleistocene European Archaeolaginae, *Hypolagus beremendensis* and five extant species *Lepus europaeus, Oryctolagus cuniculus, Sylvilagus brasiliensis, S. floridanus*, and *Pentalagus furnessi*), exhibiting a wide range of adaptations, were studied. The phyletic analysis using 98 variables clusters closely *Oryctolagus* with *Sylvilagus*. *Hypolagus* is placed outside of this group, further externally *Pentalagus* and finally, *Lepus* as the outermost species. The most conservative morphology is observed in pelvis and femur, while the structure of tibia and foot best reflects cursorial adaptations as well as the jumping ability, notably in species living in dense vegetation. In the ankle structure the good leapers express a slight elongation of the body of calcaneus, and the bone itself, also talus, cuboid, and body of naviculare are slenderer. *Hypolagus beremendensis* reveals the peculiar foot proportions with strongly elongated proximal and medial phalanxes, which is probably characteristic for

Archaeolaginae. The detailed analysis of the hind limb structure and proportions of particular segments allows inferring the palaeoecology of extinct species.

Allometric Growth in the Damselfishes of the Genus *Dascyllus* (Pomacentridae)

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The Pomacentridae, commonly known as damselfishes, is one of the most specious families of coral reef fishes (>350 species). The genus *Dascyllus* contains ten species which fall into three complexes: *aruanus, reticulatus* and *trimaculatus*. The members of the two first complexes are small-bodied with a maximum standard length (SL) of 50-65 mm and the third complex groups large-bodied fishes of 90-110 mm SL. Phylogenetic data place the *aruanus* complex in a basal position with the two other species groups as derived sister taxa. Herein, we test the hypothesis that evolutionary change throughout the large-bodied species occurs by isometry. Geometric morphometrics is used to examine the ontogeny of size and shape. This method, which allows description and statistical analysis of form, is applied for the neurocranium and mandible in the three species referencing each complex: *Dascyllus aruanus, D. reticulatus* and *D. trimaculatus*. Another closely related pomacentrid, *Chromis viridis*, was used as outgroup for comparing ontogeny. At the larval stage, the structures are rather similar. Multivariate regression of shapes on size reveals that the three *Dascyllus* species have a common ontogenetic trajectory which clearly differs from that of *C. viridis*. During growth, allometry concerns each unit (e.g., shortening of the neurocranium and the mandible) and is identical in each *Dascyllus* species. However, it appears that the largest studied specimens of *D. trimaculatus* (90 mm SL) have similar shapes and, differ only in size from the largest ones of both other species (50–60 mm SL).

Mobile Larynx in Male Mongolian Gazelle *(Procapra gutturosa* Pallas, 1777)

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This study provides the first evidence of pronounced temporary laryngeal descent in a bovid species. An elaborate acoustic display is prominent in male courtship behavior of polygynous Mongolian gazelle. During rut, rounding up of females is accompanied by continuous head-up barking by dominant males. Throughout the rut their evolutionarily enlarged larynx descends to a low mid-neck resting position. In the course of each bark the larynx is additionally retracted towards the sternum by 30% of the resting vocal tract length. The considerable distance between resting position and maximal laryngeal descent suggest a backward tilting of the hyoid apparatus and an extension of the thyrohyoid connection. Return to the resting position is done by strap muscles and by the elastic recoil of the pharynx and the thyrohyoid connection. The neck of adult dominant males is accentuated by long grey guard hairs. The passive swinging of the heavy larynx of adult males during locomotion is a handicap. Apparently, this disadvantage becomes outweighed by the profits for reproductive success.

Postcranial Anatomy of the Permian Therapsid *Suminia getmanovi*, the Oldest Known Arboreal Tetrapod

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The basal anomodont *Suminia getmanovi* from the Late Paleozoic of Russia is highly specialized in its masticatory apparatus in showing extreme adaptations for high-fiber herbivory. In contrast, its postcranial anatomy remains largely undescribed. For this study, more than a dozen mostly complete skeletons were used to provide the most complete picture on the postcranial anatomy of any basal anomodont. The newly available material indicates that in addition to its derived cranial anatomy *Suminia* also displays a large number of autapomorphic features in its postcranium. These include an elongate neck with extremely broad cervical vertebrae, a long tail, a slender, tall scapular blade, and elongate limbs. Further autapomorphic characters are displayed in the autopodium and comprise an enlarged distal carpal I, elongate penultimate phalangeal elements, as well as a reversal to the plesiomorphic condition for amniotes with a phalangeal formula of 2-3-4-5-3 (manus) and 2-3-4-5-3 (pes). This is achieved by insertion of disc-like phalangeal elements in digits III and IV. This combination of morphologically distinct characters combined with the small body size (40 cm in length) strongly suggests that Suminia was an arboreal animal capable of using its manus for grasping, and, thus, represents the oldest evidence for arboreality in tetrapods in the fossil record.

The Evolution of Preaxial Dominance in Tetrapod Limb Development—Implications for the Origins and Relationships of Modern Amphibians

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Limbs adapted for terrestrial locomotion are a hallmark of the tetrapod body plan. Despite the wide range of shapes that accompany a vast variety of limb functions, their development follows a very conservative pattern of de novo condensation, branching, and segmentation. Development of the zeugopodium and digital arch typically occurs in a posterior to anterior sequence, referred to as postaxial dominance, with a digital sequence of IV-III-V-II-I. The only exception to this pattern in all of living Tetrapoda can be found in salamanders, which display a reversed pattern of preaxial dominance. This divergence has puzzled researchers for over a century, but despite many advances in research on limb development, the divergent evolution of these two different pathways and their causes are still not understood. An examination of over 600 specimens of the branchiosaurid *Apateon* (Temnospondyli) from a wide range of ontogenetic stages formed the basis for the investigation of the pattern in its limb development. The exceptional preservation allowed for the reconstruction of ossification sequences in the fore- and hind limbs and their comparison with the patterns found in extant tetrapod taxa. The results show that preaxial dominance in limb development was already established in branchiosaurids in the Upper Carboniferous. When considered in the framework of competing hypotheses of basal tetrapod relationships, the evolution of this character provides new data for the discussion of the highly controversial relationships of the three modern amphibian groups among the possible Paleozoic antecedents and the time of the divergence of these lineages.

Reconstruction of the Elbow Joint Angle in Extinct Terrestrial Vertebrates Based on the Orientation of the Olecranon Process

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In skeletal reconstructions of extinct vertebrates, the posture of forelimbs is one of the most challenging parts of the body. It is mainly because each joint has a wide range of motion. Various different forelimb reconstructions therefore have been suggested for an extinct species such as *Triceratops* (Ceratopsia, Dinosauria), *Desmostylus* and *Paleoparadoxia* (Desmostylia, Mammalia). This study focuses on reconstructing elbow joint angle, EJA, formed by the shaft of the humerus and ulna in extinct species of quadruped amniotes. Possible elbow joint movement was studied in various species of mammals and reptiles with dried skeletons and fleshed specimens with X-ray photography. The olecranon process and the shaft of the humerus are generally oriented nearly perpendicular to each other in the support phase in mammals. Holding the angle of the olecranon process and the humeral shaft, OHA, perpendicular, major extensor muscles maximize the lever-arm at the elbow joint. The olecranon process generally is not prominent in extant species of reptiles. In these reptiles, EJA was measured with X-ray photographs at the angle when the extensor lever-arm was maximized. Orientation of the extensor lever-arm, such as OHA, can be used to reconstruct the forelimb posture for quadruped amniotes, especially for the animals with prominent olecranon process, regardless the taxa and body size. According to this method, *Triceratops* would have had a relatively flexed elbow joint with approximately 120 degrees in EJA. *Desmostylus* would have had more

upright forelimb approximately 160 degrees in EJA than that of *Paleoparadoxia* with EJA of 130 degrees.

Reconstructing Mammalian Turbinates from Noisy CT-scans

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Advances in high-resolution CT scanning have allowed us to visualize extremely fine aspects of mammalian cranial anatomy, such as the olfactory and respiratory turbinates. These structures are critical in the history of mammalian evolution, form a large part of the skull, and yet have been neglected in functional and evolutionary studies because of their cryptic location. We have underway a survey of turbinate structure across the order Carnivora. In this exploratory study, we intend to quantify the surface area of olfactory and respiratory turbinates in species that differ in aspects of their ecology, such as body size and habitat (aquatic vs. terrestrial, mesic vs. arid). The primary challenge has been the extraction of a relatively clean, 3D-image of the turbinates that can then be used for surface area measurements. Here, we report on a segmentation method that utilizes volumetric anisotropic diffusion and contrast-limited adaptive histogram equalization (CLAHE) in order to enhance the turbinates by removing noise created by the imaging process. We first use contrast-limited adaptive histogram equalization to brighten the turbinates in each image, while suppressing obvious noise. Next, we perform volumetric anisotropic diffusion, which smoothes away uncorrelated noise in the volume of images while filling in small gaps in the turbinate surface that are supported by the surrounding images. Once these steps have been taken, the images are segmented trivially by thresholding, and a surface is constructed from which we may make our measurements.

What Will be the Future of the Vertebrate Collections?

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Vertebrate specimens and collections are basic tools for most morphologists. They represent the reality behind the concept arisen by science. Therefore, these collections must be kept, protected, and still be accessible for the general public and researcher. Consequently, the collection management must be adapted to new and future goals in science and cannot ignore the evolution in research programs. Several guidelines for the care of natural history collections have been edited and are in use in many institution. They are guidelines and not rules, which gives answer. For instance, it stated that every effort must be made to minimize the level of risk facing specimens as a result of storage and use. We must keep everything but could we? The accumulation of fragile biologic collection at some point jeopardized the quality of conservation. The increasing numbers of specimens in collections represent a cost and reassess the questions of what must be preserved; how to deal with destructive inquiries; or should we restrict the access to the collections. Some authors have compared the biodiversity crisis to a new Alexandrian Tragedy. The collections represent the ultimate bastion against the mass extinction of biosystematic resources destroying irreplaceable repositories of information. Management is thus a key issue for museums.

X-ray Microtomographic Studies of Exceptionally Preserved Three-dimensional Galeaspid Endocranium from the Silurian of South China

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The sequence of evolutionary stages through which an archetypal vertebrate brain was established remains poorly known because there are few living representatives of jawless vertebrates and the relationships of those known remain poorly understood. There is, nevertheless, a rich fossil record of basal vertebrates, many of which preserve the gross morphology of the brain, sensory organs and distribution of the cranial nerves. These data are integral to understanding the establishment of the vertebrate brain and the extinct galeaspids remain the most significant outstanding source of information. Although seminal work was conducted by Halstead (1979, Nature, 282: 833–836), Wang (1991, Science Press. 41–65), the galeaspid brain still remains poorly understood, especially by comparison to osteostracans whose neurocrania were resolved at by serial sectioning by Stensio (1927, "The Devonian and Downtonian vertebrates of Spitzbergen. 1. Family Cephalaspidae." Skrifter om Svalbard or Nordishavet 12: 1–391). Three-dimensionally preserved galeaspid endocrania were collected from the Silurian of Zhejiang, China. We employed Synchrotron X-ray Tomographic Microscopy (SRXTM) at the Swiss Light Source to provide noninvasive volumetric tomographic scans of the galeaspid braincase at a high resolution. Using these datasets, detailed 3D computer reconstructions were produced, thus allowing virtual dissection and examination. Our preliminary results showed that the arrangement of the cranial nerves of galeaspids matched well the condition in osteostracans. Our studies also revealed an anteriorly located olfactory bulb and a terminal nerve, both more comparable to the gnathostome condition than that of lampreys or osteostracans. X-ray microtomographic studies of such rare galeaspid endocrania are invaluable in understanding the assembly of the vertebrate brain immediately prior to the origin of jawed vertebrates.

Scapula and Locomotion in Carnivora

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A total of ten variables were measured from 175 individuals belonging to 91 carnivore species. A factor analysis of these variables was carried out to study the relation between scapular morphology and some aspects of the biology of the studied species, specifically size, locomotor behavior and habitat. Three factors accounting for 79.71% of total variability were obtained. The first factor (F1) was highly correlated to body mass, but at the same time it seemed related to the preferred habitat: forest and jungle species, as well as those living in watery environments, presented higher values of F1 than species with similar body mass that inhabited open spaces. The second factor (F2) appeared to be in relation with cursoriality, since positive values for cursorial species and negative values for non-cursorial species were obtained. Finally, the third factor (F3) would be related to locomotor behavior, showing a tendency to increase F3 value from arboreal species to terrestrial ones (with scansorial and aquatic species displaying intermediate values). Unfortunately, this factor seemed to be highly influenced by taxonomic relationships at the family level. Consequently, no generalization could be postulated for Carnivora as a whole.

Morphological Analysis of Chondrocranial Development of *Pelodytes punctatus* Under Different Experimental Conditions

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During development, the tadpole chondrocranium modifies its form and ossifies to reach the adult cranium morphology. Environmental conditions can affect this period, altering the growth rate or the phenotype of the specimens. When *Pelodytes punctatus* is raised in competition with *Bufo bufo*, it accelerate its development and reaches is lower body mass at the end of metamorphosis. We have performed a laboratory experiment to compare the morphological development of the chondrocranium of *Pelodytes punctatus* in different competitive conditions. To analyze the shape change we used geometric morphometric methods. We digitized 12 chondrocranial landmarks, and then performed discriminant analyses to compare the grouped Gosner stages between treatments. Linear regressions of relative warps on log centroid size were also analyzed. The shape of the chondrocranium in the beginning of development shows differences between treatments. The higher shape differences are identified in the anterior region of the cranium, related with the buccal apparatus and feeding musculature. The chondrocranium of the competitive treatment at the beginning of the development is more lengthy or longer and narrow than the control treatment, meaning a more juvenile morphology. Those differences are reduced along the ontogeny, suggesting a compensatory development in the later Gosner stages to reach the same cranial shape.

Scientific Rotoscoping: A Morphology-based Method of 3D-motion Analysis and Visualization

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Despite the success of point-based tracking systems for measuring 3D-kinematics, topical landmarks are often poor proxies for underlying skeletal movement. X-ray imaging provides direct bone visualization, yet accurate quantification of non-planar motion by cineradiography or video fluoroscopy remains elusive. Scientific Rotoscoping entails aligning a computer model configured from a subject's actual anatomy (the key) with X-ray and light video images (the lock) to simultaneously animate and quantify 3D-motion. Polygonal bone models made from CT or laser scan data are articulated into a digital marionette using a hierarchy of virtual joints, for which each degree of freedom is separately controlled in the program, Maya. In contrast to point-based approaches, which quickly simplify complex organisms into a series of line segments, scientific rotoscoping is morphology-based. We do not track images of points, but images of structures, fully integrating the anatomical elements of interest into kinematic analysis. Ongoing studies of flying pigeons and walking alligators provide insights into this technique's strengths and weaknesses, as well as systems most suitable for Scientific Rotoscoping. Supported by the National Science Foundation, Brown University, and Autodesk.

Xenarthran Phylogeny and Relationships to Non-xenarthran Placentals

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The present study reviews recent morphology-based investigations of xenarthran phylogeny. Areas of broad consensus are noted, including the monophyly of the Xenarthra, of each of its three major constituent subgroups (Cingulata, Vermilingua, Phyllophaga), and of Pilosa (Vermilingua + Phyllophaga). The affinities of Xenarthra to other placental mammal groups remain controversial and in need of further investigation. Within Cingulata, the taxonomy and phylogeny of glyptodonts is poorly understood, although new insight is provided by one recent study. Two recent cladistic examinations of relationships among extinct and extant armadillos and other cingulates come to quite divergent conclusions, one supporting more traditional systematic arrangements, the other contradicting several established groupings. Regarding Vermilingua, relationships among undisputed members are uncontroversial, but there remains wide disagreement over the proper allocation of the putative anteater Eurotamandua from the Eocene of Germany. Virtually all recent investigations of sloth phylogeny support the diphyletic origin of the two extant tree sloth genera, but differ in the hypothesized relationship of the extant forms to various extinct taxa. A recent comprehensive analysis places *Bradypus* as the sister taxon to all other sloths, and allies *Choloepus* with extinct meglonychid sloths. This study corroborates the monophyly of the sloth families Nothrotheriidae, Megatheriidae, Megalonychidae and Mylodontidae, supports the alliance of nothrotheriids, megatheriids and megalonychids in a clade Megatheriodea, and within the latter group unites nothrotheriids and megatheriids in a clade called Megatheria. Relationships within these sloth families, in particular Mylodontidae and Megalonychidae, are deemed in need of additional study.

Placental Specializations in the Viviparous Lizard *Sceloporus jarrovi*

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Embryos of viviparous squamates form placentas that sustain them throughout development. Such placentas commonly are structurally simple and function in gas exchange and water uptake. We have studied placental membranes of the lizard *Sceloporus jarrovi* (Phrynosomatidae), by using semi-thin sections of resin- embedded tissues. In this species, the ovulated yolk provides most of the nutrients for development. Our observations reveal a combination of specializations never before described among reptiles. In the chorioallantoic placenta, fetal and maternal epithelia are greatly attenuated and lie in direct contact, due to loss of the vestigial eggshell; these features enhance gas exchange. In the yolk sac placenta (omphalallantoic placenta), the omphalopleure forms branching outgrowths that protrude into the uterine lumen and show structural evidence of absorptive capabilities. The apposed uterine epithelium exhibits epithelial hyperplasia and secretory activity. The chorioallantoic and yolk sac placentas appear to be adapted for distinct functional roles, in gas exchange and nutrient provision respectively. Presence in *S. jarrovi* of a true omphalallantoic placenta that persists until the end of gestation is contrary to assumptions in the literature. The occurrence of placental specializations for secretion and absorption in *S. jarrovi* suggests that morphological adaptations for placentotrophy can evolve in the absence of an evolutionary reduction in yolk.

Comparative Craniofacial Morphometry, Karyotypic and mtDNA in *Akodon cursor* (Rodentia, Muridae) from the South American Atlantic forest: Integrative Approaches

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Some Neotropical rodent species present vast karyological polymorphism. While such variation has been viewed as potentially triggering speciation, few studies tackle the problem with a multi-hierarchical approach. We analyzed craniofacial measurements, karyotypes and mtDNA sequences of *A. cursor* covering all its range in the Brazilian Atlantic Forest. 442 karyotypes showed three diploid numbers [2n = 14 (64.7%), 15 (21.5%), 16(13.8%)], with 26 karyomorphs. A nongeographic pattern was observed, with different frequencies of 2n or karyomorphs, most frequent being 2n = 14/AN = 18 and 2n = 14/AN = 19. Frequencies of rearrangements are in Hardy-Weinberg equilibrium for each locality, but not for all localities clustered. Cytochrome-b sequences from 73 specimens using neighbor-joining, maximum parsimony (4:1), maximum likelihood and median-joining analyses suggest two geographic lineages (NE/SE), with low differentiation (K2P = 0.036). Geographic variation in 19 skull measurements is pervasive, with Mahalanobis distances ranging from 2.2 to 50. Size and shape differentiation patterns across localities are similar. Morphological differentiation is independent of geographic distribution and genetic (DNA or chromosomal) distances. Geographic, cytochrome-b and chromosomal distances are highly correlated, suggesting isolation by distance at molecular and karyotypic levels. This pattern does not persist after exclusion of the only population from NE lineage with both karyotypic and DNA data available, in agreement with NE/SE clades. A quantitative genetics model applied to morphological differences among populations indicates that the null hypothesis of genetic drift can not be ruled out. Our results suggest that chromosomal variation and DNA are unrelated to morphological differences–their role in speciation, if any, would result from historical factors. Financial support: CNPq, CAPES, FAPESP and FAPERJ

The Role of the Evolution of Novel Reproductive Strategies in the Adaptive Radiation of Mesozoic Archosaurs

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The ability to rapidly produce amniotic eggs surrounded by rigid, calcium-rich shells conferred several distinct evolutionary advantages to Mesozoic crocodilians, dinosaurs, birds, and presumably, a variety of basal archosaurian taxa. Such eggs are more resistant to desiccation, microbial infection and predation than the leathery, proteinaceous shells of most other egg-laying amniotes. Also, the relatively high albumen allotment of typical archosaurian eggs provides a rich supply of water for the growing embryo, while more permeable eggs of other reptiles are more dependent on environmental water sources for development. It is probable that the evolution of hard-shelled, water-rich eggs by basal archosaurians was a crucial preadaptation to their spectacular Middle-Late Triassic adaptive radiation, a time characterized by widespread global drying that would have favored the hardier archosaurian egg. However, this adaptation likely canalized archosaurs to obligate ovipary. The early stages in the evolution of viviparity invariably relied upon extended retention of eggs in utero, and archosaurian eggs are incompat-

ible with the high oxygen conductance levels needed to ensure embryonic survival. Furthermore, nest structures and patterns of egg deposition of most dinosaurs are consistent with crocodile-like temperature-dependent sex determination, a selectively advantageous strategy in thermally equable climates of the Late Jurassic-Late Cretaceous. Global climatic instability at the end of the Cretaceous may have critically skewed dinosaurian sex ratios, contributing to their extinction. Significantly, the evolution of avian endothermy, coupled with genetic sex determination and egg incubation, would have favored survival of birds during extended periods of global cooling at the K-T boundary.

The Musculotendinous System of Pelagic Fishes: How Does Swordfish (*Xiphias gladius*) Compare to Thunniform and Carangifom Swimmers?

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Most pelagic fishes possess several adaptations for reducing drag and increasing swimming performance (i.e., streamlined, teardrop-shaped body). Despite a superficial resemblence, many pelagic groups differ significantly with respect to their swimming kinematics and mechanical design (e.g., dynamics and distribution of the locomotor musculature, red muscle-tendon relationships). Two principal types of mechanical design, the carangiform and thunniform, have independently evolved several times in gnathostome fishes and both have been identified in pelagic fishes. Surprisingly, the swordfish (*Xiphias gladius*, family Xiphiidae), a common apex predator of pelagic ecosystems, has not been investigated with respect to its mechanical design. In this initial study we present data on various aspects of the musculotendinous system of swordfish and compare our findings to those on thunniform (lamnid sharks, tunas) and carangiform species (carangids, scombrids). In all aspects investigated the swordfish represents an intermediate state between the carangiform and the thunniform type. (i) Red muscle has shifted medially and anteriorly in swordfish when compared to carangiform fishes but not to the extent of thunniform fishes. The relative maximum amount of red muscle is located at 0.6L (carangiforms: 0.8L; thunniforms: 0.5L). (ii) The identified red muscle-tendon association in swordfish suggests posterior force transmission over a distance of 0.08–0.1L (carangiforms 0.05–0.07L; thunniforms 0.2–0.25L). These morphological findings support the hypothesis that swordfish represents a third type of mechanical design in pelagic fishes. Further evidence to support this work can be obtained from studies on kinematics and red muscle dynamics.

Did Aistopods Have Pedicellate Teeth?

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Aistopods are Paleozoic snake-like limbless amphibians. A new specimen of a phlegethontid aistopod has been discovered in the MNHN collections of Montceau-les-Mines housed in the Musée d'Histoire Naturelle d'Autun. This is a juvenile individual, maybe the smallest aistopod ever described. Its preservation does not allow a specific identification but many features of the skull can be observed and this specimen is assigned to the genus *Phlegethontia*. The teeth of this animal exhibit some features that have never been observed in such lepospondyls amphibians; premaxillary teeth exhibit two fractures at their base that do not reach the sedimentary matrix around the teeth, so that these fractures seem natural. Compared to the teeth of an extant salamander, this may be interpreted as a pedicel. Such pedicellate teeth have only been documented in extant lissamphibians and two genera of dissorophoid temnospondyls and this was the last non-homoplasic synapomorphy that united them. The confirmation of pedicellate teeth among some lepospondyls would reveal that this character is more widespread than previously thought and would make it a homoplasic synapomorphy.

Variation in EMG Activity During the Reflex Pharyngeal Swallow

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The classic description of EMG activity during swallowing (Doty and Bosma, 1956. J.Neurophys 19:44-60) describes high levels of intramuscle and of inter-individual EMG variation. We reinvestigated this pattern, testing two hypotheses concerning EMG variation: 1) that it could be reduced with modern methodology and 2) that it could be explained by selective detection of different types of motor units. In eight decerebrate infant pigs, we elicited radiographically verified pharyngeal swallows and recorded EMG activity from a total of 16 muscles. Synchronization signals from the video-radiographic system allowed the EMG activity associated with each swallow to be aligned directly with epiglottal movement. The movements were highly stereotyped, but the recorded EMG signals were variable at both the intramuscle and interanimal level. During swallowing, some muscles subserved multiple functions and contained different task units; there were also intramuscle differences in EMG latencies. Variation within muscles was, in some cases, as great as variation among individuals. In this situation, statistical methods were essential to characterize the overall patterns of EMG activity. The overall pattern among muscles was similar to that of Doty and Bosma with a "leading complex." However, there were several significant differences in activity patterns that were discernable in these data.

Evolution of Asynchronous Jaw Muscle Activity in Elasmobranchs

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Jaw muscle asynchrony is an ancestral trait in vertebrates and may have arisen with the evolution of mobile jaws. Investigating this trait within elasmobranchs increased our understanding of the evolution of this trait throughout the vertebrates. Complex prey processing in vertebrates is characterized by unilateral activation of the jaw musculature, permitting freedom of movement through partial decoupling of the sides of the head. Temporal patterns of bilateral jaw muscle activity were investigated in four major groups of elasmobranchs: *Squalus acanthias* (a basal shark), *Chiloscyllium* plagiosum (a derived shark), *Mustelus canis* (a derived shark) and *Leucoraja erinacea* (a basal batoid) using electromyography. Electrodes were implanted in three of the jaw adductors: two divisions of the quadratomandibularis and the preorbitalis, as well as in a cranial elevator in sharks: epaxialis. All species process complex prey items by head-shaking, crushing or biting. All four species use synchronous activation (no difference in onset of activity) of bilateral muscle pairs during prey capture. *Chiloscyllium* uses synchronous activation during prey processing whereas *Squalus*, *Mustelus* and *Leucoraja* use asynchronous activation.. Due to differences in cranial design, *Leucoraja* are able to process prey unilaterally while the sharks process prey bilaterally, thus the batoid is more efficient in using fewer muscles. *Leucoraja* are the most derived of the three species, therefore complete unilateral activation may be a derived form of asynchrony.

Seasonal Changes of Muscle Morphology of Greenland Sled dogs

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To explore the physiological boundaries of seasonal up-and down-regulation of skeletal muscles and to analyze the combined effects of temperature, energy intake, and exercise, we studied a team of 14 dogs kept under traditional husbandry conditions at Qeqertarsuaq, Greenland. During winter, dogs were exposed to low temperatures, high work load, but normal food intake; during summer they experience mild temperatures, intermittent food supply, and no exercise. Body weight was 18.8 ± 1.6 kg in summer and 26.8 ± 2.6 kg in winter. The circumference of fore leg muscles and hind leg muscles differed significantly between summer and winter. We used transcutaneous ultrasonography to measure the muscle thickness on the scapula, the hind leg and the fore leg. All muscles were significantly thicker during winter than in summer (i.e., M. supraspinatus: 2.24 ± 0.2 cm in summer, 2.71 ± 0.2 cm in winter; lateral foreleg muscles: 0.49 ± 0.19 cm in summer, 0.94 ± 0.22 cm in

winter; the combined M. biceps femoris and M. vastus lateralis: 1.43 ± 0.159 cm in summer and 2.30 ± 0.185 cm in winter.) To explore the ultrastructural causes for these observed muscle size differences, we took microbiopsies from M. adductor magnus. Muscle histology was evaluated by the number of myofibrils per mm^2 (311.20 ± 71.52 in summer; 281.19 ± 56.01 in winter), the number of capillaries per mm^2 (804.16 ± 184.37 in summer; 682.69 ± 208.51 in winter), the diameter of myofibrils (34.17 ± 11.28 μm in summer, 50.50 ± 14.12 μm in winter), the distance between myofibrils (27.22 ± 13.87 μm in summer, 13.17 ± 10.01 μm in winter), and capillarization (ongoing). The average number of capillaries per muscle fiber did not differ between summer and winter condition. Architectural changes of myofibrils were described as the length ratio of the Z-line to the M-line. In winter this ratio was 1 compared to 0.87 in summer. Muscle fibers differed in the number of lipid droplets.

Sand-burrowing Kinematics of the Pacific Sand Lance, *Ammodytes hexapterus*

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The Pacific sand lance, *Ammodytes hexapterus,* is a small schooling fish that exhibits a peculiar burrowing behavior in which they swim rapidly into the sandy bottom. This behavior occurs for hibernation and for predator-avoidance. While burrowing, these fish experience a physical transition from water (a relatively inviscous fluid) to a sand-water mix (a relatively more viscous, granular fluid), along with which comes a significant change in Reynolds number. We used high-speed video to investigate the progression of kinematic behavior throughout the burrowing process of *A. hexapterus*. Burrowing was found to occur in four stages: 1) the initial dive stage; 2) a propulsive stage; 3) a transition from aquatic to subterranean locomotion; and 4) a glide stage in which the posterior quarter of the fish passively slides into the substrate. Size class was not found to have an effect on kinematics, but large sand lance exhibited the burrowing behavior much more readily than small individuals. The burrowing events in which the individual was resting on the bottom immediately before burrowing were executed at a lower velocity than those where the individual was higher up in the water column, indicating that momentum can be used to speed up the burrowing process.

Bite Force Estimation for *Deinonychus antirrhopus* Using Tooth Indentation Simulations

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Several methods have been used to estimate bite force values in extinct dinosaurs. These include up-scaling from living reptiles, estimates based on presumed muscle sizes, types, and mechanical configurations, and finally tooth indentation simulations. In the present research we utilized the latter to determine minimal bound estimates of bite forces produced by *Deinonychus antirrhopus* during feeding. Numerous bite marks on a recently unearthed specimen of the iguanodontian dinosaur *Tenontosaurus tilletti* from the Cloverly Formation of Wyoming were simulated by indenting a nickel alloy cast of an adult *D. antirrhopus* tooth through bovine long bones using a mechanical loading frame. These elements showed comparable microstructure and cortical thicknesses spanning the bounds of those in the bitten bones. The results reveal that this animal generated values of approximately 3000 N. *Deinonychus* teeth are relatively small, recurved, and laterally compressed, suggesting that they were not as well suited to sustaining bone impacts as those of some other dinosaurs (e.g., tyrannosaurs). Indeed, most bite marks attributed to this and related taxa consist of just shallow scrapes. All the same, the results from this study reveal that relatively high bite force generation was within the bounds of this animal's capacities and that its dentition was capable of repetitively puncturing thick bone cortices (6.5 mm).

Hindlimb Muscle Actions Over Ontogeny in Goats and Sheep

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Certain homologous muscles appear to function differently during locomotion in mammalian quadrupeds that differ substantially in body size. For example, in trotting horses, the vastus lateralis, a major knee extensor, primarily shortens when active during the support phase, whereas, in trotting goats, the same muscle undergoes a lengthening-shortening cycle. Further, in trotting rats the vastus is mainly stretched when active during support. Differences in size between newborn and adult animals are not as dramatic as those between rats and horses, but are nevertheless considerable. Does a limb muscle's function change as an animal grows from a newborn to an adult? To address this question we used sonomicrometry and electromyography to quantify length changes and activation patterns in the vastus lateralis and biceps femoris of goats and sheep ranging in size from 4–40 kg. Preliminary data suggest that activation timing remains comparable in these muscles as animals grow. In addition, strain patterns in newborns and adults are qualitatively similar: biceps fascicles generally shorten over much of stance and vastus fascicles undergo a lengthening-shortening cycle over the same period. However, levels of fascicle strain are typically slightly lower in smaller, younger animals. Thus, hindlimb muscles undergo similar strain and activation patterns in newborns, juveniles and adults, but limb joints seem to undergo smaller excursions in younger animals.

The Homology and Phylogeny of Chondrichthyan Tooth Enameloid

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The homology and phylogeny of tooth enamel(oid) within chondrichthyans and, more broadly, within gnathostomes, has long been a topic of debate. Here, a systematic SEM survey of tooth microstructure in (primarily) fossil taxa spanning chondrichthyan phylogeny demonstrates the presence of a superficial cap of single crystallite enameloid on the teeth of several basal elasmobranchs, as well as on the tooth plates of *Helodus* (a basal holocephalan). When analyzed in light of a number of competing phylogenetic hypotheses, these data suggest that the epithelial-mesenchymal interactions required for the development of enameloid during odontogenesis are plesiomorphic in chondrichthyans, and most likely in toothed gnathostomes, and provide phylogenetic support for the homology of elasmobranch and actinopterygian tooth enameloid. Furthermore, the occurrence of fully-differentiated neoselachian enameloid microstructure (including compression-resistant tangle-fibred enameloid and bending-resistant parallel-fibred enameloid) in *Chlamydoselachus anguineus*, a basal squalean with teeth that are functionally "cladodont", is evidence that triple-layered enameloid microstructure may have preadapted neoselachian teeth to a cutting and gouging function, and thus may have played an integral role in the Mesozoic radiation of the neoselachian crown group.

Segmental and Columnar Aspects of the Organization of Vestibular Projection Neurons

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Vestibular projection neurons reside within a longitudinal domain that spans much of the hindbrain, and are thus subjected to the segmental influence of the rhombomeres during their genesis and differentiation. They also have diverse targets rostral to, caudal to, and within the hindbrain. Neuroanatomical and functional studies have shown that vestibular projection neurons that project to common targets are differentially clustered within this domain, creating a mosaic arrangement in which axon trajectory and synaptic connectivity are related to neuron position. By combining axonal tracing techniques with fate mapping techniques it has been possible to map this mosaic pattern onto the columnar and segmental organization of the hindbrain, thus providing a link between developmental patterning events and function within identified circuits. Such studies provide a platform for addressing the molecular mechanisms underlying circuit formation within the vestibular system.

Actinopterygian Vertebral Characters That Aid in Taxonomic Discrimination

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Vertebrae are arguably the most common diagnostic fish remains recovered from archaeological excavations. The variation present in fish vertebrae makes the task of species identification daunting. Not only do vertebrae vary within the individual from atlas to terminal vertebra, but also clade-specific diagnostic characters compound the problem of identification. The functional interpretation of vertebral features is in its infancy. My aim is to summarize the characters that need to be considered to make accurate taxonomic determinations in the archaeological context, with fossils, and in stomach content and scat analysis. Actinopterygian fishes of California are used to illustrate vertebral variety. Features worth noting include: size of the notochordal canal; depth and shape of the recesses of the ends of the centra; smooth, pitted, perforate, and laminar texture of the bone; position and angle of the transverse processes, spines, neural and hemal arches relative to the centrum; architecture of the lateral surface of the centrum including ridging, flanges, recesses, and buttresses; relationship of diameter to length of the centrum: and dorso-ventral compression of the centrum. These features are useful in taxonomic determination but await functional analysis.

Contribution of Geometric Morphometrics to the Study of Fossil Primate Skulls: The Case of Large Adapines (Primates)

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Geometric morphometric methods are a powerful tool for the analysis of morphological diversity and its systematic implications. Three-D coordinates of landmarks taken on seven *Leptadapis* skulls were treated in a generalized Procrustes adjustment. Missing points were replaced by visual estimations, repeated twice. On the PCA analysis of Procrustes residuals, uncertainties due to these estimations are reflected by increased distances between replicated points. The uncertainties due to reconstruction being recognized, the morphometric results confirm the systematic conclusions driven from a qualitative analysis of these skulls. They suggest that the two proposed groups can be quantitatively separated by shape variables, independent of size, pointing to differences in the height between palate and orbits, the anteroposterior length of the bullar region, the overall breadth of the skull, the height of the frontal line, etc. Some of the recognized differences had not been found through visual comparisons. The large adapine skulls were also compared with a sample of living New World monkeys. The morphometric analysis shows that the large adapine skulls have a higher morphological disparity than those from several living species of one genus, giving further quantitative support to the possible distinction of two genera among them. Difficulties linked to incomplete fossils will be further analyzed, as well as the need of new landmarks or new outlines to study peculiar morphologies found in fossils.

Integrating Morphology, Behavior and Phylogeny to Determine the Mechanics and Energetics of Rorqual Lunge-feeding

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Rorquals exhibit one of the most extreme feeding methods among aquatic vertebrates. These whales generate dynamic pressure at high speed in order to stretch their mouth around a large volume of prey-laden water that is then filtered with racks of baleen. This lunge-feeding process is facilitated by highly extensible tissue located on the throat wall, thus providing a large capacity for engulfment. Because of this enhanced capacitance, engulfment volume is limited by the size and shape of the skull and mandibles, both of which are incredibly robust, making up nearly ¼ of a whale's body length. First, we develop a quasi-steady hydrodynamic model of lunge-feeding derived from first principles that predicts engulfment volume, drag, and mechanical power as a function of time. We then parameterize the model for an adult fin whale with kinematic data measured by high-resolution digital tags and morphological data. Our analysis reveals an extraordinary engulfment capacity that is larger than the body itself. However, this engulfment capacity comes at a high energetic cost, whereby drag, power and drag coefficient are severely increased over the course of a lunge. Lastly, we present a phylogenetic analysis of the scaling relationships for the various dimensions of rorqual mandibles, which range in length from 1 m (minke whale) to 7 m (blue whale). We discuss these results in a mechanical context, specifically in terms of bending beams exposed to high drag as suggested by our lunge-feeding model, and compare these allometric trends to non-lunge-feeding baleen whales of similar size.

Redescription of the Carpus of *"Bothriospondylus" madagascariensis* (Dinosauria, Sauropoda): Homology of the Carpal Elements in Sauropodomorpha

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Except for some rare exceptions, the arrangement and evolution of the carpus remain poorly understood among sauropodomorphs, mainly because of a bad preservation in the fossil record. If preserved, the other problem is the difficulty to identify the carpal elements, rarely found in articulation. Whereas the carpus of Prosauropoda is relatively well-known in regard of the remains of Massospondylus and Plateosaurus, the structure of the Sauropoda carpus is still unknown and was subject of many interpretations so far. Here, we redescribe the wrist of *«Bothriospondylus» madagascariensis*, a Middle Jurassic sauropod from the Majunga Basin in Madagascar, previously described by Lavocat in 1955. It consists of five carpal elements, an unusual feature among sauropods, which preserved most of the time three of few carpal bones. The study of some extant taxa such as Chelonia, Lepidosauria and Crocodylia, as well as that of prosauropods, leads us to test different homological hypotheses in the carpus of *«Bothriospondylus»*. These results are replaced in a phylogenetic context, in order to propose a preliminary hypothesis on evolution of the carpus within Sauropodomorpha.

Homologies of Larval Amphibians and the Evolution of the Anuran Tadpole

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The larval morphology of the extant amphibian orders has traditionally been communicated in a mixture of descriptive and homology-expressing terms. In an endeavor to reconstruct the morphology of the most recent common ancestor of the three orders in its larval form, we are revising the cranial musculo-skeletal system and associated primary homology assessments. There are fewer conflicts in reconciling the three orders than expected from traditional morphological terminology (often concealing homology) and from the profound differences in general appearance of salamander larvae, caecilians, and anuran tadpoles. However, some ambiguity remains, e.g., in the homology of the depressor mandibulae group or the nature of the caecilian pterygoideus and levator quadrati. Caecilians and salamanders preserve many plesiomorphic conditions, such as suspensorium orientation, hyobranchium, and lower jaw structure, whereas anuran tadpoles accumulated the largest amount of derived character states. The seemingly deep gap between the cranial morphology in the assumed "salamander-like" ancestor and the anuran tadpole can be bridged by processes of shape shift, translocation, parcellation, and fusion of structures. In anuran larvae, most apomorphic cranial features can be derived from a hypothetical "salamander-like" ancestor in functional continuity, despite a shift in the feeding mode from suction feeding to suspension feeding. The adrostral cartilage (only in some anuran tadpoles), however, appears to be a true innovation in the cranium without a precursor in the lissamphibian common ancestor.

Pre-stance Forelimb Retraction Versus Speed in Trotting Rats

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Spring mass models show that the rotation of the limb toward the ground in the latest part of the swing phase dramatically increases the

range of admissible parameter values that let the system run stably by fine tuning the instant of touch down. We observed behavior in rats trotting at constant speed on a treadmill and filmed videoradiographically. We make use of radio opaque markers implanted surgically to automate the frame by frame analysis via home-made computer tracking of the markers. No differences were found in the locomotion before and after the operation. Four hundred cycles were collected and analyzed and parted into five speed classes. General standard deviations of the metric parameters decreased with increasing speed. The amplitudes of motion were found larger at the wrist and at the elbow but not in the shoulder. The "limb" retraction as it has been observed in the asymetrical gaits (gallop, half bound) of different sized mammals is reduced to a speed-dependant tuning of the ulna motion during trot.

3D-reconstruction of the Quail Trunk and Limb Kinematics from 2D Videoradiographical Views

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This study aims to compare two methods that reconstruct the third spatial dimension that describes the transverse kinematics motion of a small terrestrial bird. Series of 2D videoradiographical views are available in parasagittal projection on the one hand, and in dorso-ventral projection on the other hand. The first method is based on the coordinates collected from the parasagittal view. It estimates the lengths of different useful segments of the animal's leg and body, and uses dorsoventral views to identify the times of abduction and adduction respectively in a qualitative way. The second method deals with coordinates issued from lateral and dorsoventral views, that actually come from distinct sequences of locomotion. It implements a walking-cycle matching algorithm on the longitudinal motion direction coordinate that is common in parasagittal and dorsoventral views. Both methods show similar results in matter of movement shape and amplitude. The precision of both reconstruction techniques is discussed.

The Structure of Variation and the Developmental Basis for Evolutionary Change

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In recent years, our understanding of the developmental pathways that drive development has increased enormously. The proliferation of accounts focused on the roles of specific genes in development has now created a vast field of bewildering complexity. Yet, this growth in information has not produced a fundamental change in our understanding of the developmental basis for evolutionarily significant phenotypic variation. We still do not know how selection and development interact to produce variation and evolutionary changes in features such as limb length or the shape of the skull. We argue that a new theoretical approach is needed to integrate gene-centered accounts of developmental mechanisms to a phenotypically relevant understanding of developmental systems. This approach focuses on higher levels of the developmental hierarchy such as pathways and processes as ontologically equivalent sources of developmental explanation for phenotypic variation. Development funnels the vast amount of variation at the molecular level through definable numbers of developmental pathways which influence smaller numbers of developmental processes which, in turn, often have tractable relationships with fairly restricted sets of phenotypic outcomes. We argue that understanding this relationship between developmental processes and phenotypic outcomes is a key step in unraveling the developmental-genetic basis for phenotypic variation. The results of such studies provide a larger framework within which to contextualize the massive amounts of data generated by ongoing studies on gene-specific effects on the phenotype and the dissection of the genetic networks that control or regulate normal and abnormal development.

Head-bobbing During Terrestrial Locomotion in Birds: Effects on Center of Mass

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Head-bobbing is the fore-aft movement of the head relative to the body during terrestrial locomotion in birds. Although it is considered to be a visual response, our studies show that head-bobbing also impacts post-cranial locomotor mechanics. Terrestrial locomotion and head-bobbing were evaluated in the Elegant-crested Tinamou (*Eudromia elegans*) at a range of speeds (0.43 to 2.78 ms-1) using high-speed (250 Hz) videography synchronized with ground reaction force data. The results demonstrate that the head-bobbing cycle can occur any time during the stride cycle, thus the timing of head-bobs is independent of limb movements. Yet, the cycling of head and neck protraction and retraction effects body pitch. Thus, movements of the head and neck (which constitute ~6% of overall body mass) modify the movement of the body's center of mass. [supported by NSF IOB 0520100]

Reptilian Evo-devo: Replacement Tooth Formation in the Bearded Dragon *Pogona vitticeps*

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The molecular control of replacement tooth formation in amniotes is largely unknown. Undoubtedly, this gap stems from the inability of conventional mammalian models, such as the mouse and rat, to form more than a single set of teeth throughout their lives. Accordingly, alternative amniote models must be considered. Our group has turned to snakes and lizards (Squamata), which form multiple sets of teeth and, for many species, develop oviparously. Here we describe early odontogenesis in the central bearded dragon *Pogona vitticeps*. Histological analysis reveals that tooth development in *P. vitticeps* closely parallels the stages described for mammals (*viz*., initiation, bud, cap, bell stages). In brief, a thickened oral epithelium projects into the dental mesenchyme to form the sheet-like dental lamina. This structure is larger in size compared to mammals and appears to be continuous along the length of the jaws. Teeth bud from the leading edge of the lamina, with first generation anlagen closely abutting the oral epithelium and replacement teeth forming more distally. Towards elucidating the bases for the expanded dental lamina and enhanced odontogenic capacity of *Pogona* and other reptiles, we have cloned several genes involved in tooth initiation, including the *P. vitticeps* orthologs of *Bmp2*, *Bmp4* and *Msx2*. We characterize their expression by radioactive *in situ* hybridization and compare these data with cell proliferation and apoptosis as revealed by PCNA and TUNEL assays. Collectively, our findings suggest that the unique features of the squamate dentition are the result of modulation of generalized vertebrate odontogenic machinery.

Neural-crest Derivation of the Bony Skull is Not Conserved Among Vertebrates: Data from Amphibians

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We utilize a novel transgenic labeling system to assess the contribution of cranial neural crest to the bony adult skull in the clawed frog, *Xenopus laevis*. This system can be used to trace the contribution of embryonic cells to adult structures, including those that form after a prolonged larval period. Results constitute the first direct evidence of neural crest derivation of most cranial bones in amphibians and represent only the second comprehensive fate map for the vertebrate osteocranium. Neural crest derivation of the bony skull in anurans is more extensive than that reported for any other vertebrate. Crest-derived territory extends caudally to include the entire length of the frontoparietal bone in the skull roof and the rostral portion of paired exoccipital bones at the rear of the skull. Unique features include a significant contribution from the hyoid crest migratory stream to rostral bones, which generally are regarded as derived from the mandibular crest stream. Interspecific variation in embryonic derivation of the bony skull may mean that the neural crest-mesoderm boundary has shifted within the skull during vertebrate evolution, and that a given bone in one species may form from a different precursor cell population than the homologous bone in another species. This would offer an example of evolutionary lability of neural crest biology,

which in most other respects is highly conserved among species. Alternatively, these data may indicate errors in the traditional assessment of specific cranial bone homologies among vertebrate classes. Supported by US NSF EF-0334846 (AmphibiaTree).

Modularity, Pleiotropy, and the Evolution of the Genotype-phenotype Map

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Modularity is often seen as a prerequisite for evolvability. From a population-genetics perspective, modularity can be described as a pattern of pleiotropy. In this contribution, I first describe how pleiotropy affects evolvability. I then consider and evaluate several hypotheses for how patterns of pleiotropy may evolve, and finally I discuss the implications of these hypotheses for the evolution of evolvability, and for the link between micro- and macroevolution.

Masticatory Anatomy of Felids: Stretch, Strength and Osteological Correlates of Muscle Architecture

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We studied the anatomy and fiber architecture of the chewing muscles in nine species of felids from 3.9–250 kg. The goals of the study were: 1. to understand the scaling pattern of muscle mass, cross-sectional area (PCSA), and fiber length (FL); 2. to test the relationship of these variable and diet, and 3. to find osteological proxies for these soft tissue variables so that our dietary deductions can be applied to fossil taxa. RMA regressions on logged variables show that temporalis and masseter (the largest jaw adductors) muscle mass, PCSA and a proxy for adductor force (PCSAleverage) scale isometrically with body mass. FL has a behavioral signal: those taxa that require large gape (e.g., the large prey specialist *Felis caracal*, and the felid with the relatively longest canines, *Neofelis nebulosa*) have relatively long temporalis and masseter fibers, and the taxon that specializes in the smallest prey (the rodent specialist, *Felis serval*) has the relatively shortest fibers. We found that the average of temporalis and masseter FL is best approximated by a line representing an anterior temporalis fiber (i.e., from the anterior corner of the sagital crest to the anterior most point on the coronoid temporalis scar, just posterior to the carnassial). Osteological proxies of a posterior temporalis fiber, mean of a middle masseter and anterior temporalis fiber, and mean of a middle masseter and posterior temporalis fiber also approximate true FL. Osteological proxies for muscle mass and PCSA are harder to find.

Arciferal vs Firmisternal Type of Pectoral Girdle in Frogs: An Ontogenetic View

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Historically, two basic types of anuran pectoral girdle have been described on the basis of their differing morphologies. In the arciferal type, the epicoracoid cartilages are broad, overlap each other along the ventral midline, and protrude into posteriorly directed epicoracoid horns. In the firmisternal type, the pectoral girdle lacks epicoracoid horns and the epicoracoid cartilages are fused to each other in the medial line. Later, these types proved to be generalized and simplified, e.g., because in the arciferal type the medial tips of procoracoids are fused, so they do not overlap. Also, many authors showed that a variety of intermediate conditions exist between these two types of girdles. Using cleared-and-stained specimens, I studied the ontogenetic development of the pectoral girdle in larval stages and adults of seven frog species. These species were from six families and they were selected according to their phylogenetical status among Anura and the type of their pectoral girdle (Discoglossidae, Bombinatoridae, Pipidae, Pelobatidae, Bufonidae and Ranidae). I found that the epicoracoid cartilage is not homologous in the arciferal and firmisternal types of the pectoral girdle. In the arciferal one, the epicoracoid originates from the medial prolongation of the procoracoid cartilage and broadly overlaps its counter part in the further development. In the firmisternal pectoral girdle the epicoracoids are in fact only widened cartilaginous medial ends of the coracoids that fuse together along the midline.

Origin of Anuran Jumping Locomotion: Inference from Functional Morphology and Comparative Anatomy

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Unlike extinct Temnospondyli from which frogs evolved in the Triassic, and unlike their larvae, adult frogs are capable of symmetric locomotion in water and on land. Transition to a symmetric terrestrial locomotor mode (i.e., jumping) required profound changes in the musculoskeletal system, such as the elongation of the hind limbs, a shortening of the presacral vertebral column, a posterior shift of the pelvic joint, and the fusion of the caudal vertebrae into a rod-like element. Despite the long-standing interest in the origin of jumping in frogs, it is still debated whether these features that appear to characterize jumpers evolved in water or on land. In order to gain insights into the origin of this unique morphology we investigated the locomotor apparatus and its use in frogs that differ in their locomotor specialization (jumpers, hoppers, burrowers, and swimmers) using methods of comparative anatomy (to quantify morphological differences) and developmental morphology (to understand how these differences are established during development). Additionally, we investigated the function of selected hip and thigh muscles using functional analyses (high speed videofluoroscopy combined with electromyography) in the different species, and during a range of locomotor behaviors. Finally, we address the relevance of these data in the context of the paleontological record represented by an evolutionary series of neotenic temnospondyls, *Triadobatrachus*, and Mesozoic anurans.

Vertebral Morphometry in Snakes: Implications for Developmental Mechanisms in Axial Skeleton Evolution

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Shifts in *Hox* gene expression are thought to be responsible for the limbless body plan of snakes, and reduced *Hox* regionalization has been proposed to drive an increasingly uniform axial osteology throughout their phylogeny. This hypothesis is based on a single taxon; however, patterns of morphological variation in the axial skeleton of snakes remain poorly known. We quantified intracolumnar changes in squamate precloacal vertebral morphology to determine whether changes in variation are consistent with developmental hypotheses of progressive homogenization. Procrustes aligned landmark coordinates were used to sample morphology throughout the vertebral columns of taxa representing all higher-order snake lineages. Shape variance along each vertebral column, derived from PCA ordination, was used as an index of regionalization. Evolutionary changes in the index were mapped onto snake phylogeny to test whether they were consistent with either *Hox*-mediated differentiation at the origin of snakes or with progressive growth-related changes in regionalization throughout subsequent snake history. Variance corresponding to allometric shape change demonstrated a negative correlation with patristic distance, corroborating hypotheses of decreasing regionalization throughout snake phylogeny. This pattern is more consistent with heterochronic changes than *Hox* domain shifts as mechanisms of axial evolution within snakes, however. Comparisons with successive sister taxa do not reveal a pronounced decrease in intracolumnar variance at the origin of snakes relative to other squamates, suggesting that increasing homogenization of the vertebral column may actually have occurred deeper within Squamata.

The Structure and Function of the Palatal Oral Mucosa of the Malayan Box Turtle, *Cuora amboinensis* (Daudin, 1802)

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Microanatomical structures and specializations of the palatal oral mucosa of the Malayan semiaquatic turtle *Cuora amboinensis* are described

and discussed as essential parts of the feeding system. SEM revealed that the palate has a flat surface. Taste buds are present both in lightly keratinized and non-keratinized regions and their density is highest in the anterior, prechoanal palate. Keratinization is reflected in disc-shaped keratinized dead cells with rough microplicae on the surface and is concentrated close to the rhamphothecae. The surface of the non-keratinized hexagonal epithelial cells is dotted with microvilli and sometimes with cilia. Light microscopy shows the different tissue layers of the oral mucosa and the different epithelial structures. Taste buds consist of slender epithelial cells and exhibit the typical barrel-like shape. The epithelial keratinocytes mature from basal to superficial, where they lose their nucleus to build up keratin layers with varying thickness. Secretory cells range from cuboidal epithelial cells to specialized goblet cells. Goblet cells appear diffuse, but are often organized in goblet cell fields which can be folded into crypts. All the structures of the oral mucosa act as a functional entity that includes secretion, immunological response, metabolism, as well as sensory and mechanical properties. All these functions play an important role in feeding behavior. They help determine how successfully an organism adapts ecologically to the environment and are thus essential for the species' survival.

Ontogenetic Differences Between the Winter Skate (*Leucoraja ocellata*) and Previously Described Chondrichthyans

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Batoids (skates and rays) have a highly modified body plan in comparison with other elasmobranchs, as an adaptation to a durophagous lifestyle. The developmental mechanisms that pattern their peculiar morphology have only recently received attention, and remain mostly unknown. Although the early embryology of batoids has previously been described, a complete description of later stages is still missing. This would provide an accurate tool for new developmental studies, as well as a direct comparison of ontogenetic sequences between chondrichthyans using the existing tables for sharks and chimeras. We propose a staging table for batoids based on the embryology of the winter skate (*Leucoraja ocellata*), native to the Northwest Atlantic. Using a series of embryos provided by the Biodôme de Montréal, we focus on stages 25 to 32, which are important for the development of specialized features in batoids. These stages were aligned to the generalized chondrichthyan framework developed by Scammon (1911, In G. Keibel (ed.), Normentafeln zur Entwicklungsgeschichte der Wirbeltiere, Vol. 12, pp. 1–140. Gustav Fisher, Jena) and refined by Ballard et al. (1993 J. Exp. Zool. *267: 318–336*). Although the early patterning of the body plan in skates is remarkably similar to that of sharks and chimeras, a number of differences emerge later in ontogeny and are compared here. These include the anterior progression of the pectoral fin and fusion to the head, which separates the spiracle dorsally from the gills openings in the ventral region, the migration of the eyes dorsally, the accelerated elongation of gill filaments and enlargement of the anal membrane.

Early Development of the Cephalic Skeleton in *Heterotis niloticus* (Teleostei, Osteoglossiformes)

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As the most primitive group among Teleostei, the Osteoglossomorpha super-order is of great interest due to the particular anatomy, phylogeny, biogeography and economic value of its representatives. Among this group, the African arowana *Heterotis niloticus* is not the least astonishing species. In adult specimens, the parasphenoid-tongue bite apparatus (TBA) that characterizes all Osteoglossomorpha is greatly reduced. Moreover, this species is unique in possessing a paired epibranchial organ which has a filtration function. Another surprising character is the presence of an articular connection between the parasphenoid and the hyopalatine arch: the basipterygoid articulation. In this study, the ontogeny of the cephalic skeleton was described from 6 hours until 50 days post-hatching (dph) using trypsin-cleared and stained specimens. The following results were yielded: the chondrocranium is quickly shaped (all elements are present at 96 hph), but its regression is slow and several cartilaginous elements persist in the ossified skull (at least until 50 dph). The TBA starts to develop since 48 hph and the parasphenoid is still well toothed at 50 dph. The epibranchial organ develops very slowly and doesn't appear to be functional at 50 dph. These two observations seem to indicate a progressive change in the diet, from a carnivorous to a microphagous diet. The formation of the basipterygoid articulation is a two-step process that involves various structures: first solely composed of cartilaginous elements (trabeculae + palatoquadrates), it is later composed of dermal bones (parasphenoid + entopterygoids) with few cartilaginous components.

Using Zebrafish to Investigate the Origin and Evolution of Morphological Novelty

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Exploiting the conserved developmental mechanisms seen in vertebrates, the zebrafish has become a popular model organism within the field of biomedical research. Yet, by ignoring what makes this cypriniform fish unique we are overlooking a powerful model organism for investigating the origin and early development of morphological novelties. As cypriniforms, zebrafish possess a number of poorly investigated adaptations associated with feeding: enlarged pharyngeal jaws opposed to an enlarged basioccipital process of the neurocranium instead of upper pharyngeal jaws; a muscular palatal organ found on the roof of the buccal chamber; and the kinethmoid, a rostral ossification associated with premaxillary protrusion. Taking advantage of some of the molecular tools used by developmental biologists we describe the early development, growth and possible evolutionary fates of some of these novel structures. The palatal organ, while less well-developed in zebrafish than in other cypriniforms, is apparent from early ontogenetic stages. Vertebrate morphologists have long examined premaxillary protrusion and pharyngeal jaw function in Perciformes. However, appreciably less emphasis has been placed on investigating the convergent acquisition of these functions in Cypriniformes. Given that cypriniform fishes lack oral jaw teeth, there must exist significant selection for efficient pharyngeal jaw processing in these species. The speciose Cypriniformes possess a novel median bony element, the kinethmoid, which allows for a unique mechanism of premaxillary protrusion. We have examined the development of this important feeding innovation. Identifying the developmental mechanisms responsible for the origin of these feeding adaptations will enhance our understanding of how functional novelties arise and evolve.

Lick, Shoot and Flick: the Evolution of Highly Specialized Tongue Protrusion Systems in Vertebrates

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Highly specialized, extremely elongated tongues have evolved independently in many vertebrate groups. Whereas ballistic tongues involved in prey capture are observed in many amphibians and reptiles, slower tongue protrusion systems are found in several mammals and birds (e.g., nectar feeding bats, anteaters, pangolins and woodpeckers). Although all of these designs have in common that the tongue is extremely elongated during protraction, the mechanical demands on these systems may vary dramatically. Muscles causing tongue elongation and shortening in nectar feeding bats or birds, for instance, likely have little or no demand for speed or strength. For the ballistic tongues of salamanders, on the other hand, speed is of prime importance during projection. In still other systems such as chameleon tongues, speed and force need to be combined into a single system because chameleons commonly eat very large prey. To explore these issues and to understand the morphological basis of tongues with different functional capacities, the morphology and ultrastructure of some the most extreme tongues in vertebrates (nectar feed-

ing bats, salamanders and chameleons) were examined. Our data show marked differences in gross morphology and ultrastructure that appear tightly linked to the mechanical demands imposed on the functioning of these systems and show remarkable convergence (e.g., use of helically arranged muscles) in some aspects, but striking divergence in others (e.g., presence or absence of supercontractile muscle).

Dwarfing a Giant: Allometry and Ontogeny of Elephant Limb Bones

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Elephants are the largest living terrestrial mammals. They represent the endpoint taxa for our current understanding of many inter-specific allometric relationships and the constraints imposed by large body size, particularly in locomotion. Despite ranging from just over 100kg at birth to 7,000kg in full-grown males, recent research suggests that juvenile elephants do not differ from their adult conspecifics in their kinematics. The highly derived, graviportal skeletal morphology of elephants has been closely linked with elephant locomotor abilities, and yet the intraspecific allometry and ontogeny of elephant limb bones has been little studied. This is necessary to our understanding of the morphology and adaptation of extinct elephant species, especially the dwarfed species of elephant found on islands 800,000—10,000 years ago. The smallest of these dwarf elephants, *Palaeoloxodon falconeri*, is estimated to have had an adult body mass of just 150kg (equivalent in size to a neonate African elephant), compared to its 10,000kg ancestor, *P. antiquus*. Biometric data have been collected from growth series of African elephant (*Loxodonta africana*) and fossil dwarf elephant limb bones, as well as from fossil *P. antiquus* material, to assess how dwarf elephant limb bone morphology compares with elephants of similar size. Additionally, the intraspecific allometry of extant elephant limb bones through ontogeny is assessed. These data shed further light on the effects of scaling on morphological and biomechanical adaptation.

Functional Mechanics of Cranial Sutures

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Sutures are viscoelastic joints that unite the dermal bones of the skull and provide locations for bony growth. The load-bearing elements are the collagenous ligament and bound water. Ligamentous anatomy is thus an important determinant of sutural mechanical properties. Sutures are far more compliant than the bones they join. In vivo, sutures receive quasi-static loads from soft tissue growth, cyclic loads from function, and impact loads from activities such as head-butting. Cyclic chewing strains recorded in pigs (*Sus scrofa*) demonstrate that different sutures are compressed or tensed to different levels. A plethora of experimental evidence suggests that sutural growth (and hence cranial morphology) is influenced by mechanics. Sutural growth in pigs can be studied using vital staining of replicating cells and newly mineralized matrix. Braincase and facial sutures are similar in both their in vivo strains and in their growth, despite a somewhat different development and the presence of dura mater only in the neurocranium. Tissue layers analogous to the periosteum line the bone fronts, providing a continuously renewing source of cells with osteogenic potential. In growing sagittal sutures, cell replication becomes increasingly confined to the ectocranial region, along with a general tendency for growth cessation on the dural surface of the bones and acceleration on the ectocranial surface. Exuberant ectocranial osteogenesis ultimately bridges the suture. Although there is no evidence that sutural strain causes fusion, after fusion is initiated, strain levels drop to those typical for adjacent bones. Supported by DE8513 from NIDCR.

A Comparative Study on the Functional Morphology of the Jaw Apparatus in Cyprinodontiformes (Teleostei, Atherinomorpha)

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Cyprinodontiformes represent a heterogeneous taxon of teleost fishes regarding their diverse trophic strategies. In a comparative study, the anatomy of nerves, muscles, and ligaments of the complex jaw apparatus were investigated. Examinations of 95 species including representatives of the related Beloniformes, Atheriniformes, and *Perca fluviatilis* as outgroup enabled the conceptualization of 78 soft tissue characters, most of them described for the first time. Following the new hypothesis regarding the early phylogeny of Cyprinodontiformes, the genera *Aplocheilus* from India and *Pachypanchax* from Madagascar are sister groups of all the remaining species. Additionally, the distribution of fiber types in four large muscles of the jaw apparatus of Cyprinodontiformes were studied in eleven species. The histochemical characterization (Glycogen, SDH, mATPases, NADH) resulted in the identification of four different fiber types, arranged in distinct regions within these muscles. Previous functional studies have shown that red fibers are responsible for slow breathing movements, while fast contracting fibers are activated exclusively during ingestion. The distribution pattern of red fibers is highly conserved and consists of small, sharply delimited zones surrounded by a single layer of intermediate alkali-stable fibers. In contrast, the proportions of fast-contracting fibers (white respectively intermediate alkalilabile) varies clearly among the species depending directly on trophic strategies. Fast-contracting fibers, therefore, are responsible for observed differences in the configuration of jaw muscles within Cyprinodontiformes. On the basis of the phylogenetic analysis these results show that jaw muscle characters reflect historical evolutionary adaptations correlated to changes in feeding behavior.

Effects of an Erect Posture on the Lumbar Paravertebral Musculature

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Compared to the horizontal posture in quadrupedal mammals, the erect posture of the trunk in human bipedality results in completely different loads on the vertebral column and thus in different functional demands on the musculature. The paravertebral muscles have to counteract gravitational forces acting in parallel to the body axis rather than orthogonally as in other mammals. Surprisingly, the topography of the back muscles in humans is very similar to that found in other mammals. Therefore, we investigated further characteristics of the lumbar muscles to find adaptations to the differing functional demands. We examined the ratio of the anatomical cross-sectional areas of all paravertebral muscles using CT data of a donated cadaver and compared them to data of other mammals. The results showed that the ventral musculature comprised a higher proportion of the entire cross-sectional area of all muscles (1:1 with respect to the dorsal muscle group) in comparison to quadrupedal mammals (1:3). Furthermore, the three-dimensional muscle fiber type distribution was examined in serial sections of the epaxial muscles as an indicator of a muscle's function. In contrast to other mammals, which have high percentages of slow contracting, fatigue-resistant fibers in deep, mono- or oligosegmental muscles only, a high proportion of slow fibers was found throughout all epaxial muscles in humans. This indicates a stabilizing function for both the deep, oligosegmental as well as for the superficial, multisegmental muscles.

Turtle Beaks, Bird Beaks, Croc Beaks? Parallel Evolution of Rhamphothecae in Sauropsida

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Edentulous beaks appear several times in sauropsid evolution. Although both extant examples (turtles and birds) are entirely edentulous, many extinct beaked sauropsid clades show substantial maxillary and dentary tooth rows. This results in a great deal of variability in beak form, but the number of parallel occurrences (between twelve and fifteen, depending upon topology) raises the possibility of underlying similarity driving beak evolution. In this study, specimens from 20 extant sauropsid taxa were surveyed for the morphology and topology of skin features, dermatocranial skeletal elements, and trigeminal innervation on the maxillary rostrum, using such anatomical techniques as dissection, microCT, and histological sectioning. Skeletal specimens from over 200 additional extant and extinct sauropsid taxa were also examined to [1]determine the accuracy and extent of bony correlates for these features, and (2) test for congruence between "similar" morphologies in distantly related clades.

Persistent and congruent similarities in sauropsid facial skin include the retention of a fold between the integumentary derivatives of the embryonic maxillary and frontonasal processes, which corresponds in many taxa to the separation between the ophthalmic (CN V1) and maxillary (CN V2) dermatomes. A second border occurs between the dermatomes of medial and lateral rami of the ophthalmic nerve. In cases where skin morphology varies across the maxillary rostrum, the sharpest gradients in morphology generally occur across one of these borders. Separate frontonasal and maxillary skin regions may thus vary as partially independent "modules" of integument, facilitating the parallel evolution of beak plates on the premaxilla and mandibular symphysis.

One Gland, Two Lobes: Organogenesis of the Harderian and Nictitans Glands in Deer

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Traditionally, the nictitans and Harderian glands of mammals have been considered to be two fundamentally distinct structures. However, a consistent, unambiguous distinction between these orbital glands, whether based on gross anatomical, histological or histochemical criteria, has remained elusive. The Harderian gland was originally described, and first distinguished from the nictitans gland, in adult deer, and cervine deer are still regarded as paradigmatic for the "dual gland" condition. Yet the developmental origins of their glands have never been investigated. We examined the organogenesis and histochemical development of the anterior orbital glandular mass in a total of 30 fetal specimens of two species of deer (*Muntiacus reevesi* and *Dama dama*). Four stages of glandular organogenesis were observed. Most notably, the two glandular portions developed from the same inception point, but the deep lobe developed faster than the superficial lobe. The common inception point, and the relationship of the collecting ducts clearly show that this is a single glandular mass that differentiates into two lobes, rather than two distinct glands. The histochemical profiles of the two lobes differ slightly, but both produce lipids. We propose that the terms nictitans and Harderian glands, as separate entities, be discontinued, and that the entire complex be referred to as the anterior orbital gland (glandula orbitalis anterior), with superior and deep lobes (pars superficialis and pars profundus, respectively).

Animating the Feather: A Four-dimensional Teaching Tool

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Feather development and replacement involve a bewildering series of gross morphological, histogenetic and cytogenetic events and processes taking place in three-dimensional as well as temporal space. Simultaneous and consecutive productions of different types of keratinocytes—some in continuous sheets, others subject to precisely patterned, programmed separation—are one of the most magnificent and unique manifestations of epidermal activity in sauropsids. Consideration of the processes involved demands continual change of mental perspective from anatomical to molecular levels: these processes are a challenge to scholars of development and evolution, and a pedagogic nightmare when trying to communicate them to students. Conventional two-dimensional diagrams, even at their most detailed and complete, are inadequate for illustrating the four-dimensional intricacies of feather genesis: they usually fail to generate a level of comprehension among students beyond *"... and then some complicated stuff happens."* Indeed, most available accounts of these processes in the primary literature, let alone secondary and tertiary texts, all suffer from these shortcomings. In an attempt to better illustrate the fundamentals of feather replacement, and on the premise that explaining four-dimensional processes requires four-dimensional illustrations, we have initiated the creation of a series of computer animations about these topics. Drafts of these animated shorts will be presented for evaluation.

On the Evolution of the Eyelids and Eye-licking Behaviour in Reptiles

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The reptilian eye is protected from the environment by many different structures, including a pair of eyelids (upper and lower), a nictitating membrane and a variety of orbital glands. This protective system is observed in many extant reptiles, including representatives of turtles, crocodiles, rhynchocephalians and squamates. It thus presumably is the primitive stage. Most commonly this system closes off the eye by using both a large mobile lower eyelid (often containing a translucent window), and a nictitating membrane. However, there are two alternative modifications: (1) In assorted scleroglossan lizards (including most gekkotans and also all snakes) the lower eyelid is transparent and covers the eye temporarily as a framed window or permanently as an entire spectacle. (2) In assorted Iguania (peaking in the Chamaeleonidae) and in eublepharid gekkotans, the upper and lower eyelids are both enlarged. Thus, the half-closed eyelids still permit the lizard full vision. However, within *Anolis* (Iguanidae), all three variations are observed in different species. The role of the nictitating membrane also changes with the modifications in eyelid morphology: In lizards with mobile eyelids, it wipes the cornea and conjunctiva; in lizards with immobile eyelids, and in snakes, it is reduced and finally lost. In contrast, the tongue, which in eublepharid gekkotans also plays a role in cleaning the eye (eye-licking), likewise cleans the keratinized spectacle in all other gekkotans. Thus, the eye-licking behavior probably evolved in the common ancestor of the Gekkota, and was retained in both spectacled geckos (where its function appears obvious) and eublepharids.

The Ribcage of Tyrannosaurid Dinosaurs and an Interpretation of Potential Breathing Mechanisms

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Fossil skeletons of Tyrannosauridae (Late Cretaceous theropod dinosaurs) are well suited for a study of costal aspiration breathing, due to the generally good preservation. In this study, I investigated the detailed morphology of the ribcage in tyrannosaurid fossils, in order to develop inferences regarding potential ventilatory mechanisms. Data about the anatomy of the ribcage were collected from specimens housed in the Royal Tyrrell Museum of Palaeontology and other institutes. These observations demonstrate that the tyrannosaurid ribcage extends from the 11th–23rd presacral vertebrae. Throughout the series, the 13th–15th presacral ribs are much longer than other ribs, and possess especially blunt distal ends. The distal ends of the 13th–15th presacral ribs are oriented medially (not anteriorly). These features suggest that these three pairs of ribs primarily articulated with cartilaginous sternal elements, and the sternal rocking seen in extant birds is unlikely in tyrannosaurids because the vertebral rib articulated with the cartilaginous sternal rib at an extremely obtuse angle. In addition, the rotational axis for the rib on the vertebra orients relatively dorsoventrally in tyrannosaurids, indicating that the mediolateral component was larger than the dorsoventral component in the rib rotation. Taken together, these lines of evidence suggest that dorsoventral movements of the sternum were likely limited, and lateral excursions of the thoracic wall being more integral to costal aspiration in tyrannosaurids. This interpretation indicates that the basic avian thoracic architecture was incomplete despite the possible presence of air sacs in tyrannosaurids.

From Mice to Monkeys: How Similar Are Their Dental Genetic Architectures?

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Mice are a powerful model for studying the genetics of odontogenesis. From an evolutionary perspective though, how characteristic of other mammalian taxa is mouse tooth development? Quantitative genetic analyses can be used to gain some insight to the appropriateness of broad application of the mouse model, as these analytical methods can be performed on animals that are logistically impractical for developmental genetics research. We used quantitative genetic analyses to study variation in incisor and molar size in out-bred populations of mice and

baboons. We studied tooth size variation in a pedigreed population of *Mus sp*. from the University of California Museum of Vertebrate Zoology (n = 222). All dental phenotypes returned significant heritability estimates. Through bivariate analyses we found that minor variation in mouse incisor size appears to be genetically independent of the minor variation in their molars. Given that mice have derived dentitions relative to many other mammals, we undertook a quantitative genetic analysis of homologous phenotypes in the baboon dentition. We collected data from captive pedigreed *Papio hamadryas* individuals from the Southwest Foundation for Biomedical Research and Southwest National Primate Research Center (n = 630). These analyses also return significant heritability estimates. And similar to the mice, bivariate analyses of the baboons suggest genetic independence between the minor variation in incisors and molars. These data suggest that the genetic architecture of these two species is similar in many respects despite the dramatic morphological differences between their dentitions and despite the ~75 millions years since they last shared a common ancestor.

Apical Ectodermal Ridge (AER) Development in the Pectoral Fin of the Australian Lungfish (*Neoceratodus forsteri*)

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Thorogood (1991, in Hinchliffe, J.R. *et al*. (Eds) Developmental Patterning of the Vertebrate Limb. Plenum Press, New York) proposed a model based on a heterochronic two phase shift in skeletal patterning within developing appendages as vertebrates moved from the water onto the land. The first phase involves patterning of the endoskeletal elements. During the second phase dermal skeletal elements develop in, and are unique to, fish fins. The AER is a morphologically distinct entity, present in most vertebrate fin/limb buds, and is an integral component of the proximo-distal outgrowth of endochondral elements within the developing appendages. In the chick and other tetrapods the AER persists until the end of digit formation. However, in some amphibians there is no morphologically distinct AER and yet limbs develop with the full complement of endochondral elements, i.e., humerus, ulna, radius, wrist bones and digits. In ray-finned fishes, the AER or pseudo-apical ectodermal ridge is very short lived which is coincident with a reduction in endoskeletal elements and extensive development of dermally derived fin rays. The pectoral fin of the dipnoan, *Neoceratodus forsteri*, contains both well developed endochondral and dermal skeletal elements and, as such, represents a "half way point" between appendages of primarily dermal origin, as in the actinopterygians, and the wholly endoskeletally derived limbs of the tetrapods. Scanning electron microscopy and histological investigations together with the localization of the fgf8 gene product were used to describe the form and function of the AER in *N. forsteri*. The results of this study are discussed within an evolutionary context.

The Principles of Shoulder Biomechanics in Land-living Tetrapods: Cursorial Mammals, Recent Squamata, Archosaurs and Fossil Sauropods, Analyzed with the Aid of FES

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The indirect attachment of the forelimbs to the trunk in all land-living tetrapods seems inadvantageous, because permanently energy-consuming. It implies, however, solid biomechanical advantages, which will be presented. The remarkable variation of the shoulder girdles was investigated under biomechanical viewpoints. The force flow between the weight-containing trunk and the supporting forelimb is made visible with the aid of three-dimensional Finite Element Systems (FES) analysis. Biomechanical requirements diverge between forelimbs in sprawling and in extended positions on cross sections. In sprawling postures, the m. pectoralis keeps the shoulder joint in equilibrium. Its pull leads to compression between the shoulder joint and the muscle's origin, to which the coracoid offers resistance. The extended limb position in (cursorial) mammals implies a short load arm of the weight force at the shoulder joint. The m. pectoralis can be recruited for carrying a part of body weight, especially if the sternum is shifted to a position ventral to the shoulder joint. So the ribs carry weight, and the bony connection between shoulder joint and sternum is superfluous. In sauropods, our biomechanical analysis and the morphology of the compression-resisting skeletal elements leads to adaptations: the thorax was extremely narrow, a cartilaginous sternum was present and located much deeper than the shoulder joints, the forelimbs were extended in walking, but not in reclining to resting postures; the circle of forces was closed partly through the coracoid like in reptiles, and partly through the ribs like in mammals. The implications of these traits for locomotion will be discussed.

New Fossil, *Tiktaalik roseae*, and the Biomechanical Conditions for the Evolution of the Tetrapod Bauplan

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Newly found fossils from the Late Devonian are here considered not as "primitive" limb-possessing tetrapods, retaining traits of fish-like ancestors, but as animals adapted to the special conditions in their environmaent. The external forces acting on them and the stresses inside the body are analyzed, partly by means of FESA. Our results fit with the conclusions drawn by the authors of the first description, but reach farther: The selective advantages for characteristic morphological traits and relevant movements of animals living partly submerged in shallow water and partly on firm ground are defined semi-quantitatively. The flat skull and the mobility of the neck seem to be adaptations to lateral snapping movements for catching prey. The marked development of the shoulder girdle and free forelimbs are advantageous for performing this behavior on land as well as in water. The development of strong ribs is a mechanical requirement for land-living vertebrates which shift their body weight between the forelimbs on both sides. The results of these calculations can be interpreted as explanations of morphology, or as a well-founded hypothesis about the behavior and mode of life in the fossil animal. The behavioral and environmental conditions are determined under which the energy expenditure can be calculated.

Geometric Morphometric Analysis of Intraspecific Skull Variation in *Egernia depressa* (Squamata: Scincidae)

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Landmark-based geometric morphometric techniques were used to examine intraspecific skull shape variation among three populations of the pygmy spiny-tailed lizard (*Egernia depressa*) in Western Australia. In the northern part of their range (Pilbara; 22°S), these lizards inhabit rock crevices in disjunct outcrops. Two populations were sampled in the Pilbara; one population west of the Hamersley Range (n = 10) and one east of the range (n = 9). Preliminary results indicate that the shape of the ventral aspect of the skull differs significantly between these two populations. The shape change occurs primarily around the inferior orbital foramen, and, although no shape difference exists between males and females, juveniles and adults are significantly different. The Hamersley Range that separates these two populations likely creates a reproductive barrier that may account for the divergent morphology. In the southern part of their range (Gascoyne; 25°S), where these lizards occupy tree hollows instead of rock crevices, a third population was sampled (n = 4). Preliminary results indicate that the Gascoyne population does not differ significantly from the western Pilbara population, even though the lizards utilize different habitats.

Cranial Kinesis in Dinosaurs: Significance for Functional Inferences and Evolution

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Cranial kinesis has been postulated to have been present in many non-avian dinosaurs (e.g., theropods and ornithopods). The presence of intracranial synovial joints—structures shared with extant lepidosaurs and birds—has typically been the sole indicator of kinesis, whereas the protractor musculature, which supposedly powers these joints, has received little attention. In fact, whether these hypotheses envision a powered or passive system is unclear. We reviewed the cranial musculoskeletal

systems of extant and fossil diapsids to assess inferences of cranial kinesis in non-avian dinosaurs. Intracranial synovial joints and protractor muscle are ubiquitous among dinosaurs including clearly akinetic taxa (e.g., ankylosaurs, ceratopsids). However, non-avian dinosaur taxa do not exhibit the breakdown of linkage systems of skeletal units (e.g., palatal and facial units) considered necessary for intracranial movement that kinetic birds and lizards possess. Additionally, most of the non-synovial contacts postulated to slide in dinosaurs are without extant analogs. Thus, most non-avian dinosaurs do not possess the morphology necessary and sufficient for positive inferences of cranial kinesis. Moreover, although many extant lizards bear all of the morphological features suggestive of cranial kinesis, they do not necessarily express it, which thus represents an important caveat for any fossil inferences. The widespread presence of synovial joints in non-avian dinosaurs, and diapsids in general, suggests these joints may be primarily responsible for mediating cranial growth and are only secondarily associated with cranial kinesis. This bears significance for understanding avian evolution as well as general reptilian cranial form and function.

The Microarchitecture of the Cornified Epidermal Sheath of the Cat Claw

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The microanatomy of hard cornified structures, such as claws and beaks, is notoriously difficult to analyze because of the complexity and the extreme range of hardness of the component tissues. A correlative approach using light microscopy, SEM, synchrotron x-ray micro-computed tomography (μCT with a resolution of 9 μm), and virtual 3D-reconstructions of the tomography data revealed a highly complex microarchitecture of the cornified sheath of the cat claw, which reflects the uniquely complex shape of the underlying dermal tissue and bony core. The cornified sheath is generated by the living epidermis that is supported by the dermis and its papillary body whose configuration varies depending on its location. The dermis is densely supplied with blood vessels, most of which emerge from the bony core. A single large dorsal dermal papilla points distally, and the overlying living epidermis forms cone-shaped layers of cornified epidermis, which are separated from one another by distinct breaks that appear to be formed periodically. The terminal cone forms the tip of the claw and is shed by cats through a mechanism that has been all but overlooked by science so far. The sides of the cornified sheath appear also to be formed in periodic layers and create sharp blades that frame the soft, friable sole horn of the claw and are responsible for the effectiveness of feline claws in cutting into flesh. (Supported by a Faculty Research Grant from Louisiana State University).

The Ridge Pattern of the Cornified Oral Surface of the Upper Beak of Parrots: Individual and Genus-level Character

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Parrots and cockatoos (Family Psittaciformes) are seed predators with a specialized seed-shelling mechanism using distinct beak structures, which include the patterns of ridges on the cornified oral surface of the upper beak. Transverse or chevron-shaped filing ridges cover the oral surface of the overhanging upper bill tip. A curved transverse step separates this surface from the corneous palate with its own pattern of palatal ridges, which is indicative of generic relationships within the psittaciform families. The ridges are surface structures that are initiated at the level of the underlying connective tissue with its own papillary and ridge formations and are the result of alternating juxtapositions of horn of different hardness. Whereas the filing ridges and transverse step are directly involved in the seed-shelling mechanism, the palatal ridges are not. The ridge pattern of the cornified oral surface of the upper beak of 28 live individuals of the Hispaniolan Amazon (*Amazona ventralis*) was documented through photographs with an otoscope and through casts using dental impression material at 6-month intervals over the course of one year to establish that the ridge patterns are individually unique and that they do not change with time. The complex pattern of the ridges, like that of the human fingerprint ridges, is likely the result of epigenetically determined individual patterns within a genetically determined basic ridge pattern. The ridge patterns may potentially be used as a tamper-proof identification tag to distinguish captive-bred parrots and cockatoos from illegally captured one.

Odontogenetics of Tribosphenic Molars: Developmental Background of a Major Mammalian Apomorphy

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Prismatic enamel and monophyodont multicuspidate molars represent the major dental apomorphies of mammals and one of the key factors of the ecological prospect of that group. Molar development and enamel formation were extensively studied in several model species (mouse, vole, human etc.) only little information is available on these topics in tribosphenic molars (TM) though—as it was many times demonstrated—it presents a phylotypic stage to all mammalian molar types. We analyzed architecture of TM enamel coat in several model taxa, particularly bats, and studied early stages of amelogenesis on embryonal series of *Monodelphis domestica* and *Myotis nattereri* with aid of histological and SEM techniques. The results demonstrated that: (i) the crests, which are essential characters of TM, are preformed at the early stage of IEE histodifferentiation, (ii) the later stage of TM development is characterized by considerable emancipation of particular structural modules of the tooth, and by (iii) early beginning of the formation of prismatic enamel, while (iv) the final adult shape and size of the tooth and enamel maturation are established as late as the time of tooth eruption. The delayed enamel maturation, that is an essential precondition for expansion of tooth size and fine tuning of the crest interlocking pattern at the perieruptional stage, is related to a switch of the secretory actvity of ameloblasts from a slow production of large-crystallite prismatic enamel to a rapid production of small-crystallite interprismatic matrix and aprismatic enamel, supposedly under the mechanical stress of tooth eruption.

Fossorial Locomotion in a Fossorial Specialist: The Kinematics and Kinetics of the Ferret (*Mustela putorius furo*)

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Small mammals commonly utilize burrows for sanctuary as well as predation. While the biodynamics of digging has received considerable attention, how mammals move through the constrained environment of tunnels is largely unexplored. In the present study, we used a mammal morphologically adapted for fossioriality, *Mustela putorius furo* (domestic ferret), to evaluate the effect of constrained environments on locomotor biodynamics. We simulated burrow-like conditions in the laboratory using plexiglass tunnels overlying a trackway into which a force platform was integrated. Locomotor trials simulated both epigean (overground) and subterranean (tunnel) conditions. Simultaneous high-speed videography captured limb and spinal kinematic data. Previous gait analyses have reported just two gaits in *Mustela*: walking and half-bounding. Movement through tunnels constrains *Mustela* to non-bounding gaits and reveals a greater locomotor repertoire than has been previously recorded. In addition to providing baseline data on

locomotion in tunnels, our study may provide some insight into the evolution of the short-limbed and slender morphotype typical of mustelines as well as half-bounding, a gait that is pervasive among small-bodied mammals.

Vertebral Growth Pattern in Squamates

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The inner structure and growth pattern of squamate vertebrae have rarely been studied, despite the great functional involvement of this skeletal part in locomotion. The growth in length of the vertebrae is realized by a classic process of endochondral ossification and the growth in diameter by sub-periosteal deposits of pseudolamellar bone tissue. Primary bone tissues then undergo an intense and characteristically imbalanced remodelling process: bone is extensively resorbed but is not reconstructed in the same proportion by secondary deposits. This remodelling process is particularly intense in the deep regions of the centrum and neural arch, where the reconstruction deficit makes the originally compact cortex cancellous, and the endochondral spongiosa looser. In consequence, a special inner structure, appearing on transversal sections as two roughly concentric osseous rings (corresponding to tubes in 3D), is created: one surrounds the neural canal and the other, made of the unresorbed outer part of the periosteal cortex, is in peripheral position. They are connected by thin trabeculae. Vertebral compactness is somewhat higher in snakes than in lizards, which suggests a less intense remodelling activity. Remodelling starts at an early stage of development and remains constant thereafter. Its functional meaning remains to be precised. Moreover, it appears that the growth in length of the centrum is strongly asymmetrical, the posterior (condylar) part growing much faster than the anterior (cotylar) one.

The Phyloinformatics Productivity Tool Morphster and Image Driven Ontologies

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Assembling the Tree of Life (ATOL) is a grand challenge consuming the energies of biologists around the world. Enabled by the success of the Human Genome project, ATOL promises to make remarkable discoveries about Earth's biota and its history. Further, integration of large-scale observational data with sequence data will likely contribute to critical understanding of geological change as an evolutionary force on DNA. An end goal of our project includes a phyloinformatics productivity tool, Morphster, with which systematic biologists may conduct their studies and document their observations. The tool is designed such that the supporting images and accompanying text descriptions may be transparently integrated with emerging online corpuses of scientific knowledge. Most important among these online corpuses are authoritative descriptions of anatomy (nomina anatomica) encoded as ontologies and authoritative catalogs of taxonomic names. Morphster entails productivity through the integration of web services and a user experience succinctly described as image-driven ontology editing. There are a number of image annotation systems where a user may label an image using controlled keywords drawn from an existing ontology. Morphster is designed to go a step further and enable scientists to describe and document new observations. Morphster will record those observations by extending the existing ontology. In support of collaborative endeavors Morphster incorporates the security and bookkeeping needed to maintain the identity and separation of each contributor's work including isolation from authoritative contents.

Locomotor Performance as a Target of Sexual Selection

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Intuitively it is appealing to consider locomotor performance as a trait likely to be under strong selective pressure. Many animals appear to use fast speeds while doing a number of important tasks in nature, including escaping predators, capturing prey items, and chasing rivals during resource defense. Because of the presumed importance of locomotion to individual fitness, numerous studies have attempted to link maximal locomotor performance and probability of survival (i.e., natural selection). However, far fewer studies have tested whether superior locomotor performers have higher mating success than poor performers (i.e., sexual selection). Even fewer studies have directly linked locomotor performance to a mating success advantage, suggesting that future studies should carefully design studies to determine whether sexual selection operates directly on performance ability. We discuss our work on how sexual selection operates on sprint speed in collared lizards (*Crotaphytus collaris*), where faster territorial males better defend larger territories, have access to more females, and sire more offspring. We also provide additional taxonomic examples in which sexual selection is likely important to the evolution of locomotor performance, emphasizing the logistical difficulties associated with quantifying relevant locomotor performance traits. We conclude with suggestions for future research directions in this field, including considering the role of display behavior and broadening the taxonomic breadth of studies.

Comparative Electron Microscopic Study of Bone Repair After Internal Fracture, Osteotomy and Perforation of Rat Tibia

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Comparative electron microscopic study of bone repair after internal fracture, osteotomy and bicortical perforation of tibia was performed on 72 male Wistar rats (200–220 g). Rats were subdivided in the cases of osteotomy and perforation into control, training (swimming) and immobilization subgroups. Bone repair was observed during the first post-traumatic weeks. Although the bone repair in general had similar repair stages in all groups, the repair process was dependent on the mode and degree of injury, thus being different in the experimental groups: indirect ossification after internal fracture; primary periosteal, secondary endosteal ossification after osteotomy and primary endosteal, secondary periosteal ossification after perforation were noticed. The results of the electron microscopic study on bone repair confirmed our previous reports on similar post-traumatic bone repair studies where basically routine histology, histomorphometry and immunohistochemistry were used.

Interpreting Locomotor Function From Form, and Vice Versa

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The shapes of bones are often used in paleontological studies to infer how, for example, dinosaurs stood and moved. In extant animals the converse conundrum exists: we can measure how elephants stand and move, but why are their bones shaped so strangely? We present these two case studies, of dinosaur and elephant locomotor form and function, to examine the roles of osteological data in functional morphology and evolutionary biomechanics studies. We take a hard look at the limits of such data; does bone form tell us much, or at least not enough, about locomotor function without adding additional soft tissue or biomechanical data? We use constraint-based exclusion of mid-stance limb poses for *Tyrannosaurus rex* to illustrate how limb orientation is nigh impossible to reconstruct using only skeletal data. A skeletal limb can be posed in too many configurations to non-arbitrarily identify which were used in life. Data on ground reaction forces and muscle moments are far more powerful for determining likely poses. Conversely, how do different functional parameters such as muscle and joint forces and bone orientation interact with bone form (e.g., geometry and material properties) to determine the regional stresses and strains in limb bones? We show preliminary results from collaborative studies using finite element analysis to analyze elephant bone mechanics. Although paleontological and neontological perspectives may sometimes differ, our case studies show some common themes as well; both must confront large numbers of

unknown parameters in order to unravel the complex relationship between bone form and function.

It's All in the Head. Morphological Basis for Differences in Bite Force Among Color Morphs of the Dalmatian Wall Lizard

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Males of the lizard *Podarcis melisellensis* occur in 3 very distinct colors that differ in bite performance, with orange males biting harder than white or yellow ones. Morphometric data indicate that differences in bite performance cannot be fully explained by differences in overall size or head shape. However, differences in bite force among color morphs are best explained by variation in head width, suggesting underlying differences in cranial shape and/or the size of the external jaw adductors. To explore this issue further, we examined variation in cranial shape, using geometric morphometric techniques. Additionally, we quantified differences in jaw adductor muscle mass and architecture. Orange males have larger jaw adductors than individuals of the other two morphs. However, not only the mass of the external jaw adductors, but also that of other jaw adductor groups was greater for the orange morph. Data for other cranial muscles not related to biting suggest that this isn't a consequence of an overall increase in robustness in orange individuals. These results suggest that differences in bite performance are caused by an increase in the mass of all adductor groups, which may be induced by differences in circulating hormone levels.

Tooth Replacement in Wild Atlantic Salmon (*Salmo salar* L.): A Heterochronic Shift Concealing an Ancient Pattern?

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To gain insight into the evolution of tooth replacement mechanisms, we have studied tooth replacement in the dentary of wild Atlantic salmon (*Salmo salar*), a primitive, protacanthopterygian teleost. Serially sectioned heads of early posthatching stages were analyzed. Contrary to first-generation teeth, replacement teeth develop from a placode-like thickening of the outer dental epithelium of the preceding tooth, at its lingual and caudal side. Multiple layers of epithelial cells, termed the middle dental epithelium, build up against the inner dental epithelium on the lingual side of the replacement tooth germ as it grows. Finally, a single-layered outer dental epithelium segregates from the middle dental epithelium and thickens into a new placode for the next tooth. Dental organs of predecessor and successor remain broadly interconnected. The absence of a discrete successional dental lamina in salmon stands in sharp contrast to other teleost species, even those that share with salmon extraosseous tooth replacement. We propose that the mode of tooth replacement in Atlantic salmon displays several ancient characters similar to those observed in chondrichthyans, and that differences between Atlantic salmon and chondrichthyans can be explained by a heterochronic shift. We explore the possibility that the middle dental epithelium functionally substitutes for a successional lamina, and could be a source of stem cells, whose descendants subsequently contribute to the placode of the new replacement tooth.

A Non-invasive Analysis of Head Shape Dimorphism in a European Eel Population (*Anguilla anguilla*)

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The existence of naturally occurring narrow- and broad-headed individuals within the European eel (*Anguilla anguilla*) populations is long known. Previous studies demonstrated sexual differences in growth, with females growing faster than males, but which are irrespective of the observed difference in head shape. The different head shapes have been related to different diets, where broad-headed eels would feed on bigger and harder preys. Although some research has been focusing on this dimorphism, very little is still known about how and when this dimorphism arises and what parts of the body plan are involved. To be able to follow the head shape in eels of certain populations during their growth using capture-recapture methods, we tried to establish a screening method to map variation in head shape in a non-invasive manner (without requiring decapitation). On pictures from a dorsal and lateral view of the head, contour data was used in an elliptic Fourier analysis. Shape variables obtained from this analysis where used for statistical testing, in order to see whether a bimodal distribution in head shape could be found. Comparison with positive results based on previous analyses using length measurements of eel heads allowed us to evaluate the accuracy of this method for screening eel head shape on live material, as well as to describe the variation in head shape using contour descriptors.

Selection on Biomechanical Traits; What Do We Know?

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The vast majority of selection studies focus on morphological traits, and therefore, we lack a general understanding of how selection operates on functional traits, such as performance, and related behaviors. We examined how selection on performance (sprint speed, bite force) operates within four sympatric anole lizard species to gain a general understanding of how selection differs among species, particularly in regards to performance capacity. One of our goals was to examine how selection on performance differs from selection on morphology within this group. We generally found strong evidence for selection on performance, which in some cases was stabilizing, and in other cases directional. However, selection on morphology was not always concomitant with selection on performance, indicating a possible disconnect between the two kinds of traits. Our work generally serves as a cautionary note for researchers who assume that selection on morphology is an accurate surrogate for performance. Further, we promote studies of selection on performance as being crucial to test the basic adaptive basis of morphological traits.

Para-aortic Body Plays Key Role in Renal Vascular Formation

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A kidney must be highly vascularized with having tightly organized architectures. Histologists had revealed how the fine vasculatures integrate with the nephric-tubule formation. On the contrary, gross anatomists had focused their attentions on the variations seen in the branching pattern of renal arteries and veins, and sought the developmental mechanisms causing the changes. Felix (1912, Manual of Human Embryology 752–973) speculated that the metanephros climbs upwards to the remnants of mesonephric arteries, as if on a ladder. McClure and Butler (1925, Am. J. Anat., 35, 331–383) demonstrated that the left renal and suprarenal veins are the remnants of subcardinal veins abandoned by the regressed mesonephros. Both authors explained that the arteries and veins abandoned by the mesonephros play key roles in the metanephric vascular formation of the human embryo. However, they had never shown practically how the developing primary vascular cage within the metanephros switches their connections with the mesonephric artery from one to another, or how the subcardinal veins disconnect from the highly vascularized mesonephros and reconnect with the metanephros and suprarenal gland. We pursued the mentioned vascular morphogenesis by the dye- and resin-injection methods using rat embryos from13 through 16 embryonic days. Surprisingly, the mesonephric arteries and the subcardinal veins are not involved in metanephric vascular formation, but the remnant arteries and veins originated with the para-aortic body and its derivatives generate the definitive renal artery and vein, and suprarenal artery and vein. We present the novel developmental process including the mechanism that causes the morphological variations in the renal vascular system.

Mouse Enamel From Frog Amelogenin

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Amelogenin, the major protein of the developing enamel matrix, controls enamel crystal growth and habit. While much has been contributed to our understanding of mammalian amelogenin function, little is known about how amelogenin and its unique physico-chemical features have evolved among vertebrates. We have determined that enamel hardness and elasticity and the number of Exon 6 PXQ repeats are increased in mammalian enamel as compared to frog enamel. In addition, mouse enamel contains prisms, while frog enamel does not. Here, we report the first generation of a transgenic mouse overexpressing amphibian amelogenin recombinant protein. Our data suggest that transgenic overexpression of *Rana pipiens* amelogenin results in significant changes in tooth enamel structure. In eruption-stage mouse incisors, transgenic mice lacked a transparent zone at the tip of the enamel, featured a reduced pigment zone and an Amelogenesis imperfecta resembling enamel surface. In transgenic mouse molars overexpressing frog amelogenin, the enamel layer was divided into a prismatic and a prism-less zone in comparison to the prismatic wild-type enamel. Moreover, transgenic animals featured decreased enamel thickness and a sharply separated dentin-enamel junction. Our findings suggest that the evolution of vertebrate enamel from amphibians to mammals involved the introduction of prismatic enamel, increased enamel thickness, and an interconnected dentin-enamel junction. Funding by NIH grant DE15425 and NSF grant MCB-0236226 is gratefully acknowledged.

Asking Why: Inquiry-based Learning in the Comparative Vertebrate Anatomy Laboratory

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Widely used methods of comparative anatomy instruction in the laboratory include large amounts of rote memorization, and text-intensive manuals that provide students with little opportunity for self-evaluation, concept exploration, or higher-order inquiry. As part of the Inquiry Through Blended Learning Initiative at the University of Calgary, we have developed an inquiry-based laboratory course, associated with a workbook and web-based course material including instructional videos and tutorials, which represents an innovative approach to teaching comparative vertebrate anatomy. Students discover the answers to a series of open-ended functional and biomechanical questions by completing exercises involving the sea lamprey, spiny dogfish, and domestic cat. We expand the comparative approach to include species other than focal organisms, and incorporate integrative questions designed for group discussion, in order to generate interest, crystallize concepts, and encourage students to explore beyond the basic anatomy of the specimen on the laboratory bench. We take a modular, synthetic approach, incorporating more difficult questions in later modules that require application of knowledge gained in earlier modules, and completion of the workbook exercises results in a study resource for final examinations. This approach thus provides a means to develop not only anatomical knowledge in the form of fact retention, but to inform students' approach to such topics and encourage synthesis and integration early in an undergraduate program. Despite the challenges posed by a large course (~140 students/year), this approach has been well received by students and has resulted in positive changes in students' attitudes and commitment to learning the material.

Locomotor Specializations in Sthenurine Kangaroos

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Sthenurines (Miocene—Pleistocene), popularly known as "giant browsing kangaroos", are commonly assumed to have a similar mode of ricochetal locomotion as large macropodines (e.g., gray and red kangaroos), perhaps being even more cursorially specialized as their pes is monodactyl. However, modern large macropodines (around 100 kg) appear to be at the size limit for strain on the Achilles tendon, the determining feature in hopping, and some sthenurines were twice this size. We show here some interesting differences in postcranial morphology between sthenurines and terrestrial macropodines, and suggest that sthenurines were not as specialized for hopping. We measured 27 species of extant macropodoids and 23 individuals of *Sthenurus*. Bivariate plots show sthenurines have a relatively shorter fourth metatarsal than terrestrial macropodines, and thus a shorter foot, resembling dendrolagines (tree kangaroos) in this regard, and also have more robust femora and tibiae. PCA analysis also revealed differences between sthenurines and terrestrial macropodines: the pelvis is broader mediolaterally and the ilium longer, but the ischium is shorter and the pubic symphysis less elongated; the femur has broader proximal and distal articulations, and a longer greater trochanter; the calcaneum has a shorter and thicker heel. In these features sthenurines show a greater resemblance to dendrolagines, indicative of adaptation for power rather than for speed. This suggests a different locomotor focus from the derived hopping of terrestrial macropodines. The similarities to dendrolagines, the only macropodines to move their hindlimbs independently of each other, raises questions as to whether sthenurines were capable of bipedal striding.

Quantification of Dicynodont Cranial Function Using Finite Element Analysis and Bone Histology

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Differences in cranial morphology across Dicynodontia have been correlated with changes in masticatory function, and hence, dietary preference. Although the derived masticatory apparatus of dicynodonts allowed propaliny, it has been hypothesized that *Lystrosaurus* utilized powerful orthal jaw movements to process fibrous vegetation. Cranial specializations of *Lystrosaurus*, such as a posteriorly deepened skull and a patent premaxilla-nasal suture, may have increased the efficiency of its masticatory system. This study quantitatively examines the biomechanical significance of cranial form of *Lystrosaurus*, and also *Oudenodon*, a generalized dicynodont, using Finite Element Analysis (FEA) and bone histology. In FEA, two types of bite were modeled: 1) a shearing beak bite along the maxillary rim, and 2) a propalinal grinding bite along the palate. A preliminary FEA indicates that during a beak bite, higher compressive and tensile stresses accumulate in the *Oudenodon* skull, suggesting that the *Lystrosaurus* skull could have tolerated a higher bite force necessary to masticate fibrous plants. However, during a propalinal bite, both *Lystrosaurus* and *Oudenodon* have similar peak stress values. Previous studies of extant tetrapods have indicated correlation between bone microstructure and biomechanical function. It is thus hypothesized that histological features of dicynodont cranial bone will agree with the FEA results. Several histological features are quantified and described including channel orientation, size and density of secondary osteons, and sutural types.

The Mating Call Structure of *Rana* in Libya

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The water frog of genus *Rana* in Libya has been studied by using bioacoustic analysis. When the calls recorded in Libya compared with those of *Rana ridibunda*, the call period was considerably longer in the calls from Libya than in *Rana ridubunda* calls, so that the number of pulse groups per call is higher in Libyan population than in *Rana ridibunda* population. The pulse group period, duration of pulse group, and intervals between the pulse groups are considerably shorter in the calls from Libya than those of the calls from *Rana ridibunda*. The histogram of the discriminant function scores for the Libyan *Rana* and *Rana ridibunda* showed close agreement between the two Libyan localities and both were completely separated from *Rana ridibunda*. A principle component analysis shows that Libyan populations are completely separated from *Rana ridibunda* populations. From these results, we found that there are clear differences between Libyan water frogs and *Rana ridibunda* in mating call structure.

Structure of the Heart of Snakes and Lizards

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Hearts of lizards and snakes consist of a sinus venosus, two separate atria and a single ventricle. The ventricle is divided into two major compartments, cavum pulmonale and cavum dorsale, by the muscular ridge (MR) and one or more septa. The MR arises near the ventricular wall, has a free lateral opening and can abut to the bulbus lamelle (BL) on the opposite side of the ventricle. Both the MR and BL are particularly large and well-developed in varanid lizards and pythons. The lateral opening of MR can be effectively closed in these animals by the MR abutting to the BL during ventricular contraction. This enables the ventricle of these species to sustain high systemic pressures, while keeping a low pulmonary pressure. Opposing this design are ventricles of rattlesnakes where BL is less developed resulting in identical systolic pressures in both circulations. This correlation between structure and function, however, becomes less obvious in species such as tegu lizards and anacondas where septations are pronounced; nevertheless, they do not separate pressures. Different structural designs exist and they are not correlated to pressure separation. Detailed and interspecific studies are therefore necessary to discuss possible driving forces governing cardiac design. We present the differences in ventricular structure in ball python, *Python regius*, South American rattlesnake, *Crotalus durissus*, yellow anaconda, *Eunectes notaeus*, tegu lizard, *Tupinambis merianae*, and iguana, *Iguana iguana*. Our study concludes that other finer structures than the MR contribute to the ability of having systemic pressures that exceed pulmonary pressures by 3–4 times.

Simple and Complex Complexity of Teeth

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Dentitions appear to be more complex in vertebrates that eat plants rather than animals. Increased complexity is especially apparent in herbivorous taxa that eat fibrous plants. For example, specializations to eat bamboo have evolved several times in mammals. At least primates, bears, and muroid rodents have living species that rely largely on a bamboo diet. Whereas phylogeny, size, and life history are highly divergent among these bamboo specialists, their cheek tooth morphology shows high overall complexity irrespective of the taxon-specific morphological details. The high complexity values can be related to the high number of tooth crown features, or "tools", required to process fibrous bamboo. Yet this kind of high dental complexity may require simple developmental changes. Thus, panda teeth, for example, may be morphologically complex but developmentally simple. In contrast, some of the low-level taxon-specific details of teeth, and features that allow us to tell the panda tooth from the lemur tooth, appear to require developmentally more elaborate changes. That is, ecologically and phylogenetically informative aspects of the phenotype may have a tendency to be developmentally simple and complex, respectively.

Segmental Identity Within the Vertebral Column: What Can Fossils Tell Us?

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The identity of individual segments within the vertebrate axial skeleton is determined, in part, by the expression boundaries of homeotic genes. Alterations of these genes (e.g., misexpression or deletion) can alter the identity of an axial segment, mimicking either more anterior or posterior segments (anteriorization or posteriorization, respectively). The expression of *Hox* genes has been shown to be a critical factor in establishing the anterior-posterior axis. Misexpression and/or deletion of these genes in the cervical region of mice result in a variety of anatomical malformations (including anteriorization, posteriorization, fusion, or deletion—anatomical correlates to the underlying changes in gene expression). For example, experimental anterior misexpression of *Hoxd4* in the mouse vertebral column results in the occipital region of the skull resembling the anterior cervical vertebrae. Deletion of *Hoxd3* has an opposite effect, with the anterior cervical vertebrae (atlas) coming to resemble parts of the occiput. In the 370 million year-old (Late Devonian) placoderm *Cowralepis maclachlani*, the occipital and the fused anterior region of the vertebral column, the synarcual, have a nearly identical morphology. We suggest that misexpression/deletion of *Hoxd3* and/or *Hoxd4* occurred in *Cowralepis*. The putative presence of these *HoxD* genes suggests the presence of all four *Hox* clusters in placoderms, indicating that the gene duplication generating the four clusters (*HoxA–D*) occurred phylogenetically prior to the evolution of crown group gnathostomes, within the stem Gnathostomata.

Variation on a Theme: Characteristics of Setal Fields and Associated Locomotor Substratum in the Gecko Genus *Rhoptropus*

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Species of the southern African gecko genus *Rhoptropus* are all rock dwelling, but the type of rock comprising the locomotor surface varies between species and between geographic regions. Seven species of *Rhoptropus* were field collected, and samples of rock on which they were found were taken. Scanning electron microscopy was used to image setal fields and characterize pertinent dimensions, and to generate three-dimensional digital elevation models of the substrata. These two data sets permitted calculation of average contact areas available to setal fields in relation to the rock surfaces occupied. Natural substrata are undulant and unpredictable, and provide only limited, patchy areas for setal contact. Furthermore, the amount of area available for attachment varies greatly both within a single rock type and between different rock types. The varying surface characteristics of rock substrata may present challenges that vary on a species-specific basis, which may in turn relate to variation among the configuration of the setal fields. Differences between species are compared to differences in locomotor substrata and are examined in the context of the phylogeny of the genus to endeavor to elucidate how setal field evolution is adjusted to peculiarities of the substratum.

Effects of Muscular Dystrophy on Craniofacial Shape During Growth in Mice

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The muscle forces influence the morphology of bone, particularly during growth. From extensive studies of the interaction between the muscles of mastication and the skull we know that these muscle forces, and their resultant strains, influence cellular division rates along sutures and manipulate bone remodeling. In the multi-element craniofacial skeleton, this leads to different bone shapes and affects levels of integration. In extreme cases, this can be a source of pathological dysmorphology. Skeletal anomalies are common in patients with muscular dystrophy (MD), despite an absence of mutations to genes that specifically direct skeletogenesis. In order to further understand these anomalies, we examined two strains of MD (laminin and merosin deficient) relative to controls, to determine how the weakened muscle forces affected skull shape in a mouse model through ontogeny. Shape was characterized with geometric morphometric techniques, improving upon the limited analytical power of the standard linear measurements. Through these techniques, we document the specific types of cranial skeletal deformation produced by the two strains, each with individual shape abnormalities. The mice with merosin deficiency (with an earlier age of onset) developed skulls with more deformation, but the shape change was not an exaggerated version of the laminin deficient skull shape. Measures of integration were also different between the two MD strains. By examining the ontogenetic development of these craniofacial shapes, we conclude that timing of any pathological condition is an important contributor to the amount and type of dysmorphology found in the skull.

Cranial Suture Morphology of the Lepidosaur *Sphenodon* (Diapsida: Rhynchocephalia) and Implications for Functional Morphology

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The New Zealand *Sphenodon* represents the only remaining member of the Rhynchocephalia, a group of reptiles that were both diverse and

widespread during the Mesozoic. *Sphenodon* possesses a unique combination of feeding adaptations not found in any extant taxon, notably: large chisel-like premaxillary teeth, an acrodont dentition, and enlarged palatal tooth rows that allow three-point bending to be applied to food items when the jaws close. In addition, the lower jaw is able to slide forward in order to rip food items apart. Together, these adaptations should generate distinct stresses on the skull which, in turn, may be reflected in the morphology of the cranial joints as there is increasing evidence that sutures serve to reduce and redirect stresses. A survey of *Sphenodon* skull joints demonstrates that almost all sutures remain patent throughout life, and that most midline joints are simple abutments whereas the remaining, more peripheral, joints often consist of extensive overlaps. Some joints involve substantial soft tissue (e.g., premaxillavomer) whereas others have a very close fit (e.g., postfrontal-postorbital). Similarly, facet surfaces can be smooth, ridged, pitted or striated. Some correspondence between joint morphology and predicted stress is observed. For example, the strongest joints are located in the skull roof whereas the joints of the palate are comparatively weak, corresponding to expectations of beam theory.

Stable Isotope Compositions of Extant Xenarthran Teeth and Their Potential for the Reconstruction of the Diet of Fossil Xenarthrans (Mammalia)

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Stable isotopes of carbon, nitrogen and oxygen are valuable proxies to reconstruct animal diets and ecology, as well as environmental and climatic conditions. They have been applied successfully in numerous studies to reconstruct feeding behavior and food webs from the isotopic composition of skeletal remains of both extant and fossil mammals and of human beings. In this study, we analyze teeth of mainly extant but also some fossil xenarthrans for their carbon, nitrogen and oxygen isotopic composition. Xenarthrans are mammals with either reduced small teeth like sloths and armadillos or have edentulous jaws like anteaters. In most geochemical studies tooth enamel, which is the hardest and least altered biologic skeletal tissue, is used for isotopic and geochemical investigations. Since the Eocene, xenarthran teeth have completely reduced enamel and are made up of a composite of different dentin tissues (ortho-, vaso-, and/or osteodentin) as well as of cementum. The aim of this survey is to check the preservation potential of primary isotopic compositions in the dentin of xenarthran teeth and then to test the applicability of stable isotope techniques to reconstruct dietary habits using teeth of extinct xenarthrans.

Pressures Used in the Perception of Hardness by Tongue, Teeth and Fingers

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Prior to ingestion, a food's hardness is evaluated by the hands. Immediately after ingestion it is evaluated by the teeth tongue and palate. This information is used to determine the food's subsequent processing. In this study, we measure the pressures exerted during the assessment of hardness using three model stimuli presented in the form of spheres of three different sizes. We investigated the forces deployed by the tongue teeth and fingers while assessing the hardness of spherical objects. Samples were given to subjects, who were asked to assess how hard they were on a 100-point scale either by placing them between the first finger and thumb, tongue and palate, the incisors or premolars. The degree to which they were compressed during assessments by finger and tongue was measured using image processing to determine the change in diameter. Sensory scores were highest for samples assessed by the tongue, lowest by the teeth. The fingers perceived smaller spheres as harder. Pressures deployed by the tongue varied from 3 kPa to 10 kPa, and were highest for the hardest samples, but were unaffected by size. Mean pressures measured in this study were substantially lower than previously reported in the literature by a factor of up to x10. Since larger, harder objects elicit higher forces the size and rigidity of the pressure transducers used may have had a determining role in the forces deployed and may explain this discrepancy.

Introduction, Comparative Cardiac Morphology, and Historical Hypotheses

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Reptiles have entered more fully terrestrial environments and adopted more active lifestyles than the amphibians and early tetrapods that preceded them. The cardiovascular system of reptiles supports accompanying higher metabolic rates and elevated levels of oxygen and carbon dioxide transport. Serving these physiological requirements are at least three anatomically distinct heart morphologies. The heart of birds includes primarily four anatomically separate chambers with valves between them presiding over the entry and departure of blood. The two other anatomically distinct heart morphologies are found in turtles and squamates, and in crocodiles, producing hearts with directly connecting sub-compartments and interconnections. This anatomical system of connecting compartments and vessels suggested to early anatomists that pulmonary and systemic blood streams might significantly mix in these "imperfectly" designed reptile hearts. The first experimental work instead showed little mixing and remarkable separation of these blood streams while air-breathing and cardiac shunting away from the lungs during diving. Further experimental studies related reptile (non-avian) heart morphology to maintenance of differential blood pressures, digestion, and other physiological demands. The goals of this symposium are to 1) clarify basic comparative structure and homologies of the reptilian heart, and 2) bring fresh experimental or interpretive understanding of reptile heart function, especially of the physiological role of cardiac shunting.

Changes in Egg Shell Structure and Function During Avian Evolution

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The shell of an egg contributes to successful embryogenesis in many ways, such as in protection, respiration and water exchange. The shell is also the major source of calcium for the development of highly calcium-consuming organs in the bird, such as the skeleton. Some studies show, moreover, that growth rate may play a fundamental role in the pattern of skeletal development: the faster the growth, the less ossified the skeleton becomes. We predicted therefore that slow (precocial) and fast (altricial) growing bird species should have evolved eggs encased in shells with different structures adapted to support different rates of calcium removal by the developing embryos. This prediction was tested by comparing the fine structure of the inner egg shell surface (mammillary layer) from bird species belonging to the major basal clades in the avian phylogeny. Using scanning electron microscopy we compared the mammillary layer of both preincubated eggs and eggs at the time of hatching, i.e., before and after embryonic development and accompanying calcium removal and obtained results consistent with the prediction. The number of mammillary tips per unit of surface area was associated with mode of development and growth rate. The number was higher, and calcium removal was also more extensive, in shells from precocial species than in shells from altricial species. These findings lead us to the conclusion that the major clades in the avian phylogeny have evolved different eggshell characteristics to cope with different calcium requirements imposed by their markedly different growth rates and modes of development.

Explaining the Growth of Craniofacial Skeleton Under Protein Restriction and Ligation of the Uterine Artery by Principal Component Analysis (PCA)

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The effects on craniofacial growth, of various nutritional conditions were examined in twenty timed pregnant Wistar rats and their 80 off-

spring. Rats were fed a diet containing 4% protein [Low protein diet, (LPD)], 12% protein [middle protein diet, (MPD)], 24% protein [control protein diet (CPD)], or IUGR and 24% protein (the offspring of the pregnant rats whose arteries of uterus were ligated during pregnancy). To investigate the effect of low, middle protein and IUGR on a normal growth trajectory, we radiographed four groups of rats from 22 d (post-weaning) to past adult size. The differences of weaning and final sizes of each measurement for each treatment and among treatments were analyzed. Significant differences were found for some measurements ($p < 0.05$). Furthermore, we defined four principal components among the measurements. These four components make interpretation of dietary effects on craniofacial growth easier and clearer.

Anatomy of the Facial Sexual Dimorphism in Orang-utans (*Pongo pygmaeus*)

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Adult male orang-utans have a pair of well-developed fatty cheek pads (FCP), called flanges, as secondary sexual features. Although experimental and ecological studies of the orang-utan face are frequently carried out for clarifying their significance, the only anatomical approach to the orang-utan FCP in the available literature is that of Winkler (1989). We re-examined the facial nerve supply to the FCP, particularly the fine branches of the facial nerve, supposed to be sensory, after their emergence from the stylomastoid foramen. Anatomical observation might give a clue to the nature of those nerves by examining animals with well-developed face prominences like adult male orangutan. Apart from skull measurements, we have carried out detailed macroscopic anatomical dissections of four sides of two orang-utan heads including one orang-utan head with well-developed FCP. The FCP was composed exclusively of fatty tissue and was supported by well-developed orbito-temporalis and platysma muscles, and by the temporal fascia lacking any attachments to osseous elements. The (sensory) nerve branches supplied ventral and dorsal aspects of the FCP. In addition to limited contributions of the zygomatico-temporal and third cervical nerves, the nerve supply consisted mainly of the zygomatico-facial nerve branch of the trigeminal nerve and of the cutaneous branches of the facial nerve. Skull measurements yielded pronounced sexual differences, especially regarding the zygomatico-facial and stylo-mastoid foramina. The morphological and functional significances of the morphological results will be discussed.

Thalamic Visual Nuclei in Turtles: Synaptic, Neurochemical Organization and Metabolic Activity

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The visual thalamic nuclei of the tectofugal (nucleus rotundus, Rot) and thalamofugal (nucleus dorsalis geniculatus lateralis, GLd) pathways in turtles (*Emys orbicularis, Testudo horsfieldi*) were studied with immunohistochemical/fluorescent and histochemical methods combined with tracing (HRP, BDA, Fluorogold) technique at light and electron microscopic levels. The main visual inputs to both nuclei are excitatory glutamatergic projections correspondingly from the optic tectum and the retina forming asymmetric synapses on dendrites. They both receive extrinsic inhibitory GABAergic projections from the thalamic reticular nucleus and the pretectum, forming symmetrical synapses on neuronal somata and dendrites. In contrast to Rot, GLd contains intrinsic GABAergic neurons with presynaptic dendrites, forming dendro-dendritic contacts within glomerular-like structures. In addition, Rot and GLd have multiple modulatory inputs (monoamine-, neuropeptide-, choline and NO-ergic) which are more abundant to the GLd. Projection thalamo-telencephalic neurons in both Rot and GLd are immunoreactive to calcium-binding proteins with predominance of calbindin in Rot and without remarkable predominance of calbindin, parvalbumin or calretinin in the GLd. Besides, colocalization of parvalbumin and calbindin was found in some projection neurons in both nuclei. The metabolic cytochrome oxidase activity was much higher in Rot than in GLd, correlating with a dominance of the tectofugal visual pathway in the organization of visually-guided behavior in reptiles. The work was supported by Russian Academy of Sciences (05-04-48296); Department of Biological Sciences RAS (1-OB); MNHN (USM 501); CNRS (UMR 5166); INSERM (U 616).

Accurate Measurement of Thin Membranes in X-ray Computed Tomography Data: From Trabeculae to Turbinates

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Although a rising number of morphological studies seek to utilize tomographic data to make measurements, there has been insufficient work on standardizing how these measurements are made. When small or thin features are imaged, they have a tendency to appear wider than they truly are. This is an inevitable outgrowth of the finite resolution of tomographic data. Resolution limits can be conceptually summarized as a point-spread function (PSF), usually a Gaussian smoothing kernel of a certain diameter. If all dimensions of a feature are larger than the PSF diameter, then simple thresholding is a legitimate approach for measurement, with the optimal theoretical value being the midpoint between the end-member X-ray attenuation coefficients of the feature of interest and the surrounding material. When a feature has one or more dimensions smaller than the PSF diameter, its apparent attenuation level does not reach its end-member value but its apparent dimension remains large, rendering thresholding inappropriate. In such cases, accurate measurements can be obtained by summing the attenuation surplus or deficit associated with the feature, and converting it to a linear or volumetric dimension as appropriate. Accurate calculation of this deficit can be challenging, as it depends on the interplay between the incoming X-ray energy spectrum and sample attenuation characteristics. If adequate calibration can be achieved, one can obtain reasonably accurate measurements for features with dimensions down to roughly a tenth of a voxel edge length. These principles are illustrated on data for nasal turbinates and trabecular bone.

Limb Heterochrony in the Marsupial *Monodelphis domestica*

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Heterochrony, or a shift in developmental timing, is an important source for evolutionary change. Here we utilize *Monodelphis domestica* (Metatheria), an opossum, as a model to investigate the developmental origins of limb heterochrony. *Monodelphis domestica* neonates show significant acceleration of forelimb development relative to the hindlimbs when compared to other non-metatherian amniotes. When the hindlimbs of *M. domestica* embryos begin outgrowth, the forelimbs are already well-defined buds, indicating that heterochrony arises very early. Our study aims to uncover the developmental and genetic basis of the early limb heterochrony in these neonates. As a proxy for limb field specification, we have examined the expression of genes used previously as limb field markers (Tbx5 and Tbx4), as well as downstream genes known to be involved in limb outgrowth (Fgf10 and Fgf8). Using in situ hybridization, the timing of earliest limb expression of each of these genes is compared between *M. domestica* and *Mus musculus*. We have found that the timing of first Tbx5 expression in the future forelimb region has shifted much earlier in the opossum, as has the expression of Fgf10 and Fgf8. Tbx4 is also expressed earlier in the opossum, but appears so early relative to axis development that hindlimb outgrowth may be limited by tissue availability. A subset of the Hox genes has been hypothesized to lie upstream of Tbx5/4 in positioning the limbs. We test this by examining the timing and pattern of relevant Hox expression in *M. domestica.*

A New Clupeomorph Fish from the Cenomanian (Cretaceous) of the Middle East

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A new genus and species of a double-armored †Ellimichthyiformes (Teleostei: Clupeomorpha) is described from the Cenomanian marine deposit of Ein Yabrud, near Ramallah, West Bank. Thirteen species of Teleostei, as well as a bipedal snake have already been known from this locality,

and this is the first Clupeomorph fish described. This new taxon is known from eleven acid prepared specimens. The †Ellimichthyiformes are an extinct taxa of Clupeomorph with a Tethysian geographical distribution and uniquely diversified during the Cretaceous. The new species from Ein Yabrud is the thirteenth Clupeomorph fish known from the "Cenomanian Tethys"; the other described taxa have been collected in Lebanon, Morocco, Portugal, and Slovenia. This new †Ellimichthyiformes is characterized by its extraordinarily expanded ventral series of scutes, which confers it an apex-like ventral profile, and by its elongated first dorsal fin rays. It shares both the synapomorphies of †Ellimichthyiformes Grande, 1982 and of the family †Paraclupeidae Chang and Chou, 1977. I present evidences that the new species is a close relative of the triple-armored †Ellimichthyifomes †Triplomystus Forey et al. 2003.

Temperature, Size, Performance and Fitness

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This talk focuses on three related patterns often observed in ecothermic animals. First, larger body size is frequently associated with greater fitness within populations: bigger is generally fitter. Second, greater maximal performance at the optimal temperature is frequently associated with higher optimal temperatures: Hotter is generally better. Third, higher temperatures during development typically lead to smaller adult body sizes: Hotter is generally smaller. We will discuss the empirical support (and counterexamples) for these patterns, how temperature may constrain both size and maximal performance, and the implications for selection on performance and size in thermally variable environments.

Ontogenetic Stages in the Long Bone Histology of Sauropod Dinosaurs

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In the fossil record, long bones (femora, humeri) are the most abundant remains of sauropod dinosaurs. Due to the simple appositional growth of long bones, samples taken from a standardized sampling location in the mid-shaft region are well suited for studying bone histology and growth in extinct animals. Additionally, long bone length is a good proxy for body length and body mass and therefore important in reconstruction of growth curves based on histologic data. In a comparative study of the bone histology of several sauropod taxa, including diplodocoids (*Apatosaurus, Diplodocus, Dicraeosaurus, Diplodocinae indet* from the Trendaguru Beds and from the Morrison Formation), basal macronarians (*Camarasaurus, Brachiosaurus, Europasaurus*) and titanosaurs (*Phuwiangosaurus, Ampelosaurus*), remarkable changes during ontogeny were discovered in growth rate and bone tissue types. Five biologic ontogenetic stages (hatchling, juvenile, subadult, adult, senile) have their counterparts in 13 histologic ontogenetic stages in the long bone histology of these sauropods. The 13 histologic ontogenetic stages include gradual transitions between the different ontogenetic bone tissue types as well as three adult phases (still growing, decreasing growth which finally results in a growth plateau, senile stage). Because of the relatively uniform growth of all sauropod long bones (laminar fibro-lamellar bone), taxa are easy to compare and the ontogenetic histologic stages could be identified in all studied sauropod taxa. However, there are subtle differences in the ontogenetic bone tissue types between the different taxa which reflect different growth trajectories and life histories in the sampled sauropod taxa.

Cranial Muscle Morphology in Caecilian (Lissamphibia: Gymnophiona) Larvae, Fetuses, and Adults: The Impact of Feeding Mode on Muscle Development

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Oviparity with free-living larvae and metamorphosis is considered to be the ancestral mode of reproduction in the Lissamphibia; i.e., caecilians (Gymnophiona), salamanders (Caudata), and frogs (Anura). Derived reproductive modes in amphibians comprise oviparity with direct development, and viviparity. In caecilians, the evolution of viviparity necessarily entails new demands on nutrition during development. Larvae of oviparous species are aquatic predators; viviparous species have fetal stages that feed in utero by rasping the uterus epithelium. It is shown that differences in the feeding behavior during early ontogeny are mirrored in the development and morphology of the cranial musculature. Caecilian fetuses differ from free-living larvae by: topographic relations of cranial bones and musculature; some muscles that are present in larvae are absent in fetuses; other muscles attach to different skeletal elements; the development of teeth-bearing bones in viviparous species is accelerated in relation to other cranial elements. The hyobranchial apparatus in fetuses is less elongated relative to Neuro- and Dermatocranium, compared to caecilian larvae. The cranial morphology of fetuses is similar to that of adult caecilians; free-living larvae differ notably from postmetamorphic stages. Characters that are unique to caecilian larvae are correlated to aquatic larval feeding; the accelerated development of teeth-bearing bones in fetuses is related to the early onset of intrauterinal feeding in viviparous caecilians. The evolution of viviparity in caecilians led to the loss of larval characters.

The Anatomy of the Palatoquadrate of the Lower Triassic *Proterosuchus fergusi* (Reptilia, Archosauromorpha) from South Africa

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The palatoquadrate of *Proterosuchus fergusi* consists of two ossifications, the epipterygoid and quadrate, which were joined via cartilage in life. The contours of the cartilage are well preserved in the form of grooves on the dorsal surface of the pterygoid. The epipterygoid consists of two structures: the anteroposteriorly expanded basal portion and dorsally from it extending slender ascending process. From the anterior margin of the basal portion of the epipterygoid, a plate-like structure, called the anteromedial lamina of the epipterygoid, extends anteromedially thus forming the anterolateral wall of the epipteric cavity. Comparisons with the similarly constructed embryonal and adult epipterygoid components of *Sphenodon punctatus* show that the anteromedial lamina of the epipterygoid of *P. fergusi* is an additional constitutional component of the epipterygoid of this species and that this lamina is absent in the former species. However, a structure in a topologically similar position as the anteromedial lamina of the epipterygoid of *P. fergusi* is present in the palatoquadrate of *Alligator mississippiensis.* The anterior lamina of the palatoquadrate of *A. mississippiensis* ossifies in membrane and forms the dorsolateral cover of the huge trigeminal ganglion. It is argued here that the anteromedial lamina of the epipterygoid of *P. fergusi* and the anterior lamina of the palatoquadrate of *A. mississippiensis* are with the most probability homologous structures and thus are present in the basal and one of the crown taxa of the archosauromorph clade respectively.

The Effects of Skull Morphology on Feeding Performance in Snakes: A Preliminary Study

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Uniquely among terrestrial vertebrates, snakes resemble fishes in relying largely on extensive and well-coordinated movements of complex skeletal linkage systems to feed. In recent years, ichthyological biomechanists have developed increasingly sophisticated and accurate models to predict feeding performance in fishes, and such models have even been used to predict feeding performance in fossil taxa. In contrast, no such predictive models have yet been developed for snakes. In fact, no empirically derived data have ever been published that directly link any specific aspect of skull morphology with feeding performance in snakes. In this study, I quantified intraoral prey transport performance across a wide range of prey sizes for a phylogenetically and morphologically diverse sample of macrophagous alethinophidian snakes. I then quantified the cranial morphologies of all taxa included in these performance studies through detailed craniometric analyses, in which approximately 70 linear measurements were taken across all regions of the skull and jaw apparatus. Finally, regression analyses were conducted in order to develop a quantitative model predicting prey transport performance based on the relative proportions of individual bones and functional units within the head skeleton. Contrary to previous hypotheses, the relative lengths of

neither the quadrate nor the supratemporal were found to be significant in determining feeding performance. Rather, these preliminary analyses suggest that the relative length the lower jaw is the single most important determinant of prey transport performance, explaining between 68 and 78 percent of the variance in the performance data, depending on which phylogenetic hypothesis is used for analysis.

Analyzing Modularity in Complex Morphological Structures

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Modularity is a general property of biological systems. Modules are units of a system that are integrated by many and/or strong interactions of their component parts and that are relatively independent of each other because there are only few or weak interactions between the parts of different modules. For morphological structures such as skulls, this concept can be used within the framework of geometric morphometrics. Modularity can be assessed through the analysis of covariation landmark points: a module is a set of landmarks that covary with each other more strongly than with the landmarks of other modules and that are spatially contiguous. This definition will be applied to a range of examples from relatively simple structures such as the mouse mandible to highly complex ones such as the skull of the mouse and other mammals.

Horn Size, Sexual Selection and Performance in Insects

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Weapons such as horns are widely distributed in the Coleoptera, and exhibit an astonishing diversity. Male beetles of the species *Euoniticellus intermedius* carry a single horn on their heads which they use in contests over access to females. In a series of laboratory experiments we found that horn length was a more important predictor of victory than body size, especially in larger males. Further experiments have showed that horn length is a better predictor of a male beetle's strength and endurance than body size, and is correlated with one of two measures of immunity. Thus, it seems that horn length in this species acts as a clear signal of individual quality.

Scanning Electron Microscopy of the Fetal Membranes of an Oviparous Snake

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Electron microscopy has contributed importantly to our understanding of fetal membranes of viviparous amniotes. However, such membranes have never been studied by scanning EM in oviparous reptiles. The absence of information about oviparous species hampers attempts to distinguish specializations for viviparity among live-bearing squamates. Drawing on our breeding colony of the oviparous corn snake *Pantherophis guttatus* (Colubridae), we used SEM to examine fetal membranes throughout development between the times of oviposition and hatching. Two major fetal membranes surround the developing egg, the chorioallantois and the omphalallantoic membrane. The latter is formed from the yolk sac omphalopleure and isolated yolk mass, with the allantois on its inner surface. SEM shows that epithelium lining the chorioallantois consists of broad, flattened cells that form a thin, unbroken barrier over the allantoic capillaries. In contrast, epithelium lining the omphalopleure is cuboidal and bears surface ridges suggestive of absorptive capabilities. Recent research on viviparous snakes has revealed that the chorioallantois and omphalopleure are respectively specialized for gas exchange and absorption. Our studies of corn snake fetal membranes suggest that specializations for these distinct functions may have originated under oviparous conditions.

The Avian Furcula in its Anatomical Context: Seeking Explanation for Patterns of Reduction and Loss of the Wishbone

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The avian furcula has a longstanding history of study related to interest in its form, its potential homology, and its possible multifaceted functional contributions. It is highly variable in terms of completeness of expression (spanning a range of five recognized classes from a single ossified element, joined in the ventral midline, to a completely unossified condition represented only by unmineralized connective tissue). Overall, the furcula has been regarded as an integral part of the breast-shoulder apparatus (BSA), consisting of the coracoids, sternum, furcula, scapula, ribs, vertebral column, and the connective tissues that link them, but its functional morphology has essentially been interpreted in isolation. Examination of the BSA in its entirety across the Neognathae permits contextualization of variation in pattern and form of the furcula, and provides the background for considering phylogenetic and functional correlates of its form. Interpretation of the morphological environment in which the various "classes" of furcular morphology are expressed, and exploration of patterns of reduction seemingly independently in owls, barbets, mesites, turacos, and parrots, allows a more holistic consideration of the furcular form. Parrots are employed here as a case study to investigate the potential correlate of phylogeny, flight style and other behavioral/mechanical qualities attributed to the furcula.

Heterochronical Shift of Shh Expression in Fin Buds of a Cartilaginous Fish Implies Sequential Events in Vertebrate Limb Evolution

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Evolutionary acquisition of Sonic hedgehog (Shh) expression into fin buds has been considered as a crucial step during vertebrate limb evolution (Tanaka et al., 2002, Nature 416:527–531.; Kmita et al., 2005, Nature 435:1113–1116). Here, we analyzed fin development in embryos of cartilaginous dogfish, *Scylirohinus canicula*, and examined expression pattern of genes known to be involved in fin/limb patterning. In limb buds of tetrapods, Shh expression is activated as soon as there is a morphological bud, while in dogfish fin buds Shh transcribed at a very late stage of development. Thus, temporal shifts in the expression of Shh during vertebrate limb evolution might have facilitated major morphological innovations in paired appendages. To explore this possibility further, we investigated factors that might allow fins to acquire Shh expression at this late stage of development in dogfish. Based on our findings, we will present a model for evolution of paired limbs in the vertebrate body plan.

Convergent and Divergent Evolutionary Patterns in Raking, A Novel Salmonid and Osteoglossomorph Feeding Behavior

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Concurrent analyses of morphology, muscle activity and kinematics, although relatively uncommon, isolate and highlight how changes at each organizational level directly influence organismal capabilities. We examined the patterns at all three levels in the tongue-bite apparatus (TBA) used in raking, a novel prey-processing behavior in osteoglossomorph and salmonid fishes. Electromyography on several taxa from each lineage identified the raking motor activity pattern (MAP) as statistically different from previously described feeding behavior MAPs. This analysis also provided strong evidence that a convergently derived MAP governs raking. Unusually, raking is very stereotypical in generalist feeding salmonids, while the more specialist osteoglossomorph taxa commonly modulate raking in response to prey-type differences, as manifested both in raking MAPs and resultant kinematics. Morphological variables, including pectoral girdle articulations and architectural differences in a novel cleithrobranchial ligament are key factors in explaining the observed intra and interspecific differences. Biomechanical raking models based on morphology and kinematics data from both lineages were tested empirically using EMG, high-speed video and sonomicrometry. Electromyography illustrated that activity in the basihyal protractor musculature during the preparatory phase primes the TBA prior to the biomechanically more complex power stroke, which involves both a simple lever model of cranial elevation and a 4-bar linkage model of basihyal retraction. Power-stroke models are now used to categorize taxa by the relative contribution of each mechanism. Supported by NSF IOB 0444891 and DBI 0420440.

Intramandibular Joints Help Coral Reef Fishes Have a Bite

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Coral reef fishes are, more than any other fish fauna, dominated by taxa that use biting strategies to dislodge sturdily attached, tough prey from confinements in a highly complex habitat matrix. We investigated the functional morphology of such biting strategies in the squamipinnes, a nominally monophyletic group comprising nine successful and distinctive coral reef fish families. A squamipinnid supertree hypothesis revealed independent evolution of an intramandibular joint (IMJ) at least five times in this group and we discuss the role of these joints play in facilitating biting. Character mapping revealed no less than seven gains or losses of intramandibular flexion, all associated with trophic transitions between free-living and attached prey. Generalized squamipinnid taxa are commonly suction feeders and lack intramandibular flexion, and flexion also typically decreases after reversal to suction feeding, e.g., in several secondary planktivores. The IMJ is a basal trait in angelfishes, f. Pomacanthidae, permitting over 35° of mandible flexion, which results in peak-protruded jaw closure. In all other IMJ-bearing taxa the joint functions to augment vertical gape expansion during biting behaviors. Butterflyfishes (f. Chaetodontidae) have acquired intramandibular flexion in conjunction with a major evolutionary transition from mid-water suction feeding to benthic biting. The most pronounced intramandibular flexion occurs in the coral-scraping *Chaetodon* subgenera *Corallochaetodon* and *Citharoedus* (16 ± 6.6°–49 ± 2.7°). A complex evolutionary history has led to widespread IMJ occurrences in extant biting fishes, revealing that intramandibular flexion is a major functional innovation, constituting a functional prerequisite to successful biting strategies in many reef fishes.

Ontogeny of the Beak of the Gymnodonts and Fixation of the Ethmopalatine Articulation (Teleostei, Tetraodontiformes)

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The tetraodontiform families Triodontidae, Tetraodontidae, Diodontidae, and Molidae comprise the monophyletic gymnodonts, a group characterized by their conspicuous beak-like jaws. We describe and compare the ontogeny of the beak and the ethmopalatine articulation of representatives of three families of gymnodonts, based on cleared and double-stained specimens of *Monotrete leiurus, Diodon sp.,* and *Ranzania laevis*. In adults of all three taxa the jaws have no teeth, but individual teeth are clearly present in early developmental stages, a fact which has not been recorded before. Along with the evolution of the gymnodont beak, the ethmopalatine articulation has been almost entirely immobilized. The way in which this immobilization is achieved during development has not been studied before and differs among the representatives of the three families. In the tetraodontid *Monotrete* a dorsal caudally directed splint of membrane bone encloses an anteriorly directed process of the vomer and thus fixes the articulation. In the diodontid *Diodon* a dorsally directed process of membrane bone from the autopalatine sutures tightly with the frontal. In the molid *Ranzania* the autopalatine has a caudal lamina of membrane bone that runs along the parasphenoid and a second lamina contacts the lateral ethmoid, thus restricting mobility of the joint. The different ways in which the articulation is immobilized may shed some doubt on the homology of this character among the gymnodonts.

Development of the Anterior Part of Skull in the Anura

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Two morphologically different schemes of the anterior part of the skull were recognized in the anuran larvae. The first, which occurs in the Pipidae, consists of the horizontal internasal plate which also serves as the larval upper jaw; its lower jaw consists of two elongated Meckel's cartilages interconnected by two hypomandibulars (= infrarostrals) and one basimandibular. The second, which is typical for non-pipoid anuran tadpoles, consists of a pair of trabecular horns terminated by suprarostral cartilages. Its lower jaw consists of a pair of infrarostrals, sometimes interconnected by the basimandibular. Although the second type seems to be more conservative in that it maintains two separate trabeculae, it is more deviated from the ancestral temnospondyl scheme by its modified larval jaw apparatus. In contrast, the pipid larval type is basically the same as in ancestral temnospondyls. During metamorphosis, both types undergo profound transformations in which some parts disappear, some arise new, and some are translocated and become parts of other structures. Therefore, the question arises as to which parts of these two types are homologous. To answer this question, we followed the development in *Discoglossus*, a representative of primitive non-pipoid anurans, and *Xenopus* (completed by data gained from selected stages of *Pipa*), as representatives of contemporary pipids. Here we present some preliminary results based on histological analysis and computer-assisted 3D-reconstructions. This made it possible to compare development of homologous parts from the earliest mesenchymal primordia till the structures of adults. An attempt is made to explain morphological differences of homologous parts.

Morphological Characteristics of the Glenohumeral Joint and Its Implications on Shoulder Joint Mobility in Primates

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Cineradiographic studies on primates revealed differences in the degree of glenohumeral joint mobility during horizontal locomotion. The abduction of the humerus is caused by an abduction of the scapula, while medio-lateral excursions in the glenohumeral joint are avoided in *Microcebus murinus, Saguinus oedipus* and *Eulemur fulvus*. The glenohumeral joint of *Saimiri sciureus* is characterized by additional medio-lateral mobility for a parasagittal course of the forelimb during quadruped locomotion. In *Ateles geoffroyi* the scapula is almost decoupled functionally from the humerus, offering the greatest glenohumeral joint mobility. The aim of our study is the identification of possible anatomical characteristics of the glenohumeral joint surface areas, corresponding to the differences of glenohumeral excursions during locomotion. Size, shape and curvature of the joint surface areas of 72 individuals of 12 species were determined using a newly developed method. Preliminary results of form and incongruity of glenohumeral joint surface areas showed the expected differences between quadrupeds in general and suspending primates. But, within quadrupeds no difference in glenohumeral joint incongruity could be detected between terrestrial and arboreal species. However, terrestrial primates possess a relatively broader glenoid fossa. This feature may be related to higher load carried by the forelimbs in terrestrial primates. Joint surface curvature is also related to the degree of forelimb loading. We conclude that load transmission rather than angular excursions is reflected in the morphology of the glenohumeral joint.

Comparative Primary Hair Structure in the Lutrinae (Carnivora: Mustelidae)

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The thirteen otter species known have world-wide distribution and live in very different biotopes, from tropical to arctic climates. In some regions of Africa, Asia and South America, two to four species occur sympatrically. Otters are all considered as semi-aquatic carnivores, but they are diversely adapted to the aquatic environment. In this study, we analyzed primary hairs (PH; length, width, morphology, cross-section, medulla and cuticle structures), in order to control whether otter species can be identified using hair morphology, and to see how hair characteristics correlate with geographic distribution, foraging behavior and taxonomic position. The identification of otter species using hair structure

analysis was difficult because of great similarities in the medulla and cuticle structures, and it was not possible to identify every species confidently. The most divergent feature was the cuticle scale pattern of the pars intermedia of the hair shaft. No exact correlation could be found between hair characteristics and the above listed parameters; however, some tendencies became obvious: *Pteronura* and *Enhydra*, which are the most divergent taxa, show the most specific PH. All the *Lutra* members have the same cuticle pattern, but the tropical species and subspecies have thinner and shorter PH, with shorter cuticle scales. In the two clawless *Aonyx* and the small clawed *Amblonyx*, which live in the tropical and subtropical regions and feed mainly on invertebrates, the PH differ clearly from those of the three species, which live in the colder northern regions and spend more time foraging in the water (*L. canadensis, L. lutra, E. lutris*).

Bone Remodelling Response to Mechanical Strains in the Developing Primate Craniofacial Skeleton

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Postnatal growth of the mammalian craniofacial skeleton is influenced by mechanical stimuli. This study addresses the possible link between the local masticatory strain environment in the primate face and bone surface remodelling fields as well as the emergence of structures such as browridges. We developed three-dimensional finite element analysis (FEA) models of the skulls of two Old World monkey species, *Macaca fascicularis* and *Cercocebus atys*, at different ontogenetic stages. The models were subjected to masticatory muscle forces estimated from physiological cross-sectional areas of *M. fascicularis* cadaveric specimens. The models were sequentially constrained at each working side tooth to simulate the variation of the bite point applied during the masticatory cycle. We applied a custom voxel-based FEA package to compute engineering parameters of interest including strain energy density (SED). Quasi-dynamic cumulative maps of the peak strain environment throughout the face were created by registering the maximum SED value in each finite element from each of the loading regimens. These maps were compared with bone surface remodelling maps in the faces of the two species. Our findings show some correspondence between regions of high and low SED and resorptive and depository areas (e.g., in the maxilla). There are also regions in which there is no obvious relationship between SED and remodelling (e.g. the suprarorbital browridge). These findings suggest that, at least in part, remodelling activity might be predicted from FEA and are a stimulus for future investigation. Supported by the BBSRC, The Leverhulme Trust, the Australian Research Council and the Max-Planck-Gesellschaft.

Developmental Background for the Origin of Turtles

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The turtle carapace is made of dorsolaterally expanded ribs. Due to this dislocation, the topographical relationship between the rib cage and scapula in turtles has been reversed as compared to other amniotes. For this turtle-specific pattern, an inductive function of the lateral edge of carapace, or the carapacial ridge (CR), has been assumed. By comparative observation and cell labeling studies, we found that the CR mesenchyme is derived from the dermomyotome, representing the ventrolateral limit of the axial domain. The CR is thus unique to turtles, different from the Wolffian ridge that develops from the body wall. Turtle ribs are also unique since they never invade into the body wall as in other amniotes. Neither ablation or implantation of CR altered the dorsoventral pattern of ribs, but only the turtle-specific fan-shaped pattern of ribs was arrested. By differential screening, we have isolated CR-specifc genes, including Sp5, CRABP-1, Lef-1 and APCDD1. Overexpression of the dominant negative form of Lef-1 in the CR epithelium resulted in arrested development of the carapace at the site of electroporation. We conclude that the CR does not have an inductive function as has been suggested, but is rather functional in the marginal growth of the carapacial primordium with its specific gene expressions. We also note that the CR does not express all the genes known to be functional in the limb bud, and therefore the CR cannot be regarded as a structure simply obtained by a co-option of the limb developmental program.

Evolutionary Pathway of Developmental Mechanisms of Skeletal Muscles, with Special Reference to the Lampreys

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Protochordates such as amphioxus and larval tunicates possess trunk or tail muscles that form bilateral rows flanking the notochord. However, this striated musculature in these animals does not undergo such a complicated processes for morphological patterning as those of vertebrates, especially gnathostomes. The somitic skeletal muscles of the gnathostome vertebrates are categorized into epaxial and hypaxial parts morphologically separated at the level of the notochord. During evolution, the hypaxial part undergoes conspicuous elaboration to give rise to the migratory precursors which give rise to the tongue muscles, the trapezius muscles, and the limb muscles, all of which are absent in agnathans and invertebrates. We investigated the molecular basis for evolution of the complicated and diverse morphology of the gnathostomes, mainly using the Japanese lamprey *Lethenteron japonicum*. This animal would represent the ancestral state of vertebrate which had already established a far more complicated skeletal muscle system than those of protochordates. We have examined the patterns of expression of the genes encoding the major contractile proteins and the muscle-related transcription factors in the lamprey. The results revealed that the lamprey myotomes consist of multiple regions in which muscle-specific genes are differentially regulated during development. Cells at the lateral edge of the somites, directly underneath the epidermis, express Pax3/7 gene, a lamprey cognate of gnathostome Pax3 gene which plays an important role in hypaxial muscle development. Our data implied that a cell layer homologous to the amniote dermomyotome, with respect to the gene expression, might already have been acquired in agnathans.

Morphofunctional Observations on the Mandibular Arch Bones in Fishes with Different Food Habits

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Three fresh water fish species were examined: *Stizostedion lucioperca* (L. 1758), *Cyprinus carpio* (L. 1758) and *Ctenopharyngodon idella* (Cuv. et Val., 1848). They display significant biodiversity: *S. lucioperca* is a predator, its food consist of other fish or fish juveniles. *Cyprirus. carpio* is omnivorous, feeding essentially on small crustaceans, worms and seeds, while *C. idella* is herbivorous. As a result of different food sources those species have also developed a different way of taking prey. Morphofuncional analysis of mandible bones as well as four points in the syncranium (cranial end of Premaxilla, Hyomandibulare connection with neurocranium, Quadrate-articular facet, cranial end of Dentale) and angles between them, was done in order to explain differences between chosen species in the moment of mouth opening.

Histological Study of Carabelli's Cusp

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The Carabelli's complex refers to enamel features present in the lingual aspect of the protocone of permanent and deciduous molars of primates. There are some interesting aspects of the development of Carabelli's trait and its potential association with the topography of the enamel dentine junction (EDJ). Several authors have indicated that not all features recorded on the enamel surface are mirrored at the EDJ level. Given that cusps develop through the differential folding of the epithelium, we prepared six histological sections of modern human molars to investigate developmental and morphological aspects of Carabelli's cusp and its association with the EDJ topography. Results from this study show that all

specimens show the presence of a topographic feature at the EDJ level underlying the Carabelli's cusp. This feature is identical in morphology to those found in the main cusps. Using marked striae in the protocone and Carabelli's cusp, we were able to discern a delay in the development of Carabelli's cusp with respect to the protocone of about 4.2 to 5.6 months. Furthermore, in at least one specimen, we identified marked striae present in Carabelli's cusp but this line was absent in the protocone suggesting that the mineralization of Carabelli's cusp was independent of the protocone. In the remaining specimens Carabelli's cusp mineralized from the ameloblastema originated in the protocone. We suggest that at least in cases where Carabelli's cusp is strongly expressed, this cusp most likely develops through the activity of the same signaling molecules that control the development of the main cusps.

Isolated Mammalian Fossil Remains of Petrosals and Teeth: What to Do With? Morphometric and Phylogenetic Analyses of Metatherian Petrosal Bones from the Paleocene of South America

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The systematics of extinct mammals is mostly based on teeth, which are better preserved than skull bones. Nonetheless, petrosals (paired bones of the ear) are more frequent than the latter, and proved to bring significant phylogenetic signal. Paleocene layers from Tiupampa (Bolivia) and Itaboraí (Brazil) have yielded partial to complete metatherian skulls with associated petrosal bones (assigned to the pucadelphyds *Pucadelphys* and *Andinodelphys*) and isolated metatherian petrosals, respectively. Both localities are of a main importance in the understanding of the Notometatheria (South American and Australian metatherians) evolutionary history, since they provide the most abundant and the oldest metatherian assemblage of South America. An attempt at assigning the isolated petrosals to tooth-based taxa from Itaboraí was made by combining parsimony and morphometric methods. Morphometric studies show that molar proportions are correlated with that of petrosals; however, the assignation of an isolated petrosal to a dental-based taxon remains difficult. A parsimony analysis highlighted the close relationship of petrosal Types I, V, VI, VII, *Caenolestes* and Australidelphia. The identification of australidelphian taxa (petrosal Types V and VII) among the Paleocene fauna of Itaboraí makes the stratigraphic origin of Australidelphia older than it was thought.

Msx Genes are Important Effectors Downstream of Gli3R in the Shh/Gli3 Pathway Controlling Antero-Posterior Development of the Limb

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Msx genes encode homeodomain transcription factors. In the mouse embryo, Msx1 and Msx2 are expressed in limb bud ectoderm and mesoderm. Accordingly, the Msx1:Msx2 double mutant limbs are deeply affected. Abnormalities along the antero-posterior axis are prominent, leading either to oligodactyly or polydactyly but always with absence of digits with anterior identity (thumb or big toe). This led us to hypothesize that Msx genes might play a important role in the Shh/Gli3 pathway that controls antero-posterior patterning of the limb. Indeed, Msx gene expression is affected in the Shh and Gli3 mutants, suggesting that Msx1 and Msx2 are downstream targets of Gli3R. To analyze the genetic interactions between Msx and Shh, we produced Shh:Msx1: Msx2 compound mutants and showed that diminishing Msx activity in Shh mutants leads to a partial rescue of the Shh limb phenotype. The precise role of Msx genes in the Shh/Gli3 pathway is currently investigated and will be discussed.

Breathing Inside a Box: Turtle Locomotion and the Evolution of Alternate Lung Ventilation Mechanisms

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Turtles are unique because their shoulder blades lie inside the rib cage and the fused ribs make costal ventilation impossible. Two main lung ventilation mechanisms are known in turtles: 1) antagonistic pairs of sheet-like abdominal muscles alter lung pressure as they contract; and 2) protraction and retraction of the limb girdles drives air in and out of the lungs. We studied ventilation during treadmill locomotion in two emydid turtles to see if they breathe during locomotion and whether they use locomotor-respiratory coupling. Both species had very high ventilation rates during locomotion, but neither species showed signs of coupling. Consequently, limb movements cannot be driving lung ventilation and the abdominal ventilation mechanism appears to function independent of the limbs. The terrestrial species (*Terrapene carolina*) didn't show any differences in breathing patterns between locomotor bouts and the short pauses between bouts; however, the semi-aquatic species (*Trachemys scripta*) took smaller breaths more frequently during locomotion. The comparatively gigantic green sea turtles (*Chelonia mydas*) don't breathe during terrestrial locomotion (Jackson and Prange, 1979). Thus, all three turtle species studied to date reveal different relationships between breathing and locomotion. The derived abdominal breathing mechanism found in turtles may have evolved as an accessory mechanism to circumvent the ancestral locomotor/ventilation constraint seen in lizards (Carrier, 1987). Once established, this mechanism could have allowed the ribs to abandon their role in breathing and fuse to form the carapace.

Two Fulcra in a Common Joint—the Mammalian Jaw Joint

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The primitive form of the Therian jaw joint is a transversely elongated mandibular condyle fitting into a corresponding transverse groove in the squamosal bone of the skull. The lateral and medial ends of the joint appear to be adapted to two different functions. The lateral end is the fulcrum for the lever arm of the jaw in biting by the cheek teeth, while the medial end is the fulcrum for the lever that plunges the canine. The comparison is most easily made in carnivores where the biting function is concentrated at a single tooth, the carnassial. Here, the plane of the cuting edge can be projected backward to cross the outer edge of the jaw joint. A line drawn from the innermost side of the joint to the tip of he canine is almost parallel to the sagittal plane of the skull. Just behind the medial fulcrum is a massive post glenoid process which braces against the backward push of the mandible when the canine is being plunged.

The Evolutionary Morphology of Lizard Weaponry

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In many vertebrate taxa, males attain larger body size than females and possess comparatively robust heads, often with more developed jaw musculature, exaggerated dentition, or other modifications. The elaboration of such structures frequently reflects their role as weapons in male-male combat, motivating the hypothesis that sexual selection for superior weapon performance may be responsible for some patterns of sexual dimorphism. Our research on collared lizards (*Crotaphytus*) demonstrates that harder-biting males (i.e., those that have greater weapon performance) enjoy larger territories that overlap more females, more social interactions with females, and greater reproductive success compared to similarly-sized but more weakly biting males. These results are corroborated by laboratory experiments showing that harder-biting males are dominant in staged interactions. The signaling system of collared lizards provides additional support for the importance of bite force in sexual selection. Male collared lizards include gaping displays as part of their behavioral repertoire during territorial interactions. This display posture reveals to rivals the size of the jaw-adductor musculature, the primary effector of bite-force performance. This index of weapon performance is visually amplified by the exposure of white patches that delineate the dimensions of the jaw musculature and contrast conspicuously with the surrounding integument. Based on these results, we suggest that sexual selection for weapon performance can have substantial consequences for sexual dimorphism, and that signaling systems and the performance capacities that they advertise may offer clues to understanding the origin of much morphological diversity.

Morphological Evolution of Vertebrates in the Conquest of Land

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Over the last ten years, many discoveries have overturned long-held ideas about morphological transformations associated with the conquest of land by vertebrates and the first evolutionary radiation of terrestrial vertebrates. Among these are the description of the Devonian sarcopterygian *Tiktaalik* and new, well-preserved remains of *Panderichthys*. The morphology of their pectoral fins has led some authors to suggest that the autotpod is not neomorphic. Also exciting is the discovery of several fragmentary remains that document an extensive evolutionary radiation of Devonian vertebrates that may have had limbs. The idea of a diphyletic origin of pentadactyly (once in amphibians and once in reptiliomorphs) has been rejected on the basis of the most recent phylogenies that favor a monophyletic origin, before the origin of the tetrapod crown-group. Ongoing work on the microstructure of appendicular long bones suggests that the many limbed vertebrates were aquatic and that the conquest of land by vertebrates occurred later than is often thought. The phylogeny of limbed vertebrates has been controversial since the discovery, in the mid-1990s, that the established consensus was not the most parsimonious tree. All phylogenies published after 1996 indicate that the basal dichotomy between amphibians and reptiliomorphs (and hence, the origin of the tetrapod crown) had been misidentified. The main controversy revolves around the origin of extant amphibians, either among "lepospondyls", among "temnospondyls", or among both groups in the context of a polyphyletic origin. However, comparisons between morphological and molecular trees rule out a polyphyletic origin.

Origin of the Murine Dental Pattern in Muroidea (Rodentia, Mammalia): Contribution of Palaeontology, Functional Morphology and Development in the Study of an Evolutionary Innovation

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The origin of the murine dental pattern (presence of supplementary cusps on upper molars) in Muroidea (Rodentia, Mammalia) shared by Deomyinae, Cricetomyinae and Murinae, is studied in order to illustrate how functional continuity that necessarily accompanies a modification of a dental pattern was maintained. Murinae originated in Southern Asia, and the genus *Potwarmus* (ca. 18 MA old) could be considered as the oldest representative of the subfamily. This genus showing close affinities with the Early Miocene genus *Primus*. Morphometric analyses (3D reconstructions of scanned fossil teeth with X-ray microtomography, Procrustes methods applied on homologous points related to cusps, topographical maps of the tooth crowns) support the gradual origin of the murine dental pattern. It is demonstrated that functional continuity during the transition towards the murine pattern has requested the acquisition of new contacts between cusps that are allowed by changes in their position and form, and at the same time by change in the direction of the chewing movement, which implies a new position of the molar rows at the beginning of the chewing cycle and that this modification was made easier by the tooth morphology of the likely insectivorous *Potwarmus*. Recent progresses in the knowledge of the odontogenesis of the mouse can be used to better understand the pattern of morphological change documented by fossils. If several aspects of the origination of the murine dental pattern could be related to heterotopic and heterometric changes of the patterning cascade regulating the cuspidogenesis, changes of cusp shape remain to be explained.

Physical Performance and Fitness in Lizards

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Considering one of the basic tenets of evolutionary physiology, i.e., that physical performance and fitness are tightly linked, one may expect phenotypes with exceptional physiological capacities to be promoted by natural and sexual selection. Our analysis of locomotor performance in the common lizard (*Lacerta vivipara*) demonstrates that endurance (running time to exhaustion) is highly heritable, yet selection in favor of this trait can be unexpectedly weak. In juveniles, the expression of a genetic predisposition to high physical performance at birth strongly depends on dietary conditions experienced early in life. This caused shifts in natural selection regimes between poor and rich environments. In subadults and adults, physical performance was also a poor predictor of natural and sexual selection. Altogether, these results could explain why physical performance remain considerably variable in animal populations.

A Predictive Model of Paleobiological Estimation of Bone Growth Rate from Bone Tissue Types in Extinct Amniotes

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Amprino's rule (according to which the diversity of periosteal bone tissue types is the expression of different growth rates) has been previously used to infer bone growth rates of extinct diapsids by using information obtained only in extant birds. This procedure is problematic because at least the first two extant sister-groups of an extinct taxon (the extant phylogenetic bracket) should be used to estimate character states of this extinct taxon. Here we present a predictive model of paleobiological estimation of bone growth rate based on data obtained from a sample of 44 growing individuals belonging to 13 species of amniotes (3 species of mammals, 3 cheloniens, 4 lepidosaurs, 1 crocodile and 3 birds). This model allows the estimation of bone growth rate in extinct amniotes by taking into account the phylogenetic position of the fossil under analysis, as well as a number of histological variables such as the density of primary osteons, the density of simple vascular canals and the shape of osteocytes. The application of this model may help to elucidate the evolution of bone (and overall) growth patterns in amniotes.

Comparative Anatomy: Paths to the Future

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Comparison is an elementary process of science. However, this process leads to different kinds of investigations according to what is compared: experimental situations or biological things. If the goal of science is to rationally explain the real world, then comparison of biological things leads to explain their origins. Among natural sciences comparative anatomy illustrates the kind of inference to which comparison of static things is devoted. Functional anatomy is more devoted to compare dynamic processes, or experimental representations of dynamic processes, than to compare static objects. The social challenge of comparative anatomy today is that it is not taught anymore. In the past, we used to teach separately the pure acquisition of knowledge of anatomical structures in one hand, and pure comparative methods disconnected from any anatomical background or realities in the other hand. There is no place where we teach theoretical and practical comparative anatomy devoted to explain patterns of characters through the diversity of living things. Paradoxically, huge amounts of undiscovered anatomical structures remain to be exploited (just think about myology!). The future of systematics is neither in comparative genomics nor in labs of molecular systematics, but in those museums that will be able to maintain the mutual enlightment between comparative anatomy and molecular systematics.

Interplay of Growth and Mechanics on Dinosaur Bone Histology

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Bone histology of extinct tetrapods is microstructurally diverse. That diversity is influenced by extrinsic (e.g., mechanics) and intrinsic (e.g., ontogenetic and phylogenetic constraint) factors. Over two decades of investigations have begun to disentangle the interplay of those factors in dinosaurs and emphasize the relative importance of ontogeny. Although ontogeny in dinosaurs can be quantified using skeletochronology, the uncertainty of growth estimates remains largely unknown. Here, I present a framework to assess the uncertainty in growth estimates of dino-

saurs. Uncertainty in growth estimates of dinosaurs exists because no single bone preserves a complete record of cortical deposition. Medullary expansion and cortical remodeling remove or obscure lines of arrested growth (LAGs), which are measured to estimate ontogenetic status. Several models of periosteal deposition were used to estimate the number and spatial location of missing LAGs. Median age estimates were calculated. Standard errors of those medians suggest that age uncertainty for the assessed dinosaurs is lesser for younger specimens and greater for older ones. Histological parameters, such as vascular canal orientation and proportion of secondary remodeling, in the assessed dinosaurs relate strongly to ontogenetic status. Increased deposition of radial vascular canals positively correlates with the acceleration of limb growth within independent lineages of dinosaurs. In addition, the proportion of secondary remodeling strongly correlates with both the ontogenetic age of the specimen as well as the rate of medullary cavity expansion. Those histological parameters in dinosaurs suggest the relative importance of ontogeny over mechanics on vascular organization and bone remodeling.

The Conditions Required for an Economic Standing Position in Humans: Key Role of the Pelvic Parameter: The Sacral Incidence Angle. Growth, Evolution and Plasticity of This Parameter

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Human bipedal adaptation, more than any other locomotor adaptation, lends itself to a study of its optimization. The main problem is to achieve a sagittal balance of the trunk on the lower limbs using minimal energy. We test the hypothesis that the analysis of the mechanical and morphological relationships between pelvis and vertebral column would permit us to understand the factors involved in its economy. We measured the standing postures of men and women using barycentrometer measurements and full spine radiograph with a single referential system, as well as in vivo measurements of the weight and center of weight supported by each vertebra and the coxo-femoral joints. The position of the center of weight in front of or behind the vertebrae or the coxo-femoral joints requires an opposite muscle force to ensure mechanical stability. The results suggest that, in the sagittal plane, there is a tendency to maintain the most efficient position of the body in terms of muscle fatigue and vertebral strain. A new sagittal pelvic parameter, the sacral incidence, is the most significant parameter. This angle (35°–75°) determines the adequate values of sacral slope, lumbar and dorsal curvatures. These four parameters are tightly correlated. Incidence increases during postnatal growth and with the associated changes in spinal curves. We present the lower values of this parameter in non human primates and its significant increase in young Japanese macaques trained for bipedalism. We conclude that adequate correlations between the degree of incidence and of vertebral curves ensure an economical balance for standing position.

The Amphibian Anatomical Ontology

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The need for terminological standardization is particularly important in amphibian anatomical research. Amphibians are commonly used for gene expression and embryological studies, yet the three orders—Salientia (frogs and toads), Caudata (salamanders and newts), and Gymnophiona (caecilians)—are so morphologically distinct that studies of one order are rarely applied to another. Moreover, three different anatomical lexicons are used for the three orders. As a consequence, research on amphibian gene expression, embryology, and comparative anatomy is limited. The solution to this problem lies in the development of an amphibian anatomical ontology, which will accommodate the diversity of structures present in the group and facilitate consistent use of vocabularies in the annotation of amphibian morphology. An amphibian anatomical ontology will allow morphologists to determine the preferred name for a given anatomical structure, evolutionary biologists to find similar morphological structures of phylogenetic significance present among different species, and embryologists to compare gene expression among embryos of different taxonomic groups. Herein we describe our community-based efforts to develop the Amphibian Anatomical Ontology, including software-based text mining, community contribution, curation, and acceptance, and database access and integration. We also describe the project website—www.amphibanat.org—which includes discussion boards, links to contacts and mailing lists, and the user interface for searching, browsing, and navigating the ontology.

Patterns of Cranial Skeleton Ontogeny in Syngnathidae: A Comparison Between *Syngnathus rostellatus* and *Hippocampus capensis*

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The special reproductive strategies, the elongated snout without teeth and the fastest food intake ever recorded among teleosts, make pipefishes and seahorses (Syngnathidae) very remarkable fish. Despite their exceptional appearance, little is known about their morphology and ontogeny. The aim of this study is to compare the ontogeny of the head skeleton in *Syngnathus rostellatus* (Nilsson's pipefish) and *Hippocampus capensis* (Knysna seahorse). First, a detailed morphological study was performed using cleared and stained specimens. In addition, serial histological sections were used to create graphical 3D-reconstructions. Second, a biometrical study was carried out to analyze growth patterns in the head region of both species. The obtained osteological results were compared with those of *Gasterosteus aculeatus*, which has a basal position within the same order. Based on the results of this study and data from literature it could be concluded that: (1) already at the moment of being expelled from the brooding pouch, the juveniles are provided with a feeding-apparatus comparable to the adult situation, (2) *S. rostellatus* and *H. capensis* both grow isometrically and have an almost similar growth rate, (3) apart from the seahorse braincase being tilted with respect to the ethmoid region during early ontogeny, most dissimilarities between *S. rostellatus* and *H. capensis* are related to the more elongated snout of the first; and (4) the differences with *G. aculeatus* involve a series of structural specializations in *S. rostellatus* and *H. capensis* that can be related to powerful and fast suction feeding.

Integration of the Head and Forelimb in Bipedal Hominids

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Integration, a fundamental property of organisms, occurs via multiple mechanisms and for diverse reasons. Although there has been substantial work on the genetic and epigenetic mechanisms by which developmental integration occurs, we have less of an understanding of the evolutionary relationships between functional and developmental integration. In this respect, human evolution provides an interesting test case. In quadrupedal mammals, there is considerable functional integration among and between the limbs, but little functional integration between the limbs and the skull. The evolution of bipedalism in hominids, however, provided new opportunities for novel forms of integration by emancipating the forelimbs from any major role in locomotion. Here we consider how the forelimb and head become increasingly integrated in the genus Homo because of the biomechanical challenges of running. While the arm and the head interact little during walking, we have found that, during running, the stance side arm acts as a counterbalance to the head, stabilizing it against impulsive pitching forces generated by the heel strike transient. Moreover, the functional properties of this linkage may have driven several developmental changes in the proportions of the arm and the anatomy of the shoulder girdle during human evolution. Thus, evolutionary changes in arm and head morphology during human evolution may be more integrated than previously considered.

Scaling of Locomotion in Dogs

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The scaling of locomotion has long been under investigation and from many diverse points of view. All previous works share one limitation: the samples used included animals from diverse groups, so that the differences observed could not be characterized clearly whether they are due solely to the different size of the animals, or to a different phylogenetic signal. Domestic dogs increasingly represent a well established evolutionary model group for genetic as well as zoological questions. The entire genome is now sequenced and the history of the different breeds is also well known. In a short time, breeds of different size and shape were bred. The resulting large size range (e.g., Chihuahua at 0.5 kg to English Mastiff at 90 kg) and the fact that all breeds belong to the same species makes this group an ideal sample to investigate how animal size influences locomotion, especially kinematic parameters. Representatives of 30 breeds, with 10 animals per breed, were studied. The proportions of the limb segments as well as of the trunk were measured. Despite the different sizes and shapes of the breeds, intralimb proportions are very similar, such that it seems that intralimb proportion escapes selection. Animals were filmed during locomotion using highspeed cinematography coupled with a marker based motion analyzing system to calculate kinematic parameters. As with the intralimb proportions, the kinematic parameters were also found to be relative independent from the sizes and shapes of the different breeds.

Morphometric Geographic Variation in the Three-toed Sloth *Bradypus variegatus* (Mammalia, Xenarthra)

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The three-toed sloth *Bradypus variegatus* Schinz, 1825 is the most widespread species among the extant sloths. Strictly arboreal and folivorous, they are found in tropical forests and also non-forested regions of Brazil, such as the Caatinga and Cerrado. Recent studies on populations of the Atlantic forest observed a high genetic diversity across its geographic sampling, representing a north-south divergence. This genetic gradient has raised the question of the possible existence of a morphocline when comparing populations on different geographic regions. This study investigated, using univariate and multivariate analyses of cranial morphometric characters, the geographic variation in *B. variegatus* among four areas throughout Brazilian territory: East and West Amazon, North and South Atlantic forest. The geographic variation seems to be clear between the Amazonian populations and those from the Atlantic forest. The East Amazon sample may be characterized by smaller overall cranial size, and relatively smaller rostral and mandibular width. Although there was no significant size divergence among the other three regions, there were differences regarding cranial shape between the West Amazonian sample and the one from the South Atlantic forest. The discriminant analysis separated the four geographical regions and the rostral width also had the highest loading in CAN1. In general, there were two main clades grouping the Amazonian populations and those from the Atlantic forest. Both seem to differ in overall cranial size and in some aspects of cranial shape. Our results, therefore, suggest the existence of a morphocline throughout *B. variegatus* distribution along Brazilian territory.

Mechanism of Sound Production in *Oreochromis niloticus* (Cichlidae)

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The mouthbrooding cichlid *Oreochromis niloticus* (Nile tilapia) is one of the best studied fishes in the world, and is considered to be an important economic species. During courtship, males form dense aggregations where they defend nets to which they attract females. This behavior is accompanied by sounds made principally towards conspecifics males. Currently, different studies in *Tramitichromis intermedius* and *Oreochromis mossambicus* have hypothesized that the pharyngeal jaw apparatus and the swimbladder were involved in sound production. The aim of our study was to determine the sound producing mechanism in males of *Oreochromis niloticus*. The coupling of kinematic data input from high-speed X-ray videos (250 and 400 fps) and sound recordings have allowed us to observe the movements of different skeletal pieces (pelvic and pectoral girdle, cleithrum, pharyngeal jaws, basis of the caudal fin, etc.) during sound production. The analysis will allow determining how skeletal pieces are involved in the sound production mechanism.

Quantification of Physical Properties of Foods in Vertebrate Diets

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The physical properties of foods form the stimulus for tooth and jaw adaptation. They have had little attention, but it is difficult to see how adaptation will be understood without them. There are two aspects: (i) external physical attributes (particle shape and size, the volume of food in the mouth and abrasiveness), united by describing the food surface, and (ii) internal mechanical properties that define the resistance of a particle to the formation of new surface. Such new surface forms mainly by fracture. In foods with linear stress-strain curves, the best mechanical measures are the elastic modulus (E) and toughness (R), where the latter refers to the energy expended per unit crack area. In such foods, the fracture force is proportional to their product, (ER) 0.5, whereas displacement is proportional to their ratio: (R/E) 0.5. In such foods, it is possible to relate the bite force at failure to these property groups via a relevant measure of food particle size. The ease of fracture is less easy to define when energy imparted by loading can be dissipated in time-dependent behavior, and thus not available for cracking, or stress-strain curves are very nonlinear. The presentation will involve a demonstration of techniques for measuring moduli (tension, compression, bending, indentation), toughness (notching, cutting, wedging, wires) and friction, plus indicate how load-unload cycling studies can help in establishing energy partitioning during food deformation.

Pelvic Fin Locomotion in Benthic Batoids

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Studies of locomotion in batoids have largely focused on pectoral fin movements. However, pelvic fin "punting," has been described as an important locomotive mechanism in skates. Other benthic batoids have been observed performing similar punting movements despite lacking the skate's specialized pelvic fin structure. In this study, we compared the use of pelvic fins in locomotion among three benthic batoid species: Bancroft's numbfish, *Narcine bancroftii*, the yellow stingray, *Urobatis jamaicensis*, and the Atlantic stingray, *Dasyatis sabina*. These species allow for comparative analyses across the three benthic batoid swimming styles: axial undulation, pectoral undulation and an intermediate between pectoral undulation and oscillation, respectively. To determine structural and locomotory differences between the pelvic fins of these species, we compared the pelvic fin to pectoral fin surface area ratios, skeletal morphology, and swimming kinematics, including punting distance (body length (BL)), speed (BLsec-1), glide duration (sec), and thrust duration (sec). The relative size of the pelvic fins may indicate their importance in locomotion, as the fins of *N. bancroftii* ($n = 10$) were significantly larger than those of *U. jamaicensis* ($n = 6$) and *D. sabina* ($n = 10$). In fact, whereas speed is highly variable, *N. bancroftii* punted a significantly greater distance (0.80 ± 0.26 BL; $n = 4$) than *U. jamaicensis* (0.69 ± 0.39 BL; $n = 4$) and *D. sabina* (0.32 ± 0.17 BL; $n = 4$), without any difference in duty factor. Moreover, punts by *U. jamaicensis* and *D. sabina* were always accompanied by pectoral fin movement. To better understand the components contributing to punting ability, we also described and compared pelvic fin musculature and skeletal elements.

Teeth: Part of a Complex System

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Teeth form an integral part of the masticatory system. Although they are subject to phylogenetic constraints, they are also well-adapted to cope

with the cyclical forces encountered during mastication. Owing to their complex 3-dimensional structure it is difficult to determine which microanatomical feature may constitute a functional adaptation, an epigenetic epiphenomenon or a phylogenetic artefact. Histological and morphometric techniques have been instrumental in shedding light on these questions, but each has their limitations. Here we propose that a better understanding of tooth function and phylogeny may come from isolating certain structures and by subjecting them to functional (and phylogenetic) analyses separately. Using finite element stress analyses, such an approach has allowed us to make predictions about the functional and phylogenetic importance of the unique, i.e., scalloped, morphology of the dentino-enamel junction in primates and has enabled us to infer kinematic parameters of the mandible from enamel microstructure alone. While engineering techniques employed on biological structures can only aid in the formulation of hypotheses, the results presented here highlight the significance of such multidisciplinary approaches for the study of dental microstructure, on the one hand, and for the elucidation of (possible) dietary adaptations of extinct species, on the other. This work is supported by The Leverhulme Trust (F/00 025/A) and the Natural Environment Research Council (NER/A/S/2003/00347/2).

Observations on the Turbinal Elements of the Ethmoid Bone of Marsupials

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The skeleton of the nose and associated sinuses and recesses are virtually unrepresented in phylogenetic analyses. This is partly because this portion of the skull, particularly the ethmoid, is structurally complex and difficult to observe in situ and intact. Here, I present some potentially phylogenetically informative observations based on comparative examination of the ethmoid from nearly every major clade of extant marsupials. High resolution X-ray computed tomography was utilized to visualize the ethmoid of intact skulls to document this anatomy. The ethmoid bone of mammals comprises several turbinal elements (maxilloturbinal, nasoturbinal, ectoturbinals, endoturbinals) that coalesce caudally to form the cribriform plate. The shape and complexity of the maxilloturbinal is variable between different marsupial taxa. For instance, the maxilloturbinals of the koala and wombat are simple, without many scrolls, and are tube-like in form caudally. In contrast, the maxilloturbinal of the Virginia opossum is complex, possessing many branches and scrolls throughout its rostrocaudal length. The nasoturbinal and corresponding maxillary recess also show considerable variability in dorsoventral extent, shape, and rostrocaudal placement in the nasal cavity relative to the maxilloturbinal. Presence of five endoturbinals (not counting the nasoturbinal) and two ectoturbinals appears to be the ancestral condition for Marsupialia. However, the number of endoturbinals ranges from four to six and the number of ectoturbinals ranges from one to three among marsupials. In conclusion, there is great potential for phylogenetic signal of the ethmoid bone for marsupials, particularly the maxilloturbinal and nasoturbinal elements.

Histological Microstructure of the Claw of the African Clawed Frog, *Xenopus laevis* (Anura: Pipidae)

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Claws, or homologous structures (e.g., nails and hooves), are consistent components of amniote anatomy. Claws are also present in certain extant non-amniote taxa, such as the African clawed frog, *Xenopus laevis*. Claws in amphibians are rare and these non-amniote heavily cornified systems are often overlooked when discussing tetrapod integument evolution. The histology of the integumentary component of the claws of *X. laevis* is described, and is the first of its kind for an amphibian heavily keratinized system. The claw sheath is composed of a localized thickening of the corneous region of the epidermis that envelops the entire terminal phalanx of pedal digits one to three. Differences in the non-cornified layers of the epidermis of the claw and non-claw region of the digit include an overall grainier appearance of the cytoplasm and increased abundance of desmosomes on the intermediate spinosus cells. The microstructure of the claw sheath of *X. laevis* differs from that of amniotes in several respects, including corneocyte orientation, which suggests a distinct mode of growth in each group. Further experimental work may confirm a conserved pattern of cornification in these structures in tetrapods, making rare amphibian heavily cornified systems such as claws critical to gaining a complete understanding the evolution of tetrapod keratinization.

Feather Growth and Renewal—F.R. Lillie's Unhappy Legacy

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Publications by Lillie and/or his Chicago colleagues during the 1930s and early 1940s underlie most available accounts of adult feather development in secondary and tertiary texts. As introduced in 1932, Lillie's invocation of the principle of concrescence in the context of feathers was allegedly "modified" in later papers through changes in figures and accompanying legends: in fact, text meaning remained fundamentally unchanged throughout (Maderson, Int Comp Biol 42:1270–1271). The phrase "concrescence theory" is absent from Lillie's widely quoted 1942 Biological Review, but its implications remained integral to this paper. From 1934–1939, Lillie's concrescence theory of feather development was extensively criticized by two English workers, Paul 'Espinasse and Ann Hosker, but their papers were ignored or cited inappropriately in publications from Chicago. Archival correspondence between Lillie and 'Espinasse elucidates the background of these matters. The original "concrescence theory" derived from Wilhelm His' writings popular in Boston during Lillie's early career: its unstated implication of independence of two parts of a bilateral structure led Lillie to a fallacious assertion, which was identified by 'Espinasse. Lillie claimed to have "new morphological data" that led him to contradict classical conclusions concerning direction of cell movement during feather growth: these claims remain unsupported to this day—Lillie's "concrescence" was an ad hoc assertion facilitating interpretation of his endocrinological data. Lillie was aware of published criticisms and he and his colleagues chose to ignore or downplay them. The relevance of these historical events to recently proposed models of feather evolution and development will be discussed.

The Developmental Significance of a Neglected Feather Component

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Largely ignored in most anatomical and even ornithological texts, the superior umbilicus (SU) is a median pit or slit located within the proximal, U-shaped end of the rachidial groove (PURG). On the feather's inner aspect a semi-circle of short plumulaceous barbs continuous with the two lateral rows of barbs along the rachis always delineates the PURG. In patent SUs an α-keratogenic pulp cap may protrude through the lumen; remnants of more distal caps may sometimes occur along the PURG. Reflecting interspecific variability, SUs may be small or absent leaving only the smooth, ß-keratogenic surface of the rachis. Adjacent to the PURG, a few captured caps may be found closely embedded in pith within the rachis. We interpret these features of a newly-defined "superior umbilical region" (SUR) as results of the transition from spathogenesis (when differentiating barb ridges, arranged spirally around a column of pulp caps, separate) to calamogenesis (when cells remain adherent producing a tubular calamus). During cortical cell epithelialization in both barbs and rachis, additional ß-keratogenic cells swell to form pith tissue that has several functions: 1) facilitating cortical cell flattening and elongation; 2) strengthening beam structures of barbs and rachis at a fraction of the mass of a solid structure; and 3) in SUR specifically, enveloping α-keratogenic pulp caps derived from regressing dermal core to seal the hole in the rachis that would otherwise represent a wound after spathe deployment. This last feature also ensures mechanical continuity between the rachis and calamus.

Interlimb Coordination in Dogs: Time and Space Variations Related to Speed and Gaits

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Mammals are able to modify their velocity within a large range of speeds, by modifying their interlimb coordination, or gaits, in time as well as in space. Many of them use symmetrical gaits for slow locomotion and asymmetrical gaits for faster locomotion. In this work, we studied the relationship between gaits and speed by describing the time and the space interlimb coordination in dogs, within a large range of speeds. We proved that the coordination within the pairs of limbs, in time as well as in space, depends only on the kind of gait: symmetrical gaits require an increase of lags or gaps within the pairs with an increase in speed to maintain a perfect alternation between the limbs of the same pair. To the contrary, asymmetrical gaits require a relative consistency in the lags and gaps between the limbs of the same pair whatever the speed. On the other hand, the temporal coordination between the pairs is specific to the gait and is not related to the speed, whereas the spatial coordination between the pairs is strongly related to the speed, due to the increasing occurrence of one or two suspension phases. Moreover, at the highest speeds, the sagittal flexion of the vertebral axis is responsible for the increase in the stride length whereas there is no change in the time variables because they have already reached their limit.

MorphologyNet, the Digital Library of Interactive, 3D-images of Animal Anatomy

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Technological developments in the generation of three-dimensional (3D), high resolution animations and interactive images are increasing at an exponential rate. The importance and potential of these tools has not escaped the biological community, wherein 3D-visualizations of anatomical structures are being generated for use in research and education. By creating realistic 3D-reconstructions of anatomy, researchers are better able to examine small and internal structures, study modifications to structures through development, describe diversity in anatomical structures in various groups, and share their findings with colleagues. Herein, we describe the development of MorphologyNet—www.morphologynet.org—a community-based digital library of 3D, interactive digital reconstructions of anatomy. MorphologyNet was created in response to the growing need of the scientific community to share 3D-anatomical reconstructions through the web, and serves as a depository for researchers generating 3D-images. MorphologyNet also includes an easy-to-use interface that allows high resolution animations to be rotated, resized, "dissected", and customized for color, texture, and opacity. Additional functionality, including linear, geometric, and volumetric analysis tools currently are under development.

Feeding Kinematics and Performance of Hawaiian Stream Gobies, *Lentipes concolor* and *Awaous guamensis*: Implications for Habitat Distribution

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Distributions of Hawaiian stream fishes are typically interrupted by waterfalls that divide streams into lower and upper segments. Hatched larvae are flushed into the ocean, and must climb these waterfalls to reach adult habitats when returning back to freshwater streams. Stream surveys and studies of climbing performance show that *Lentipes concolor* can reach fast-flowing upper stream segments, but that *Awaous guamensis* reaches only slow-flowing lower segments. Gut content analyses indicate that diet differs only by 10% or less dry weight for most major components (green algae and invertebrates). This might suggest that feeding kinematics and performance of these two species would be similar. Alternatively, feeding kinematics and performance of these species might be expected to differ in relation to the different flow regimes (faster feeding for *L. concolor*, slower feeding for *A. guamensis*). To test for such differences, we compared suction feeding kinematics and performance between *A. guamensis* and *L. concolor* through analysis of high-speed video footage. *Lentipes concolor* showed significantly faster jaw opening performance which may facilitate suction feeding in the fast stream reaches where *L. concolor* typically inhabits. Morphological differences between the feeding apparatus of these species appear to contribute to the differences in performance, which might also help to explain the absence of *L. concolor* from lower stream reaches where *A. guamensis* inhabits.

Relationships Between Skeletal Mechanics, Bone Geometry, and Histomorphology in the Limb Bones of Vertebrates

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How do skeletal mechanics and growth interact to influence bone morphology? Can mechanics be predicted from skeletal morphology and histomorphological features? These are questions that have intrigued functional anatomists, paleontologists, mechanical engineers, and skeletal biologists for years, leading to numerous quantitative, functional, and histological analyses relating form and function in the vertebrate skeleton. Integrative approaches to these questions, combining analytical functional and quantitative morphological data often inform us most about these relationships in the skeleton. Through a series of experiments, we investigated ontogenetic relationships between limb bone form and skeletal mechanics in a diversity of vertebrate taxa (goats, emu, monitor lizards). We measured *in vivo* bone strains in various limb bones during ontogeny in each taxon. Bone strain patterns and magnitudes were related to ontogenetic changes in cross-sectional bone geometry. Reconstructions of the cross-sectional strain environment throughout each bone's cortex were compared to regional patterns of bone growth and histomorphology, including bone porosity, remodeling, and collagen fiber orientation. In general, cross-sectional bone geometry and periosteal bone growth corresponded to the overall loading patterns at the bones' mid-shafts. Limb bones loaded predominantly in axial bending had more asymmetrical cross-sections than those loaded in torsion, which were fairly circular in cross-section. In contrast, histomorphology generally did *not* relate to mechanical loading or regional strain distributions within the bones. This lack of correlation could possibly relate to other influences affecting bone modeling and remodeling, including growth physiology, bone metabolism, or other mechanical influences unaccounted for here.

Dental Microwear in Domestic Sheep and Goats: Implications for Palaeodietary Analysis

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Dental microwear has been widely applied to dietary reconstruction in palaeontological contexts. More recent research has, however, begun to explore the potential of this method for reconstructing animal diet during the Holocene. Here, the focus is on the role of animal diet in understanding past husbandry regimes, including domestication, and their impact on the environment. This research has demonstrated that microwear analysis has the potential to identify particular foddering and grazing regimes but has also begun to question established theories of microwear formation in ungulates. In this paper, I will review research undertaken on diet-microwear relationships in modern and archaeological domestic sheep, goats and pigs and will explore the significance of this work both for the understanding of animal-human relations in the past and for microwear studies in general.

Variation in the Inner Ear Skeleton in Squamates: A Preliminary Report

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The inner ear serves both hearing and equilibrium functions. The bony skeleton of the inner ear of squamates (lizards, snakes, amphisbaenians) comprises the semicircular canals and their associated ampullar recesses, the vestibule, the lagenar (cochlear) recess, and various ducts and nerve passages. The generation of digital endocasts (three-dimensional representations of void spaces) from high-resolution X-ray computed tomographic (HRXCT) datasets permits the visualization and qualitative and quantitative comparison of the inner ear skeleton. Almost 200 HRXCT

datasets have been generated as part of the National Science Foundation Assembling the Tree of Life project for squamates (Deep Scaly). These represent extinct and extant taxa spanning the full spectrum of body size (skull lengths from <1 cm to 0.5 m), lifestyle (fossorial to aquatic to arboreal to gliding), and phylogenetic position within Squamata. Significant differences exist in the relative size of the vestibule and the statolithic mass, the relative diameter of the semicircular canals and their radii of curvature, and the degree of differentiation of the lagenar recess, among other things. These differences are discussed as they relate to body size and lifestyle, all in the context of current hypotheses of squamate phylogeny.

The Postorbital Palatoquadrate Articulation in Elasmobranchs

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Among modern elasmobranchs (neoselachians), a postorbital palatoquadrate articulation occurs only in hexanchiforms. However, a similar postorbital articulation is present in many Paleozoic chondrichthyans. Thus, the articulation in hexanchiforms has been widely considered to be an ancient, conserved feature and became secondarily conscripted as a component of the classsical "amphistylic" jaw suspension pattern. It is also widely assumed that this articulation was secondarily lost in the majority of modern elasmobranchs. These assumptions are challenged by morphological differences in this articulation between modern hexanchiforms and early chondrichthyans, particularly its relationship to cartilages forming the postorbital process. One pattern is widespread among Paleozoic chondrichthyans (including xenacanths, "ctenacanths", symmoriiforms, *Cladoselache*, *Pucapampella*, and probably *Doliodus*). By contrast, a postorbital articulation is absent in hybodonts (the putative sister group of neoselachians), and the peculiar "sub-postorbital" articulation of *Tristychius* (possibly a sister to hybodonts plus neoselachians) resembles the ancient pattern rather than the hexanchiform one. A hexanchiform-like articulation occurs only in a few extinct galeomorphs (e.g., *Synechodus*, *Paraorthacodeus*); paradoxically, it was weak or perhaps even absent in some early hexanchiforms (e.g., *Notidanoides*). Although a postorbital articulation is probably a very primitive chondrichthyan feature that was conserved in several early elasmobranch lineages, the articulation pattern in hexanchiforms is not widely distributed among elasmobranchs (including extinct forms), and is resolved most parsimoniously as a cladistically derived condition within neoselachians.

Chordate Mechanoreceptors and Origin of Vertebrate Hair Cells

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Urochordates and cephalochordates are simple non-vertebrate chordates, the study of which, based on comparison of homologous structures, may contribute toward understanding the origin of vertebrates and the characteristics of the common ancestor. A recently debated issue regards the presence, in non-vertebrate chordates, of cell populations homologous with cranial placodes and the neural crest, considered evolutionary innovations in vertebrates. Data are accumulating to demonstrate that both the genetic machinery involved in placode/neural crest differentiation and ectodermal homologues are found in non-vertebrate chordates. In the oral region of urochordate ascidians, we have found the coronal organ, perhaps a counterpart of the vertebrate lateral line, composed of mechanoreceptors which share, with vertebrate hair cells, a number of features supporting their possible common derivation from an ancestral type of sensory cell. These features regard comparative analysis of position, cytological characteristics (mechanoreception ability, row alignment, presence of cilia, presence of afferent and efferent synapses) and developmental gene expression. All these aspects indicate that cell populations with some characteristics of acoustico-lateral placodes also occur in non-vertebrate chordates and, in particular, that the rudiment of the oral siphon has the properties of a neurogenic placode. By extension, the last common chordate ancestor also possessed neurogenic placodes. We discuss the possibility that the hair cell is an old acquisition, the origin of which may be traced back to the chordate ancestor and which evolved independently in the different chordate lines.

The Atypical Hindbrain: Molecular and Morphological Segmentation of the Medulla Oblongata

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The vertebrate hindbrain has a metameric organization, appearing subdivided into segments or rhombomeres along its rostrocaudal axis. At early neural tube stages, these rhombomeres express given combinations of developmental genes and are limited by boundaries that display specific cellular characteristics. However, these features are not fully shared by the rostralmost hindbrain units (whose development depends on the isthmic organizer) nor by the caudal hindbrain units, which form the medulla oblongata or myelencephalon. The latter appears as a homogeneous, non-subdivided region, as shown by the expression pattern of several molecular markers, i.e., those related to neuronal differentiation. There is overt regionalization along the dorsoventral axis, that is, involving longitudinal columns, but not along the rostrocaudal axis. However, quail-chick fate maps of caudal hindbrain show that it is subdivided rostrocaudally into 5 pseudorhombomeres (Cambronero and Puelles, 2000, J Comp Neurol 427:522) which were empirically defined according to adjacent half-somite boundaries. These pseudorhombomeres lack overt interneuromeric boundaries, but have a metameric nature, since they correspond to serial developmental units of the medulla oblongata, sharing a fundamental dorsoventral organization and showing a correlation with morphological boundaries of given nuclei. We have analyzed at late stages of differentiation this medullary segmental map in relation to the expression of molecular markers, such as genes coding for transcription factors or enzymes involved in neurotransmitter metabolism. We propose a synthetic neuromeric framework for the developmental pattern of this brain region, integrating results from fate-maps, gene expression patterns and morphological analysis of medulla oblongata nuclei.

Ventilation is Metabolically Expensive in Resting and Running Guinea Fowl

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Avian ventilation may be metabolically costly because the mechanical work required to overcome the inertial and gravitational resistance to movement of the mass of the sternum, associated flight muscles, and viscera is expected to be high. A novel method was used to measure the cost of ventilation (COV) in resting and running guinea fowl (*Numida meleagris*). Birds' caudal air sacs were cannulated and air was pumped through the lungs and out the nares and mouth (unidirectional artificial ventilation: UAV) until the flow rate was sufficient to decrease ventilatory drive and stop ventilatory movements. The difference in oxygen consumed with and without ventilation was assumed to be COV. The COV of guinea fowl was found to be considerably higher (23% of resting metabolism, 32% of running metabolism) than estimates in mammals and reptiles (1-6% of resting metabolism, up to 15% in running mammals). Expired PCO_2 did not decrease drastically during UAV, suggesting that high the COV measured is not to due to UAV induced metabolic suppression. Additionally, the COV per unit ventilated was the same in resting and running birds (20.3 ml O_2 l^{-1} ventilated), although higher volumes of air were moved in running than resting birds (at rest: minute ventilation 0.31 l min^{-1} kg^{-1}, tidal volume 16 ml kg^{-1}; during running: minute ventilation 1.5 l min^{-1} kg^{-1}, tidal volume 25 ml kg^{-1}). These data raise the question of why the ancestors of birds shifted from the primitive mechanism of breathing, which is very economical, to one that consumes more energy.

Do Patterns of Correlated Divergence Resemble Intraspecific Patterns of Covariation? A Study of Skull Evolution in a Clade of Ecologically Diverse Rodents

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The variational properties of complex structures such as the vertebrate skull largely reflect developmental and functional interactions among their components. Such variational properties, e.g., degree of morphological integration, canalization, or developmental stability, ultimately shape the structure of morphological variation within populations and potentially their evolutionary trajectory. Alternatively, divergence may be

relatively insensitive to these attributes, reflecting mostly particular responses to current selective pressures. To assess these hypotheses, variational attributes of skulls were estimated for a clade of Neotropical rodents spanning a wide range of lifestyles. Variances and multivariate correlations were computed for shape attributes for each species using geometric morphometric methods applied to 32 partitions of the skull, corresponding to localized anatomical regions. Intraspecific patterns of (co)variation were then compared to patterns of clade disparity (i.e., net amount of interspecific divergence) and co-divergence. Results indicate that intraspecific correlation patterns are poor predictors of the patterns of morphological divergence among related species, so that skull regions that appear more correlated within species do not diverge jointly. However, magnitudes of intraspecific variance and interspecific divergence appeared correlated in certain regions, such as the molar alveoli, both hypo-variable and phylogenetically conserved, and the mandible, palatal, and frontal-parietal regions, both hyper-variable and highly diverse. These results suggest that while trajectories of skull shape divergence may not be constrained by the structure of population variation, regulation of variation within populations, e.g., via canalization, might still affect long term evolvability. Results are discussed in terms of the traits' functions and the ecological diversity of the sampled species.

Using Morphological Techniques to Quantify Fishing Impact on Populations: The Case of Illegal Shark Finning in Northern Australia

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Arial surveys have clearly shown an increase in illegal shark fishing across Northern Australia, mainly by foreign fishing vessels. Vessels intercepted by Australian Fisheries Management Authority (AFMA) surveillance have their illegal catch, which includes dried fins, confiscated. Identification of the shark species represented in these seized fin collections is crucial to estimation of exploitation rate for north Australian sharks as the real catch is highly likely to be significantly greater than estimated from legal harvest. A consequence of this illegal fishing is that Australian shark fisheries managers do not have a sound estimate of the total shark catch in northern Australia. To improve the estimates of illegal species harvest, species identification from dried fins is required. A variety of approaches, including genetic and morphological, have been suggested, each with advantages and disadvantages. The aim of this project is to assess whether morphological techniques can identify species found in confiscated fin collections. Morphological characters such as denticle shape, and fin size and shape have been evaluated for their ability to identify shark species from dried fins using morphological analysis software and multivariate statistics. From these results, morphological identifications will be tested against genetic identifications of apprehended fins. If useful, the resulting morphological techniques will be used to construct diagnostic keys to facilitate improved stock structure/stock assessment estimates for species. This project is part of a large initiative with a large number of collaborative organizations.

Selection Patterns Driving Human Skull Evolution: Insights from Quantitative Genetic Models

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Modern human skull morphology is the result of many evolutionary changes within the hominid lineage. Derived morphological features in *Homo sapiens* are a globular and expanded cranial vault, a strong cranial base flexion, and a smaller retracted face. It had long been accepted that modern human craniofacial form had evolved as an adaptive response to bipedal locomotion, to brain and sensory capsule evolution, as well as to dietary changes. However, this view is currently challenged. In this study we use quantitative genetic methods to provide insight into the genetic basis of the architecture of human skull and to test which selective forces may have driven modern human evolution. A cranial sample from Hallstatt (Austria) with 350 complete skulls falling into multigenerational pedigrees was analyzed by means of 3D geometric morphometric techniques. Skull shape was recorded as a hemicranial configuration with 28 left landmarks. Phenotypic, additive genetic and environmental variance covariance matrices were computed following an animal model and by applying restricted maximum likelihood methods, and these were introduced at the multivariate animal breeder's equation to simulate the response to selection. In a retrospective analysis, different selection differentials were designed in order to test the likelihood of specific adaptations (bipedalism and encephalization) being responsible for modern human skull autopomorphies. The response to selection analysis highlighted that directional selection for a larger anterior neurocranial region together with the morphological changes derived from bipedalism could have been sufficient forces to trigger human skull evolution.

Cranial and Central Nervous System Morphological Integration and Evolution in Birds

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Since the works of Cuvier, Dubois, Lapique and Jerison (to name but a few researchers), the characterization of central nervous system (CNS) phenotypic evolution has been on allometric grounds, being currently portrayed as a phenomenon of deviations of its size relative to body size. On these allometric bases, and regardless if we speak of birds or mammals, CNS allometric evolution appears associated with differences in life-history strategies of development whereby the altricial developmental strategy appears to promote larger positive deviations from the mean (i.e., larger CNS proportional sizes relative to body mass). However, studies on CNS morphology approaching the evolution of its shape are rare. Among several facets, exploring CNS shape evolution is important if aiming to gain insights on cranial phenotypic evolution, since both systems are physically and developmentally integrated through complex epigenetic processes. We have explored this whole matter in birds using shape analysis (Procrustes-based geometric morphometrics procedures and associated multivariate statistics). The avian CNS fits so tightly within the endocranial cavity that its imprint on bone allows making inferences about its external shape. Thus, we have first analyzed endocranial shape (and, by inference, CNS shape) disparity and allometric patterns among birds, and then challenged the null hypothesis that developmental strategies (altricial or precocial) are also related with evolutionary shape differences of both systems. The covariation between patterns of CNS proportional disparity (proportional size differences) and braincase shape disparity patterns has been explored in order understand the way in which they might be morphologically integrated in avians.

Effects of Erect Bipedal Standing on the Rat Femoral Neck

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Effects of erect bipedal standing exercise on femoral neck cross-sectional morphology was investigated in seventeen growing male rats, divided into control group and exercise group. For that purpose, 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 bipedal standing exercise from 64 days to 140 days of age, totaling 136 to 138 sessions. At the age of 140 days, the left femur was removed. By using pQCT (peripheral quantitative computed tomography), a cross section of the femoral neck was scanned 0.4 mm below the femoral head. Cortical thickness of the cross-section was examined in anterior, posterior, superior, and inferior parts of the cross-section. Cortical thickness of the inferior part showed larger value in the exercise group than in the control group and the difference was statistically significant ($p < 0.05$). This result corresponds to the feature of the cross-sectional morphology of femoral neck in bipedal humans that have larger cortical thickness in inferior than in superior part. The result demonstrates the relationships between mechanical load on femoral neck and the cross-sectional morphological feature of the femoral neck in bipedal humans.

Kinematic Analysis of Operant Bipedal Rat Measured in X-ray Cineradiography

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The aim of this study is to examine the bipedal standing behavior of rats by using an improved bipedal training box with cineradiography. Five operant conditioned bipedal rats of Wister strain (female, body weight of 240 g in average) were used for this study. A rat stands bipedally in the box for 5–10 seconds and pushes up a lever from beneath. Serial pictures of bipedal standing and lever pushing up behavior of the animals were recorded from lateral side by X-ray cineradiography (Siemens). Changes of the posture were analyzed from squatting to full stand position, measuring serially on the parameters of an angle of entire postural axis, magnitudes of knee and hip joints angles, lumbo-sacral, tholacico-lumber, and cervico tholacic angles. As the head position of the animal became higher, the lumbo-sacral angle gradually decreased from around 180 to 160 degrees and lordosis was observed in this region. In the first half of a movement of squatting to full standing, cervico-thoracic and thoracico-lumber angles rapidly increased preceded to the increase of knee and hip joint angles. In the second half of a movement from the squatting to full stand, magnitude of the angles of knee and hip joints increased faster than the increase of cervico-thoracic and thoracico-lumber angles. These relationships in changes of the magnitude of angles among the joint angles of lower limbs and vertebra regions showed almost the same pattern as in each individual and in their every bipedal standing behavior.

Ontogeny of Swimming Movements in Relation to the Skeletal System Development in *Clarias gariepinus*

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The swimming mode of *Clarias gariepinus* is anguilliform. Fish larvae, like most adult fish, undulate their bodies to propel themselves. However, their functional morphology and efficiency are distinct from adults because different anatomical structures are not yet fully developed. Study aim is to characterize ontogeny of swimming movements in relation to the development of the skeleton. Such an approach could highlight relations between structures and function during swimming ontogeny. seventysix fishes from 4 mm to 13 mm total length (TL) or from 0 to 312 hours post-hatching respectively were divided in 21 developmental stages. For each stage, undulatory movements were recorded using a high speed camera (400–800 fps) to characterize the swimming establishment and improvement. Moreover, 25 fishes of each stage were deeply anesthetized. Osseous and cartilaginous structures were stained with alizarin red and alcian blue respectively. Anguilliform swimming movement appears first at 4.6 mm TL and is fully established at approximately 7.5 mm TL, corresponding to the appearance of basidorsals 3, 4, 5 and hypurals 1 and 2. For fishes longer than 7.5 mm, the efficiency of the undulatory movements become better and better effected during growth, and could be correlated with the development of anatomical structures. At 9 mm TL, vertebral centra appear and ossify from the front to the back. First ossification in the caudal complex was observed at around 9.6 mm TL. Maximum efficiency in swimming is reached at approximately 13 mm TL when 1/3 of the vertebral column is fully ossified.

Hearing Capacity in Extinct Grounds Sloths: Does Size Limit Plasticity?

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Recent work by Blanco and Rinderknecht has demonstrated the application of techniques for calculating the expected lower frequency, best frequency and higher frequencies of hearing in the extinct ground sloths. Calculations of these frequencies are based on the surface area of the tympanic area as defined by the enclosed area of the ectotympanic ring. Based on their initial work we have examined a selection of extinct ground sloths to see if the range of hearing in different taxa is related to their ecology, with taxa living in open habitat having hearing in the lower frequencies, including subsonics, while forest taxa utilized higher frequencies for communication. We compared the range of frequencies in all major groups of ground sloths and focused on closely related taxa with different inferred habitat preferences. The sample included the largest ground sloths, *Megatherium* which inhabited open country in temperate climates and *Eremotherium* which is found in tropical to subtropical forest, as well as megalonychids, mylodonts and nothrotheres. Since the extinct ground sloths range in size from a few kilograms to thousands of kilograms we can examine whether an animal's increase in size and the concurrent increase in the area of the tympanic limits a taxon's ability to hear higher frequencies. Our examination of ground sloths over a large range of body mass indicates that the range of hearing is directly related to size and the range of frequencies that an animal can hear does not reflect its preference for a particular environment.

Is Iroquois-1 Involved in Specifying Digit Identity?

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We are investigating the hypothesis that digit patterning in vertebrates is analogous to a signalling cascade in *Drosophila* wing development. We are focussing on Iroquois-1 (Irx1), a vertebrate homologue of a gene that is expressed in response to Hh signalling in the fly and contributes to a transcription factor code specifying different veins in the wing. Previous work in mice has suggested that Irx1 may be expressed in different digits. We are comparing Iroquois expression in different vertebrates. We have found that Irx1 is expressed in the distal part of the chick wing during digit development, with expression initiating at the posterior region, then sweeping across the handplate where it is finally seen at high levels in the primordium of the most anterior digit. We have found that when Shh is applied to early wing buds to induce extra digits, ectopic Iroquois is associated with these extra digits. In insects, Hh signalling is mediated by Dpp (a homologue of Bmp2), and we have shown that the effects of Shh on Irx1 expression in chick may also be mediated by Bmps. We are currently testing whether Irx1 plays a role in determining digit identity by carrying out genetic manipulations in the chick limb.

Lizard Legs and Locomotion: Linking Leg Morphology, Gait, and Mechanics in Terrestrial Locomotion

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Terrestrial locomotion occurs when the musculoskeletal system moves the legs, producing coordinated footfall patterns (gaits) which output forces to the substrate resulting in center of mass movement (mechanics). While the links among these components have been studied in a handful of bipeds and large quadrupeds they remain poorly understood in other groups. To address this problem we quantified locomotor morphology, gait, and mechanics in a sample of 14 lizard species. Radio-graphs were used to quantify the lengths of 16 skeletal elements related to locomotion. Principal components analysis revealed 1 size axis and 2 shape axes that accounted for $\sim$ 90% of the variance in morphology. To quantify locomotor function, each species was filmed over their entire range of speeds while moving down a 3 meter racetrack with an incorporated force platform. *Ameiva* differed from all other species in having a significantly longer fourth toe and metatarsus and a shorter fifth toe, humerus and ulna. This unique morphology was clearly related to a unique function. *Ameiva* used a lateral sequence diagonal couplet gait over all speeds and mechanics. Species from the Iguania clade clustered together in morphospace and they were clearly specialized for trotting gaits and running mechanics. The relationship between locomotor morphology and function was more complicated among other species; however, there was some indication that morphology was related to function. We discuss how morphological variation might be causally related to functional variation across the diversity of lizards and the evolutionary implications of this relationship.

Comparative Bone Microstructure and Its Significance: Evidence from Primates

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The microscopic structure of bone records a history of its development, and thus, represents an important source of information concerning ontogenetic, local/functional, and environmental factors which influence its formation. Recent research has demonstrated the potential of bone microstructural analyses for deciphering growth strategies and behaviors characterizing organismal life histories. This approach has contributed significant insight into the paleobiology of several vertebrate groups (e.g., dinosaurs; non-mammalian therapsids). Despite the promising results of this work, however, aspects of bone microstructure in many mammalian groups remain relatively unexplored. We present results from an ongoing effort to systematically characterize taxonomic, ontogenetic and intra-skeletal variability in bone microstructure within a single mammalian order, Primates. Focusing here on primary bone microstructure at mid-diaphyses, ontogenetic series and adults of 21 extant genera (including humans) were examined. Color-coded tissue type maps were created from same field-of-view brightfield and polarized light images, permitting quantification of tissue type proportions within whole cross-sections and among bone regions. Adults of many taxa exhibited a preponderance of parallel-fibered and lamellar bone. However, results also demonstrated significant taxonomic, ontogenetic and element variation in tissue type proportions, including the presence of fibro-lamellar bone, which reflect systematic differences in postnatal growth and bone-specific ontogenies. Variability in depositional rates may also be discriminated from features observed qualitatively, including vascular patterns, growth lines, and collagen fiber orientation. These data provide important baseline information concerning variability in primate bone microstructure, and establish a comparative foundation for extending analyses to primates and other mammals in paleontological contexts.

Moray Eel Feeding Behavior: The Relationship Between Character Suites and Functional Innovation

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Moray eels (Family Muraenidae) comprise a large radiation of predatory fish that occupy crevices of coral reefs. This major radiation of teleost fishes does not appear to use suction as a prey capture mechanism and recently I discovered that morays exhibit a functional innovation in their pharyngeal jaw apparatus. In a prey transport study using *Muraena retifera* I observed that the pharyngeal jaws protracted from behind the skull into the oral cavity to grasp prey and transport it back into the esophagus. The pharyngeal jaws of moray eels have the greatest mobility of any teleost fish documented to date. Morays exhibit several major anatomical novelties of the head region associated with the absence of suction during prey capture, including marked reduction of the hyoid bar, pectoral girdle and sternohyoideus muscle. The reduction of important character suites associated with suction production may have increased functional diversity of the pharyngeal jaw apparatus. Morays appear to have modified the general teleost feeding condition in order to eat large prey that they capture while hunting within the confined spaces of coral reefs.

Ontogeny of the Cephalofoil in Four Species of Hammerhead Sharks (Elasmobranchii: Sphyrnidae) from Southwestern Atlantic

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From the six species of hammerhead sharks present in Southwestern Atlantic, we examined the neurocranial osteology and the ontogeny of four species (*Sphyrna lewini, S. tiburo, S. tudes* and *S. zygaena*). As in all Sphyrnids, those species are easily recognized by the presence of a wing-like head shape. In this paper, we studied the ontogenetic development of the cephalofoil and present new data for a better characterization of the different species. The changes in neurocranial ontogeny were observed. Those changes refer especially to the complex composed of the preorbital, intraorbital and olfactive cartilages, pre- and postorbital processes and mediorbital anterior and posterior conexions, in its proportions, size and angle in the cephalofoil. It was possible to list characters that will allow future phylogenetic studies, refering to: the presence and shape of the rostral window, the shape of the rostral wing, the presence of a curvature in the medial portion of the posterior mediorbital connexion, the presence of the nasal groove, the presence of lateral indentations and the angle of the posterior margin of the head.

Sensorial System of Lorenzini Ampullae in Four Species of Hammerhead Sharks (Elasmobranchii: Sphyrnidae) from the Southwestern Atlantic

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The wing-like shape of the head is the principal charachter of hammerhead sharks, being important for studies on its origins, evolution and diversity. The cephalofoil shape in Sphyrnids changes during its ontogeny, being necessary to establish other taxonomical charachters to determine correctly its species. The present work studied the distribution of electrosensorial pore regions in ventral surface of the cephalofoil (VSC) in *Sphyrna lewini, S. tiburo, S. tudes* and *S. zygaena* from the Southwestern Atlantic. Those pores in VSC represent a specialized electrosensorial network capable of catching subtle variations of electric field. Electroreception is used in orientation when swimming and in prey localization. In this study new data were collected for a better characterization of hammerhead sharks, resulting in a list of new anatomical data required for future phylogenetic studies with Sphyrnids. It was observed that the topographic pattern of electrosensorial pores on the VSC is conserved from juvenile to adult stages and between species. Thus the pattern of elecroreceptive pores on the VSC of the studied hammerhead shark species occuring in Southwestern Atlantic (c.f. *S. lewini, Sphyrna tiburo, S. tudes* and *S. zygaena*) can be used together with head morphology as an aid to identify species.

Relationships Between Palaeoenvironment, Palaeodiet, and Morphology in Eurasian Bovids

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Because their diets tend to reflect habitats, the ecology of fossil bovids is often investigated to better characterize past environments. Here, I combine two approaches, i.e., dental microwear and ecomorphology, to reconstruct the diet of late Miocene bovids in Eurasia. The masticatory and tooth morphologies inform on the global dietary adaptation while the dental microwear signature provides details on the physical properties of last food items consumed within a short period of time. Because they are common in fossil assemblages, the presentation emphasizes the Boselaphini subfamily. The microwear pattern of fossil species is compared with that of modern ungulates belonging to the "Ungulates" database. Molar facets were digitized using a CCD camera connected to a white-light stereomicroscope, and microwear scars were recorded and measured. While ecomorphologic features suggest that the two main Boselaphini (*Tragoportax* and *Miotragocerus*) browsed, the dental microwear analysis suggests wider ranges of feeding habits. In fact, the species of *Miotragocerus* usually have a high pit percentage and especially very few scratches on shearing molar facets. This undoubtedly indicates browsing habits. In contrast, the populations belonging to *Tragoportax* display a different microwear pattern. Some populations were indisputably more engaged in grazing than others. The spatial environmental dynamics along the West-East gradient and the climatic changes due to the pre-Messinian Mediterranean may explain such dietary variations between populations. While the masticatory and tooth morphologies may not have displayed the ecological plasticity of *Tragoportax*, the combination with the dental microwear analysis furnishes an efficient tool to investigate the palaeobiology of these extinct ruminants.

Mechanics of the Alligator Mandible: How Well Does in vivo Bone Strain Approximate Stress Patterns?

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In vivo strain gauge technology has been an extremely valuable experimental tool for interpreting loading patterns in bones. However, a major limitation of strain gauge studies is that when strain data are examined in isolation they do not provide direct information regarding bone stress. This deficit arises from the fact that calculation of stress is dependant upon both data on deformation as well as the material properties of skeletal elements. Because bone is an anisotropic material, its structural properties are different in different directions. This has the potential to cause misinterpretation of strain data because principle strain axes may not be aligned with principal stress axes. In this study, we compare strain and stress magnitudes and orientation data from the alligator mandible. Principal strain magnitudes and orientations were recorded from three experimental animals during forceful biting using rosette strain gauges. These were combined with material properties data (elastic and shear moduli, Poisson's ratios) from the mandibles of five alligator specimens, collected in vitro utilizing an ultrasonic pulse transmission technique to determine principal stress magnitudes and orientations. Due to the anisotropy of skeletal tissues, our understanding of loading patterns from in vivo bone strain studies can be clarified by applying material properties data to calculate bone stress. This methodology serves as an example of how these experimental techniques can be combined to produce the most accurate interpretation of in vivo skeletal function.

Food Material Properties, Tooth Form and Jaw Movements in Human Mastication. Perspectives on the Perception of Food Texture

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Among the sensory attributes of foods, texture is considered to be one of the significant features that influences consumer acceptance and therefore its evaluation is important in food product development and quality control. Although the physical properties of foods have been extensively studied within the field of rheology, less attention has been devoted to determine how humans interact with foods of varied physical properties. This poster presents research tools to study various aspects of the human food interaction. In particular, research on the development of a mastication/biting robot is presented for the study of firmness perception of gelatin gels and cheese. We present evidence that biting motions measured via electrognathography are very variable among individuals and that this variability has an impact on the stresses developed in food samples while biting and ultimately on the perception of food firmness. In addition, a study of molar teeth morphology and its impact on both the stresses developed in foods while biting and the resulting perception of firmness in food gels is presented. Finally, we present results from a study on the relationship between the perception of meat toughness and both jaw motion and muscle activity during mastication which demonstrates that the mastication function is modulated by meat physical properties. These studies contribute to the body of research existing on the interactions between human body function and sensory perception.

An Integrative Analysis of Elephant Foot Biomechanics

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As in all legged land animals the pes and manus of elephants are specialized to act at the animal: substrate interface, although, in this case, the relationship is tested to extremes. Their large size, and ability to travel at moderately high speeds on hard ground without injury, suggests a high level of functional adaptation within the manus and pes to withstanding repeated high loads and accelerations. Our previous work concentrated on describing the changing shape of internal musculoskeletal features of the manus and pes through ontogeny (scaling), and here we present data from three sets of methodologies designed to test the inferences made from these results. Motion analysis and force plate data were coupled for quantification of external deformation in live subjects, and contrasted with motion analysis of known load application to cadaveric specimens, allowing comparison of structural reactions to load under active and passive conditions. These methods quantify deformation in the fibrous foot pad, a complex structure which, to date, has been difficult to analyze. Application of a series of known loads to cadaveric specimens was also used to produce sequences of commuted tomography (CT) scans, allowing visualization of the changing orientations and locations of internal musculoskeletal features during loading. This technique provides direct comparison of loading conditions with results from previous scaling work.

Biochemical Muscle Characteristics of the Minute Forelimb and Enlarged Hindlimb of the Quokka (*Setonix brachyurus*, Macropodidae)

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The Quokka is a threatened species of marsupials now restricted to mainland South-Western Australia and two nearby islands. It looks like a small, dumpy kangaroo with minute forelimbs and enlarged hind limbs. Like macropods, the quokkas can hop with their powerful legs, but can also walk on all four limbs. We looked for evidence of adaptive changes in the fiber-type composition of extensor limb muscles like those of bipedal hopping eutherian mammals (Jerboas) as compared to quadrupedal ones (Jouffroy et al., 2003, J. Anat. 202:373).The different types of myosin (MyHCs) were investigated by immunofluorescence, given that marsupial limb muscles express the same slow,[1] and fast (2A, 2B, 2X) myosins as eutherians (Zhong et al., 2001, Electrophoresis, 22:1016). In the Quokka's forelimb, as in the Jerboa's, the elbow extensor triceps caput mediale comprises a very low percentage of type 1 fibers (6%), those fatigue-resistant fibers that characterize this postural (antigravity) muscles of the quadrupedal eutherians. Thus, relieving the forelimbs of their locomotor role is accompanied by similar biochemical muscle modifications in eutherians and metatherians. Unlike eutherians, all Quokka's knee and ankle extensors contain few type 1 fibers (< 30%). Gastrocnemius lateralis and vastus medialis (95% type2 fibers) are the best equipped for providing leaping energy.

Convergence and Constraint in the Evolution of Carnivore Skull Shape

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Phenotypic similarities between distantly related marsupials and placentals are commonly presented as examples of convergence and support for the role of adaptive evolution in shaping morphological and ecological diversity. Here we compare skull shape in a wide range of carnivoran placentals (Carnivora) and non-herbivorous marsupials using a 3D geometric morphometric approach. Morphological and ecological diversity among extant carnivorans is considerably greater than is evident in the marsupial order Dasyuromorphia with which they have most commonly been compared. To examine convergence across a wider, but broadly comparable range of feeding ecologies, a dataset inclusive of non-dasyuromorphian marsupials and extinct taxa representing morphotypes no longer present was assembled. We found support for the adaptive paradigm, with associations between morphology, feeding behavior and bite force, although skull shape better predicted feeding ecology in the phylogenetically diverse marsupial sample than in carnivorans. Further, we show that consistent but differing constraints have influenced the evolution of cranial shape in Carnivorans and marsupials. These, which correlate with brain size and bite force, are maintained across the full range of morphologies and feeding categories, from small insectivores and omnivores to large meat-specialists.

A Geometric Morphometric Analysis of the Xenarthran Humerus with Reference to Digging Ability

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The digging ability of living armadillos has been shown to be strongly related to the proportions of their olecranon process with respect to the ulnar length (Index of Fossorial Ability - IFA). This geometric morphometric study of the xenarthran humerus uses the IFA to determine features of the humerus which are likely related to digging ability. Twenty, 3-dimensional landmarks were digitized on the humerii of 38 extant and 11 fossil xenarthrans. For all the extant and for some of the extinct specimens the ulna was available and the IFA was calculated. There is a large size range among the specimens under study and the data was analyzed in size and shape space where all the size related variability is concentrated in the first principle component (PC1). Multivariate regression of IFA on PCs 2 to 6 clearly reveal the digging related variation in shape of the humerus. The analyses reveal that a long deltopectoral crest that is anteriorly placed and extends well past the middle of the humerus, a larger medial epicondyle, a large posteriorly directed supinator crest, larger articular surfaces, and a larger greater tubercle are all features strongly associated with digging ability.

Comparative and Experimental Analysis of Trigeminal Nerve Development in Duck, Quail, and Quail-Duck Chimeras

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Japanese quail, *Coturnix coturnix japonica* (Aves: Galli), and white Pekin duck, a domestic race of the mallard, *Anas platyrhynchos* (Aves, Anatidae) have undergone considerable craniofacial evolution. In particular, regions such as the jaw complex have become highly specialized for feeding and as a result display clear species-specific differences in the size and shape of skeletal elements, musculature, and associated cranial nerves. To explore the developmental basis for such differences, we focused on the trigeminal nerve, which innervates the jaw adductor muscle complex. First, we compared trigeminal morphogenesis from about Hamburger-Hamilton (HH) stage 15 onward using whole mount immunostaining and 3D-reconstruction. We find that the ganglion develops species-specific morphology from a relatively early stage, and developmental events shift temporally relative to the appearance of outer morphological characters (staging criteria). We observed an early additional branching in the mandibular branch of the quail and massively more robust ganglionic parts in the duck. To investigate further developmental mechanisms that might pattern the trigeminal as well as facilitate the striking evolvability of the jaw complex, we grafted cranial neural crest cells, which normally participate in the formation of the trigeminal, from quail donors into stage-matched duck hosts. Preliminary results show that chimeras develop a less robust trigeminal ganglion in association with quail donor cells. This would be consistent with our observations about the patterning of soft and dense connective tissue in other transplant experiments, which suggest that the spatiotemporal integration of jaw elements results from neural crest-mediated hierarchical organization and modularization.

Musculoskeletal Modelling and Finite Element Analysis of Lizard Skulls

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Multibody dynamics analysis (MDA) is a relatively new computer modelling technique that can be used to model the external forces and internal musculature responsible for skull loading. Here, it was used in a preliminary study of jaw muscle forces in the skull of the herbivorous agamid lizard *Uromastyx*, which is part of a larger project to understand lizard skull architecture. The analysis included multi-segment representations of the jaw adductor and pterygoideus muscles and temporal ligaments, which were specified with representative force-length relationships. For simplicity in this model, constant muscle force-velocity relationships were assumed. The geometry of the skull was obtained from microCT, and the model was constructed so that the quadrates were mobile with hinge joints at the cranium and mandible. A quasi-dynamic analysis of the skull then returned the respective muscle forces and maximum bite force for different gape angles. The results of the MDA analysis are now being applied to high resolution finite element models of the skull to predict the variation in skull strain during loading.

Evolutionary Integration and Modularity in the Mammalian Mandible: Evidence from Experimental and Natural Systems

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The mammalian mandible is a complex morphological structure, composed of six morphogenetic components with different embryological origins (three posterior processes, two alveolar regions and the masseteric region) integrated during development. The mandible has been proposed as a paradigm for the development and evolution of complex structures, and its embryological division into morphogenetic components has inspired investigations regarding the division of mandible components into modules (genetically and functionally independent sets of characters). In this work, we reviewed the evidence regarding modularization of the mandible and present new data from two of the most morphologically and ecologically diverse mammal families: Echimyid rodents and Phyllostomid bats. Several studies have attempted to determine the modular organization of the mandible by testing hypotheses in which characters are organized in independent modules. The division of the mandible in two modules (ascending ramus and alveolar region) has been both supported and challenged by evidence from experimental data. A different proposition considers each morphogenetic component an independent module, and is supported by evidence from experimental and natural systems. In the long run, modularity in the mammalian mandible is not fixed and the hierarchical structure of integration among different components is not necessarily conserved through evolutionary time. The macroevolutionary data sets analyzed in this study show a convergent evolutionary integration pattern, where shape variation in the anterior alveolar region is correlated with shape variation in the posterior processes, suggesting that function might be more important than genetics and development in determining evolutionary integration patterns in a large time scale.

Relationship Between Bone Growth Rate and Bone Vascular Density in Amniotes: A First Test of Amprino's Rule in a Phylogenetic Context

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The diversity of bone microstructures in vertebrates results from multiple factors. Although this diversity has been studied for several centuries, its determinism is still far from a complete understanding. In response, studies considering phylogeny and different functional factors have brought some new insights in this area. As far as the development is concerned, it has been shown that bone histological organization was the expression of different growth rates, but this hypothesis has never been tested in a phylogenetic context. In order to do that, we quantified periosteal bone growth rate and bone vascular density in 56 juvenile individuals belonging to 13 species of Amniota. We used the recently developed method of variation partitioning analysis and showed that a portion of the variation of bone vascular density is explained by bone growth rate, a portion by the phylogeny, and there is an important overlap between the fractions explained by these factors (the phylogenetically structured functional variation). Using Independent Contrasts, which also take phylogeny into account, we were able to specify the existence of a linear positive relationship between bone vascular density in primary bone tissue, and periosteal bone growth rate.

Evidences for a Tongue-based Prey Transport in a Scleroglossan Lizard (*Tupinambis teguixin*)

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Within the squamate lineage, two major clades are characterized by two different feeding strategies: iguania are considered as sit-and-wait predators, whereas the majority of scleroglossa is active forager. Moreover, prey acquisition mode in iguanian lizards is based on lingual prehension, contrary to scleroglossan lizards which combine a vomeronasal chemosensory system and jaw prehension. Thus, the specialized tongue of a major number of scleroglossan lizards is not used during prey capture, but only for collecting chemicals into the environment. Based on high speed films, the specialized tongue of Teiidae has been reported to play a major role in transport and swallowing phases of the feeding behavior. By using high speed cinefluoroscopy, we tested the action of the tongue during these phases. We studied prey (freshly killed grasshoppers and mice) processing pattern in two individuals of *Tupinambis teguixin*. We observed that prey transport within the oral cavity is strongly related to movement of the hind tongue during transport cycles. Also, this part of the tongue helps to move the prey from the pharynx to the esophagus during swallowing although the mouth remains closed. The prey transport and swallowing were analyzed by measuring variables depicting movements of the mouth and hyobranchium (i.e., gape opening angle and distance, prey position between snoot and esophagus) to compare kinematics of trophic system in scleroglossan and ignuanian lizards with differently specialized tongues.

Functional Morphology and Physiology of Tail Vibration in Snakes

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Rattling by rattlesnakes is one of the fastest vertebrate movements and involves some of the highest contraction frequencies sustained by vertebrate muscle. Specifically, the shaker muscles in the tails of rattlesnakes can sustain contraction frequencies up to 90–100 Hz for extended periods. To study the evolution of these high-performance muscles, we compared the activities of the enzymes citrate synthase (an indicator of aerobic capacity) and lactate dehydrogenase (an indicator of anaerobic capacity) in the tail muscles of rattlesnakes (*Crotalus atrox*) and successive outgroups (*Agkistrodon contortrix, A. piscivorus, Elaphe obsoleta*, and others). Rattlesnake tail muscles contracted at the highest frequencies and had the highest aerobic capacity, but only moderate anaerobic capacity. In other species that vibrate their tails, contraction frequencies and enzyme activities varied. Among species, there appears to be a clear relationship between muscle contraction frequency and aerobic capacity, but not between contraction frequency and anaerobic capacity. We have not detected any relationship between aerobic capacity and the duration of tail vibration bouts. These results suggest that moderate to high aerobic capacities in the tail muscles evolved gradually in viperid snakes, before the evolution of rattlesnakes, rattles, and highly specialized shaker muscles. We are currently testing for relationships among tail morphology, muscle physiology, and mechanical energy output.

The Consequences of Having a Long Trunk: Functional Morphology in the Ferret

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Ferrets, as well as weasels and polecats, possess relatively short legs and a long, slender trunk. These body proportions enable them to enter the burrows of voles and rabbits upon which they prey. The long back has been suggested to facilitate locomotion in small tubes; however, no conclusive evidence was presented. Instead, a long trunk actually reduces manoeuvrability because the higher rotational inertia hampers turning ability. In our study, we analyzed the functional consequences of this unusual body shape. Back posture and back movements were studied using cineradiography, revealing profound differences between overground and underground locomotion. During overground locomotion, the back is arched, resulting in a functional trunk length comparable to normally proportioned small mammals and thus leading to similar muscular demands and manoeuvrability. During underground locomotion, by contrast, the back is straight, resulting in greater rotational inertia and higher stabilisation requirements. This unusual load situation is reflected in the morphology of the paravertebral muscles, which differs clearly from that of all other mammals investigated so far. The metabolic profile showed that all paravertebral muscles can act as either mobilisers as well as stabilisers independent of their anatomical position. By contrast, normally proportioned mammals show a clear morphological and, thus, functional separation between the superficial, force-generating mobilisers and deep, fatigue-resistant stabilisers. We suggest that the observed pattern reflects the adaptation of the back muscles to the functional demands of a long trunk in meeting the increased stabilising needs during both overground and especially underground locomotion.

Gene Expression During the Development of the Postcranial Skeleton of the Red-eared Slider Turtle, *Trachemys scripta*

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Consideration of the developmental origins and patterning of the postcranial skeleton in turtles illustrates several important principles in evolutionary biology. The presence of a shell, composed of plates of dermal bone organized into a dorsal carapace and a ventral plastron, has altered the body plan of turtles from that of a typical tetrapod. The vertebral column, ribs, and girdles of the appendicular skeleton lie within this dermal armor. Questions about the developmental origin of these tissues and their integration into the vertebrate body plan are addressed here. What is the embryonic origin of postcranial dermal bone? How have the developmental pathways used to pattern the vertebrate body been conserved, and how have they changed in chelonian vertebrates? I address these questions using developmental genetics as a line of evidence. I investigate regulatory gene expression during the development of the skeleton in the red-eared slider turtle, *Trachemys scripta*. The expression of Pax and Twist genes in the ventromedial sclerotome of *T. scripta* is conserved compared to other vertebrates, while dorsal sclerotome lineages express Bmp-4 but not Msx genes. These data suggest a conservation of genetic patterning of ventral elements of the axial skeleton and that differences in the dorsal mesenchyme could be related to the juxtaposition of mesenchyme that will form the dorsal neural arches and the shell. The expression of Twist genes in the carapacial mesenchyme suggests a dermatomal origin for the carapace; however, a contribution to the shell by neural crest cells is not excluded.

Development of the Skull in the Chinese Soft-shelled Turtle, *Pelodiscus sinensis* (Reptilia: Testudines: Trionychidae)

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Soft-shelled turtles (Trionychidae) are among the most distinctive and derived recent turtles. We investigated the development of the skull in *Pelodiscus sinensis*, with particular emphasis on the pattern and sequence of the ossification. Ossification starts at late Tokita-Kuratani stage 18 with the ossification of the maxilla, followed by the dentary and prefrontal. The quadrate is the first endoskeletal ossification and appears at TK stage 22. All ossifications found in the adult skull are present by TK stage 25. Compared to *Apalone spinifera*, the only other trionychid for which extensive data on the development of the skull are available (Sheil [2003] J. Morphol. 256:42–78), most ossifications seem to develop later in *P. sinensis*. Differences in ossification sequences between the two species are also present: in *P. sinensis* the jugal develops relatively early and before the frontal, whereas it appears later in *A. spinifera*; the frontal appears shortly before the parietal in *A. spinifera* whereas in *P. sinensis* the parietal appears several stages before the frontal. Further differences are in the morphology of the chondrocranium: the nasal capsule is more extensively developed in *P. sinensis*, which further lacks a crista sellaris, resulting in a common pituitary and basicranial fenestra. Integration of these data into a comparative analysis of

the sequence of cranial ossification in cryptodire turtles using event-pairing methods and based on published sources and our ongoing work on seaturtles, reveals heterochronies some of which reflect the hypothesized phylogeny of the taxa considered.

Morphology of Larval Caecilians (Amphibia: Gymnophiona)

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Adults of all living caecilians have skulls in which the temporal region is either completely covered by bone (stegokrotaphy) or with a gap present between the squamosal and parietal (zygokrotaphy). In non-rhinatrematid, zygokrotaphic taxa, the primary jaw adductor musculature is confined to the adductor chamber and does not extend onto the dorsal side of the skull. This is in contrast to the condition in the Rhinatrematidae, the sister group to all other living caecilians, where the adductor musculature extends through the temporal opening onto the dorsal side of the skull. The implications for the ancestral condition of the morphology of the caecilian head have been widely discussed based on the observed adult morphologies, their phylogenetic distributions and putative sister group. Several clades of living caecilians, however, are characterized by the presence of morphologically distinct, free-living larvae that undergo a metamorphic transformation into the adult-like morphology. Little attention has been paid to larval morphology and metamorphosis and its implications for the reconstruction of the ancestral condition of the caecilian head. We have investigated the morphology of larvae and adults of rhinatrematid, ichthyophiid, uraeotyphliid and caeciliid caecilians, covering all genera for which free-living larvae are known. Several features of caecilian larvae are unreported or have previously been overlooked. The implications of our data for the evolution of stegokrotaphy in caecilians will be discussed.

Development and Evolution of the Trunk Muscles: New Understanding of the Turtle Body Plan

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All the skeletal muscles in the vertebrate trunk arise from somites. In gnathostomes, they have traditionally been classified into epaxial and hypaxial muscles, innervated by dorsal and ventral spinal nerve branches, respectively. Recent developmental analyses have implied another classification, by which the muscles can be divided into those developing directly from dermomyotomes (primaxial) and those that differentiate after delamination and migration from the dermomyotome. The latter muscles are generally attached to distantly related skeletal elements that do not share the same somitic origin. To this class of muscles belong the tongue (or more appropriately hypobranchial) muscles, limb muscles, and the trapezius muscles. Could such a basic configuration and developmental patterning of the trunk muscles explain the anatomical patterns of entire vertebrate species? Turtles have often been cited as an example of evolutionary novelty, in which the anatomical pattern was fundamentally altered as seen in the reversed topographical relationship between the scapula and rib cage. By comparative anatomical analyses, we will show that turtles can be viewed as animals with shared amniote anatomical pattern that merely have experienced different ways of "folding" during development, specifically at the lateralmost primaxial elements (involving the muscles innervated by suprascapularis and long thoracic nerves). Curiously, this folding takes place at the lateral edge of the carapacial primordium, or the carapacial ridge, which is specific to turtles. Thus, the novelty in turtle can be seen as a new pattern of folding of shared embryonic patterns.

Feeding Patterns of Asian Box Turtles—A Comparative Study on *Cuora amboinensis* and *Cuora flavomarginata* (Chelonia, Emydidae)

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This study examines the anatomy and histology of the feeding apparatus of two closely related turtle species, the Malayan box turtle (*Cuora amboinensis*) and the yellow-margined box turtle (*Cuora flavomarginata*). The focus was on the kinematic patterns of terrestrial and aquatic feeding. Feeding patterns were analyzed by high-speed cinematography. Both species are able to feed on land as well as in water and are omnivorous. During terrestrial feeding (analyzed for both species), the initial food prehension is always done by the jaws, whereas intraoral food transport and swallowing actions are lingual-based. In aquatic feeding (analyzed for *C. amboinensis* only), the prey is captured by a fast forward strike (ram feeding) of the head. Compensatory suction by hyoid depression prevents the prey from floating away during the head approach. In *C. amboinensis*, food transport under water involves inertial suction; additional compensatory suction movements occur. Despite the close phylogenetic relationship of the investigated species, there are differences in their head morphology—weaker jaw adductor muscles and a simplified trochlear complex in *C. flavomarginata*—as well as in their terrestrial feeding modes. *Cuora amboinensis* exhibits head and neck movements that are very similar to the inertial movements in aquatic feeding, but have no real effects on food transport on land. We hypothesize that these movements represent relicts of basic aquatic feeding patterns.

Feeding Patterns in *Cuora galbinifrons* (Bourret, 1939)

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The Indochinese box turtle *Cuora galbinifrons* is a purely terrestrial species in its natural habitat; aquatic feeding has not been described for this species. The present study examines aquatic and terrestrial food uptake, intraoral transport and swallowing using high-speed films and cineradiography. These patterns differ from those in other box turtles. In both media, food uptake involves jaw prehension. Intraoral transport mechanisms under water differ depending on prey size: small items are transported by inertial suction, whereas larger items are moved by the tongue—normally a clear terrestrial strategy. Intraoral transport on land is lingual based. Pharyngeal packing phases are detectable prior to swallowing in both media. Swallowing mechanisms are similar under water and on land. Within the swallowing act, a further static phase could be detected. It is termed esophageal packing here (the bolus is retained for a certain time in the posterior third of the esophagus). The described feeding modes are highly variable in the measured parameters (time and kinematic patterns). The appearance of lingual transport mechanisms under water is correlated with the well-developed hyo-lingual apparatus of the species; *C. galbinifrons* (known as a highly terrestrial turtle) presumably also uses this terrestrial pattern secondarily in the aquatic environment.

Evolution of the Shell Coat and Oocyte Yolk; A Marsupial Perspective

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Two features characterize early marsupial embryos, the shell coat and oocyte polarity. Extracellular embryonic coats are found in all vertebrates, aiding fertilization, preventing polyspermy and keeping blastomeres together. Presumed tertiary amniote egg coat homology is based on time and place of deposition. Within the amniote oocyte, yolk platelets and droplets are often polarized. Reptile, bird and monotreme oocytes contain both yellow (large complex platelets and lipid bodies) and white yolk (smaller platelets and variable vesicular products) arranged in concentric layers. Marsupial oocytes are characterized by a polarized accumulation of vesicles and granular material that are similar to white yolk. Two novel proteins, Coat Protein 4 (CP4) and Vesicle-Associated Protein 1 (VAP1), have been isolated from the Common Brushtail Possum, *Trichosurus vulpecula*. CP4, the first marsupial shell coat protein to be identified, is synthesized by the luminal and glandular epithelium of the uterus under the influence of oestradiol and progesterone and stimulates epithelial proliferation in vitro. In marsupials, the oocyte vesicles contain extracellular matrix material and stabilizing proteins which enable formation of the epithelium during early cleavage. This suggests that white yolk provides the substrate for epithelial construction during early lineage allocation, when the blastoderm spreads over the yolk in birds and reptiles and lines the zona pellucida in marsupials and monotremes. The evolution of the marsupial shell coat and

oocyte polarity will be discussed with reference to the presence of cp4 in the genome of a variety of vertebrate species and the role of vesicular material in early embryonic development.

Genetic Architecture of the Mandible Shape: Insights from Fine Mapping QTLs in a Heterogeneous Stock of Mice

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The mouse mandible has been intensively used as model of complex traits. This structure of great importance for feeding consists of parts that have different functions in the process of biting and chewing. Its developmental set-up and genetic architecture are therefore important factors influencing its evolutionary potential. Precise data on genetic architecture are required to understand properties of the genotype-phenotype map and its relationships with the development. Quantitative trait locus (QTL) mapping provides such data by detecting genomic regions that affect a given phenotype and estimating their effects. Conventional genetic designs for QTL mapping suffer from weak resolution and power to achieve this goal. There are, however, newly available designs and genomic resources that overcome these difficulties and afford unprecedented statistical power and genetic resolution. We attempt to map loci affecting mandible shape using 1,700 mice from a heterogeneous stock, which were each genotyped for 12,000 single nucleotide polymorphisms. Geometric morphometric methods are used to quantify and analyse mandible shape. We find 258 potential candidate loci. Averaging multiple QTLs models yields fifty to seventy loci having an effect on mandible shape. The effects of different alleles of a given QTL on shape differ not only in their magnitude, but are also qualitatively different from each other in that they change different shape features. QTL effects show a varying proportion of their total effect on the mandible affecting preferentially the ramus or the alveolar regions. The overall pattern of integration of QTL effects therefore reflects the developmental set-up of the mandible.

Affinities and Morphology of a Poorly Known Chondrichthyan from the Upper Cretaceous

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Upper Cretaceous sediments yield vast numbers of isolated teeth belonging to the family Ptychodontidae, Genus *Ptychodus*, Aggassiz 1835. The teeth are morphologically unique among chondrichthyans. Despite isolated teeth being quite common in Asia, Europe, Africa and the Americas, articulated jaws are rare. Teeth found in association have revealed heterodonty, which is common but not ubiquitous among chondrichthyans. Postcranial material is almost entirely restricted to dermal denticles with only a few associated vertebra having been recorded. Although 11 genera have been assigned, heterodonty and lack of material mean that synonymy is probably high. Due to the lack of material, post-cranial morphology remains completely unknown and although Ptychodontidae is currently assigned to the Superfamily Hybodontoidea, it is currently uncertain whether they are more closely related to sharks or rays. This study serves to compare and contrast *Ptychodus* species both with each other and with other chondrichthyans in an attempt to clarify its systematic affinities and propose the first reconstruction of whole body morphology.

Life on the Edge: Craniofacial Mesenchymal Interfaces

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Craniofacial mesenchyme is of dual origin—neural crest and mesoderm—and each of these populations is heterogenous with respect to cell behaviors (e.g., stationary vs. motile) and fates. In addition to a changing, dynamic relation to each other, these mesenchymal populations abut surface and neural ectodermal and pharyngeal endodermal epithelia, and with each of these epithelia there are ongoing reciprocal interactions. Changes in the location of these interfaces, in the timing of interactions among or between them, or in the qualitative character of signals passing between them underlie much of the diversity of outcome, assayed as variations in craniofacial morphology. This presentation will highlight the locations and nature of cell:cell relations between crest and mesodermal populations, contrasting the behaviors associated with neural, connective tissue, myogenic, and angiogenic lineages in several species. In addition, the interplay between these populations and adjacent epithelia will be discussed, with particular focus on myogenesis and neurocranial skeletogenesis. Data from avian cell lineage analyses using quail-chick transplantations and plasmid/retroviral infections to follow crest and mesodermal lineages will be integrated with the results of murine transgenic studies using tissue-specific reporter genes, and the utility of these data in identifying homologies discussed.

Food Material Properties and Feeding Niche Differentiation in Neotropical White-faced Sakis and Bearded Sakis (Platyrrhini; Primates)

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Seed predation is an ancient feeding strategy of the South American pitheciin primates. Diverging from other platyrrhines about 17 million years ago, early pitheciins exhibit the same dental morphology that characterizes modern taxa: procumbent incisors, robust canines and low-cusped, sometimes crenulated, molars. Morphologically, these adaptations are strikingly similar among the three extant genera and permit access to and mastication of nutritionally rich seeds from well-protected fruit. Ecologically, sakis and bearded sakis are sympatric throughout a large part of their range, but differ in group size and ranging patterns. Sympatry among taxa may have led to sub-niche differentiation in diet, which is not reflected at the morphological level. Using a Rimac spring tester (Rinck-McIlwaine Inc., Dumont, NJ) fitted with a 1mm 2 diameter attachment, we measured the puncture resistance of fruit pericarp and (removing the pin) estimated crushing resistance of seeds ingested by bearded sakis and white-faced sakis from two field sites in South America, Raleighvallen-Voltzberg in Suriname and Lago Guri, Venezuela. We found that the smaller-bodied species (white-faced sakis) opens softer fruit, but masticates harder seeds than the larger-bodied species (bearded sakis). The crushing maximum for white-faced sakis was 52.3 kg (n = 230) compared with 23.2 kg for bearded sakis (n = 153); the puncture maximum was 6.8 kg/mm 2 for white-faced sakis (n = 347) and 33.8 kg/mm 2 for bearded sakis (n = 592). These data provide further support that field tests of physical properties of fruit and seeds are valuable supplements to both comparative feeding ecology and morphological studies.

Koalas, Papionines and Humans: Understanding Variation and Diversity in Human Evolution

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The number of species that occurred in hominin evolution is still debated. Positions of various researchers range from a single lineage through just a few species to well over 10 species and several genera. The debate can be resolved only when a common standard of intraspecific variation is applied to the now abundant hominin fossil record. We use here multivariate measures of craniometric variation (11 dimensions of neuro- and splanchnocranium), multivariate coefficient of variation (MCV) and average multivariate deviation (d), calculated for an undisputed single arboreal mammalian species, the koala (*Phascolarctos cinereus*), a set of six species of *Papio*, modern humans and a sample of all hominin fossil crania dated to the period 1.5 to 2.0 Ma who may contain as many as three genera and several species. These measures describe variation within two single known species (a marsupial and modern human), in a sample of multiple species and in a sample of unknown, and debated speciosity, hominins (dated 1.5-2 Ma). The MCV and (d) values are: *Papio* 19.2(56.8), koala 10.6(35.6), hominins 11.8 (27.9) modern humans 5.4(20.1). Differences between *Papio* and both single known species are significant. Hominin variation is significantly less than *Papio*, not different from koalas, and larger than in modern humans. It should be, however, noted that hominin specimens cover over 500 ka time span and thus must include chronological variation. This indicates that Plio-Pleistocene hominins were not as speciose as most commonly accepted in the literature.

Whole Body Lift and Ground Effect During Pectoral Fin Locomotion in the Northern Spearnose Poacher

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The northern spearnose poacher, *Agonopsis vulsa*, is a heavily armored, negatively buoyant fish that uses pectoral fins to propel it just above the bottom. We used high-speed video, kinematic analysis and flow visualization to study how *A. vulsa* overcomes negative buoyancy and generates forward thrust during pectoral fin locomotion. When slowly swimming (0.7 body lengths/second [bl/s]) more than 2 cm above the bottom the poacher maintains a high body pitch angle of 22° (mean of n = 5 individuals, 5 trials per individual). This angle of attack decreases steadily with increasing swimming speed to 5° at 1.7 bl/s. These results suggest that pitch angle is important in lift generation which allows *A. vulsa* to overcome its negative buoyancy. These results are remarkably similar to a previous study on the white sturgeon, also a negatively buoyant fish and another benthic species. The mean angle of attack in white sturgeon was found to be about 20° when swimming at 0.5 bl/s and 5° at 2 bl/s (Wilga and Lauder, 1999, JEB 202:2213–2432). In contrast, when poachers swam within 2 cm of the bottom the mean body pitch angle was zero, suggesting that they are taking advantage of a ground effect. Using suspended particles to visualize the flow around the pectoral fins, and between the fish and the ground, we established that the poacher does shed vortices that allow it to take advantage of ground effect.

The Functional Morphology of the Two-toed Sloth's (*Choloepus didactylus*: Tardigrada) Locomotor Apparatus: A Videoradiographic Study

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Although suspensory quadrupedal locomotion with hook-like autopodia is restricted to the tardigrada, it probably evolved independently in two- and three-toed sloths after the two lines leading to modern sloths and deriving from an arboreal ancestor separated about 35 million years ago. We currently investigate the kinematics of two-toed sloths using biplanar high-speed videoradiography. Preliminary results suggest forelimb kinematics in two-toed sloth locomotion to range between two modes. The "long pendulum mode" is characterized by extended forelimbs and propulsion is mainly achieved by scapula rotation contributing to stride length. The "short pendulum mode" is marked by a strong flexion in the elbow joint and forelimb propulsion is realized by movement of the lower arm. The "short pendulum mode" is used predominantly for "browsing", while the "long pendulum mode" is utilized for "faster" locomotion. Clavicula and sternum are connected by a long and loose ligament we expected to facilitate translational movement of the shoulder as known for aclavicular mammals. Hindlimbs display just one kinematic mode. Concomitant to locomotory studies and macroscopic anatomy, we are looking for fiber type distribution. Enzyme histochemical analysis of fiber-type distribution in limb muscles revealed extraordinary high proportions of oxidative fibers. A metabolic distinction of regions indicative for differential activation as shown for muscles with "anti-gravity role" is not yet identifiable. In sloths the long flexors are assumed to act against gravity-induced extension of the joints. As three-toed sloths are extremely difficult to handle, insights into possible convergent evolution can only be derived from the functional morphology of the musculo-skeletal system.

Locomotion on Sloped Arboreal Substrates: A Comparison of Gait Parameters in Cotton-top Tamarins and an Arboreal Australodelphid Marsupial

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Arboreal quadrupedal primates display a suite of locomotor adaptations to move and balance on narrow substrates, including prehensile extremities and a particular footfall sequence. It has been documented that this set of attributes evolved convergently in some arboreal marsupials. To date, the majority of experimental set-ups designed to investigate arboreal locomotion feature horizontal poles, although this orientation represents the minority of substrates in the habitat of tree-dwelling animals. Therefore, we used high-speed cinematography to analyse the influence of different substrate inclinations on the locomotion of two distantly related arboreal mammals, the cotton-top tamarin (*Saguinus oedipus,* Callitrichidae) and the brush-tailed possum (*Trichosurus vulpecula,* Phalangeridae), to test for convergent solutions for walking on sloped substrates. Unlike other primates, tamarins correspond to arboreal marsupials in having claws instead of nails on all digits except the hallux. Brushed-tailed possums and tamarins display the same footfall pattern on horizontal arboreal substrates. On inclined substrates, gait parameters of both species also correspond in many aspects, notably the degree of limb protraction and retraction depending on inclination and being strongly related to the braking and propulsive role of each limb. But, substantial differences are also apparent. Whereas cotton-top tamarins display an inclination dependent shift in some gait determinants leading to the utilization of different gaits on inclined (diagonal sequence) and declined substrates (lateral sequence), brushed-tailed possums did not show such a shift. Therefore, we suggest that the greater behavioral plasticity of primates that is not present in arboreal marsupials was an important aspect of primate locomotor evolution.

Evolution of the Archosaurian Bauplan: Non-pulmonary Adaptations of an Air-sac Based Breathing Apparatus

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Sauropsids exhibit extraordinary variability in the structure and function of the respiratory apparatus, including the degree to which pulmonary air sacs are present. Living birds represent the only extant sauropsids in which pulmonary air sacs pneumatize the postcranial skeleton, thereby allowing a direct correlation between skeletal morphology and a specific type of pulmonary system. By comparing skeletal morphology in birds with osteological features preserved in fossil specimens, it has been inferred that certain extinct archosaurs (saurischian dinosaurs, pterosaurs) possessed an air-sac based pulmonary system. This not only provides insight for reconstructing large-scale pulmonary organization, but allows for the formulation of hypotheses regarding pulmonary function (e.g., ventilatory dynamics) in addition to addressing structural constraints with regard to body size evolution in Archosauria. For example, body size variation in extant birds is directly related to the relative amount of pneumaticity in the postcranial skeleton. The largest flying birds (otids, vultures) exhibit increased pneumaticity (e.g., distal limb pneumaticity) relative to smaller members of their respective clades. Not only are similar patterns repeatedly observed in different groups of living birds, but also in select clades of both Saurischia and Pterosauria among extinct archosaurs. As a fundamental organizing system, skeletal pneumaticity reduces certain structural constraints on body size by allowing volumetric increases without concomitant increases in body mass. This would not only be critical for taxa exploiting the energetically demanding aerial environment (pterosaurs, birds), but would be beneficial for any large bodied terrestrial vertebrates, the largest of which are known among saurischian dinosaurs.

Definite Number of Ova for a Lifespan is Established During Juvenile Period of Anuran Amphibians

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Because amphibians produce rather big numbers of eggs during several breeding seasons, there is a common belief that oogonia from germ patches renew the pool of oocytes after each spawning by a wave of oogonial mitoses. However, our studies on *Rana temporaria* indicate that the definitive pool of early diplotene oocytes is established during the juvenile period, and is sufficient for the whole life of a female. The ovaries of one-year-old females contained in average 28,500 diplotene oocytes at the beginning of the season, and then their number increased to 54,480. In two-years-old frogs this number dramatically decreased to 34,666, and eventually reached 23,440 in three-year-old females. The

sharp decrease was accompanied by massive intrafollicular atresia. The average number of eggs oviposited by a female was about 2 000, which gives a pool of oocytes for 11–12 breeding seasons. The oldest female from this population was 9 years old, and the oldest *R. temporaria* from another population reported by Plytycz et al. (J. exp Zool. 273:451–460, 1995) was 12 years old, which gives a reproductive life span ranging from 6 to 9 years. In conclusion, we can say that the number of oocytes is established during the second year of a female life, and is sufficient for about a dozen of spawnings, i.e., for the whole life span.

Infants Anthropological Parameters in Correlation with Maternal Body Mass Index (BMI)

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We investigated correlations of maternal anthropological parameters with newborn's body weight at birth as well as correlations of maternal BMI before pregnancy with newborns' BMI by gender at birth and at 1, 3 and 6 months of age. In 2005–2007 in the Riga Maternity hospital we performed anthropometrical measurements of 503 newborns and infants. Study survey included maternal weight and height before pregnancy. Children were measured at the time of delivery, at 1, 3 and 6 months. BMI were calculated and processed by the means of SPSS/PCT software and compared by t-test, statistical significance $p < 0.05$. Results: from examined women 22.3% showed normal BMI, 52.2% overweight, 25.5% obese. T-test of BMI boys to girls: newborns 2.9; 1 month 4.5; 3 months 5.5; 6 months 3.1. Pearson correlation of maternal BMI to infant BMI in girls: neonate 0.2, at 1 month 0.167, at 3 months 0.159. Conclusions: Maternal BMI before pregnancy showed statistically significant impact on female offspring's BMI at birth, 1 and 3 months of age and no reliable impact on male offspring's BMI. BMI gradually increases in both genders from the birth till 6 months of age. The mean of male BMI at birth, 1, 3 and 6 months of age is statistically significantly higher than mean of female BMI in those age groups.

Numerical Evaluation for the Stress and Deformation of Theropod Dinosaur Skull Against Feeding Loads

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Theropod dinosaurs generally have skulls with large openings such as the antorbital fenestrae. These openings are believed to have lightened the skull. A series of studies using finite element analysis (FEA) has recently revealed that the openings might have dispersed the stress to a wider area in the skull and as a result made the skull structurally more stable. These previous studies analyzed the skull and the lower jaw as separate units and the force was applied only on a few large teeth in the anterior tooth row in order to overcome technical difficulties in three-dimensional FEA. We believe that these previous analyses have some problems. The stress caused by feeding might have been exaggerated by applying the force on only a few teeth. The high bending force might have also been exaggerated by considering mainly adductor mandibulae muscle group, not M. pteygoideus acts nearly perpendicular to the adductor mandibulae muscles. Although it is still two-dimensional, we have analyzed an *Allosaurus* skull and lower jaw together with a proxy for food between the jaws. Our analyses produced significantly different results from previous studies. The skull experiences less stress overall and does not have a concentration of bending stress in the dorso-posterior portion of the skull. This indicates that the upper skull shape basically has robustness against bending stress: the upper skull has acquired the optimum shape.

Conservation and Innovations in Amphibian Head Development

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Our research on the evolution of head development focuses on understanding the developmental origins of morphological innovations and involves asking questions like: How flexible (or conserved) are cell fates, patterns of cell migration or the timing of developmental events (heterochrony)? How do changes in timing or changes in life-history affect head development and growth? Our "model system" is a comparison between lungfishes and representatives from all three extant groups of amphibians. Within anuran amphibians, major changes in life-history such as the repeated evolution of larval specializations such as carnivory, or indeed the loss of a free-swimming larva, allows us to test for developmental constraints. Cell migration and cell fate are conserved in cranial neural crest cells in all vertebrates studied sofar. Patterning and developmental anatomy of cranial neural crest and head mesoderm cells are conserved within amphibians and even between birds, mammals and amphibians. However, radical changes in the timing of cranial neural crest stream emergence and migration occur, at least in anurans, even within a genus. The evolution of carnivorous larvae is correlated with changes in both pattern and timing of head skeletal and muscle development, and sequence-heterochronic changes are correlated with both feeding mode and phylogenetic relatedness. Supported by the Deutsch Forschungsgemenschaft (OL 134/2-4) and COST B23.

The Fundamental Structure of the Alimentary Tract and the Arterial Blood Supply in the Adult Zebrafish

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Zebrafish (*Danio rerio*) is proving itself as a useful animal model system for studying human diseases, especially in elucidating the molecular basis of congenital diseases. Some mutants with diseases that closely resemble human genetic diseases have been collected in the field of cardiovasology, and successfully positional cloned. However, the vascular anatomy of adult zebrafish that is essential to understand the malformation accurately and compare the results with those of human, has not been clarified yet. We here intend to make an anatomical atlas of vasculature distributing to the abdominal organs, which have variable features depend on fishes. The alimentary tract between esophagus and anus is characterized morphologically and histochemically. The standard pattern of the gut looping was defined by dissecting 100 adult fish, which was divided macroscopically into four sections. We designate them: (I) bulbar part of proximal intestine, (II) recurrent part of proximal intestine, (III) distal intestine, and (IV) rectum. The dye-injected specimens revealed that the unique coeliacomesenteric artery gives arterial branches to the four sections, other abdominal organs and gonad. Based on the observations, we tried to give the proper names of 15 branches from it to provide an invaluable foundation for future genetic and experimental studies.

Does the Snout Disc Make the Pig?

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The family Suidae is traditionally characterized by the presence of a snout disc, moved by the strong muscles of the rhinarium. This highly specialized structure, implicated in the digging actvity of pigs, leaves strong muscle impressions on the face of the skull, which can be interpreted and reconstructed in fossil specimens. The morphology of the snout of some fossil suids belonging to the subfamilly Listriodontinae is detailed and compared to extant suid species to infer the structure of the rhinarium of this extinct group. The peculiar features of the listriodontine snout indicate weak rhinarium muscles and suggests that some of them were most likely devoid of snout disc. The lack of this suid structure triggers the question of the ancestral morphology of the suid snout.

Morphological Study of the Otic Region and Petrosal Bone of Listriodontinae (Suidae, Mammalia)

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The basicranial region, and in particular the petrosal bone, proved to be of interest in therian mammals systematics (e.g., Carnivora, Primates, Marsupialia). The petrosal is the most complex bone in the mammalian skull, resulting from an endochondral ossification of the basicranium. It contains a variety of soft-tissue structures (muscles, nerves, arteries and veins) that are likely to leave impressions on the petrosal bone and can be interpreted and reconstructed in fossil specimens. The otic region of suids is characterized by the presence of a very long external auditory

conduct, placing the opening of the meatus dorsally, in a very high position. The morphology of the otic region of fossil suids has been studied in depth by Pearson (1927), but no suids from the subfamilly Listriodontinae were included in her work. Moreover, the otic area of those extinct suids, thought to be similar to extant ones, has never drawn attention since that study. The auditory area of members of the three listriodontine tribes is detailed and compared, together with petrosal bones from the genus *Listriodon* and *Eurolistriodon*. It appears unexpectedly that listriodonts exhibit various morphologies, triggering the question of the plasticity of the otic region of suids.

Hagfish Embrology Project

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Hagfish and lampreys are the sole members of the extant jawless vertebrates occupying a critical position on the phylogenetic tree. Since the 1870s, when the scientific importance of hagfishes was already well recognized, many embryologists have endeavored to sample hagfish embryos at various locations including the North Sea and off the California coast. Despite abundance of the adult hagfish populations, however, no detailed embryological report has been made since 1899 when Bashford Dean described a whole series of *Eptatretus stouti* embryos. The reason for this paucity of information is at least derived from inaccessibility of their deep sea habitat. Even now, although a few modern scientists try to collect hagfish embryos applying sophisticated techniques, there has not been major success. To obtain hagfish embryos, we have picked up an inshore hagfish species *Eptatretus burgeri*, and contacted a local fisherman familiar with the seasonal behavior of these animals in the Japanese coastal area. We collected adult hagfish individuals in the candidate spawning season with the fisherman and maintained collected animals in the aquarium tank designed for their spawning. We will report the details of our hagfish project, and developmental patterns of obtained embryos with a new scenario for neural crest evolution.

Inspiratory Mechanisms in Reptiles: Primitive or Derived, Primary or Accessory?

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Costal aspiration is the basal mechanism of lung ventilation in amniotes. Most amniote taxa evolved accessory mechanisms, some of which have become primary means of inspiration (e.g., the diaphragm in mammals). We discuss two cases of such inspiratory mechanisms in extant reptiles, whose role in lung ventilation is challenged by new findings. Gular pumping, as a ventilatory mechanism, was first observed in monitor lizards during and after exhaustive locomotion. A recent survey, by videoradiography, found that most extant lizard species exhibit gular pumping as a threat/defence display, or during forced exercise. This suggests gular pumping behavior is a primitive squamate character. Interestingly, when the gular pump was obstructed in juvenile savannah monitors, maximum aerobic capacity and exercise endurance were only reduced in larger animals. This suggests gular pumping does not provide an aerobic benefit to small lizards, may have evolved initially as a defence behaviour and was subsequently co-opted as an accessory inspiratory mechanism by larger lizards. Crocodilians possess a unique diaphragmaticus muscle, which powers the hepatic piston mechanism. Previous studies have shown the diaphragmaticus to contract with every inspiration, and construed that it is a primary muscle of inspiration. In contrast, we have found by electromyography that the diaphragmaticus is often quiescent, even when animals are hyperventilating (during hypercapnia or recovery from exercise). Neither maximum aerobic capacity, tidal volume, nor exercise endurance were reduced when the diaphragmaticus was surgically severed. This suggests that the hepatic piston is an accessory inspiratory mechanism, and is not necessary for adequate lung ventilation.

Developmental Plasticity of the American Alligator in Response to Atmospheric Oxygen Levels During Incubation

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Adequate oxygen supply to the embryo is necessary for normal growth and development, and hypoxia is known to constrain embryonic growth in many amniotes. However, embryos of ectotherms can remain viable and hatch successfully at lower oxygen levels than embryos of endotherms. Recent models of atmospheric composition through the Palaeozoic suggest large-scale fluctuations in oxygen levels, including a significant drop (from approx. 30% to approx. 12%) at the Permo-Triassic boundary. To investigate the effect of such an atmospheric change on whole-body morphology of embryonic amniotes, we incubated eggs of the extant American alligator *(Alligator mississipiensis)* under different laboratory conditions: hypoxia (12–13%), normoxia (20–21%) or hyperoxia (29–30%). All embryos were incubated at 30°C and were litter-matched. There were no significant differences in skull, total and snout-vent lengths between hyperoxic and normoxic hatchlings, but hypoxic hatchlings were significantly smaller. Hypoxic hatchlings also had a smaller yolk-free body mass and a greater unutilized yolk mass. Mass-specific wet heart mass was significantly greater in hypoxic hatchlings than in other hatchlings. No significant differences existed between groups in mass-specific wet liver mass. In comparison to their normoxic and hyperoxic siblings, hypoxic hatchlings showed reduced skeletal growth, indicative of lower endochondral and periosteal bone formation rates. This suggests Palaeozoic oxygen levels may have had a profound influence on growth patterns of extinct amniotes, e.g., acting as a constraint on growth rates in some Triassic taxa. Thus, attempts to infer growth rates of extinct taxa from their fossil bone microstructure should consider contemporary oxygen levels when offering alternative explanations.

Aquatic and Terrestrial Locomotion of the Ropefish

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Locomotion in amphibious fishes is an interesting (and understudied) paradigm to examine locomotor flexibility, adaptation, and evolutionary trade-offs. The ropefish, *Erpetoichthys calabaricus*, is an elongate polypterid that is known to make terrestrial excursions. Work on another elongate amphibious fish, the eel, has shown differences between aquatic and terrestrial locomotion and it is possible that elongate amphibious fishes move similarly between aquatic and terrestrial habitats. To compare movements in each habitat aquatic and terrestrial locomotor trials of the ropefish were captured using high-speed digital imaging. The midline of the fish was digitized using the computer program Didge and movements of the body were plotted through time. Aquatic trials showed a gradient from high amplitude undulations at the posterior end of the animal to low amplitude undulations at the anterior end of the animal, with undulations decreasing progressively from the posterior to anterior ends. Therefore, typical of swimming undulation, not all points of the animal travel in the same direction. This is in contrast to terrestrial movement of the ropefish. Terrestrial locomotion more closely approximates terrestrial lateral undulation than swimming undulation in that generally, all points travel in the same direction and progressively decreasing amplitudes of undulation are not seen from the posterior to the anterior ends of the animal. These preliminary results are similar to results found for eels, suggesting that elongate fishes may move similarly on land irrespective of phylogeny.

The Role of Amelogenin in Enamel Formation

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With the clonings of cDNAs to amelogenin, ameloblastin, enamelin, MMP20, KLK4 and amelotin, all of which are relatively enamel-specific gene products, our understanding of enamel matrix assembly, and the role the enamel matrix plays in biomineralization, has been greatly enhanced. Of the structural enamel matrix proteins, the biological function of amelogenin is best understood. Amelogenin self-assembles into nanospheres, which can then align into a linear and branching gel-like structure that are capable of guiding enamel crystallite growth. While much of our understanding of amelogenesis has been derived from either rodent or *in vitro* experimentation, all findings relate to enamel formation in higher mammals. I will discuss recent advances in amelogenin biochemistry and function.

Muscle Attachments of Ribs in Extant and Extinct Species

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The goal of our research is to predict the tidal volume of dinosaurs on the basis of resting position of the ribs, intercostal muscle coordinates,

swing plane of the ribs and functional morphology of breathing mechanisms in modern analogs. Data on the latter two are available and the resting position of the ribs can be deduced if the orientation of the intercostal muscles is known. Sharpey's fibers are collagenous extensions from the periosteum that penetrate the bone surface. Their orientation reflects that of the muscles to which they attach. Assuming that the orientation of Sharpey's fibers of external and internal intercostal muscles is known, they can be used to predict the resting position of ribs in extant and fossil material. As an extant model we used Bennett's Kangaroo (*Macropus rufogriseus*), in which both layers of intercostal muscles are well developed. Cross sections of ribs were prepared using paraffin histology and palaeohistological methods (thin-ground sections). These were observed using polarized light and compared with fossil rib fragments of *Plateosaurus engelhardti*.

Evolutionary Genetics of Zebrafish Pigment Pattern Development

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Pigment patterns of *Danio* fishes are a tractable system for studying the evolution of developmental mechanisms and how these mechanisms influence patterns of phenotypic variation. *Danios* exhibit a diverse array of adult pigment patterns ranging from horizontal stripes in the zebrafish, *D. rerio*, to a uniform pattern in *D. albolineatus*, to vertical bars in *D. choprae*. Here, I report on recent progress in understanding the genetic and cellular bases for pigment pattern diversification in this group, and how genetic approaches can be used to reveal homology and evolutionary novelty during pigment pattern development.

The Impact of High-throughput Morphometrics on Phenotypic Analyses with 3D-micro-computed Tomography

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The biological sciences have lately seen a switch of emphasis away from individual genes and isolated pathways towards the analysis of complex interactions that produce phenotypic variation. This past era produced an increasing demand for and creation of high-throughput techniques capable of analyzing vast amounts of data; likewise, high-throughput approaches that involve the study of variation will be crucial to phenotypic analysis realizing its potential in post-genomic biology. Here, we present such a tool and its application to craniofacial phenogenomic studies. Further, our technique provides a platform for data sharing and standardization. To these ends, we have begun to develop first, software capable of high-throughput phenotypic analysis and second, a community-wide database of high resolution micro-computed tomography data. Our software employs a new non-landmark morphometric method that superimposes volumetric datasets into a common orientation to create a single mean shape or generalized shape image (GSI). Shape differences between two GSIs can be visualized using surface-to-surface distance measures between the superimposed images. Within-sample shape variation can be quantified using the image gradient of the average shape and visualized by superimposing the gradient magnitude on an isosurface representation of the average shape. Current research using this method has focused on craniofacial development and the analysis of morphological variation at different developmental stages—embryonic, neonatal and adult—in several mouse strains. Additionally, an internet-based system for the storage and retrieval of volumetric data that incorporates both this high-throughput method and traditional geometric morphometric output will enhance this 3D morphometric method.

The Contribution of Differential Epistasis to the Variation in Pleiotropy

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Differential epistasis describes the situation where epistatic effects involving the pleiotropic locus are different for the different traits this particular locus influences. (Cheverud et al., 2004). Pleiotropy is an aspect of the genetic architecture responsible for the coordinated variation between phenotypic traits and thus for the modular organization of the phenotype. However, the evolvability of the phenotypic covariance structure requires that the underlying genetic architecture is variable. Differential epistatic effects on the pleiotropic loci result in genetic variation in the covariance and therefore variation in the observed pleiotropic effects. Differential epistasis thus offers a way of maintaining genetic variation in the phenotypic organization. We concentrate on the continuous population-level genetic variation in the modularity of adult phenotypes. We first address the variation in pleiotropy by mapping relationship QTLs (rQTLs; Cheverud et al. 2004) for tail and limb bone lengths in relation to weight at necropsy in pooled F2 and F3 generations of a cross between two inbred mouse strains. These are the loci at which alleles affect the relationship between pairs of traits, rather than contributing variation to any one trait itself. When considering morphological traits, such loci affect shape, or in this case allometry. We found altogether 11 rQTLs. Genetic variation in relationships between traits stems either from the interactions with genetic background or environment. We focus on epistatic effects upon the rQTLs. Epistatic scans for specific loci that interact with rQTL in affecting the traits of interest revealed multiple interaction loci. The effects of these loci upon the allometry are presented.

Tracing Segmental Boundaries in the Adult Mouse Hindbrain

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We have used data from the rhombomeric analysis of the chick hindbrain to formulate hypotheses on the occult rhombomeric borders of the adult mouse brain. We have used transgenic mice to validate some of these hypotheses. In the embryonic vertebrate brain, seven segments (rhombomeres r1 to r7) can be identified on the basis of constrictions in the developing hindbrain. In the chick, it has been shown that homeobox (hox) genes are responsible for much of this segmentation process. We have investigated the rhombomeric origin of the adult brainstem nuclei in the mouse by studying the lineage of several transcription factor genes by cre/lox recombination and subsequent labelling of the relevant cell lineages with LacZ and GFP. We have mapped the boundaries and derivatives of rhombomeres 3, 4 and 5 by studying the expression of hoxb1, hoxa3, and egr2. The contents of these rhombomeres in the mouse are very similar to those in the chick but there are some differences. We have also found evidence from normal histology and hoxb8 expression in the mouse suggestive of the existence of four additional "hidden" rhombomeres caudal to r7. The presence of rhombomeres r8 to r11 was originally suggested by Cambronero and Puelles (J. Comp. Neurol, 427:522, 2000) on the basis of chick-quail grafting experiments. Overall the organization of the rhombomeres of the mouse is very similar to that in the chick, and we believe that most data derived from avian studies can be confidently transferred to mammals.

Skin Structure in the Dwarf African Clawed Frog *Hymenochirus boettgeri*

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The skin structure of adult specimens of *Hymenochirus boettgeri* investigated in SEM and LM shows great diversity between the dorsal and abdominal part of the body including the surface, distribution and size of different glands and melanin structure. SEM studies show that the surface of the dorsal part is covered by three types of protuberances: the largest protuberances (mean diameter = 321.5 μm) always have one outlet of a serous gland and 2–4 outlets of mucous gland on their lateral part; the medium sized protuberances (mean diameter = 159.38 μm) have only outlets of mucous glands, and the smallest (mean diameter = 41.98 μm) have no outlets at all. The skin on the abdominal part of the body has medium and small protuberance types; the presence of outlets of the serous glands is sporadic. The semithin sections stained with methylene blue show that the superficial layer of epidermis on protuberances forms cusps of completely keratinized cells, whereas the remaining cells are less keratinized and possess many microridges on their apical surface. The melanophores are present beneath the epidermis of the

dorsal part, but single or aggregated melanosomes are observed between and within the epidermal cells. Ventral skin is almost devoided of pigmentation. In the stratum spongiosum we identified mucous glands and two types of serous glands which differ from each other both in size and the nature of their secretion. Gland are mainly located under protuberances.

Evidence for Sertoli Cells in the Testes of *Bombina variegata* (Anura: Bombinatoridae)

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Because Sertoli cells (SCs) are inherent to the germinal epithelium in all male chordates, reports on their absence in *Bombina* required careful scrutiny. We reexamined the testis structure in *B.variegata* using light microscopy, transmission and scanning electron microscopy in breeding males, tadpoles (Gosner 35+) and metamorphosed juveniles. Adult male testes contained mature sperm amid a heterogeneous assembly of cysts varying in size and gametogenetic stage of the enclosed cells, as expected in a species with a prolonged mating season (April-September). Contrary to Obert's (1976) report, the SCs were readily identified. They separated germ cells from the basement membrane and formed the walls of gradually enlarging cysts. The SCs morphology underwent profound changes during spermatogenesis. Nuclei of SCs that surrounded early spermatogonia were positioned adjacent to the basement membrane, whereas in later spermatogenesis the nuclei were located next to the lumen of the testis. Phagocytosis of the residual bodies and in the degenerating cells was observed. Examination of the developing gonads in tadpoles revealed that the SCs originated, as in other amphibians, from the celomic epithelium. Based on morphological and functional criteria, our study demonstrates the presence of SCs in *B.variegata* testes, where they assist in sperm formation, and thus confirms the tripartitate structure of the germinal epithelium in this species.

First Articulated Skeleton of a Terrestrial Paleogene African Mammal: *Saghatherium antiquum* (Hyracoidea) From the Early Oligocene of Libya

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Complete or partially articulated skeletons of a dozen of mostly juvenile individuals of the hyracoid *Saghatherium antiquum* from the early Oligocene of Jebel al Hasawnah (Tarab Formation, Libya) are described. This is the best preserved mammal material known from the Paleogene of Africa. It provides the first data on the postcranium of Paleogene hyracoids and a primary reference to their locomotor adaptations. The overall construction of the skeleton of *S. antiquum* is very close to that of extant procaviids, which indicates a remarkable old and stable pattern. This is especially true of the intracarpal and intratarsal construction (taxeopody and relationships of proximal and distal rows). Unlike extant species, *S. antiquum* is characterized by a lengthened foot and hand (metapodials, astragalar neck, and cuboid), and a hoof-like morphology of the distal phalanges that, among other features, suggest an overall unguligrad stance. The postcranium of *S. antiquum* displays striking cursorial specializations which are also well distinctive from procaviids. Some of these are well advanced in *S. antiquum* (e.g., tridactyl mesaxonic pes) and suggest a pattern established very early in hyraxes. Other characters, like the presence of an asymmetrical and oblique trochlea on the astragalus, indicate that *S. antiquum* was not a rapid cursor. *Saghatherium antiquum* has a high number of thoraco-lumbar vertebrae as in other paenungulates, but a lower number than in extant hyraxes. It therefore illustrates an intermediate structural pattern between the noticeable derived condition of modern hyraxes and the more primitive condition of tubulidentates and other paenungulates.

Non-occlusal Dental Microwear, Enamel Microtopography and Tooth Crown Morphology in Neanderthals: Evolutionary Determined or Ecologicaly Constrained?

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Recent analyses have shown that enamel 3D-topography is highly sensitive to taphonomic processes. Restrictive sample selection criteria need to be adopted prior to microwear analyses in order to prevent the effect of post-mortem damage on fossil specimens' dietary interpretation. However, well preserved enamel surfaces show a significant variability in enamel roughness that can be used to trace dietary differences among fossil human populations. In addition, differences in tooth crown morphology between hominin species may be interpreted as biological adaptations to ecological conditions and dietary habits. Buccal enamel dental microwear, enamel roughness and tooth crown geometric morphology have been analyzed in a sample of Neanderthals and modern humans fossil remains from Europe and the Near East. Significant associations among all the variables analysed were obtained, suggesting that a coevolutionary model between dental morphology and ecological conditions can be applied to the Middle and Upper Palaeolithic transition. The dietary and morphological indicators analyzed suggest that adaptation the overall climatic conditions was not fully tempered by cultural factors, but significantly conditioned by natural selection. Neanderthals, as modern humans, fought a parallel, never-ending struggle for survival determinant of both cultural and biological adaptations.

Synthesis of Current Data in Growth of Early Jawless Vertebrates

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Recent published works on the growth of the heterostracans (armored jawless vertebrates) led us to present a synthesis of current data concerning the ontogeny (from juvenile forms to adults) of these siluro-devonian vertebrates. Data are now sufficiently documented to propose a general scheme of the dermal skeleton development and histology for the two main heterostracan groups: the Cyathaspidiformes and the Pteraspidiformes. The horizontal cyclomorial development of the head shield is now established on growth series. It is completed by new evidences of vertical bony tissue growth which results generally in homogeneous histology of the dermal plates in adult specimens. Variations of speed in cyclomorial development and heterochronies can explain some remarkable forms such as the huge *Gigantaspis* or the aberrant *Doryaspis* (Pteraspidiformes). Finally, it provides an explanation for the general trends of evolution within the heterostracans.

Masticatory Anatomy of Strepsirrhines: Selection for Stretch or Strength?

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We studied the anatomy and fiber architecture of the chewing muscles in 25 strepsirrhine primates. The goals of the study were to: 1. understand the scaling pattern of muscle mass, cross-sectional area (PCSA), and fiber length (FL), 2. test the relationship between PCSA and dietary preference, and 3. test the relationship between FL and a behavioral measure of gape. We found that jaw adductor muscle mass, PCSA, and FL scale isometrically with body mass (RMA log slopes = 0.943, 0.707, and 0.269, respectively; r-squared values = 0.898, 0.841, and 0.734, respectively). The relationship between PCSA and dietary preference is poor. However, of the large-bodied strepsirrhines, those that eat tough foods (leaves) tend to have greater PCSA than those that eat fragile foods (fruits). Multiplying a muscle's PCSA by its leverage changes the distribution of data points very little: those strepsirrhines that have greater PCSA tend to have greater muscle leverage too. We performed an experiment on a subset of our sample to estimate Preferred Bite Size (PBS), the size of the largest block of food a strepsirrhine will ingest without biting it apart first. We found that PBS scales isometrically with body mass for most foods tested. However, among large-bodied strepsirrhines, leaf-eaters have a much smaller PBS for their body size than do fruit-eaters. This matches the pattern we see for chewing muscle FL,

suggesting that the size of food items ingested by these animals may select for chewing muscle fiber length.

An Avian-style Respiratory System for Sauropod Dinosaurs

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Previous attempts to model lungs of giant sauropods (Dinosauria: Saurischia) have been based on either a crocodilian (Hengst et al., 1996. In: Keller and MacLeod, eds. Cretaceous-Tertiary Mass Extinctions: Biotic and Environmental Changes. W.W. Norton & Co. NY: 327–347.) or mammalian model (Gunga et. al., 1995. Naturwissenschaften 82:190–192). Not surprisingly the predicted lung structure was either of such low diffusing capacity that the dinosaur could not have survived at present-day oxygen levels or so small that the dead space provided by the long neck would have compromised the efficiency of gas exchange. Since birds are the direct descendants of theropods (Dinosauria: Saurischia), a modified avian model is likely to produce more plausible predictions of lung function in dinosaurs (Hicks and Farmer, 1998. Science 281:45). Extrapolating avian values for respiratory anatomy and physiology to a sauropod reveals that the diffusing capacity of the lung would become incapable of matching the increase in metabolic rate at body masses between 10 and 50 tonnes, depending on temperature control mechanisms and whether the animal is resting or moving. Thus, the pulmonary diffusing capacity could set the anatomical limit to gigantism. We further propose that sauropods had an active cooling mechanism, possibly involving the neck and sac-like lung regions, and that the latter also made previous weight estimates systematically too high. Financial support: DFG FOR 533 TP U5.

Micrornas and the Evolution of Vertebrate Complexity

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The notion of complexity is often easy to appreciate but difficult to quantify. Nonetheless, given their almost 3-fold increase in the number of cell types, vertebrates are clearly more complex than invertebrates (Valentine et al. 1994 Paleobiololgy 20:131–142). Sempere et al. (2006 J. Exp. Zool. 306B:575–588) recently showed that Osteichthyes are characterized by a dramatic jump in the number of microRNAs, ~22 nucleotide non-coding RNAs that control gene expression by negatively regulating the stability or translation of target mRNAs, as compared to other animals including cephalochordates and urochordates—only a handful of new miRNAs evolved at the base of Chordata, but at least 75 new miRNAs evolved between the last common ancestor of vertebrates and other chordates and the last common ancestor of Osteichthyes. Because microRNAs (miRNAs) seem to control the balance between cellular proliferation and cellular differentiation, the evolution of new cell types might be controlled, at least to some degree, by the evolution of new miRNAs, and indeed, many of these new vertebrate-specific miRNAs are expressed in vertebrate-specific tissues and tissue specializations. Here, we show that many of these osteichthyian miRNAs are also detected in Chondrichthyes, and we will report data concerning their detection in lamprey. We argue that lying behind the origin of vertebrate complexity might be the dramatic expansion of the non-coding RNA inventory including miRNAs, rather than an increase in the mRNA-encoding inventory due to genomic duplication events.

Lateralized Behaviour and Mauthner Neuron Asymmetry: Is There a Link?

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Many tadpoles have a turning bias and turn about twice as often to their left side than their right when either startled or diving after taking a breath of air. This turning bias does not appear to be linked to any external asymmetry such as position of the spiracle. Wassersug and Yamashita (2002. Laterality 7:241–260), however, suggested by that the asymmetry in behavior may correlate with asymmetry in Mauthner neurons. Moulton et al. (1968. J Embryo Exp Morph 19:415–431) have previously asserted that Mauthner neurons are asymmetrical in tadpoles, but provided no data to support that claim. Here, we test the Wassersug and Yamashita hypothesis with *Rana sylvatica* tadpoles from Nova Scotia, Canada. Turning bias was measured after tadpoles surfaced to breathe air. Their Mauthner neuron size was then assessed from serial sections stained with Bodian silver stain. Consistent with Moulton et al. (1968), we found that Mauthner neuron size, as represented by nuclear size in cross section, is commonly asymmetric with a mean difference between the left and right neurons of 13% (N = 107). We were not able to show though that behavioral differences in turning bias correlated with the amount or direction of the asymmetry in the Mauthner neurons. Although Mauthner neuron asymmetry may contribute to lateralized behaviors in tadpoles, other parts of the nervous system must be involved in the lateralization of turning bias. Factor influencing lateralized behaviors in tadpoles will be discussed.

Skeletal Derivatives of the Somites in the Mexican Axolotl (*Ambystoma mexicanum*)

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The axial skeleton of vertebrates as well as the occipital region are derivatives of the sclerotomal regions of somites. The segmentation of the axial skeleton is shifted compared to the original segmentation of the somites by a process called resegmentation. Transplantation experiments in the quail-chick chimera system have revealed that cranial and caudal halves of the somites are lineage restricted and retain their axial information while forming single vertebrae. This is in contrast to a less strict resegmentation observed in zebrafish. Further comparative data for resegmentation modes are needed for a better understanding of this process and its variability among gnathostomes. The somitic fate in species other than chicken has been analyzed mostly using classical histology. We mapped the fate of somites two to five by injection of dextran-fluorescein in an urodele amphibian, the Mexican axolotl. After 10 to 40 days of development the marker was detected and amplified by immunofluorescence on paraffin sections. We were able to determine the contributions of single somites to different vertebrae as well as to the occipital region. We also tested if somitic material contributes to the shoulder skeleton. This has been shown to be the case in chicken and mouse and also is assumed for other species, but has so far never been confirmed in an amphibian. Furthermore, we investigated the muscular derivatives of single somites, which revealed only small differences between the Mexican axolotl and chicken. Our data support a conserved pattern of somitic derivatives at least within tetrapods.

Growth Factors in the Esophagus in Children with Esophageal Atresia (EA)

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Incidence of esophageal atresia is reported in one case from 3000 newborns. The morphopathogenesis of this malformation still is not clear. Aim of work was investigation of innervation and growth factors in esophagus in children with EA. Material was obtained from 15 newborns during plastic surgery. Control material was taken from children who died from non-gastrointestinal diseases. PGP 9.5, VIP, SP, NF, M, TGFß and NGFR were detected by use of immunistochemistry. Results showed vacuolized epitheliocytes and hyperplasia of basal cells, disorganization of muscle, vacuolization of gangliocytes in Auerbach's plexus in all patients. Esophagus showed weak staining of myelin- and NF-containing nerve fibers in submucosa, Auerbach's plexus and adventitia. Numerous PGP 9.5 nerves were seen in affected tissue. Occasional SP-, VIP-containing nerves were seen only in two cases. Control subjects demonstrated strong and abundant distribution of above mentioned neuropeptide-containing nerve fibers in muscle layer, around esophageal glands, and in adventitia. NGFR was richly expressed in nerves of controls, but varied in patiens. FGFR was equally expressed in patients and controls, but expression of TGFß varied again in patients. Conclusions. Weak NF and M staining for nerves, decrease of SP-, VIP-nerves and various expression of NGFR characterize EA disordered tissue despite

generally rich neuropeptide-containing innervation that indicates involvement of other neuropeptides in EA. FGFR expression is unchanged, but decrease of TGFß proves possible significance of other growth factors in EA pathogenesis. The main changes of esophagus in EA are abnormality of epithelium, disorganized muscle coat, and vacuolization of ganglion cells in Auerbach's plexus.

Skin Regeneration and Degeneration Factors After Implantation of Different Biomaterials in Subcutis of Experimental Animals

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The appearance of tissue regeneration and degeneration factors after the implantation of biomaterials is still unclear. The aim of this work was to reveal the distribution of growth factors, neuropeptides, matrix metalloproteinases (MMPs), apoptosis, and genes in tissue around the implants. Methods: PGP9.5, VIP, SP, TGFß, FGFR1, BMP2/4, MMP, barx1, msx2 and apoptosis were detected in soft tissue after subcutaneous implantation of hydroxyapatite ceramic (HAP), glass ceramic (4N, 4NK) in Wistar rats, and in the vertebrae and ear cartilage perichondrium after implantation of HAP and by use of immunohistochemistry. Results: In rats, some connective tissue cells expressed TGFß. FGFR1 was expressed by epithelial cells, connective tissue, hair follicles, and sebaceous glands. Appearance of neuropeptide-containing nerves correlated with duration of implantation time. White blood cells, cells of the connective tissue and glandulocytes were positive for MMP2. Neovascularization, proliferation of nerves and sclerotization of blood vessels were observed around the implants. Epithelium, cells of the connective tissue and skin derivatives, chondrocytes and muscles demonstrated apoptotic changes. Rabbits showed massive neochondrogenesis with bone fragments. Chondrocytes and a moderate number of connective tissue cells expressed BMP2/4, FGFR1, TGFß, MMP2, MMP9, barx1, msx2. Conclusions: A decrease of immunoreactive innervation is correlated with the increase of implantation time of the biomaterial. Degeneration and selective expression of FGFR1 are characteristic changes for soft tissue around biomaterial implants. Implantation of HAP and perichondrium elicites neochondrogenesis and osteogenesis. However, a rich expression of growth factors and matrix degradation enzymes, and massive apoptosis in newly formed cartilage/bone, give rise to questions about the quality of the structure that develops.

Competition, Mating Systems and Sexual Dimorphism in Primates

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Primates show a great deal of variation in sexual dimorphism in canine size and body mass. Many comparative analyses have evaluated the hypothesis that sexual dimorphism in primates is a consequence of sexual selection. It has long been noted that analyses employing one of the most common measures of sexual selection—breeding system—consistently demonstrate that monogamous species show little dimorphism (as expected), while single-male and multimale species show highly variable degrees of dimorphism. This large degree of unexplained variation in dimorphism has led other comparative studies to investigate the relationship between dimorphism and estimates of intrasexual competition, socionomic sex ratios, group size and operational sex ratios. While categorical estimates of intrasexual competition are the strongest correlate of dimorphism in primates, careful consideration of the relationships between these various behavioral and demographic measures and dimorphism helps resolve some of the traditional conundrums arising from past analyses, and provides a deeper understanding of the relationship between intrasexual competition and other behavioral and demographic measures. Especially important is consideration of selective pressures independently affecting male and female traits. Phylogenetic comparative analyses support the model that ultimately for males, sexual selection is a function of the monopolization potential of females as a function of the spatial and temporal distribution of females, coupled with female counterstrategies to male coercion. Dimorphism is also affected by patterns of female intrasexual competition and selection for female life-history traits that impact female size and reproductive success.

4d-analysis of Mouse Pelvis Morphogenesis

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Today the respective knowledge of body axis and limb morphogenesis in vertebrates is in-depth, whereas the establishment of the axio-appendicular junction—the morphogenesis of the pelvic girdle—is still vaguely comprehended. Not only from the evolutionary and the developmental perspective is the establishment of the pelvic girdle elements of crucial importance, but also from the medical point of view in terms of human pelvic malformations. The present study examines the developmental dynamics of the pelvis anlage in the mouse (*Mus musculus domestica*), with respect to axio-appendicular conjunction, addressing the questions of the origin of the elements (axial versus appendicular origin), the tripartition and the attachment process. Specimens from developmental Theiler (Theiler, 1972)1 (TH) stage 19 to 25 were sectioned in series for histology and were examined by light microscopy. From this histological series we generated computer-based 3D-models2-3. By subsequent 4D-reconstruction the entire developmental process of early pelvis morphogenesis was visualized and qualitatively and quantitatively analyzed. Our results confirm that the pelvis anlage is of uniform origin, emerges in intimate association with the limb, and only secondarily attaches to the body axis. By virtue of 4D-visualization a yet unknown developmental process is revealed and characterized: the rotation of the pelvic element from its position at origin, to its final inclined, functional position. 1. Theiler K., The House Mouse, Springer, Berlin (1972): 1–168; 2. Streicher J. et al., Anat. Rec. (1997) 248: 583–602; 3. Streicher J. et al., Nat. Genet. (2000) 25: 147–152.

Locomotor Energetics in Chimpanzees, Humans, and Extinct Hominins: Contributions of Muscular and Skeletal Anatomy

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What are the relative contributions of skeletal anatomy and muscular anatomy to the energy cost of locomotion, and how can their independent effects be measured? In this study, we measured the energy cost of locomotion during both quadrupedal and bipedal walking in chimpanzees, and during walking in humans. We then compared differences in cost to differences in contact time (i.e., stance duration) and the volume of muscle activated per unit of ground force, measured via kinematic and inverse dynamics analyses. As expected, differences in contact time and active muscle volume reliably predicted differences in cost between humans and chimpanzees, and between bipedal and quadrupedal walking in chimpanzees. Importantly, the combined inverse dynamics and energetics analyses enabled us to assess the relative contributions of skeletal and muscular anatomy to locomotor cost. Skeletal anatomy contributed significantly to differences in cost via the effect of hip height on contact time, and the effect of posture (particularly knee and hip flexion) on active muscle volume. Muscular anatomy affected differences in cost as well, with the relatively longer muscle fibers of chimpanzees contributing to their greater cost of locomotion relative to humans. We then used these results to model locomotor energy cost for early fossil hominids, since energetic efficiency has often been proposed as an important selection pressure in early hominin evolution. Results generally support the hypothesis that early hominins had lower locomotor costs than apes, but assumptions regarding muscular anatomy in these species greatly affect their predicted energy costs.

The Development of Osseous Tooth Support: What are the Functional Cues?

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Young, compliant bone adapts to loading through apposition and increased stiffness. This study investigates the biomechanical effects of tooth loading on developing alveolar bone as a tooth erupts into occlusion. Loading of an erupting tooth was hypothesized to generate greater strains in alveolar bone than loading of a tooth in occlusion. Mandibular segments from miniature pigs, *Sus scrofa,* containing M1 either erupting

or in functional occlusion, were loaded in compression using a materials testing machine. Simultaneous recordings were made from rosette strain gauges affixed to the lingual alveolar bone and the M2 crypt. Principal strains were compared at 440N. In both groups the crypt distal to M1 showed higher strains than in the lingual region. In the crypt the largest principal strain was tension for specimens with erupting teeth (500 to 2300 με), but compression for specimens in occlusion (−300 to −700 με). In the lingual region, compression was the dominant principal strain, and had a similar range in both groups (−20 to −500 με). These data indicate that lingual cortical plates are stiff and supportive even before functional occlusion, whereas alveolar bone distal to the tooth is less stiff. In contrast to expectation, the major change with functional occlusion was an alteration of strain pattern rather than magnitude. During eruption, the loaded M1 crown generates high tensile strains in the distal alveolar bone that may trigger osteogenic augmentation of the alveolar ridge. In contrast, the roots of erupted teeth deform distal bone through transmission of occlusal loads. Supported by NIH/NIDCR DE015815-02.

Cranial Biomechanics of a Primitive Ornithischian Using Finite-element Analysis

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Ornithischian dinosaurs were the most diverse and abundant herbivores of the late Mesozoic, developing a range of jaw mechanisms to process plant matter; yet the jaw mechanism utilized by the primitive clade Heterodontosauridae is uncertain. Heterodontosaurs are rare and poorly understood herbivorous dinosaurs distinguished by a heterodont dentition and robust cranium. It is commonly believed that heterodontosaurs used a transverse power stroke in mastication, achieved by long-axis rotation of the mandibles. Propaliny and cranial kinesis have also been proposed as possible jaw mechanisms. However, lack of tooth microwear and limitations in the field of biomechanics have prevented testing of these hypotheses. Because of their phylogenetic position as the most basal ornithischians, uncovering the feeding strategy used by heterodontosaurs would shed light on the origin and early evolution of herbivory within Ornithischia. This study applies the engineering technique of finite-element analysis to visualize stress and strain within the cranium of *Heterodontosaurus tucki* during feeding, allowing us to determine which jaw mechanism best corresponds to skull morphology. Additional evidence for relative jaw motion was obtained from skull and dental morphology, suture analysis, and tooth microwear, providing a holistic approach in determining the jaw mechanism of *Heterodontosaurus*. Our results suggest that mastication did not involve rotation of the mandibles but instead scissoring of the mandibles with lateral splaying of the posterior skull elements. These results illuminate key structural changes in cranial morphology that may have evolved in early ornithischians during the transition to herbivory.

Material and Structure: The Influence of the Mineral Component on Mechanical Properties of Elamobranch Vertebrae

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Mineral content and arrangement are significant predictors of material properties in mammalian bone. Increasing mineral content increases stiffness and strength, and the arrangement of bone, as in trabeculae, has effects on both properties as well. Shark vertebrae, although made of cartilage, are heavily mineralized tissues. They have material properties and mineral fractions which near those of trabecular bone. The mineral in shark vertebrae varies interspecifically in amount and also arrangement within the centra. Our goal was to determine the influence of mineral content and mineral arrangement on the mechanical properties of mineralized shark vertebrae. We examined the effect of structure on material properties by testing seven species of elasmobranch, including six shark species and one species of axially undulating electric ray. We also examined the influence of mineral content on material properties. We serially demineralized vertebrae from one species to determine the effects of mineral content on material properties in the absence of interspecific structural variations. We found mineral content in mineralized vertebral cartilage varies significantly both intraspecifically by as much as 35% and interspecifically by as much as 24%. Mineral is a significant predictor of material properties when taking both content and arrangement into account. However, the magnitude of the mineral arrangement effect is greater than the effect of amount, suggesting mineral arrangement is more influential in determining the material properties of elasmobranch vertebral cartilage than amount.

Evolution of Complexity Across the Vertebrate and Teleost Genome Duplication Events

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Whole genome duplication (WGD) events provide special opportunities for increasing organismal complexity in two ways: first, WGD copies all of each gene's cis-acting regulatory elements, whereas gene duplication by retrotransposition or local tandem duplication duplicates either none or an unknown amount of cis-acting regulatory elements, respectively; second, WGD preserves the stoichiometry of genes in a regulatory network. Ohnologs (paralogs arising from a WGD event) begin to revert from two copies to single copy after the duplication, but if only a few genes in duplicated networks survive in duplicate, and if ohnologs survive in duplicate because they are at least partially non-redundant, then linkages among surviving genes may become more complex than before duplication. What types of developmental genetic regulatory networks evolve after WGD? Is one set of ohnologs used in one group of cells or developmental processes and the duplicate set in other cells or processes? Or does the pathway evolve in an interrelated array of interacting components much more complex than the original network? To explore these questions, we investigate developmental regulatory changes across two episodes of WGD: those occurring at the base of the vertebrate revolution (R1 and R2) and the one at the base of the teleost radiation (R3). Urochordates appear to be the sister group of the vertebrates, diverging from them prior to the R1 and R2 WGDs; we investigate the larvacean urochordate *Oikopleura dioica*, which retains a chordate body plan throughout its life, as a model for pre-R1 developmental mechanisms, and compare results to other urochordates (ascidians) and vertebrates to infer evolutionary change in developmental mechanisms across WGDs. Likewise, we investigate developmental gene functions in the teleosts zebrafish and stickleback, with tetrapod gene function as the unduplicated outgroup, to infer the evolution of regulatory complexity and its relationship to diversity with respect to the teleost WGD. We will present explorations on ohnologs, regulatory change, and complexity regarding the origin and diversity of placodes and the evolution of skeletal gene networks.

Food Grasping in Primates: Evolutionary Perspectives

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The evolution of primates, including human evolution, is linked to the development of the grasping behavior allowing organisms to exploit resources of their environment. The relation between the evolution of primates and grasping has been investigated through a kinematic analysis based on observations and experimental work in one arboreal species of Platyrrhini (the capuchin), five species of Catarrhini, and human. The questions were: (i) do actual primates present specific functional characteristics linked to their modes of grasping?, and (ii) is it was possible to trace an evolution of functional characteristics through studied species in relationship with the structures of the hand? We focussed on the areas of contact between the grasping fingers and the object to assess the relationship between grip types and the volume of the food item. Quantitative analysis were used (i) to determine the grasping techniques, (ii) to test the effects of the volume on the digit areas used in the various grasping techniques, and (ii) to compare the kinematic properties of limb and digit movements during each of these techniques. This analysis permits us to show that all primates use a large variety of grasping techniques. Results show that all primates were able to modulate their grasping techniques in strong relationship with food volume, independently of their phylogenetic relationship ant the structure of the hand. These data are finally used to discuss the simplest model of grasping usually proposed as the evolutionary scenario of the functional and cognitive grasping capacities of primates.

Odd Carboniferous Iniopterygian Anatomy Revealed by Synchrotron Radiation Microtomography

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Living chondrichthyans, or cartilaginous fishes, include 813 species of elasmobranchs (shark and rays) and only 33 species of chimaeroids (sea rabbits). Apart from the marked difference between sharks and rays, these two respective groups show little morphological diversity. In contrast, during the Carboniferous and Permian, 251–358 million years ago, chondrichthyans underwent an evolutionary radiation that gave rise to amazingly diverse morphologies, notably among the presumed early relatives of chimaeroids, such as the iniopterygians, which are odd-looking chondrichthyans hitherto known from poorly informative flattened impressions. Here, we report the first iniopterygian skulls preserved in three dimensions in concretions from the Pennsylvanian of Kansas. Their study by means of synchrotron radiatio–microtomography (SRμCT) reveals their extremely peculiar anatomy, although they do share unique characters with living chimaeroids.

The Biomechanical Function and Stressing of Ribs in Terrestrial Quadrupeds, Especially Sauropods, With the Aid of FES New Fossil, *Tiktaalik roseae*, and the Biomechanical Conditions for the Evolution of the Tetrapod Bauplan

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Ribs are much better developed in land-living tetrapods (beginning with the earliest, most ancestral forms) than in fish-like vertebrates. We analyzed the force flows between the thorax and the shoulder girdle with the aid of basic biomechanical principles. In simplified models of squamates, crocodiles, cursorial mammals and sauropods, the mechanical loading of the trunk was made visible by three-dimensional Finite Element Systems analysis (FES). Sprawling as well as extended limbs were taken into consideration. While quadrupedal standing yields causal explanations for the axial skeleton and m. rectus abdominis, the lifting of one or two limbs shows the necessity of ribs and the oblique muscles of the trunk wall: Ribs fulfill, in combination with the oblique abdominal and intercostal muscles, the requirement to resist compressive and tensile stresses derived from torsion in the trunk, that means the body segment between fore- and hindlimbs of tetrapods. These torsional stresses are independent from the lengths and weights of neck and tail. Torsional stresses are confined to the periphery of the trunk and leave the spaces in their center (the body cavities) unstressed. The shapes of individual ribs in cursorial mammals can be explained on the basis of the stress patterns which occur under common biomechanical loads. In sauropods, the anterior ribs are slightly longer than the more posterior ribs, while curvature is about the same. The strongest ribs are the numbers 3-8. This makes them well suited to carrying a considerable part of body weight—which is not the case in modern reptiles, but similar to the situation in cursorial mammals.

Morphbank, an Avenue to Document and Disseminate Anatomical Data: Phylogenetic and Paleohistological Test Cases

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MorphBank (www.morphbank.net) is an open web repository for digital images utilized in specimen-based biological research. Established in 1998 by a consortium of systematic entomologists, MorphBank serves as a permanent archive to store and distribute images from any of the anatomical sciences. Here, we show examples of its application to phylogenetic and paleohistological studies. In the phylogenetic example, each character state scored in a matrix can be documented using specimen images. Each cell of the character matrix also can be linked to a collection of images stored in MorphBank. Annotations, such as labels, can also be added to the images to explain one's interpretation of the morphological character states. Likewise, in the paleohistology test case, images of specimens, such as whole skeletons, elements, and thin-sections, can be stored. From these, element selection, section planes, and information describing the specimen (histology, ontogenetic stage, stratigraphic information, etc.) can be annotated. An ancillary goal of this project is to establish a user friendly, standardized template to help histological researchers document their work. In summary, MorphBank provides for a useful means to storage and distribute morphological information on a long term basis. It presently has the capability to build and illustrate character matrices supported by images, adding a visual dimension to the documentation of morphological characters in phylogenetic studies. The organization of the paleohistological portion is currently under development and we welcome suggestions on how to best meet the needs of MorphBank users. In our presentation we will demonstrate how all these features are being implemented.

Comparison of the Carpals in Subterranean Hystricognath Rodents from Africa and South America

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Subterranean mammals have evolved several morphological adaptations to the fossorial lifestyle such as a cylindrical body, reduced pinnae and tails, and digging tools like prominent teeth, enlarged forefeet or the "mole's thumb" of some talpids. Data for digging adaptations in the autopodials of subterranean rodents are scarce even though recently several authors discussed some morphological aspects of limb morphology in hystricognaths and tested their phylogenetic relevance. Hystricognaths show elongated phalanxes, which lead to highly derived morphology of the musculature and tendon insertion sites. We used histological serial sections of the forelimbs of five species of burrowing rodents, which represent two major clades (the South American hystricognaths *Ctenomys opinus, Spalacopus cyanus* and the African bathyergids *Heliophobius argenteocinereus* and *Fukomys mechowii*) to make 3D-computer reconstructions of the manus of juvenile stages and compared them with adult macerated skeletons. We describe the development and the arrangement of carpals and sesamoid bones and found several variable features some of which represent convergent evolution. Although the studied rodents mainly use their teeth to loosen the soil, digging is performed with their feet. All species show fusions of different carpals (for example the lunate and scaphoid), interpreted as adaptations to fossorial lifestyle to stabilize the carpus during digging.

A Novel Scenario for Hindbrain Interpretation by Complementary Columnar and Segmental Approaches

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Classical anatomical subdivision of the hindbrain into metencephalon (pons-cerebellum) and myelencephalon (medulla) is over 100 years old, and impedes progress in structural and functional understanding. A new scenario has resulted from recent results, informing on differential fate and molecular specification of hindbrain segmental units, with hidden segmental patterns in motor nuclei, sensory nuclei and reticular formation, and showing the segmental subunits of the larger plurisegmental formations to be functionally specialized. Accordingly, it is confusing and undesirable to continue thinking of the hindbrain in units larger than the rhombomeres. Moreover, the scheme of morphological columns (longitudinal zones), originated in the analysis of functional components in cranial nerves, is also about 100 years old, and does not consider the real sources of neuronal types and their radial and tangential displacements in the mantle layer. Modern analysis of dorsoventral patterning and fates of specific derivatives has highlighted not only rhombic lip migrations, but also some unexpected tangential migrations (notably of efferent preganglionic and branchiomotor neurons into the alar plate). These novelties, jointly with segmental subunits, justify a cautious but progressive correction of the classical columnar scheme. Essential aspects of the old conceptions survive, but we dispose now of a much more precise paradigm for rethinking structure-function relationships in the vertebrate hindbrain. Many detailed aspects of this model still need

to be explored and established on a firm basis. The hindbrain again becomes a frontier in neuroscience.

Development of the Olfactory Skeleton of *Spea multiplicata* (Anura: Scaphiopodidae)

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The paired nasal capsules of *Spea multiplicata* are located in the anteriormost section of the cranium, the olfactory region, which comprises the anterior fourth of the skull. In the adult, the nasal capsules are formed by an intricate set of sac-like cavities that house the olfactory organ and constitute the beginning of the respiratory system. In tadpoles, nasal capsules do not have a respiratory function, but each is composed of a single cavity formed by soft tissue covered with olfactory epithelium. Our study of the developmental patterns of the nasal capsule skeleton has revealed that the nasal cartilages and septomaxillae are de novo adult structures that chondrify dorsal to the larval skeleton of the ethmoid region. The only larval-skeleton derived structure of the adult nasal capsule is the solumn nasi, which is formed by the trabecular plate. In *S. multiplicata*, the process of nasal skeletal development begins during mid-premetamorphosis (around Gosner Stage 31), with chondrification of the septum nasi and lamina orbitonasalis. Of the anterior nasal cartilages, the alary cartilage and superior prenasal cartilage are the first elements to chondrify at Gosner Stage 37. By Gosner Stage 40, all of the major elements of the nasal capsules are chondrified, and most structures have attained a morphology that closely resembles that of the adult.

Neogene Sloths from Bolivia: Northwestern South America's Importance in the Evolution of Tardigrada

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As for most South American mammalian clades, knowledge of xenarthran evolution during the Neogene is based mainly on Argentinian remains, a circumstance related to the history and development of paleontology in this continent. The southern area of South America has generally been considered as the cradle of sloth evolution, and Argentinian taxa as phylogenetically and morphologically central among sloth lineages. Recent discoveries in the Deseadan SALMA Bolivian localities Salla and Lacayani, as well as revision of material from the Laventan SALMA (middle Miocene) of Quebrada Honda, Huayquerian SALMA (late Miocene) of Achiri and Monterhermosan SALMA (early Pliocene) of Ayo Ayo-Vizcachani and Pomata, indicate that this Patagonian model is an oversimplification. The oldest true Tardigrada is recognized in the Tinguiririan SALMA (early Oligocene) of Chile and the first sloth faunas are present in the Deseadan SALMA levels of Bolivia (Salla) and Argentina (La Flecha). We have identified at least two new Laventan SALMA *Hapalops*-like forms, several new Huayquerian SALMA *Xyophorus* specimens, two new peculiar Mylodontidae genera from the Huayquerian and Montehermosan SALMAs, and several indeterminate Montehermosan SALMA Megatherioidea. These new sloths, in addition to the well known *Pseudoglyptodon sallaensis* (Deseadan SALMA), *Xyophorus villarroeli* (Huayquerian SALMA), *Megatherium altiplanicum* (Montehermosan SALMA), and *Eremotherium sefvei* (Lujanian SALMA), confirm a distinct evolutionary pattern during the Neogene in west-central South America that was probably related to a distinct environment. Bolivian faunas could facilitate the correlation of more southern faunas with tropical faunas, such as the La Venta fauna from the middle Miocene of Colombia.

On the Revision of *Octodontotherium*: The Oldest Mylodontoid Sloth

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Oligocene sloths are not common. The Deseadan SALMA records the first appearance of mylodontid and megalonychid lineages. *Octodontotherium*, from the Deseadan of Patagonia, was first discussed by F. Ameghino at the end of XIXth century. The detailed description by R. Hoffstetter over 50 years ago is the last work on this genus, which is the only Oligocene sloth known from cranial and postcranial elements. A revision of the material assigned to *Octodontotherium*, collected by E. Riggs at the beginning of the XXth century and deposited in natural history museums in Chicago, Paris, La Plata, and Buenos Aires, allow the study of numerous postcranial elements (e.g., tibia and astragalus), as well as mandibles and a well-preserved skull. A preliminary revision of this material suggests the existence of a single species, *O. grande* Ameghino, 1895 (of which *O. crassidens* Ameghino, 1895 is a synonym). The discovery in Salla (Deseadan SALMA of Bolivia) of several remains closely related to *Octodontotherium* (probably a second smaller species) markedly increases the geographical distribution of the genus during the Deseadan SALMA. The recent discovery in late Miocene of the Peruvian Amazon of an M5 similar to *O. grande* suggests, in contrast with Hoffstetter's opinion, that this lineage survived the Oligocene-Miocene transition. A phylogenetic analysis of Tardigrada, including *Octodontotherium* and based on cranial and postcranial characters, is in process and will test Gaudin's (2004) hypothesis of mylodontine affinities of *Octodontotherium.*

Falsifying Functional Hypotheses for Fossil Fishes: Microwear Analysis of Trophic Ecology Over Evolutionary Timescales

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Rigorous functional analysis of fossil organisms is fraught with difficulties. Because functional hypotheses cannot be tested through direct observations of structures in use, arguments often become somewhat circular. Analyses of feeding mechanisms in fishes provide some of the best examples of these problems. Consequently, it has not been possible to investigate the role of trophic ecology as a driver of speciation and diversification of fishes over evolutionary timescales. This is unfortunate, given that short-term experimental and ecological studies suggest that feeding plays an important evolutionary role, causing divergence in food gathering traits and ecological character displacement, leading to morphological change and speciation. Quantitative analysis of dental microwear in fishes has the potential to provide independent evidence of function in fossils, and analysis of fossil fishes could thus provide a long-timescale test of ecological models linking microevolution to shifts in trophic resource use. Results derived from experimental feeding and field sampling of threespine stickleback (*Gasterosteus*; an important model organism in studies of evolution, adaptation and speciation) indicate that microwear analysis can detect subtle differences in trophic niche. These analyses include fish from various trophically distinct lake populations, and from sympatric benthic-limnetic species pairs. Microwear analysis of fossil stickleback populations sampled from a high-resolution Miocene age sequence in Nevada provides the first documented example of shifts in diet and habitat correlated with rapid microevolutionary change in fossils. Quantitative microwear data is also starting to provide new insights into the evolution of feeding mechanisms in other fossil vertebrates previously thought unsuitable for analysis.

What Complexity Is Not: Can We Measure Phenotypic Complexity Through Stem Lineages of Vertebrate Clades

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A general idea of complexity underlies much of the current research into the origins and early history of vertebrates, particularly hypotheses linking genomic evolution, phenotypic evolution, and diversification. This area is currently a major research theme in evolutionary biology, with a great deal of research effort expended in testing the hypothesis that increases in pre-tetrapod vertebrate complexity (and diversity) were driven by increases in genomic complexity resulting from multiple rounds of gene or whole genome duplication (citations of Ohno's Evolution by Gene Duplication, 1970, now exceed 150 per year). However, this research is rather one sided. With very few exceptions the burgeoning literature focuses on genetic aspects of the hypothesis, with very little consideration of the question "does vertebrate phenotypic complexity increase through time?." The question is more difficult to address than it might appear, not least because defining complexity is a non-trivial

problem. However, we contend that any meaningful investigation of the evolution of vertebrate complexity must address three issues: Firstly, some operational concept of phenotypic complexity and a means by which it can be measured is required. Secondly, the nature of trends through time must be determined, and if hypotheses that complexity increases are driven by genomic events are to be tested then null models must be established against which to compare observed patterns. Finally, measures of complexity and methods of analysis must be applicable to and incorporate fossils, because sampling of vertebrate diversity based on extant taxa alone will inevitably produce biased and unreliable evolutionary patterns.

Dinosaur Cardiovascular Dynamics and Heart Function

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There is no reliable, objective evidence for the structure of the heart in dinosaurs. However, a variety of data can be used to draw conclusions about likely cardiac structure and function in theropod (carnivorous) dinosaurs. These center around the probable structure and function of theropod lungs as suggested by the morphology of their rib cage, pelvic apparatus and other elements. Living archosaurs, the closest extant relatives of dinosaurs, possess lungs with vascularized and non-vascularized regions, although the crocodilian lung (and cardiovascular system) is markedly less specialized than the avian lung air-sac system and heart. The lung in extant birds requires an extensive, dorsally situated abdominal air sac which is ventilated by an expansive sternum and hinged costal ribs with specialized sternocostal joints. Alternately, the theropod rib-cage-pectoral complex lacks skeletomuscular modifications seen in modern birds: there existed neither avian-like sternocostal articulations nor a large caudally expanded sternum. Furthermore, in extant birds, the thin walled, posterior abdominal air sacs must be supported laterally and caudally to prevent paradoxical collapse during generation of negative, inhaltory pressure. The synsacrum and posteriorly directed, laterally open pubes provide such support and largely prevent inhalatory collapse. Theropods exhibited none of these attributes and were probably unable to have been able to ventilate an abdominal air sac. By extension, they were unlikely to have possessed a specialized bird-like, air-sac lung. In the absence of an avian-style lung in theropods, there is little or no evidence suggesting that they were capable of cardiovascular function more sophisticated than that of modern crocodilians.

Variation in the Morphology of True Porpoise (Odontoceti: Phocoenidae) Pterygoid Sinuses

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Details of the three-dimensional anatomy of pterygoid sinuses in extant true porpoises (phocoenids) provide insight into the evolution and development of this specialized cranial feature. The pterygoid sinus is one component of a complex of bilateral air-filled sinuses extending from the medial portion of the ear into the pterygoid and palatine bones in cetaceans. In phocoenids it consists of three main regions that vary across species. Computed tomography scans were used to non-invasively visualize and measure the morphology of the pterygoid sinuses within skulls of all six extant porpoise species. Endocasts of the sinuses were digitally extracted from within skulls. Asymmetry is noticeable between left and right sinuses; the right sinus has a larger total volume than the left among all species. Volumes of both sinuses show a relationship with phylogenetic arrangement, with the earliest diverging phocoenid (*Neophocoena phocoenoides*) having the lowest total sinus volume. Volumes correlate with shape and extension of the preorbital lobe of the sinus, which penetrates the frontals and maxillae to a greater extent in later-diverging species. The preorbital lobes broaden mediolaterally to varying degrees, particularly in Phocoenoides dalli which has the largest dorsal extension of the preorbital lobes. The pterygoid/palatine sinus regions are mediolaterally broader in *Neophocoena phocoenoides*, while in later-diverging species they are thinner and dorsoventrally long. The sphenoidal regions of the sinuses lengthen anteroposteriorly and dorsoventrally in later-diverging phocoenids. These data suggest that variation in morphology of the pterygoid sinuses in phocoenids is influenced primarily by phylogeny.

The Evolution of Mammalian Locomotor Biomechanics: Adaptations or Spandrels?

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The evolution of mammalian locomotor biomechanics is often viewed through an adaptive framework. However, adaptive views require biomechanics to be heritable, a characteristic difficult to test. Here, we suggest an alternative view of locomotor evolution. Several locomotor traits thought to be adaptive may in fact be byproducts of anatomical adaptations, and are therefore better described as spandrels. We explore this possibility by examining the evolution of quadrupedalism in primates, a topic that has generated a great deal of research into the adaptive value of biomechanics. Several researchers have suggested that primate quadrupeds share a unique suite of biomechanical characteristics that appear adaptive for small-branch arboreal locomotion. Here, we suggest that primate quadrupedal biomechanics may have evolved as byproducts of anatomical adaptations for the small branch niche and therefore, might best be viewed as spandrels rather than as adaptations. We present several cases of primate locomotor spandrels tied to morphological adaptations. For example, primates have heavy distal limb muscles used to control grasping hands and feet. From a study of ontogeny in infant baboons, we show that distally heavy limbs influence primate kinematics through the pendular mechanics of limb motion, and lead to long swing periods, low stride frequencies and long strides (considered "unique" primate characteristics). We also examine primate kinetic patterns as spandrels. Primates support more body weight on their hindlimbs compared to their forelimbs and body mass distribution likely explains these patterns. Finally, we explore the implications of spandrels for understanding how selection has shaped mammalian locomotion in general.

Morphology of the Forelimb Skeleton and Locomotory Behavior in Birds: Pelecaniformes and Procellariiformes

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Previous research has documented how whole wing parameters (e.g., wing loading, aspect ratio) correlate with flight style; however, it is less clear how forelimb skeletal morphology varies within clades that exhibit divergent locomotor modes. The objectives of this study were to conduct intralimb proportional and cross-sectional geometric analyses of the forelimb skeleton in pelecaniforms and procellariiforms, two groups of distantly related birds, to investigate whether differences in skeletal morphology may co-vary with flight mode. Basic linear metrics (n = 122) and cross-sectional geometric (n = 13) data were collected on skeletal elements comprising the three forelimb segments. In the proportional analysis, pelecaniforms exhibit more variation in brachial and antebrachial length, whereas procellariiforms show more variation in carpometacarpal length. Moreover, cross sectional properties also vary within and between taxa and flight modes. For example, pelicans exhibit relatively thinner humeral cortices (K value = 0.86) than either the within clade cormorants (K value = 0.71) or the distantly related albatrosses (K value = 0.71), suggesting an inherent functional signal among birds employing distinct flight modes. In contrast, humeral circularity indices (HCI) may track both functional and phylogenetic influences, with the pelican (HCI = 0.87) and cormorant (HCI = 0.86) having a relatively more circular cross section than the dynamic soaring albatross (HCI = 0.72). These data suggest that forelimb skeletal morphology does not merely reflect phylogeny, but records a functional signal related to differential flight mode. These results will be discussed in the context of both histological and other cross-sectional geometric properties.

In-vitro Strain in Bird Skulls and Validation of the Finite Element Method

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How well do our Finite Element model results reflect reality? We cannot definitively answer this question in extinct animals, but we can phylogenetically and functionally bracket extinct animal FE-models with data from living animals detailing (a) how well FE-models replicate experi-

mentally recorded in-vivo/vitro bone strain; and (b) which parameters matter the most for accuracy. FE-model validation against bone strain data is currently underway for macaques and crocodiles. To close the phylogenetic bracket around dinosaurs and pterosaurs—the subject of much functional analysis—extant birds are an obvious candidate for FE-validation. Futhermore bone strain data for the avian cranium is currently unknown. Here, I present preliminary data into bone strain in the ostrich skull, as an avian model system. Four ostrich skulls were CT scanned and subject-specific Finite Element models created. Models were subject to semi-realistic bite loads experienced during grasping and pecking behavior (but static rather than dynamic loading). The skulls displayed a reasonable strain-stress strain response, thus some confidence could be applied to the models. Similar magnitude loads were applied to isolated ostrich mandibles, clamped posteriorly and loaded at the beak tips. Gauges recorded in-vitro strain, which was then compared to FE-model strain in models loaded with the same boundary conditions. The results show a reasonable correlation between in-vitro and FE-strain, although the effect of modifying model parameters (material properties, boundary conditions) will be discussed, to gain a comprehensive understanding of the ability of FEA to replicate strain in a complex system such as the vertebrate cranium.

Quantifying the Modulation of Mastication with High-resolution, Three-dimensional Kinematics

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Mammalian mastication is distinguished from the intra-oral processing of other amniotes in part by the way it is modulated. The fusimotor system and periodontal afferents mediate a feed-forward or anticipatory control mechanism in mammals, which we have suggested is associated with reduced variance in cycle lengths in mammals. Reduced cycle length variance is in part attributable to rate-modulation of bite force in mammals; however there should also be kinematic and electromyographic mechanisms for modulating cycle length to food material properties. Primates are ideal for studying the modulation of chewing to food material properties because of their diverse natural diet. A system which combines high-resolution, three-dimensional kinematics with electromyography and bone strain has been developed to investigate modulation of chewing in primates. Using methods developed for the precise measurement of three-dimensional displacements of the molars, we are examining the effect of food material properties on jaw kinematics in *Cebus capucinus*. Analyses show a significant relationship between closing angle and the food material property (square root of Young's modulus multiplied by toughness; $r = -0.683$, $p < 0.01$). A significant relationship between the angle of the neutral axis of strain normal to a coronal cross-section of the mandible and this material property has also been found ($r = 0.816$, $p < 0.001$).

Morphological Evolution of the Mouse Mandible on Islands: A Balance Between Canalisation and Plasticity

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The major directions of the within-population variation, estimated by the P matrix, have been suggested to channel evolution along "lines of least resistance." We investigated the signification of these directions, and their role in channelling evolution, by confronting several scales of phenotypic differentiation of the mouse mandible: (1) the plastic response in laboratory mice fed hard vs. soft food, (2) the insular differentiation of mice from Corsica, Sardinia, and a nearby islet from the continental pool; and (3) the adaptive difference between omnivorous and herbivorous murines. The major directions of the P matrix were indeed found to parallel the directions of insular evolution, but the signification of P as a surrogate of the matrix of genetic variance G is challenged since pmax coincides with the plastic differentiation. The differentiation on the islet parallels this direction, and is therefore possibly the result of a plastic adaptation to local conditions. The second direction of P parallels (1) the difference between herbivores and omnivores within the familiy of the murine rodents, as well as (2) the differentiation from continental to insular mice from Corsica and Sardinia. This supports an adaptive interpretation that the mandible changes on these islands, in relation to a niche widening. The role of plasticity in shape changes of skeletal features may contribute to the exceptionally high evolutionary rates recorded in cases of insular evolution.

Understanding Hominin Use of Topographically Complex Landscapes at Sterkfontein (South Africa) During the Last 3.5 Million Years

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We examine possible correlations between topographically complex terrains in Africa and the presence of hominin sites. Previous research has emphasized the role of large-scale climatic changes (specifically cooling, drying periods during the Plio-Pleistocene) and also of various mediating effects, such as volcanic and tectonic activity, on localized environments in regions where hominids evolved. We present a case study from the Sterkfontein Caves (Gauteng province, South Africa) to illustrate the important relationship between topography and hominid use of the landscape in the Plio-Pleistocene. Areas of topographic complexity adjacent to open plains appear to have been favored as locations offering a variety of living and food-gathering opportunities for hominins to exploit. This pattern may explain why a significant feature of the environments present during the time of hominid evolution at Sterkfontein (and elsewhere) appears to be the near constant existence of "mosaic habitats" (i.e., combinations of open grassland and closed woodland). Likewise, isotope studies of Sterkfontein hominin diets suggest high variability in food sources. Rather than these habitats being "incidental" to hominin site locations, this habitat variability should be interpreted as a function of the topographic complexity and, more importantly, a primary reason for the hominin occupation of the area through time. However, any species (including hominins) that is dependent on specific landscape features cannot readily migrate in response to climate, and subsequent vegetative shifts, but must instead adapt its diet to changing environments. These ideas suggest that understanding the evolution of hominins in Africa requires an interpretive framework of the topography, vegetation and climatic changes that happened during the Plio-Pleistocene and these effects on the evolution of our own species.

Digit Identity—A Comparative Developmental Approach

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The homologies of digits in the tetrapod manus and pes is a subject of controversy, particularly in cases where digit reduction has taken place. We have examined digit development in a wide range of tetrapods, using gene expression profiling and transplantation experiments to try to clarify the evolutionary patterns in various lineages. While some evidence supporting the frameshift hypothesis is found in cases of digit loss, it appears that each limb in each species may have a fixed repertoire of digit types that cannot be easily modified.

Tadpole Morphological Phenotypic Plasticity in Complex Environments

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In most organisms a single genotype can produce distinct phenotypes in response to the environment, a property known as phenotypic plasticity. Several studies haven shown that anuran larvae are plastic for a remarkable array of ecological traits, ranging from diverse aspects of life-history (such as development and growth rate), behavior and morphology. Most of these studies focused on the adaptive significance of plasticity in the presence or absence of one factor; however, environmental factors rarely act alone. Here we analyze phenotypic plasticity of *Pelodytes punctatus* in a wide range of environments to elucidate the way in which plasticity has evolved. We designed a laboratory experiment to reproduce all combinations of factors observed in nature: drying, predation and competition. In these treatments morphological changes

and life-history plasticity (development and growth rates) were measured. Morphological changes were analyzed by both multivariate and geometric morphometric methods. Results obtained by the two methods were in concordance. Shape analysis allows us to discriminate predator-induced, competitor-induced and drying-induced morphotypes. Life-history traits under isolated environmental factors were also consistent with precedent studies. In complex environments we observed that life-history plasticity was governed by abiotic factors, whereas a mixture of morphological traits was observed in response to exposure to complex environments.

Developmental Basis of Morphological Integration of Brain and Skull in Craniosynostosis

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Skull and brain are commonly studied separately, building upon a perception of these tissues as developmentally and genetically distinct. The evolutionary history of Mammalia provides strong evidence that the morphology of skull and brain change jointly in evolution. In a recent study we used 3D computed tomography and magnetic resonance images of human children diagnosed with two types of premature closure of cranial sutures (craniosynostosis) and found evidence of strong phenotypic integration of brain and skull. We have expanded this study to examine patterns of association between neural and skull tissues in other forms of isolated craniosynostosis and some forms of syndromic craniosynostosis. Though patterns of association between skull and brain differ between diagnostic categories, the basis for these relationships is unknown. To initiate analyses of the genes and their regulatory programs responsible for the phenotypic associations that we have discovered, we introduce our work with a knock-in mouse model for Apert syndrome that has a S252W mutation in fibroblast growth factor receptor 2. The $Fgfr2^{+/S252W}$ mouse model provides the opportunity to closely investigate proliferation, differentiation, and altered cell fate determination of progenitor cells in cranial phenotypes while monitoring the various signaling networks that are responsible for development of the head.

Gross Anatomical Brain Region Approximation (Gabra): A New Technique for Assessing Brain Structure in Dinosaurs and Other Fossil Archosaurs

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Tracking brain evolution through the fossil record is difficult, because the bony endocranial cavity is the only proxy available for study. Although for some groups (mammals, birds) a cranial endocast is a fair representation of brain size and morphology, for many reptile groups the brain does not fill the cavity and an endocast is a poor proxy. Thus, quantitative studies of relative brain size or qualitative studies of brain region evolution often require untested assumptions and speculation. We present a new technique called Gross Anatomical Brain Region Approximation (GABRA) which addresses these problems using 3D digital analysis to estimate brain morphology in fossils based on a variety of comparative anatomical criteria. 3D digital endocasts are extracted from CT scan datasets of fossil archosaurs and then imported into modeling software (Maya). Virtual models of the underlying brain regions are produced using 3D ellipsoids based on the osteological correlates of various soft-tissue structures within the cerebral cavity, as identified by comparison with extant taxa. These discernable structures (neurovascular canals, dural sinuses, fossae produced by the brain itself, etc.) provide limits on the location and size of major brain regions (e.g., cerebral hemispheres, cerebellum, optic lobes, olfactory bulbs). GABRA allows moving beyond studying the cranial endocast as a singular entity to studying the evolution of the brain and its different parts, allowing hypotheses of neurological mosaic evolution to be better tested. Moreover, revised estimates of brain (and brain region) size will put quantitative analyses of relative brain size on a better footing.

Comparative Ontogeny and Phylogeny in Reptiles

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Statements of homology are low-level theories of character evolution that are based on a variety of empirical criteria such as those obtained by comparative ontogenetic investigations. Reptiles provide a number of classic examples that illustrate the importance of comparative ontogeny for the inference of homology. One famous example is the ontogeny and evolution of the manus in the transition from theropod dinosaurs to birds. Another example concerns the evolution of the astragalus, which involves two consecutive events of ontogenetic repatterning, one in lepidosaurs and turtles, the other in chameleons. Controversy also surrounds re-development of limbs, or parts thereof, in squamate taxa nested deeply inside limb-reduced lineages. The recent push towards broad-scale phylogenetic analyses as are required for the assembly of the tree of life highlights further difficulties of homology assessment. The AToL "Deep Scaly" Project aims at the reconstruction of squamate (lizards, amphisbaenians and snakes) interrelationships using genomic and morphological data. This approach reveals morphological homology statements to be restricted in scope. A striking example is provided by the developmentally and functionally tightly integrated palatobasal articulation between the dermal palate and the base of the braincase. I will argue on both developmental and functional grounds that the basipterygoid process in snakes, where present, is not homologous to that of other gnathostomes. The consequence of such argument is the creation of an "incomplete" character for phylogenetic analysis.

Forelimb Muscle Activity in Swimming Sliders and Sea Turtles: Are Neuromotor Patterns Conserved?

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Tetrapod limbs have been modified numerous times through evolution to yield a diverse array of forms. New locomotor behaviors might arise through evolutionary changes in anatomy, changes in activation of muscles producing limb motion, or a combination of both. Turtles provide an excellent model to test for such changes because they display diverse locomotor styles and morphologies. Most freshwater turtles swim via asynchronous anteroposterior forelimb rowing, but sea turtles swim via synchronous dorsoventral flapping of forelimbs modified as flippers. Muscular arrangements differ between these groups, but comparisons of their forelimb motor patterns have not been performed. We collected high-speed video and electromyographic (EMG) data from forelimbs of swimming red-eared sliders (*Trachemys scripta*) to provide a baseline for comparison to previous motor pattern data from the derived, flipper-shaped forelimbs of loggerhead sea turtles (*Caretta caretta*). Limb cycles were defined as a recovery phase (sea turtles: abduction, sliders: protraction) followed by a thrust phase (sea turtles: adduction, sliders: retraction). Although relative durations of these phases differ between the species (recovery phase = 30% cycle duration in sliders, 50% in sea turtles), aspects of their motor patterns are similar relative to landmark kinematic events. For example, latissimus dorsi (humeral abductor and protractor) becomes active about 10% before the start of protraction and remains active until 10% before maximal humerus protraction and abduction in both species. These data indicate the potential for conservation of motor patterns in the evolution of turtle limb function despite dramatic evolutionary changes in anatomical structure. Supported by NIH (R01-DC005063-06A1).

Schmelzmuster of *Alticola strelzovi* and *Lasiopodomys brandtii* (Arvicolinae, Rodentia) and Its Evolutionary Polarization

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Enamel Schmelzmuster offers plenty of information for phylogenetic and mechanical interpretations. Although the arvicoline Schmelzmuster is taxonomically well known, it remains undetected in some species. In this study, we analyzed the Schmelzmuster of the first lower molars of two Asiatic arvicolines, *Alticola strelzovi* and *Lasiopodomys brandtii*, using SEM. In *A. strelzovi*, the leading edges are built of a very thin layer of inner radial enamel, middle layer of a thick lamellar enamel and an outer layer of relatively thin radial enamel. The trailing edges

are thin and consist only of radial enamel. So, its Schmelzmuster fully corresponds to *A. roylei* (Koenigswald, 1980) from the subgenus *Alticola*. The same Schmelzmuster in *A.* (*Platycranius*) *strelzovi* could indicate either its closer affinity to the *Alticola*-subgenus or a convergence in this character. We did not notice individual Schmelzmuster-polymorphism as Koenigswald (1980) did in *A. macrotis*. In *L. brandtii*, the Schelzmuster does not differ from that in *A. strelzovi*, except for a small region of tangential enamel in the middle part of the trailing edges. It fully corresponds to the Schmelzmuster of *L. mandarinus* (Koenigswald, 1980) that belongs in Microtus to the more advanced forms with reduced trailing edges composed of radial and vestigial tangential enamel. We also tried to associate Schmelzmuster with arvicoline phylogeny and to their food supply (*Alticola*-species prefer forbs, whereas *L. brandtii* grasses). For the final evolutionary polarization of the voles' Schmelzmuster, the Schmelzmuster-sampling should include more *Microtus*- and *Alticola*-species.

Visceral Dimorphism on Three Neotropical Xenodontinae Snakes

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Even though most studies on sexual dimorphism in snakes focus on overall body size and shape, males and females may also differ in their body composition (e.g., relative sizes and position of different organ systems). Here, we studied the topographical anatomy of three species of xenodontinae snakes (*Atractus pantostictus, Helicops modestus* and *Sibynomorphus mikanii)*. SSD was found only on *S. mikanii*. Regarding organ positions, *A. pantostictus* and *S. mikanii* females had most organs in a more caudal position when compared to males. Strong sex differences were apparent in relative sizes of some body components. In all three species, the females had a larger right gonad than the males at the same SVL. Also, *A. pantostictus* and *H. modestus* males had larger left kidneys than females and *S. mikanii* females had larger lungs than males. Females had larger gonads, which are expected to enhance their reproductive success. The liver, important in energy processing and larger in females of some species, displayed no significant difference in any of the three analyzed species. Conversely, males seem to benefit from the enlargement of systems important to sperm competition, such as the kidney. Therefore, our results partly support the hypothesis that predicts that particular body components should be differentially enlarged in the two sexes.

High-speed Kinematics of Feeding Behavior in the Seahorse *Hippocampus reidi*

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Despite the strong physical constraints of the aquatic environment, an astounding diversity in cranial form can be observed among teleosts. Undoubtedly, one of the most exceptional cranial morphologies is represented by members of the Syngnathidae. Syngnathids (seahorses, pipefishes, seadragons) are characterized by a long, tubular snout with relatively small jaws at its end. Here, we used high speed video recordings (2000 fps and higher) and high speed X-ray recordings (up to 2000 fps) to quantitatively analyze suction feeding in *Hippocampus reidi*. First results have shown that the feeding act of *H. reidi* consists of an extremely rapid rotation of the hyoid, of which the onset precedes an equally fast elevation of the neurocranium and opening of the jaws. This feeding sequence differs from the typical rostro-caudal wave of expansion used by most fishes. The time needed to catch a prey item is often less than a few milliseconds, making them one of the fastest suction feeders among vertebrates. It is believed that storage of elastic energy is required to achieve such rapid movements in a viscous medium like water. The remarkably high accelerations of the neurocranium and hyoid support the use of an elastic energy storage mechanism during feeding in seahorses as proposed by previous morphological studies.

Quantifying Feed-forward Modulation of Mastication in Mammals and Lizards

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Modulatory ability is an important determinant of chewing performance in amniotes. Mammals possess fusimotor systems and periodontal afferents that are used in feed-forward control of bite force and muscle activity. We have argued that this feed-forward control explains the fact that mammals have less variable chewing cycle lengths and shorter average chewing cycle lengths than lizards. The relationship between possession of fusimotor and periodontal afferent systems and feed-forward control of chewing has only been established in human subjects or in anesthetized rabbits during cortically evoked rhythmic jaw movements. Here, we present and evaluate methods for using jaw kinematic, EMG and bone strain data to demonstrate the presence or absence of feed-forward control in chewing in awake, alert animals. We show that anticipatory control can be demonstrated in awake alert primates: Anticipatory EMG (EMG activity occurring prior to tooth-food contact) is correlated with corpus shear strain from the previous cycle but not from two cycles prior. We predict that anticipatory EMG will not be correlated with prior corpus strain in lizards. Development of these techniques will allow evaluation of hypotheses regarding the evolution of feed-forward modulation of motor behavior during chewing.

Evolution of the Transcriptional Repressor Domain of Vertebrate Hoxa-11

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Hox proteins play an essential part in metazoan development and are likely to be involved in the evolution of novel body plan features. Hoxa-11 is expressed in the developing embryo along the primary (anterior-posterior) axis and the secondary axis (fin-limb buds, female sexual organs, and male genitalia). Interestingly, in humans it is also expressed in the adult during gestation and loss of Hoxa-11 expression at this stage is associated with infertility in women. Since the function in the adult seems to be a mammal-specific characteristic, we wanted to investigate if it is correlated with changes in the domain architecture of the mammalian Hoxa-11 protein. We compared therefore the transcriptional activity of zebrafish, chicken and mouse Hoxa-11 proteins. The analysis showed that all three proteins function as repressors in artificial recruitment assays. However, the size of the repressor domain changed in evolution. In mouse repressor activity is solely mediated by the homeodomain while in zebrafish and chicken a region N-terminal to the homeodomain also contributes to the repressor activity. We therefore conclude that the size of the repressor domain was reduced in the stem lineage to placental mammals, perhaps as a consequence of the adaptive changes previously found to have occurred in the sequence N-terminal to the homeodomain.

New Information From HRXCT on the Origin of Monotremes

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New evidence from high-resolution X-ray computed tomography has identified an assemblage of Early Cretaceous fossils from Australia as basal members of the platypus clade (Ornithorhynchidae). Whereas molecular estimates of the divergence between platypus and echidnas range from 17–80 ma, these fossils indicate that divergence of the two monotreme clades had occurred in or before the Early Cretaceous. The fossils represent Ornithorhynchidae in both phylogenetic and ecological aspects, as they preserve evidence of an electro-receptive duckbill. Both HRXCT data and phylogenetic analysis suggest that monotremes inherited from Mammalia ancestrally an adult mandible consisting of only the dentary bone, a middle ear whose ossicles hung suspended from beneath the cranium, an elaborate olfactory system, and a comparatively huge neocortex. Monotremes subsequently evolved a novel array of rostral electroreceptors. Monotreme monophyly is further supported by postcranial skeletal morphology, brain architecture, karyotype, and mitochondrial and nuclear gene sequences. The origin of monotremes is a classical problem, but much of the new evidence bearing on early monotreme history was generated with developing 3D visualization tools designed specifi-

cally to enhance knowledge visualization and representation in phylogenetic morphology.

Development and Growth of Long Bones in Amphibians (Anura: Ranidae)

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Differentiation and development of long bones were studied in European water frogs: *Rana lessonae, R. ridibunda,* and *R. esculenta*. The study included premetamorphic larvae (Gosner Stage 40) to frogs that were 5 years old. Femora, metatarsal bones, and proximal phalanges of the hind limb exhibit the same pattern of periosteal bone differentiation and the same pattern of growth. Longitudinal and radial growth of these bones was studied by examination of the diaphyses and epiphyses. The periosteum seems to be responsible for both longitudinal and radial growth. Investigation of the formation, length, and arrangement of lines of arrested growth (LAGs) reveals that the first line is present only in the middle 25–35% of the length of the diaphysis of an adult bone. Comparison of the shapes and histological structures of epiphyses in the femur, metatarsal bones, and phalanges revealed that epiphyseal cartilages are composed of an inner and outer part. The inner metaphyseal cartilage has distinct zones and plugs the end of the periosteal bone cylinder; its role in longitudinal growth is questioned. The outer epiphyseal cartilage is composed of articular cartilages proper, in addition to lateral articular cartilages. Differences in the symmetry of the lateral articular cartilages of distal epiphyses of the femur and toes may reflect adaptations to different kinds of movements at the knee and in the foot.

Having a Closer Look: Micro-CT Analysis of the Bony Labyrinth in Rodents

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High resolution 3D-computed tomography (Micro-CT) plays an increasingly important role in mammalian craniology. This innovative and non-invasive technique provides the possibility to get a close look inside the heads of intact adult specimens. It is particularly suitable for small and complex organ systems whose macroscopic preparation is very delicate, for example the petrosal bone labyrinth that houses the cochlea and vestibule, the organs of hearing and sense of balance. Recent studies on anthropoids and marsupials using Micro-CT show significant correlations between semicircular canal dimensions and body size as well as locomotion types. Rodents, the largest mammalian order in numbers of species with a wide range in body size and locomotion types, have not yet received much attention. For the first time otical regions of 16 rodent species representing seven families (glirids, castorids, zapodids, cricetids, murids, thryonomyids, hydrochoerids) were scanned. The studied specimens contain both macerated skulls and non-macerated heads. These data were used to create computed 3D-models of the bony labyrinth. First, size-dependent variation was investigated by studying allometric correlations. For this reason length and width of the semicircular canals as well as length and number of turns of the cochlea were measured and analyzed by multivariate statistical methods. Regression analyses show significant allometric correlations between body size and length and width of the semicircular canals. Second, selected measurements and morphological features of the semicircular canals were correlated with locomotion types of the studied taxa. However, no significant correlations were found.

Scales Across Scales: The Adhesive Capacity of Geckos in Its Environmental Context

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Many taxa of gekkonid lizards have subdigital pads bearing fields of adhesive setae that allow them to bond to and climb on a wide variety of surfaces in any orientation. Measurements of the maximal adhesive force that can be produced by individual setae and, in turn, by entire setal fields exceed the force necessary to support the body mass of these animals by as much as several thousand times. This enormous safety margin may be related to the types of surfaces that have been employed in studies of the adhesive capacity of geckos. Such studies have used primarily smooth or microscopically rough surfaces; however, the natural substrata of geckos may be qualitatively and quantitatively very different. On natural surfaces the adhesive system may be limited to very small patches of contact, and on any given footfall the actual adhesive contact made may be very modest. Here we evaluate the microtopography of rock surfaces used by a southern African species of gecko of the genus *Rhoptropus*, and compare this to the form, configuration, compliance and functional morphology of its setal fields. *Rhoptropus* is diurnal, clawless and rock-dwelling, making it an appropriate subject for initial observations of the relationship between substrate microtopography and setal field morphology. Our results suggest that the design and adhesive capacity of gekkonid setal fields may be adaptive for undulant irregular surfaces, rather than smooth ones, because *Rhoptropus* exhibits setal field surface area very similar to that of other pad-bearing geckos.

Emerging Complexity at the Fish-tetrapod Evolutionary Transition: Cladistic and Morphometric Approaches

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Increasing complexity in vertebrates, such as is exemplified by local bursts in character acquisitions, is perhaps nowhere better illustrated than at the fish-tetrapod transition. This is chronologically the last of the major evolutionary transitions that resulted in the establishment of a radically new metazoan body plan, and led to the vertebrates' occupation of subaerial environments. But just how much more complex is the tetrapod body plan relative to that of tetrapods' fish-like ancestors? Different measures of complexity are inextricably related to different definitions of this otherwise poorly circumscribed concept. A simple way of measuring phenotypic complexity relies on the pattern of character distribution on phylogenetic tree branches. A series of recent, outstanding fossil discoveries of intermediate fish-tetrapod species and the substantial new amount of comparative data generated by recent, large-scale phylogenetic analyses allow us to address tetrapod complexity quantitatively. Two examples using a whole-skeleton data matrix and a smaller matrix focussing on the appendicular skeleton illustrate emerging patterns of tetrapod complexity. Morphometric approaches (Principal Coordinate Analysis; Pairwise Morphological Dissimilarity Analysis) applied to these data sets indicate that tetrapod emergence from piscine ancestors was more complicated than previously surmised. Among the major results, the acquisition of an autopod impacts very little the pattern of morphospace occupation, implying that a significantly greater portion of phenotypical variance concerns proximal regions of the appendicular skeleton. Fish-tetrapod intermediates do not necessarily occupy an intermediate position between limbed vertebrates and piscine ancestors, and discrete clustering in morphospace suggests a large amount of variance in plesia.

Methodological Issues in Comparative Analyses of Trabecular Bone Morphology

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Quantitative analyses of the three-dimensional (3D) structure of trabecular bone have become more common with the increased availability of high-resolution computed tomography. Even though methods for quantifying the 3D fabric structure of trabecular bone are well-established, comparative morphological analyses of trabecular bone present a host of potential problems related to data acquisition, processing, and analysis. One of the most significant problems when comparing bone structure across specimens and species of different size, shape, and developmental stage is the difficulty of selecting volumes of interest (VOI) that are homologous in both size and location. Here we present a method in which multiple, non-overlapping VOIs are used to characterize bone structure across the proximal metaphysis of the femur and humerus in a sample of juvenile humans ranging in age from neonate to 12 years old. The proximal 25% of the femoral and humeral metaphyses were scanned with high-resolution x-ray computed tomography for 45 individuals from an archaeological skeletal collection. Between 10 and 30 non-overlapping, contiguous spherical VOIs were defined within each dataset and

the fabric structure was quantified. In addition to providing a way to compare trabecular bone fabric structure across bones of different size, shape, and developmental stage, this method also allows the characterization of bone structural variation across an entire bone or joint region. This approach has broad applications to intra- and interspecific comparative analyses and will help to reduce problems associated with global segmentation techniques, VOI scaling and positioning, and finite element modeling.

Development of the Unique Frontal Sinus in the Spotted Hyena (*Crocuta crocuta*)

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Spotted hyenas (*Crocuta crocuta*) are highly durophagous animals capable of cracking open bones of large diameter. One characteristic unique to both extinct and extant bone-cracking members of the family Hyaenidae is a vaulted and caudally elongated frontal sinus that completely overlies the braincase. Although the function of this elongated sinus remains unclear, one hypothesis suggests that the sinus provides structural support necessary for bone-cracking. Here we used computed tomography (CT) to examine the course of frontal sinus development. The extent and volume of the frontal sinus were analyzed and reconstructed based on CT scans of 35 *Crocuta* skulls ranging in age from 2 months to 18 years. The frontal sinus is present as early as 2 months of age, occupying a small cavity rostral to the braincase; this pneumatic cavity is separated into right and left sinuses by a thin bony strut at the midline. As development proceeds, the sinus elongates caudally and by 16 months, it already overlies 50% of the braincase. Although hyenas reach adulthood by 24 months, the sinus continues to grow past 36 months of age. The adult sinus extends as far as 14.5 mm lateral from midline, and elongates caudally within the parietal bone to end at the superior nuchal crest. The slow growth of the sinus may reflect constraints on skull development as well as changes in diet and feeding performance in the maturing hyena. (This work is supported by an IRGP grant from Michigan State University).

Scaling Bite Force in Predatory Animals: Bite Force is Proportional to Body Mass 2/3

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Bite forces of terrestrial predatory vertebrates are shown to scale with increasing body size at a scaling factor of 2/3. This negative allometry indicates that bite force increases less-than-proportional to increase in body mass. This scaling factor of 2/3 can be observed in many instances of scaling: scaling of surface area to its volume in isometric bodies is one obvious example, but more relevant is that of muscle force with body mass. Since the contractile properties of muscle are generally agreed to be constant throughout vertebrates with varying scale, muscle force is most likely proportional to the physiological cross-sectional areas (PCSA) of muscles (length 2) and since body mass is essentially volume (length 3), muscle force is proportional to body mass 2/3. This coincidence in identical scaling factors enables us to suggest that muscle force, not the lengths of moment arms, is the determining factor of scaling trends in bite forces. A simple biomechanical model is used as an attempt to explain this. The model predicts that scaling factors would be most affected by parameters with the highest dimensions: in this case, body mass (length 3) and muscle force (length 2) but not distances (length 1).

Different Types of Pattern Formation Mechanisms Lead to Different Types of Genotype Phenotype Maps: Understanding the Effect of Development on Morphological Evolution

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This talk presents a wide classification of the developmental mechanisms that have been shown experimentally to generate pattern and form in metazoan organisms. Simulation and experimental studies in some of these developmental mechanisms have lead to identification of which kind of morphological variation they can produce and which kind of relationship between genetic and phenotypic variation they imply. Herein it is proposed how the combination of many of these mechanisms over the whole process of development can be used to understand many aspects of the genotype phenotype map and morphological variation possible from whole animal organisms. In silico artificial selection experiments were performed on populations of individuals characterized by a genotype, a group of developmental mechanisms (whose genes and interactions are specified by the genotype) and a resulting morphology (in the form of a spatial distribution of different cell types). This study shows how development affects morphological evolution, by determining possible variation and the genotype phenotype map, but also how different kinds of selection regimes affect the evolutionary change in used developmental mechanisms and resulting genotype phenotype maps. Overall, the intention of this study is to give some theoretical hints and boundaries for the complex interplay between selection pressures and development that leads to morphological evolution. Specific examples will be given for organs such as teeth and early insect blastoderm.

Molecular Data and the Ancestry of Living Amphibians

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Determining which of the extinct groups of Paleozoic tetrapods are the ancestors of the living amphibians (caecilians, frogs, and salamanders) essentially remains a paleontological enterprise, but the recent contribution of molecular data is shedding new light on this debate. The use of new molecular markers combined with state-of-the-art phylogenetic and dating methods has allowed inferring new timeframes and phylogenetic relationships for the major lineages of living amphibians, and ultimately, has provided support for hypothetical scenarios of their ancestry. However, credibility intervals for the critical nodes are still rather broad (over 50 my) in all recent molecular clock studies addressing the question. The study we are carrying out aims to assemble the largest and most comprehensive molecular dataset (not in terms of taxa included, but in terms of number and heterogeneity of sequence characters) combining mitogenomic and nuclear information for a sufficient dense taxon sampling with the major key lineages of living tetrapods. The analysis of this new molecular dataset with the most sophisticated dating and phylogenetic methods will yield more accurate and reliable estimates of the sequence and timing of the divergence of the ancestors of living amphibians. Preliminary results suggest that the divergence between caecilian and batrachian ancestors occurred about 360 mya, and that frog and salamander ancestors separated shortly thereafter (about 350 mya). These (relatively) old age estimates appear to be in line with the hypothesis of Lissamphibian polyphyly, although other hypotheses (the Temnospondyl or the Lepospondyl) may also be compatible if some ghost lineages are considered.

The Comparative Anatomy and Function of the Odontocete Flipper

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During the terrestrial limb to aquatic flipper transition in odontocetes, mobility at the elbow joint and manus was lost leaving the shoulder girdle as the only movable articulation. This study analyzes a larger data set of odontocetes (31 species, 6 families) than previous studies. The structure of 7 muscles responsible for flipper movement and 13 morphological characters was examined using dissections, radiographs, and osteological specimens. Specifically, muscle and bone morphology was compared with external shape of the flipper, allowing functional implications of flipper design. Results include detailed morphological descriptions of characters studied. Differences across families in the anatomy of the deltoid and subscapularis muscles correspond to variations in shape and size of the acromion process and scapula. The deltoid muscle exhibits differences in extent and thickness of fibers, covering from 1/3 to 1/2 of the scapula. The subscapularis is composed of 4, 7, or 9 muscular columns. The specialization of the subscapularis muscle allows for greater mobility suggesting relatively independent control of each column. A linear relationship was found between flipper area and body length, scapula length and width, and other osteological elements. The degree of hyperphalangy and the encasing soft tissue of the flipper were found to determine three external morphologies. These results provide

support for flipper morphology associated with ecology. Thus, species with broad flippers are found in shallow areas where more maneuverability is needed, narrow flippers in deep offshore areas requiring speed, and the intermediate form (broad base, distally narrow) a combination of both habitats.

Palaeoecology of *Apateon* (a Temnospondyl from the Lower Permian of Europe) Suggested by Bone Histology

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Apateon Meyer, 1844 is a small aquatic temnospondyl from the Permian-Carboniferous (300 My ago) of Europe. The palaeobiology, ontogeny and palaeoecology of this well-known dissorophoid have long been studied. The aim of this work is to address the life history traits of *Apateon* species by bone histology and skeletochronology. A sample of 22 individuals belonging to *Apateon caducus, A. pedestris,* and *Apateon sp.* from the Saar-Nahe Basin, Western Germany (Erdesbach, Odernheim/Pfalz and Niederkirchen/Pfalz, respectively), have been studied and their long bones sectioned at mid-diaphyseal level. Bone histology of *A. caducus* and *A. pedestris* shows juvenile features such as a relatively high growth speed and a significant primary vascularization. *Apateon pedestris* shows also juvenile-like features: persistence of Kastschenko's line and calcified cartilage, perhaps suggesting a neotenic condition. Bone growth rate is expressed by a simple pattern of lines of arrested growth (LAGs) in *A. pedestris,* whereas *A. caducus* and *Apateon sp.*, from Niederkirchen/Pfalz, show a peculiar double-line pattern. Such a pattern is observed in high elevation Portuguese populations of the extant newt, *Triturus marmoratus*, expressing hibernating and aestivating arrests of growth every year. This suggests that the latter *Apateon* species had to hibernate and aestivate every year because of drastic climatic conditions. The Saar-Nahe Basin was situated in the tropics, where seasonality would have been enhanced at high altitudes. This suggests that the Erdesbach and Niederkirchen localities may have been at higher elevation than the Odernheim locality, and that the aquatic tetrapods from both first localities underwent relatively more extreme conditions.

Autopodial Development and Evolution in Turtles

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The manus and pes of turtles have experienced numerous evolutionary transformations, as exemplified by the flippers of marine species, the sturdy autopodials of tortoises, and the soft-shelled turtles' hyperphalangy. We examined patterns of variation across several pleurodires and cryptodires and found synapomorphies that support several clades. The manus is more variable than the pes. Variation in adults included separated or fused astragalus and calcaneum, separated or fused distal carpals 3, 4 and 5, variation in number and arrangement of centrals, and presence of accessory ossifications on the radial and/or ulnar side. The pattern of chondrogenesis and ossification sequence was examined in several cryptodires (e.g., *Pelodiscus sinensis, Graptemys nigrinoda, Chelonia mydas, Caretta caretta*). Ontogenetic data tested hypotheses of primary homology. We identified both the primary axis and the digital arch. No distal condensations connected with the radius and tibia were found, supporting the hypothesis that the radiale and tibiale are absent. There is variation in the chondrification and ossification pattern in the proximal tarsal row, suggesting different compositions to the element identified in adults as the astragalus. The 5th hooked metatarsal resulted from the fusion of the fifth distal tarsal with the 5th metatarsal. The dt4 is the first element of the tarsus to start to ossify, but there is otherwise much variation in ossification sequences (and the state at hatching), correlated with phylogeny and function. The reported homologies of the carpal elements in the basal fossil pleurodire *Notoemys laticentralis* are revised.

The Ontogeny of Adaptive Characters in *Anolis* Habitat Specialists

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Evolutionary developmental biology, or evo-devo, has primarily focused on trying to understand the developmental bases of macroevolutionary innovations. However, if we wish to understand the developmental mechanisms underlying morphological adaptation we must also focus our attention at the population level. Comparing the developmental bases of variation within a species to variation among closely related species in ecological and phylogenetic contexts will potentially yield a seamless understanding of the evolutionary process. Previous studies on the ecology and evolution of Caribbean *Anolis* lizards make them an ideal system for a unified investigation of the ultimate and proximate causation of morphological diversification. This study specifically examines the mechanisms underlying the divergence of the canopy and trunk specialists from each island in the Greater Antilles. More specifically, have the same developmental processes been modified on each island during the adaptive radiation of this genus? Divergence in quantitative characters may be the result of changes at any stage of development, morphogenesis through to juvenile growth. To determine the developmental processes that have been modified during evolution we have performed an allometric study of the relative growth of limb and cranial dimensions, characters known to correlate strongly with habitat. Different measurements of body size give similar, but not identical, results whereby character divergence on each island occurs during the earliest stages of morphogenesis. Forelimbs and hindlimbs tend to be evolving identically on each island except Jamaica where forelimb cannot be distinguished between habitat specialists.

The Relationship Between Embryonic, Juvenile, and Adult Variation in Murine Long Bones

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Understanding variation across time and space is a primary goal of evolutionary biology. Within a particular species, selection can act on heritable variation at any stage of development. Thus, quantitative differences between closely related species could, in theory, be the result of changes at any stage of development, morphogenesis through juvenile growth. An increasing number of studies in vertebrates, invertebrates, and plants are finding that adaptive differences between closely related taxa are the result of changes during the earliest phases of morphogenesis. This repeated pattern of evolutionary modification of morphogenesis implies that there is a common statistical relationship between the variation generated early in development and variation in the adult form. This observation is, however, contradictory with observations from (mammalian) quantitative genetics and evolutionary biology and needs to be investigated in more detail. A fundamental question remains unanswered for many taxa; what is the statistical relationship between variation generated during different times in development and variation present in the adult form, and hence, the variation most often examined by biologists. We have performed a pseudo-longitudinal study of mammalian long bones using recombinant inbred strains of mice generated from a cross of LG/J and SM/J strains. Preliminary examination of long bone growth shows that there is heritable variation at all stages and that shared genetic effects decrease as time between measurements increases.

Osteostracan Phylogeny and Gnathostome Characters: Early Evolution and Loss of Paired Fins

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The evolution of gnathostomes represents a massive overhaul in the vertebrate body plan. A huge morphological gap exists between extant cyclostomes and gnathostomes; thus, our only recourse is to the fossil

taxa if we want to answer questions about this episode of increasing complexity and genome duplication. A growing body of evidence indicates that the Osteostraci are the closest relative of jawed vertebrates. Controversy surrounds the ancestral morphotype of the group, be it non-cornuate with developed pectoral and dorsal fins or finless trematapsid. Incomplete knowledge of osteostracan phylogeny currently impedes understanding of this important transition. Here, novel observations, new taxa and global parsimony techniques are used to construct the first comprehensive phylogeny for the Osteostraci and related taxa. This enables not only a test of previous hypotheses of ostestracan intra- and inter-relationships but also reconstruction of the gnathostome characters prior to the evolution of jaws. Osteostracan/jawed vertebrate sister relations are supported and the non-cornuates are confirmed as the basal-most osteostracans. The finless trematapsids are strongly supported as a derived clade and thus paired fins have been lost within the Osteostraci and are homologous for Osteostraci and jawed vertebrates. The upshot is that the finless trematapsids can now be added to the already well charactized examples of pectoral fin/limb loss in vertebrates such as snakes, caecillians and eels. What makes the trematapsids exceptional however is that the loss occurs almost immediately after the initial evolution of this crucial character.

Development of the Dermomyotome: The Cradle of Vertebrate Skeletal Muscle

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Somites are a common feature of the phylotypic stage of vertebrate embryos. They reflect the metameric organization of the paraxial mesoderm and give rise to a variety of derivatives including skeletal muscle, cartilage, endothelia and connective tissue. The dorsal somitic compartment, the epithelial dermomyotome, is patterned by signaling cues from adjacent embryonic structures like neural tube, ectoderm and lateral mesoderm, thus localizing cell fate decisions that lead to the various dermomyotomal derivatives. All dermomyotomal cell lineages have to undergo an epithelio-mesenchymal transition and subsequent cell migration prior to the onset of differentiation. Here, I will discuss our recent results on the molecular regulation of early dermomyotomal differentiation which is the prerequisite for the development of the locomotory system of the vertebrate body.

Modeling Physical Properties of Joint Arrays in Batoid Wings

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Formed by arrays of serially repeating skeletal elements (radials), the pectoral fins (wings) of batoid elasmobranchs (rays, skates, guitarfish) provide the opportunity to study the effects of small-scale morphological changes on large-scale structural properties. I used the spatial arrangement of the radials as a basis for models of local and whole-wing stiffness as well as the passive bending properties of the wing. Both analyses focused on single inter-radial joints as points of action, and summed local and global interactions. Stiffness calculations were based on a constrained linear spring model minimized for stored energy after perturbation. Direction of passive bending was based on the spatial relationship between neighboring joints. Comparing data from the wings of six species of batoid fishes, whole wing stiffness is higher in oscillatory swimmers than in undulatory swimmers. There was substantial variation in stiffness in different areas of the wing, with leading edges of oscillators being stiffer than trailing edges and the medial area of the wing of undulators being stiffer than the lateral area. It appears that the spatial arrangement of radials can be linked to swimming performance in a way that might have application in robotics and deployable structures.

Shoot or Swallow; Consequences of a Highly Specialized Prey Capture System on the Efficiency of Prey Transport and Swallowing in the Lizard *Chameleo calyptratus*

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The use of the tongue as a specialized organ to capture prey is generally restricted to iguanian lizards. Although there are a few exceptions, most other lizards use their jaws for prey capture. Among iguanian lizards, chameleons are unique in the use of ballistic tongue projection to capture prey. Their tongue is protruded out of the mouth on the elongated entoglossal process and then projected off the entoglossal process of the hyobranchium by the highly modified, helically arranged verticalis musculature. We predict that due to the presence of the extraordinary degree of morphological and functional specialization of the prey capture apparatus, prey transport and swallowing will be less efficient in chameleons in comparison to closely related agamid lizards. Moreover, we predict that the ability to modulate prey transport kinematics in accordance to different prey types, will be limited in chameleons. We tested these hypotheses using cineradiography to record the movements of the jaws, the hyoid and the tongue during prey transport and swallowing while eating prey differing in size and mechanical properties.

Structural Attributes Contributing to Locomotor Efficiency in the Ostrich (*Struthio camelus*)

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The bipedal ostrich exhibits exceptional cursorial ability as the only animal capable of achieving steady speeds of approximately 60 km/h for durations exceeding 20 minutes. This distinction is dependent on numerous intertwined physical and physiological subsystems. We concentrated on identification of structural and functional attributes contributing to the ostriches' locomotor performance. Our prior morphometric analysis of 83 ratite skeletons revealed that ostiches' leg-segment ratios are optimized for efficient long-endurance locomotion when taking into consideration its unique supra-jointed toe posture (Schaller et al., Proc. 3rd Intl. Ratite Science Symp., Madrid 2005:83–90). Subsequently, we investigated in vivo toe function using an RSscan pressure mat recording load distribution at high spatio-temporal resolution (Schaller et al., Comp. Biochem. Physiol., in press). When running, the two-toed ostrich establishes a tripod-patterned footprint showing load concentrated at the proximal part of 3rd toe, claw and 4th toe-tip with all elements making ground contact near-simultaneously. This may deliver increased stability while minimizing contact surface and implies claw function as positional anchor. Observations regarding 3D range of motion among hind limb segments in running ostriches appeared consistent with the maximal excursions measured from manipulation experiments on freshly slaughtered specimens. This suggests inherent morphological constraints that passively manage limb position during locomotion. Further examination of ligament function revealed the presence of an "auto-return" mechanism located at the intertarsal joint. This presumably provides the distal limb elements with a rapid forward impetus to re-establish ground contact in the shortest possible timeframe. Ongoing analyses seek to quantify the exact impact of this mechanism.

Habitual Loading Conditions of the Shoulder Joint in *Pan troglodytes* and *Homo sapiens* and Its Implications on Humeral Trabecular Architecture

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Habitual movements of the upper limb cause specific loading conditions in the bones of the shoulder joint. External and internal differences between chimpanzees and humans in these bones are connected with habitual loading conditions as a result of functional adaptation of bone to applied loads. Trabecular architecture enables us to recognize the load direction and magnitude and is used to discriminate the effects of habitual humeral loading conditions on cancellous bone in *Pan troglodytes* and *Homo sapiens*. Thus, the effects of locomotor loads applied on humeri in chimpanzees during vertical climbing, arm-swinging, and suspensory behavior are in contrast to the relatively low humeral loading conditions in humans, which occur primarily in connection with manipulatory activities. On the basis of qualitative and quantitative comparisons between humans and non human hominoids, models of different humeral loading conditions can be developed, enabling the interpretation of proximal humeral trabecular architecture of fossil hominids with regard to their preferred loading condition. Thus, the dominance of hoisting or

manipulating habits can be differentiated in their internal bone structure. This project is based on comparisons of biomechanical capacities of bone structures and represents a new field of investigation that can be used together with classical analyses.

Comparative Bone Histology of the Turtle Shell (Carapace and Plastron): Implications for Turtle Systematics, Functional Morphology, and Turtle Origins

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The bone histology of the turtle shell is valuable for addressing osteoderm and shell formation, reconstruction of fossil integumentary soft-tissue structures, phylogenetic hypotheses and functional aspects of the turtle shell, with both carapace and plastron showing similar results. The microstructural properties of turtle shell bones are proposed to be influenced by a mosaic of phylogenetic and functional factors. The ratio between phylogenetic and functional constraints is variable among major turtle groups, and only where functional aspects are less dominant, phylogenetic signals can be deduced from the bone histology. The bone histology can thus be used to verify existing intra-specific phylogenetic (e.g., morphological, molecular and serologic) hypotheses among turtles. Groups that are well defined based on shell bone microstructures are, e.g., paracryptodiran Pleurosternidae and Trionychidae. The systematic position of problematic taxa or poorly known shell material (e.g., Kirtlington turtles) can be evaluated. Part of the Kirtlington turtle material belongs to Pleurosternidae, thus extending the fossil record of Pleurosternidae from the Upper Jurassic back into the Middle Jurassic. The bone histology of other major turtle groups does not show clear phylogenetic signals, because functional factors override existing phylogenetic signals respectively. One functional aspect that profoundly influences turtle shell bone microstructures is the adaptation to an aquatic habitat/life-style. In this respect, all turtles were grouped into four categories (I "terrestrial environment" to IV "extreme adaptation to aquatic/marine environments"), based on their ecology/palaeoecology. Comparison of the oldest known turtles with recent aquatic and terrestrial turtles independently revealed a terrestrial palaeoecology for the basal Testudinata.

The Ontogeny of the Shell in Side-necked Turtles, With Emphasis on the Homologies of Costal and Neural Bones

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Although we are starting to understand the molecular basis of shell development based on the study of cryptodires, basic comparative ontogenetic data for the other major clade of living turtle, the pleurodires, had been missing. The developmental and phylogenetic relation between the bony shell and endoskeleton of Pleurodira is examined by studying histological serial sections of thirteen specimens of five different species. Emphasis is given to the portion of the carapace in which ribs and vertebral spinous processes become part of the carapace. Central questions are whether the development of neurals and costals of pleurodiran turtles is homologous to cryptodirans, if the costals and neurals are of endo- or exoskeletal origin, and what ontogenetic causes relate to neural reduction in Pleurodira. The neurals and costal do not develop as independent ossification centers, but they are initial outgrowths of the periosteal collar of endoskeletal ribs and vertebral arches. Later in development, the mode of growth switches to metaplastic ossification of soft-tissue integumentary structures. Through ontogeny, ribs of the turtles studied are confined within the epaxial musculature. The reduction of neurals in *Emydura* spp. may be linked to heterochrony, accompanied by a restricted influence of epidermal-dermal interaction in shell bone formation.

Functional Morphology of the Trunk in Small Mammals

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Mesozoic mammals were small to very small in body size and in their body proportions and mode of locomotion similar to recent small mammals such as voles or tree shrews. A comparative study of several small therian mammals revealed some general principles of their trunk use during locomotion. At asymmetrical gaits such as gallop or halfbound, the last 7 ± 1 intervertebral joints, independent of their anatomic classification as thoracic or lumbar, contributed to the intense sagittal bending comprising half of step length. Based on their topography, different paravertebral muscles are thought to be responsible for mobilizing the vertebral column and, thus involved in fast and forceful trunk motions during locomotion. Since the metabolic profile of a muscle is connected to its function, the hypothesized functions of the paravertebral muscles were tested by investigating the muscle fiber type composition and distribution in several small, therian mammals. The overall distribution of fiber types was highly similar among the species indicating comparable functions of the muscles. Deep, mono- to oligosegmental muscles contained the highest proportion of oxidative, fatigue resistant fibers and are therefore well suited to stabilize the intervertebral joints and fulfill a postural role by counteracting gravity enduringly. Superficial, polysegmental muscles were mainly composed of glycolytic, fast contracting fibers suggesting that they have a mobilizing role during locomotion and are involved in the sagittal oscillations of the trunk. A similar fiber type distribution and thereby functional classification of the paravertebral muscles is hypothesized for the ancestors of the stem lineage of mammals.

Eya1 and Six1 Regulate Neurogenesis in *Xenopus* Placodes

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Cranial placodes contribute to many sensory organs and ganglia of the vertebrate head and give rise to neurons and a variety of other cell types. Recent studies indicate that all placodes originate from a common precursor region immediately peripheral to the anterior neural plate. The transcription factors Eya1 and Six1 are initially expressed in this preplacodal region and continue to be expressed in placodes at later stages suggesting that they play a central role in placode development. Here we use gain and loss of function approaches in *Xenopus* to analyze the role of Eya1 and Six1 in placodal neurogenesis. Knockdown of Eya1 by morpholinos results in reduced placodal expression of genes promoting neural progenitors (SoxB1 genes: Sox2, Sox3) and neurogenesis (Ngnr1, NeuroD, N-Tubulin, Delta1). In contrast, overexpression of Eya1 results either in reduction or in ectopic expression of NeuroD and N-Tubulin in the vicinity of placodes. Overexpression of Eya1 also enhances ectodermal proliferation and promotes ectopic ectodermal expression of SoxB1 genes. Analysis of sections as well as dosage response experiments indicate that high levels of Eya1 inhibit Ngnr1, NeuroD, N-Tubulin, and Delta1 expression but favor ectodermal proliferation and low-level Sox3 expression. Coinjection of Eya1 and Six1 results in similar but stronger effects suggesting that these two genes affect placodal neurogenesis synergistically. Taken together our results suggest that Eya1 and Six1 synergistically promote the formation of proliferative placodal neuronal progenitors but must be downregulated to allow for neuronal differentiation.

Vestibular Labyrinth Diversity in Diprotodontian Marsupial Mammals

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The bony labyrinth of specimens representing eight diprotodontian species was visualized by high-resolution computed tomography. Linear measurements of the labyrinth were taken, e.g., the height and width of the arc of each semicircular canal. The relative sizes and spatial arrangements of the semicircular canals were compared and some of the variation was atomized into 17 characters, which were then phylogenetically interpreted. There has been a change both in size and in relative arrangement of the semicircular canals that for some aspects maps onto the ecological change from arboreality to terrestriality. In particular, there are differences among diprotodontians in the height of the anterior semicir-

cular canal in relation to the posterior one. In arboreal species, the lateral semicircular canal is relatively longer than the equivalent semicircular canals of terrestrial species. A rounder anterior semicircular canal is widespread for Diprotodontia with a shift in Pseudocheiridae, where it is more flattened. *Dendrolagus* shows features typical of terrestrial species in spite of its arboreal lifestyle. The fact that it shows the derived character state is congruent with the fact that it has secondarily and only recently evolved an arboreal lifestyle.

Locomotion of the Short-eared Elephant Shrew, *Macroscelides proboscideus* (Macroscelidea, Mammalia): Effects of Elongated Hind Limbs

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Elephant shrews were filmed on a treadmill using high-speed cineradiography to investigate the effects of different limb proportions on basic principles of locomotion in small mammals. Like in most saltatorial mammals, the hind legs of *Macroscelides proboscideus* are 25% longer than the front legs. Despite this disproportion in limb length, the extension of the forelimb and flexion of the hind limb results in the scapular pivot and the hip joint having the same vertical distance from the ground. As in other mammals, the proximal and distal segments of each limb (scapula/lower arm, femur/metatarsus) also operate in matched motion. Hence, both limb pairs have the same functional length and pivot height is independent of limb proportion. Thus, the body's center of mass is maintained at an energetically advantageous, almost constant height. In contrast to previous studies, we documented that the shoulder and ankle joints reduce dominant vertical ground reaction forces that act during touchdown, whereas the elbow joint action results in a forward propulsive movement. The longer distal elements (ulna, metatarsus) contribute 22% and 30%, respectively, to step length due to their high effective angular displacement and elevated pivot at the end of the stance phase. A striking feature in the locomotion of *M. proboscideus* is the use of a "non-defined" footfall pattern, where one hind limb is sustained in a constant position and is out of phase to the contralateral limb.

Dissociated Modules and Developmental Plasticity During Early Embryonic Development of *Danio rerio*

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During early embryogenesis, vertebrate embryos pass through a period of remarkable morphological similarity, the phylotypic stage. In zebrafish, *Danio rerio*, developmental constraints were identified as multiple correlations among embryonic characters that stabilize morphology during the phylotypic stage. However, a certain degree of phenotypic variation was observed among individuals raised in the same conditions. Here, we studied zebrafish raised under different experimental conditions to (1) see if developmental plasticity could be elicited during the early embryogenesis, and (2) if certain structures respond as coherent modules. Embryos of zebrafish were raised in: (1) different temperatures, (2) different salinities; and (3) different levels of oxygen concentration. Up to 14 morphological characters of individual embryos were measured during the phylotypic stage (i.e., 12–24 hours post fertilization). At low temperature and low oxygen levels growth rate was reduced as compared to normal condition. Plasticity was detected in the overall size of the embryo and the size of somites in the oxygen and temperature experiment. In hypoxia, size and shape of the developing eye and otic vesicle were not affected but the onset of development was heterochronically shifted to a later stage. Therefore, we identify the eye and the otic vesicle as developing modules which obviously have been dissociated from the other characters of the developing embryo. Changes in raising condition affect early development of the zebrafish on three levels (1) developmental rate (2) size and shape, and (3) dissociation of modules.

Limb Geometry in Quadruped Mammals: Biomechanical Versus Developmental Determinants

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The evolutionary transformation from the two-segmented amniote limb to the three-segmented mammalian limb occurred differently in the fore- and hindlimbs. Here, a proximal segment was added to the "old" forelimb (mobilization of the scapula), whereas the tarsometatarsus was elongated in the hindlimbs. Consequently, the serially homologous elements (e.g., femur and humerus) no longer correspond functionally such that the developmentally determined covariation between serially homologous elements conflicts with their biomechanical constraints. Mathematical simulations of a three-segmented, z-shaped limb show that the relative length of the middle segment is important for a stable translation. A flexed limb is stable if all segments are equal in length, but an extended limb requires an asymmetrical segmentation with shorter proximal or distal segments. We investigated intralimb proportions in 150 mammals with different locomotory modes to test these theoretical expectations. Hindlimb geometry is highly conserved in all mammalian quadrupeds except artiodactyls (femur is relatively shorter). In all species, femur and foot proportions are strongly correlated and the relative length of the tibia always approximates 38 ± 2% of total limb length. The middle forelimb segment, the humerus, also approximates 38 to 40% of forelimb length in primates, rodents, and marsupials, but is relatively shorter in artiodactyls. The correspondence of the femur and humerus in artiodactyls might be explained by covariation between these serially homologous elements. We suggest that hindlimb proportions are determined primarily by biomechanical demands (stable limb translation). Forelimb proportions are, instead, a compromise between biomechanical and developmental constraints with hindlimb geometry as acting as a pacemaker.

Contractile Properties of Limb Muscles in the Slender Loris (Primates: *Loris tardigradus*) Related to Climbing Performance

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Although it was reported recently that slender loris can engage in a fast walk, they are—like all members of the family Loridae—unable to gallop or to jump. Instead, their overall locomotor performance can best be described as adapted for climbing for which lorises use large limb excursions. Hand and foot morphology indicate powerful grasping capabilities and therefore, enhanced abilities for permanent momentum transfer between the body andsubstrate axes (= balance). Large limb excursions and powerful permanent grasping should demand that particular contractile properties of the limb muscles are different from the muscular properties of fast running primates. We tested this hypothesis by investigating the distribution and proportion of fatigue-resistant, slow contracting muscle fibres (Type I) in the fore- and hindlimb muscles of the slender loris using immunohistochemistry. We found that proximal limb muscles that move and stabilize the shoulder, elbow, and knee joints contain 50% or more Type I fibers in the loris, whereas the corresponding muscles of other primates exhibit such a high proportion in small, distinct regions only. The oxidative capacity of distal limb muscles securing substrate contact is much lower than expected (30% Type I fibers at most). Flexors and extensors of the distal limb joints consist mainly of fast and powerful contracting Type II muscle fibers. We conclude that proximal limb muscles serve for stabilization of the whole limb posture in the slender loris, but that the distal muscles are designed to react quickly and with high flexibility to meet the balancing demands of the acrobatic climbing performance.

Center of Mass Movements During Walking in a Prosimian Primate

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The walking gaits of most primates are unusual compared to other mammals. Primates use diagonal sequence footfall patterns, bear more weight on their hindlimbs, exhibit highly protracted arm positions, and have deeply yielding elbow and knee joints that decrease the stiffness of their limbs during stance phase. Because of their high joint yields, primates may experience minimal vertical oscillations of the center of mass and may be unable to exchange gravitational potential (PE) and kinetic

energy (KE) in the manner of other terrestrial mammals. To test this hypothesis, center of mass (CoM) movements derived from force plate recordings were collected for five adult ring-tail lemurs (*Lemur catta*) walking on a runway and simulated arboreal supports across a wide range of speeds (0.38–0.82 ms-1). Contrary to expectations, lemurs had significant vertical displacements of the CoM and moderate levels of percentage energy recovery on both ground and poles. The values for our subjects were not substantially lower than that of many other quadrupeds studied. These results may be explained by the fact along with high joint yields that would reduce vertical oscillations, primates have relatively long limbs and high values of limb protraction that facilitate large limb excursions during arboreal locomotion but could also increase vertical oscillations of the CoM. The interaction of joint yield, long limbs, and large angular excursions may serve to facilitate exchange of PE and KE during walking. This implies a dynamic solution to the challenge of navigating arboreal and terrestrial substrates economically. Supported by NSF BCS-0452217, BCS-00525034.

Vertebral Centra Lost—A Synapomorphic Feature Within the Stomiid Genera?

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Fishes of the marine teleost family Stomiidae are meso- and bathypelagic predators, which show highly specialized modifications of their feeding mechanism. Their most striking external feature is elongate jaws studded with long dagger-like teeth. In most stomiid genera the internal anatomy shows a variable number of anterior vertebrae reduced or absent. This rare feature among teleost fishes obviously enables extreme dorsal expansion of the gape. The phylogenetic intrarelationships of stomiids remain poorly resolved. Earlier hypotheses of relationships within the stomiids are based primarily on osteological characters and parts of the soft anatomy. However, the restructuring of the anterior portion of the vertebral column has never been included, because it is poorly understood. The family Stomiidae comprises 28 genera, and only 15 of these have been studied with regard to vertebral reduction. The number of reduced or absent vertebrae varies among these 15 genera and presumably offers great potential for phylogenetic systematics. Preliminary studies on *Stomias boa* indicate that ontogenetic data and analysis of the insertion of the myosepta provide new and meaningful insight into the reductive restructuring of the vertebral column in stomiids. An additional counting of spinal nerves provides an exact determination of reduced vertebrae. This study, based on dissection, serial sections and clearing and double staining methods, includes 9 previously studied and also previously unstudied genera so far. Their complex structure of the anterior part of the vertebral column and the varying absence of vertebrae appears to be a new character in phylogenetic studies.

Ontogenetic Changes in Novel Functions: Waterfall Climbing in Adult Hawaiian Gobiid Fishes

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All Hawaiian freshwater fishes exhibit an amphidromous migration of juveniles into streams after they are swept into the ocean by rapid stream currents. For three of these species, this migration is obstructed by waterfalls (up to several hundred meters tall) that must be climbed to reach adult habitats. However, adult fishes in upstream island habitats also face downstream displacement by periodic disturbances, making retention of climbing ability advantageous even for adult stream gobies. Climbing performance might be expected to decline among adults due to the tendency for mass specific muscular power production to decrease with body size, and a lack of positively allometric growth in the pelvic sucker that supports body weight against gravity. To evaluate size-related changes in waterfall climbing in stream gobies, we compared climbing performance and kinematics between adults and juveniles from all three climbing Hawaiian species (*Awaous guamensis, Sicyopterus stimpsoni, Lentipes concolor*). For species in which juveniles climbed using "powerbursts" of axial undulation, adult performance and kinematics changed markedly: adult *A. guamensis* failed to climb, and adult *L. concolor* used multiple pectoral fin adductions to crutch up surfaces at slow speeds, rather than rapid powerbursts. Adult *S. stimpsoni*, like juveniles, still alternately attached oral and pelvic suckers to "inch" up surfaces and climbed at speeds comparable to juveniles. However, adult *S. stimpsoni* also add pectoral fin crutching to every climbing cycle. Thus, although powerburst species show size-related declines in climbing performance, the addition of compensatory mechanisms prevents complete loss of this novel function in some species.

Finite-elements-analysis on a Sauropod Cervical Vertebra—Understanding Long Neck Biomechanics

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Finite-Elements-Analysis (FEA) was carried out on a cervical vertebra of the sauropod dinosaur *Brachiosaurus brancai* in order to study the vertebral design in context with biomechanical behavior of the long neck. Our aim was to reveal the distribution of stresses and the internal pneumatic cavity system within the vertebra, to deduce a possible biomechanical role of the long, overlapping cervical ribs and to find a biomechanical explanation for the overall vertebral design. FEA was carried out for load cases of dorsal, ventral and lateral flexion of the neck, and included considerations of muscle reconstructions and sauropod neck weights. Because of only rough calculations of the involved masses, uncertain soft-tissue reconstructions and an oversimplified geometry of the studied vertebra, absolute values obtained are rather imprecise, whereas distribution and direction of stresses are correct. In all load cases, the vertebra is mainly compression loaded. The zygapophyses form a sort of "dovetail"-guidance in the neck, which prevents torsion and lateral buckling of the neck. Internal pneumatic cavities in the vertebra formed only in areas of lowest stress, and FEA shows no peak stresses around these cavities. The biomechanical role of the long, overlapping cervical ribs of *Brachiosaurus* can be explained as a support structure for the neck musculature and tendons around the vertebral joints, but only if they are elastically interconnected. The results of this analysis are integrated into a model for neck support in *Brachiosaurus*, combining dorsal and ventral bracing structures in a relatively inflexible neck.

Image Management for Effective Collaboration Using Presently Existing Web Tools in Morphbank (www.Morphbank.Net)

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MorphBank is an open web repository of biological images available to the research community for documenting specimen-based research in comparative anatomy, morphometrics, morphological phylogenetics, museum studies, taxonomy and related fields. The project receives its main funding from the Biological Databases and Informatics program of the National Science Foundation. Its goal is to develop cyber infrastructure to serve as a permanent archive allowing storage and sharing of digital images. At the same time, MorphBank allows for effective management of these images. It is a collaborative platform supporting international groups of scientists by creating tools to work with images, allowing scientists to share specimen images, add information to existing images by annotating them, remotely curate natural history collections based on specimen photographs, and create, manage, and share collections of digital images. There is inherently a great deal of flexibility in the system. Images stored in MorphBank can be used in a variety of ways. Unique identification numbers given to each specimen and image in the system create unique links to each record allowing the user to embed these links in journal publications, WebPages and sequence data on GenBank. This presentation will focus on effectively managing images for morphology using MorphBank tools. The system will be used as an active image

database in connection to project/users own research, Web based publications and journal articles.

Effects of Temperature on Skeletal Growth in Mice

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Ambient temperature impacts limb and body growth in mammals. Animals chronically exposed to cold have stouter bodies and shorter extremities than littermates housed at warmer temperatures. The mechanisms underlying this response are unknown. This study tests the hypothesis that cold temperature reduces bone vascular supply and thereby elongation, while warm temperature enhances vascularity and growth. Methods: Male CF-1 mice (N = 65) were housed at 7, 21, and 27°C from weaning (3.5 wks) through maturity (12 wks) and diet/activity levels were recorded. Prior to euthanasia at 4.5, 6.5 and 12 weeks of age, mice received an intracardiac injection of fluorescent microspheres to measure regional bone blood flow. Results: Ears, limbs, and tails of warm-reared mice were significantly longer than in the cold with no change in body mass. Cold-reared mice had the shortest extremities, consumed the most food, were most active, and had enlarged hearts and kidneys. Hindlimb bone blood flow was significantly decreased in young-cold mice suggesting that vascular factors underlie these differences. In vitro experiments demonstrate that cold temperature inhibits, and warm temperature enhances, growth of cultured metatarsals absent intact vasculature indicating a direct influence of temperature on the growing tissue. Conclusion: Hindlimb vascular supply is significantly correlated with ambient temperature, but this may not be the primary mechanism causing temperature-induced alterations in skeletal growth. Analyses of apoptosis and proliferation in the growth plate are under investigation. These results have important implications for interpreting skeletal morphology of mammalian species living at climatic extremes. Funded by NSF-0524899 Doctoral Dissertation Improvement Grant.

The Biomechanical and Evolutionary Adaptation of the Lateralized Hip Joint Surface in Birds

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In birds, fracture of the femoral neck is rarely observed compared to the frequency of the same fracture in mammals and man. We studied the anatomical variation of the lateralized hip joint surface in relation to the femoral neck in birds as an evolutionary adaptation to high impact loads, e.g., during landing. Materials and Methods: 1. Comparative vector analysis of the forces in the hip in birds and mammals, including man. 2. FEA simulation using Catia and ABAQUS in 3D-dynamic presentations of CT-models. Observations and biomechanical consequences: 1. The hip of birds is not spheroidal, but a variation of a saddle-shaped joint. It is therefore more stable and axially stiff, but with reduced rotational movements. The axis of the moment (M) of a force in flexion/extension does not cross the axis of abduction/adduction. 2. The resultant force (R) is positioned laterally to the femoral head and directed axially to the diaphysis, which reduces possible shear stress in the neck region and consequently presents a predisposition to fracture. Force reduction to the femur head decreases proportionally to the head size in birds compared to mammals. Results: 1. Certain morphological features aid in differentiation of species, bone rudiments or pathological changes. 2. Exploration of the morphological and the force data may allow the development of biomechanical/bionic models for applications in joint and bone surgery.

Flight Feathers of Birds Act as a Cantilever Beam Model of Constant Strength

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A mechanical model of flight feathers should describe stress and strain distribution according to minimum/maximum law. With this concept in mind we have examined the geometric distribution of feather material and compared these to variations of V in shear diagram and M in the bending moment diagram respectively. Materials and Methods: 1. Basic mechanical models of cylindrical and fusiform tube shapes with different thicknesses of tube plates were all compared with feather and presented as FEA simulations. 2. FEA simulation of the models of feathers obtained from micrographs data. Preprocessing was carried out using program CATIA and ABAQUS was used for subsequent analysis. It was observed that there were: (a) variations of V in shear diagram and M in bending moment diagram according to the shape, (b) variation of calamus and rachis thickness of different cross sections of feather shafts according to the polar moment of inertia and (c) variations of densities of feather tissue and Young's modulus of elasticity distribution according to previous data. The results from these models indicate that the local feather tissue volume mainly correlates with the bending moment stresses. Feathers avoid higher local stresses by distributing the internal forces and feather volume according to a minimum/maximum law which continously optimizes the feather shape to one with constant strength.

Morphology and Biomechanics of a "Three-wing" Flying Fish: *Parexocoetus brachypterus*

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Flying fishes (Exocoetidae: Beloniformes) have a highly specialized morphology that gives them the ability to leap out of the water and soar through the air to escape predators. The basis for their impressive aerial performance is two-fold. A large hypocaudal lobe on the caudal fin allows the fish to accelerate as the body emerges from the water. In the so-called "two-wing" flying fishes hypertrophied pectoral fins are held abducted as wings to produce lift and keep the fish airborne during the glide. In "four-wing" species enlarged pelvic fins add significantly to the total lifting surface. Recent observations on the "two-wing" species *Parexocoetus brachypterus* show that the enlarged dorsal fin (the largest of any flying fish species) is held in a horizontal position on the windward side of the body, such that it could be used as an additional lift generating surface. We measured the fin morphology in two adult specimens (12.9 cm standard length, 26 g) caught near the Hawaiian Islands. Pectoral wing area averaged 25 cm^2, while dorsal fin area was 8 cm^2. Aspect ratios for these fins were 2.2 and 1.8 respectively. Accounting for the dorsal fin acting as a third wing reduced the computed wing loading from 110 to 80 N per m^2. These data are used in a biomechanical model to predict a corresponding improvement in lift and flight performance.

Effect of Mechanical Loading on Bone Morphology During Growth

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Long bones grow in length by endochondral ossification, in which a cartilage anlage or template is slowly replaced by well vascularized bone. Previous studies have shown that this process is influenced by mechanical stresses and strains in the developing bone. In particular, hydrostatic stress inhibits the growth process and maintains cartilage while octahedral shear stress accelerates growth and promotes ossification. We applied these mechanobiological principles to a three-dimensional finite element model of the human femur to predict how forces on the joint surface alter growth front morphology and ultimate bone shape of the proximal and distal femur. Results accurately predicted growth front morphologies in the proximal and distal femur. In the distal femoral growth plate, asymmetric stresses result in asymmetric growth with the medial side of the femur growing faster than the lateral side, indicating the formation of the bicondylar angle. In the proximal femur the direction of the resultant hip force influenced both the neck-shaft and the anteversion angle. These concepts have broad implications for understanding normal morphogenesis and also deformity under various loading conditions. These mechanobiological principles may also help to explain the morphological variations in skeletal structures of different species with different functional activities during development.

Neocortical Cell Types in Anteaters and Sloths (Xenarthra: Pilosa)

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A current limitation to interpreting the evolution of cellular types in the cerebral cortex of placental mammals is the paucity of data from two

major phylogenetic groups that diverged close to the base of this adaptive radiation, the Xenarthra and Afrotheria. In this study, we used immunohistochemistry to examine the distribution and morphology of cells in the neocortex stained for nonphosphorylated neurofilament protein, calcium-binding proteins (calbindin, calretinin, parvalbumin), neuropeptide Y, and glial fibrillary acidic protein in three species of xenarthrans (*Myrmecophaga tridactyla, Tamandua tetradactlya, Choloepus didactylus*). Overall, these species shared many similarities, suggesting that such features are representative of xenarthrans in general. Neurofilament-positive cells predominated in layer V. These cells expressed diverse morphologies with regional variation, including some with typical pyramidal shapes, but more often, multiple dendrites were seen arising from the soma and ascending towards layer I. In addition, many pyramidal cells in layers II/III were found to contain calbindin and calretinin, but parvalbumin-positive pyramidal cells were not observed. Among interneurons, there was a high density of large multipolar parvalbumin-stained cells, whereas densities of calbindin- and calretinin-immunoreactive cells were low. When these results are put into broader context, it is possible to trace the evolution of cortical architectural traits using phylogenetic analysis. Different aspects of the chemoarchitecture of xenarthran cerebral cortex resemble both Laurasiatheria and Euarchontoglires. This suggests that the stem boreoeutherian might have had an assemblage of traits that were elaborated upon differentially in the evolution of each descendent clade.

Embryonic Analysis of WISE, a Wnt Modulation Factor in Trigeminal Ganglion Formation

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A secreted Wnt modulator, WISE, binds to the extracellular region of LRP5/6 co-receptor in a similar way to Wnt, and modulates the Wnt signaling pathway. Wise is characteristically expressed in the head ectoderm in the periocular region. To analyze the function of WISE in an embryonic aspect, a retrovirus infection was performed in the chicken. As a result, ectopically formed ganglia were observed on both sides at a level of midbrain, and they were connected to the intrinsic cranial nerves by their own neural branches. This result was also confirmed by ectodermal electroporation of WISE, and with using the earliest trigeminal placode marker, it became apparent that WISE overexpression assembled delaminated-trigeminal placode neurons underneath the head ectoderm. On the other hand, the ectodermal electroporation of morpholino oligonucleotide against WISE caused a partial deficiency of the trigeminal ganglion. WISE seems to function to migrating neural crest cell (NCC) as well. An implantation of WISE-producing cell aggregate into the head mesenchyme revealed that the NCC exhibits strong affinity to WISE. An in vitro explant culture of the midbrain under WISE protein supports this idea, since WISE enhanced the outgrowth of filopodia and lamellipodia on migrating NCC. A possible partner, Wnt6 has the same function to WISE's described above, and electroporation of Axin and Dishevelled deletion constructs into the neural tube revealed that the non-canonical Wnt pathway is used for WISE and/or Wnt6 ligand in migrating NCC and is thus involved in trigeminal ganglion formation.

Molecular Evidence That the Lungs and the Swimbladder are Homologous Organs

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Both land vertebrates and aquatic fishes possess organs that are filled with air: the lungs and the swimbladder. They have been postulated to be homologous organs. Both the lungs and the swimbladder are air-filled sacs that derive from the digestive tract. On the other hand, the lungs are a paired structure while the swimbladder is a single sac. The lungs extend from the ventral side of the digestive trace, while the swimbladder extends from the dorsal side. Due to lack of fossil evidence, it has been difficult to determine whether they are actually homologous organs and if so, what they were like when they were first acquired in the ancestral vertebrate. We are comparing gene expression patterns during lung and swimbladder development in *Xenopus*, Australian lungfish, *Polypterus* and zebrafish, to test this hypothesis. So far, we have found that TBX4, FGF10 and NKX2.1, which have been identifed as key regulators of aminiote lung development, are also specifically expressed in the swimbladder of the zebrafish. This suggests that both the lungs and the swimbladder evolved from a lung-like organ that was present in the common ancestor of teleosts and tetrapods. We are now trying to identify the enhancer elements governing the tissue-specific expression of these genes to examine whether they are also evolutionarily conserved.

New Features of the Amphibamid *Doleserpeton* (Temnospondyli), and Its Implications for the Origin of Frogs

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Since it was first described in the late sixties, the Lower Permian (Leonardian) amphibamid *Doleserpeton* has repeatedly been suggested as a close relative to lissamphibians, although the specific nature of this relationship has been in question. The proposed relationship with modern amphibians was mostly based on the presence of pedicellate teeth and the morphology of the vertebrae. More recently, doubts have been expressed as to whether lissamphibians are related to temnospondyls at all. I have restudied the available material of *Doleserpeton*, with focus on previously overlooked features. Initial studies of the postcranial skeleton show a relatively primitive configuration, apart from the nearly monospondylous vertebrae. However, several new informative features were found in the braincase and otic region of the skull. The otic capsules are laterally expanded, and the opisthotics have a pronounced ventrolateral ledge, giving it a very anuran appearance in posterior view. The ledge may be connected to the presence of an operculum, although the latter has not been found in the material so far. Furthermore, an interpretation of several lateral ridges on the paroccipital process leads to the assumption that the tympanic annulus was partly attached to the otic capsule as seen in modern anurans. The stapes has previously been described as being very similar to that in frogs, and thus the picture that emerges is that of a very frog-like hearing system. The strong resemblance of the whole hearing apparatus points to affinities between *Doleserpeton* and the Anura specifically.

Functional Implications of the Locomotor Morphology of Paleogene (Oligocene) African Fossil Anurans

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Studies of extant frogs have documented a number of morphological features linked with particular locomotor modes and other behaviors. For example, anurans that rely predominantly upon leaping in the terrestrial environment exhibit longer tibofibulae and/or longer hind limbs relative to their forelimbs. Tree frogs possess expanded toe pads, whereas aquatic forms tend to have more fully webbed feet. And morphologies such as the presence of spade-like metatarsal tubercles, relatively short tibiofibulae, skull modifications such as a snout with a hardened tapered tip and stout robust forelimbs have been associated with digging behaviors in living forms. Yet limb indices and girdle morphology have been explored for functional correlates in only a fraction of anuran species. This study tests the utility of morphological features of the postcranial skeleton in a sample of modern species of known locomotor style that have not previously been examined. Based on the use of these modern analogues, the locomotor behavior of fossil anurans is then reconstructed, using specimens recently discovered in Oligocene deposits in the Rukwa Rift Basin of Tanzania. Specimens consist of postcranial elements found both isolated and in articulation. Specimens range in snout-vent length between 20 mm and 80 mm. A preliminary examination of pelvic morphology indicates at least one taxon exhibits posterolaterally oriented, cylindrical sacral diapophyses and prominent dorsal crests on the ilia. These features have been associated with forceful jumping in modern forms.

Morphological Integration in the Mandible of *Pan* and *Homo*: a 3D-geometric Morphometric Study

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Shape variation in human mandibular form has been a recent subject of investigation, but little work has been done on the integrative aspects of its morphology. Following a study by Nicholson and Harvati (2006, Am. J. Phys Anthropol. 131:368–383) on the human mandibular shape, this study examines the pattern and level of integration in the mandible of modern humans and chimpanzees. Studies on mouse mandibles show that the mandible consists of two modules—alveolar and ascending ramus (Atchley and Hall, 1991, Biol. Rev. 66:101–157; Klingenberg, 2003, Evolution & Development 55:522–531). Here we used two mandibular landmark sets corresponding to these two regions. Given the different mechanical demands placed on the masticatory system of chimpanzees and modern humans, we hypothesized that pattern and level of integration will be different between the two groups. Twenty-seven 3D landmarks were collected on 141 modern human (Nicholson and Harvati, 2006) and 26 chimpanzee mandibles. Specimen landmark configurations were superimposed using generalized Procrustes analysis. Fitted coordinates were analyzed using partial least-squares analysis so as to estimate the co-variation between the two regions. PLS axis 1 account for 99% of the total co-variance in the sample, with chimpanzees having higher scores along the regression line. Inter-specific correlation between the anterior and posterior regions was high, with $r = 0.90$. This indicates a high level of integration between the two parts. Overall, preliminary results suggest a similar pattern of integration among chimpanzees and modern humans. Supported by "EVAN" Marie Curie Training Network MRTN-CT-019564.

The Morphology and Ultrastructure of the Placenta of the Iberian Mole (*Talpa occidentalis*)

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This study focuses on the morphology, morphogenesis and ultrastructure of the placenta of the Iberian mole (*Talpa occidentalis*) in five gestational stages (17, 18–19, 19–21, 21–27, 24–27 days after conception) using light and transmission electron microscopy. *Talpa occidentalis* has a discoidal, definitive chorioallantoic placenta, situated in an anti-mesometrial position. The placental disc is divided into a labyrinthine zone on the fetal side, a centrally located feto-maternal junctional zone and a highly secretory active uterine gland zone towards the myometrium. The labyrinth is composed of fetal mesenchyme carrying capillaries, maternal vessels and an intermediate bilayered trophoblast, thus confirming the endotheliochorial nature of the interhaemal membrane. A specific structure of the mole placenta are the so called "areolae" situated above uterine gland mouths. These columnar, haemophagocytic trophoblast cells take up extravasated maternal erythrocytes and hence may play an important role for the iron supply of the embryo. The permanent yolk-sac consists of a bilaminar omphalopleure and a yolk-sac splanchnopleure, which becomes incompletely inverted due to the growing embryo. In early pregnancy a temporarily existing choriovitelline placenta develops lateral to the embryo, but decreases as the chorioallantoic placenta establishes. The mode of placentation of *Talpa occidentalis* strongly resembles this of *Talpa europaea* (Malassiné and Leiser, 1984, Placent 5:145–158). This study contributes to the reconstruction of the placental stem species pattern of Laurasiatheria.

Genetic Differentiation of the Neural Tube and the Neural Crest in Amniotes

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A consistent relation exists between the site of origin of cranial neural crest cells and their eventual location in the face and pharyngeal arches. This specificity applies to both the three major crest streams in the head as well as to specific subpopulations within the first arch crest. Further, neural crest cells, and ultimately the pharyngeal arches they populate, express patterns of gene expression that emulate the region from which they originate; proper gene expression is critical in proper morphological patterning. In marsupials, previous studies have shown that much neural crest migration, in particular to the facial and mandibular regions, begins before the morphological differention of the brain is established. In this paper, we report results of studies of the genetic differentiation of the neural plate in the marsupial, *Monodelphis domestica*. Specifically we map the expression of genes that are important in establishing regional differentiation, including Pax 6, Engrailed 1, Fgf8, Otx 2 and several Hox genes. We show that in most cases gene expression in the neural plate suggests regional specificity exists long before there is recognizable morphological differentiation and that the majority of region specific genes show first expression shortly before or at the same time neural crest migrates. These patterns are compared to those observed in other amniotes. We conclude that in marsupials, genetic differentiation of the brain is accelerated relative to morphological differentiation, suggesting that the heterochronies observed in morphological studies extend to shifts in the expression of major genes.

NESCent, the National Evolutionary Synthesis Center

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The National Evolutionary Synthesis Center, NESCent, is a collaborative initiative among Duke University, the University of North Carolina, Chapel Hill and North Carolina State University. The Center is sponsored by a grant from The National Science Foundation's Emerging Frontiers program. NESCent's mission is to facilitate broadly based, synthetic work in Evolutionary Biology. The Center sponsors a number of programs including: 1) workshops which bring several individuals together to work on a targeted project (database development and analysis, new analytical tool development, theoretical modeling) in several meetings over a two year period, 2) catalysis meetings, which are larger scale, cross-disciplinary meetings addressing "grand challenge" questions in evolutionary biology, 3) postdoctoral positions focused on integrative and synthetic work, and 4) sabbatical scholars and visiting scientists. Awards for these activities are made on the basis of an open grant competition by a peer-review panel. Deadlines for proposals are June 15 and December 1 annually. In addition, NESCent sponsors a number of informatics initiatives, and has an active program in education and outreach. NESCent Director, Kathleen Smith will be at the meeting to discuss funding opportunities, and more information may be found at www.nescent.org.

Building the Marginal Dentition of Lungfish in a Stereotypic Osteichthyan Pattern

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Lungfish tooth plates in upper and lower jaws are radically different from all other osteichthyan dentitions. This difference is in the pattern of teeth and their addition, conserved since 400 Ma when lungfish diverged from the osteichthyan stem. However, these palatal and lingual plates of fused teeth begin their early development from individual separate teeth, as do those of the single symphysial tooth and two dentary tooth rows. The early pattern of tooth loci in the position of the dentary in *Neoceratodus* is observed from timed stages to be a single pioneer tooth in position two of each row; then sequential teeth added in adjacent tooth positions, first three and then one. This is also the sequence identified in *Oncorhynchus* for the dentary bone, preceded at tooth initiation stage by activation of *Omshh*, *Ompitx2* and *Ombmp4* in a different spatial-temporal expression pattern for each dental field. In *Neoceratodus*, different levels of *Nfshh* expression reveal cryptic timing of dentary tooth initiation at critical developmental stages. Cyclopamine inhibition of *shh* prevented tooth formation in relation to stage specific initiation of teeth. Sequential tooth buds also form from the dental epithelium of the previous tooth germ, as noted for successive teeth in the trout, rather than from a dental lamina. This provides evidence that lungfish dental pattern for the lower jaw marginal teeth is derived from a stereotypic osteichthyan tooth row on the dentary as observed from appropriate early timed stages of development together with in situ studies of deployment of *Nfshh*.

Le Moustier 1 Dental Development and Enamel Thickness

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Anthropological assessments of tooth development and enamel thickness have yielded contradictory results regarding differences between Neanderthals and modern humans. The aim of this study was to estimate crown formation, enamel thickness, and age at death in an adolescent Neanderthal (Le Moustier 1), and to compare it to other Neanderthals and two modern human populations. Long-period incremental features (perikymata) were counted from high-resolution casts. Linear cuspal enamel thickness was determined for each unworn/lightly worn tooth from virtual slices, generated from high-resolution micro-computed tomography (micro-CT). Crown formation time was assessed using estimates of cuspal enamel formation rate and a range of long-period line periodicity values. Average and relative enamel thicknesses were determined from micro-CT data according to established procedures. Age at death was determined from the upper third molars using a range of estimated initiation ages, crown formation times, and root formation rates. The results suggest that perikymata numbers are generally similar to or slightly less than other Neanderthals and modern humans from northern England, and are greater than modern humans from southern Africa. Linear cuspal enamel thicknesses are similar to or slightly less than modern human populations. Crown formation times were likely to have been within the lower end of the modern human range if the periodicity of Le Moustier 1 was similar to other Neanderthals. Enamel thickness increased from the anterior to the posterior dentition, but was less than modern humans values for respective tooth types. The age of this individual at death was approximately 12–14 years.

Skull Stress Imposed by Craniocervical Feeding Motions in *Tyrannosaurus rex*: A 3D Finite-element Analysis

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High-powered bites of adult *Tyrannosaurus rex* instigated a suite of trophic behaviors involving the neck, including flesh excision and inertial feeding. *Tyrannosaurus rex* neck muscles had high calculated moment-generating capacity, and kinematic comparison suggests head and neck feeding motions broadly similar to those of extant predatory archosaurs. Using a 3D finite-element model of a large. *T. rex* skull, we test hypotheses that the cranium and teeth could effectively resist forces imparted by postulated craniocervical movements. Loading regimes include cranial retraction, lateroflexion, and torsion analogous to the initial twist of the crocodilian "death roll." Stress levels were generally low, but concentrated in the posterior palatal region when the teeth were embedded in resistant prey tissues. Results have implications for puncture-and-pull feeding and its effects on intracranial joint function (corroborating previous 2D studies), and powerful shake-feeding proposed for this taxon. Despite tremendous feeding loads imparted directly or transmitted through the neck musculature, we suggest that the broad skull of adult *T. rex* maintained stress levels within the range of narrower-skulled ontogenetic and phylogenetic precursors.

The Carnivorous Mammals ("Creodonta", Carnivoramorpha) from Le Quesnoy (mp7, Early Eocene of France)

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The locality of Le Quesnoy (Oise) has yielded the most diverse continental biotic association known from the Earliest Eocene. The study of the carnivorous mammal fauna shows the presence of: three species of Hyaenodontidae: *Arfia gingerichi* Smith and Smith, 2001; *Prototomus minimus* Smith and Smith, 2001; *Prototomus girardoti* Smith & Smith, 2001; two Oxyaenidae: *Palaeonictis gigantea* de Blainville, 1842; *Oxyaena woutersi* Lange-Badré and Godinot, 1982; and two 'Miacidae': *Miacis latouri* Quinet, 1966; and *Miacis sp*. Moreover, the enigmatic species *Dormaalodon woutersi* Lange-Badré, 1987 from Dormaal is shown to be synonymous with *P. gigantea*. A possible synonymy for the two species of *Prototomus* is considered. We cast doubt on the generic attribution of *O. woutersi*, which might be referred to *Dipsalidictis*. Our cladistic analysis of primitive early Hyaenodontidae roots the Limnocyoninae within the "Proviverrinae." The European "Proviverrinae" belong to two main lineages. The cladistic analysis supports an African origin of "Proviverrinae", and its subsequent dispersal in Europe and North America. The origin of the Asiatic Hyaenodontidae is still unsolved. The discovery of a new large species of *Miacis* (*Miacis sp*.) suggests an European origin of the "Miacidae." Besides this, we propose an ecological reconstruction of the carnassial fauna using body-mass, locomotion and diet classes. The carnivorous taxa from Le Quesnoy confirm the faunal correlation with the MP7 reference locality of Dormaal (Belgium). Indeed all the taxa are known in the Belgian locality. It supports a significant gap between the levels MP6 and MP7.

What Do We Know About the Carnassial Mammals ("Creodonta", Carnivoramorpha) From the Early Eocene (mp7-mp10) of the Paris Basin?

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In Europe, carnassial mammals of the orders "Creodonta" and Carnivoramorpha appear right after the Palaeocene/Eocene boundary (e.g., Dormaal and Le Quesnoy, MP7). Several sites from the Paris Basin have yielded fossils of carnassial taxa (e.g., Meudon, MP7; Mutigny and Avenay, MP8+9; Grauves, MP10). Current knowledge on the Eocene carnassial mammals from the Paris Basin, based mainly on the study of Rich (1971, Univ. Calif. Publ. Geol. Sci. 88:1–72) and published faunal lists of mostly undescribed fossils, allows several preliminary remarks on the early evolution of the European creodonts and carnivorans: the MP7 Oxyaenidae show body-mass increasing, but no noticeable morphological changes. They disappear during MP8+9. The Hyaenodontidae do not diversify during MP7 and MP8+9. Thereafter, during the MP10, they increase in size and show morphological innovations, as exemplified by the first hypercarnivoran *Francotherium lindgreni*. "Miacidae" identified taxa from the Paris basin include the primitive genus *Miacis* and *Uintacyon*. They do not show significant morphological diversification during the Early Eocene. Some Viverravidae (*Viverravus*) and Limnocyoninae (*Prolimnocyon*) are reported from younger sites than Le Quesnoy. These families are otherwise unknown in Middle Eocene of the Paris basin. In North America all these groups were well diversified (taxonomically and morphologically) during the beginning of the Eocene. They survive there until the end of Middle Eocene. A detailed revision of the rich creodont and carnivoran material of the MNHN collection (including unpublished fossils) from the Paris Basin will allow a better understanding of the evolution of the European carnassial fauna during the early Eocene.

Oral Morphogenesis in Axolotl and the First Evidence of Endodermal Teeth for Gnathostomes

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The textook schemes explain that the oral cavity of vertebrates is formed via an ectodermal invagination that forms a stomodeum. Tooth buds are thought to arise exclusively in the ectodermal area where the ectodermal epithelium contributes to tooth enamel and the neural crest mesenchyme to dentin. We studied oral and tooth development in the Mexican axolotl (*Ambystoma mexicanum*) and found a very different situation. The stomodeum is not shaped by the ectodermal invagination; instead, it is a solid tube of the pharyngeal endoderm that loads the oral area. Only later does the ectodermal layer populate surface of the anterior part of this endodermal tube as a "stomodeal collar." Since the ecto- and endoderm are histologically unidentifiable, in seach for a role of them in odontogensis we used orthotopical transplants of oral ectoderm from GFP+ transgenic to wild-type embryos. Interestingly, our results demonstrated conclusively that only the anterior half of the tooth germs were GFP positive, meaning that enamel of more posterior teeth of the Mexican axolotl is generated by the endodermal epithelium. Several times we also noticed epithelium of tooth germs to be of mixed ecto- and endodermal origin. Despite vivid discussions on the subject, to our knowledge this is the first evidence of tooth development from the endoderm. The evolutionary context of our findings will be discussed with respect to germ-layer origin of odontodes and a possible co-option of ancient patterning mechanisms from endoderm to oral ectoderm.

Functional Morphometry of the Pelvic Joint (Articulatio Coxae) of the Quail (*Coturnix coturnix japonica*)

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Birds' large amount of diversity among tetrapods makes them an ideal group to study vertebrates' adaptation modality. Whereas the functional morphology of the locomotor apparatus of extinct and extant terrestrial theropods has long been studied, the important role of joint structure appears to be largely unaddressed in modern studies. In depth description of articular kinetics and degrees of freedom should systematically consider the significantly altering impact of soft parts. Here, our goal is to characterize the morphology of the pelvic joint of the quail (*Coturnix coturnix japonica*) using modern imaging and 3D-geometric morphometric tools, in order to understand and describe its function as guide of the movement. For that purpose, a set of homologous landmarks was defined to model the acetabulum. We compare the shape of the fresh joint (with cartilage) to the shape of dry bone (without cartilage) and interpret the results using a three-dimensional kinematic analysis of the walk, performed using high-frequency cineradiography. The results illustrate the significance of such structures in biomechanical and kinetic studies of living animals' motion, and the relevance of reconstructing cartilage in functional arthrology of fossil vertebrates.

Mammalian Baculum—Its Ontogeny and Evolutionary Distribution

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Baculum is a bony element situated in the glans' tissue of penis in many members of some mammalian orders. Monotremes, marsupials (except wombat), and most basal placentals, Afrotheria (except some tenrects) and Xenarthra, do not possess a baculum. So this element appears to be typical for more derived placental mammals (except lagomorphs, tree-shrews, cetartiodactyls, perissodactyls and pangolins and some particular exceptions in bats, carnivores, insectivores and primates). In our research, we studied the morphology of baculum in selected common rodent species from Czech Republic. Up to now, we have analyzed 120 specimens of 7 rodent species (*Clethrionomys glareolus, Microtus agrestis, M. arvalis, M. subterraneus, Sciurus vulgaris, Micromys minutus* and *Apodemus sp.*) The whole glans of penis was dissected, double-stained with alizarin and alcian blue and stored in glycerol. We especially concentrated on the bacular size and shape (variability). Moreover, in *M. agrestis* we also investigated the bacula of males of different age, so we could study the ontogenetic development of baculum in this species. The rudiment of the baculum is a simple elongated cartilaginous element with a widened proximal end. The ossification begins in the distal end of the baculum and continues proximally. When the ossification of this element is nearly complete, a small cartilaginous rudiment of a medial rod appears distally. During the ossification of this element the lateral cartilaginous rods also develop and ossify consecutively. Furthermore, we tried to map the baculum distribution in the mammalian phylogenetic contex. Some mammalian species also possess os clitoridis, but its distribution and ontogeny remain largely unknown.

Structure of a Unique Scent Gland Among Spiny Rats (Rodentia: Hystricognathi: Echimyidae)

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Although echimyid rodents (spiny rats) comprise some 75 species and represent a significant proportion of Neotropical non-volant mammalian fauna in rainforests, little is known about their physiology and behavior. The phylogenetic relationship within the clade also remains controversial. Most species in the group primarily occupy rainforest habitats but some species, e.g., *Clyomys bishopi* and *Trinomys yonenagae* inhabit dry environments, such as the Cerrado and the Caatinga, of Brazil. We have previously described in *T. yonenagae* a sebaceous eversible anal scent gland that appears to play an important role in social cohesiveness. The present study extends these investigations to other species of spiny rats that differ in ecology and life-styles, such as solitary vs social living, fossorial vs terrestrial dwelling, size of the individuals of a given species. Financial support: FAPESP.

Cardiac Shunting in Ball Python (*Python molurus*)

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Snakes, like other ectotherm sauropsids, have a complicated heart anatomy, with five functional chambers: The Cavum venosum and the Cavum pulmonale are connected by a wide opening, but, during ventricular systole, are functionally separated by a muscular ridge. The Cavum arteriosum has no arterial exit ejecting oxygenated blood through the intraventricular canal into the Cavum venosum and the Cavum pulmonale. A functional hypothesis suggests that the muscular ridge acts as central shunt that directs oxygenated blood from the Cavum arteriosum into the left and right aorta, and deoxygenated blood from the right atrium through the Cavum pulmonale into the pulmonary artery. The direction of the shunt supposedly is condition dependent. I have studied the functioning of the heart of ball python (*Python regius*; N = 10 adult individuals) by (I) investigating the heart anatomy using macroscopic dissections and microscopic anatomy, and (II) by using non-invasive Doppler-ultrasonography to record direction, velocity, and volume of the blood flow during the heart cycle of snakes in different physiological conditions, i.e., fasting vs. digesting and resting vs. exercising. Oxygen consumption of the snakes was recorded simultaneously. The functioning of the muscular ridge, the arterial valves, the pattern of blood flow, and the separation of the blood stream into the three major arteries are described using real time Doppler-ultrasonography. Quantitative measures of blood flow volume in the left and right aorta, and in the pulmonary artery are presented for all four physiological conditions. The functional significance of the muscular ridge and concepts of central shunting are discussed.

Functional Morphology and Patterns of Blood Flow in the Heart of Snakes and Crocodiles

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Hypotheses about the functioning of the "reptilian" heart are typically derived from morphological descriptions or highly invasive physiological measurements. Both traditional approaches have provided highly valuable data and have resulted in a number of testable hypotheses about the functioning of the "reptilian" heart, supposing methods are available that allow testing of heart function in undisturbed condition. In this talk, I first discuss some methodological aspects of Doppler-ultrasonography as a (relatively new) tool in functional morphology and then present results from Doppler-ultrasonographic studies of the heart of the Nile crocodile (*Crocodylus niloticus*) and ball python (*Python regius*). Doppler-ultrasonography is a fully non-invasive technique, usually applied in human and veterinary medical diagnostics that allows visualizing the pattern and quantify the volume of blood flow in the heart, the great vessels and peripheral vessels. Blood flow was studied under different physiological conditions (i.e., fasting, digesting, diving in crocodiles; fasting, digesting and exercise in python) to test functional hypotheses about cardiac shunting and functional changes of blood flow when the animals are exposed to different conditions.

The 3D-architecture of Muscle Fascicles in Selected Muscles and Its Relevance to Force Production

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Biomechanical models describing muscle characteristics are complex and different techniques like inverse kinematics and finite element method were used in the past. None of them describes all necessary 3D-features such as the fiber type distribution or the geometrical arrangement of the muscle fascicles. In particular, the arrangement of the fascicles has an influence on the force production of the muscle. Even

slight changes of the fascicle's curvature can cause differences. The aim of this study is to reconstruct and compare the 3D-architecture of the muscle fascicles between relaxed and contracted muscles. The data will be incorporated into a 3D-muscle model in order to get a better understanding of the contraction behavior of muscles. As a result, complex courses of muscle action can be simulated and help to understand pathological alterations or changes regarding the energy efficiency and the mobility of the musculoskeletal system. The muscle fiber bundles are reconstructed and evaluated as 3D-curves from frozen cross-sections. In addition, the muscles are shock-frozen in relaxed or stimulated conditions. The variation of the space curves provides information on the curvature of the fascicles and their geometrical deformation during contraction. The results showed that muscles cannot be characterized by one specific angle. This has special importance to the determination of the physiological cross-section area (PCSA) and the Hill-type-model (with inclination of elements). Additionally, a geometrical change caused by the contraction must be heeded during simulations.

Tooth Micorwear in Recent Hyenas (Carnivora)

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The study of tooth microwear has become an important tool particularly for paleontologists to reconstruct diets of extinct animals. To do so, the microwear signals of recent animals with well known diets have to be understood and distinguishable. Most studies so far deal with primates and ungulates and only few with rodents, insectivores and carnivores. As far as feeding habits are concerned, hyenas certainly stand out within the carnivores due to their ability to break bone and the associated bone consumption. This requires high biting forces and certainly enforces high stresses on the teeth. The specialized enamel ultrastructure of hyenas have been described and interpreted in functional and biomechanic ways. Hyenas use the individual teeth in a very consistent and predictable way and differences in the enamel structure can be seen between teeth. Initial studies of the microwear in hyenids showed a high proportion of pits to scratches. This study of microwear in *Crocuta crocuta* and *Hyaena bruenna* aims to see if differences in the enamel microstructure within the dentition correspond to different microwear signals. The study will also check for differences in microwear between adult and juvenile *Crocuta crocuta* with very different diets.

Evolution of Placentation in Australian Lygosomatine Skinks (Squamata: Scleroglossa)

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Viviparity and placental nutrient provision have evolved on numerous occasions in squamate reptiles. Five lineages are substantially placentotrophic and two of these, the genera *Pseudemoia* and *Niveoscincus*, are closely related scincid lizards geographically distributed in the highlands of southeastern Australia. Histological comparison of placental ontogeny of placentotrophic species of these genera with oviparous outgroups indicates a high level of homoplasy in derived structures, yet the degree of structural similarity is variable. The terminal placental stage of each lineage consists of an omphaloplacenta (yolk sac) and a chorioallantoic placenta. The omphaloplacentae and chorioallantoic placentae are each regionally diversified and exhibit both identical and distinguishable characteristics. In general, the most similar structures have embryonic components that are also most similar to those of oviparous species. Thus, regions of hypertrophied embryonic epithelial cells, which do not occur in oviparous species, are most distinct structurally in the two lineages. Each lineage also has an embryonic structure, the interomphalopleuric membrane, which forms a boundary between the two placental regions. This structure is identical in the two placentotrophic lineages but does not occur in oviparous species. The functional characteristics of specific placental structures are not known but the morphology of the placental interface suggests that placentotrophic species have evolved regions or zones that are functionally specialized. Differences in the degree of structural similarity of these regions among placentotrophic species are explicable if selection favors retention of some functional characteristics, in addition to the enhancement of novel functions.

***Parotosuchus* from the Triassic of Antarctica and 3D-morphological Reconstruction of Temnospondyl Skulls**

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Antarctic amphibian fossils remain rare and are currently limited to a handful of specimens of uncertain taxonomic relation: only an unnamed brachyopid lower jaw, a possible juvenile mastodonsaurid (*Cryobatrachus kitchingi*), and some isolated fragments of tentatively identified lyddekerinids and rhytidosteids are known from the lower Fremouw Formation (Lower Triassic). A new specimen, the first vertebrate fossil from the upper Fremouw Formation at Fremouw Peak (Lower-Middle Triassic), was recently discovered. It consists of a partial snout, with its articulated lower jaw, of a very large, adult temnospondyl. This specimen displays typical mastodonsaurid features (e.g., part of the infraorbital sensory canal traversing the maxilla and the lacrimal; strongly transversely expanded marginal teeth) and is unambiguously referred to *Parotosuchus* on the basis of an autapomorphy (slit-like choana). The discovery of *Parotosuchus* in Antarctica is a new record for the genus, significantly extending its geographic range during the Triassic and having important paleobiological implications. Scaling of the Antarctic specimen against complete skulls of *Parotosuchus* gives an estimated total skull length of roughly 85 cm. Although incomplete, the material also allows for a 3D morpho-anatomical reconstruction of the whole skull, by comparison with the well known *Parotosuchus orenburgensis* from Russia. The new version of the modelling software "Zbrush" allows us to restore of the eyeballs, the mouth cavity, and the cranial myology. This novel modelling system has also been applied to the reconstruction of other temnospondyls such as *Watsonisuchus*, a mastodonsaurid from the Triassic of Madagascar.

Morphology of the Eutherian Nasal Region and Its Relevance for Higher-order Eutherian Phylogeny

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The nasal region comprises a complex part of the mammalian skull that has long been supposed to bear information on higher-order phylogenetic relationships. In the past 100 years, representatives from 15 of the 18 higher eutherian taxa have been studied. Here we present the morphology of the ethmoidal region from representatives of the three undescribed "orders." We examined the nasal region of the aardvark (*Orycteropus afer,* Tubulidentata), African elephant (*Loxodonta Africana,* Proboscidea) and rock hyrax (*Procavia capensis,* Hyracoidea) using serial sections and three-dimensional reconstruction, compared our data with those of other mammalian species from the literature and performed a cladistic analysis. Striking characters of our species include hypertrophy of the nasal skeleton, nine ethmoturbinates, 21 frontoturbinates, missing Foramen epiphaniale, reduced Cupula nasi anterior and anterior Paries nasi, missing Processus cupularis, and derived Crista semicircularis in *O. afer*; six ethmoturbinates, six frontoturbinates, missing Foramen epiphaniale, reduced rostral nasal skeleton without Processus alaris superior, Processus lateralis ventralis and Processus cupularis, reduced Ductus nasolacrimalis, and reduced Ductus nasopalatinus in *L. africana*; and three ethmoturbinates, three frontoturbinates, and Commissura alicupularis in *P. capensis*. We show that aardvarks and African elephants are highly derived macrosmatic mammals with a large number of nasal turbinates covered with olfactory epithelium, whereas the rock hyrax approximates the more basal eutherian character state. Our cladistic analysis only supported already well established eutherian sister groups (e.g., Tethytheria) so that the ethmoidal region appears to be of only limited utility in clarifying current systematic debates.

Segmental Organization of Hindbrain Functional Circuits in Adult Anamniotes

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Mapping of motor, reticular and central vestibular neurons by retrograde tracing in frogs and teleosts shows that the rostro-caudal distribution of many neuronal populations within the adult hindbrain is conserved when compared with their segmental positions within the embryonic and larval rhombomeric scaffold. This indicates that the segmental organization of diverse neuronal phenotypes is not a transient motif during early development but is retained throughout ontogeny, despite the disappearance of macroscopically visible segmental boundaries at later stages. This topographic stability holds for both, the anterior, overtly rhombomeric, hindbrain as well as the caudal hindbrain where the neuroepithelium is not parceled by morphological borders. It also holds for cases with extensive caudal branchiomotor migration as in teleosts or with no branchiomotor migration as in frogs. Quantitative adult segmental maps that mirror the organization of the rhombomeric framework can be created using the borders of adjacent efferent (frogs) or reticular (teleost) nuclei within a coordinate system based on external landmarks. Plotting morphologically and physiologically identified hindbrain neurons onto these maps shows a high degree of congruence between the physiological properties of adult hindbrain neurons and the underlying genetically specified segmental framework. For neuronal populations that comprise the sensory-motor network of vestibular information processing, this facilitates understanding how the different functional populations that process particular spatial and dynamic aspects of head/body motion in space develop from particular positions within the hindbrain. Thus, adult anamniote models are ideal for linking molecular and developmental aspects of hindbrain formation with the physiology of specific neuronal circuits. Support: NIH and CNRS.

Contributions of Rhombomere 4 and *Hoxb1* to Hindbrain Sensorimotor Structures

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The contribution of single rhombomeres (r) to the various structures in the mature hindbrain is not as well characterized as well as the relationship between the early segmental plan and the establishment of mature circuitry. *Hox* genes are crucial determinants of rhombomere identity and of the subsequent specification of cell identities along the dorso-ventral axis. Because of its restricted expression in r4, *Hoxb1* is an ideal candidate for studying how a single rhombomere contributes to hindbrain circuitries. We have generated a transgenic line containing the *Cre-recombinase* gene under the control of an r4 enhancer. This line was crossed to a conditional reporter line to generate a long-term fate map of all r4-derivatives from their origin to their final locations. We have identified more neuronal populations than previously described migrating out of r4 and contributing to nuclei of the auditory and vestibular systems. Furthermore, different neuronal tracts originate in r4 and project anteriorly to the forebrain and posteriorly to the spinal cord. This transgenic line was crossed with conditional and null *Hoxb1* homozygous mice to assess the role of *Hoxb1* in the specification of the various subpopulations deriving from r4. Interestingly, we found that most of the structures forming the auditory circuit were affected and *Hoxb1* mutant mice have problems in hearing. In summary, our genetic fate map analysis has unraveled previously unidentified nuclei and axonal pathways originating from r4 and has contributed to the anatomical correlation between a rhombomeric compartment with functionally distinct cell groups in the mature hindbrain.

Segmentation and Analysis of 3D-data Sets

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Three dimensional morphological data from CT and MRI consists of voxels with intensity data. The process of assigning voxels unambiguously to a tissue or structure is called segmentation. Typically segmentation requires a 3-dimensional array of the same dimensions as the data set, which in many cases can represent a significant memory requirement. There are no useful completely automated segmentation techniques for non-human data, but partial automation techniques can be exploited to make segmentation of useful data sets a realistic goal. The advantages of segmentation are several—removing an element of interest can reduce memory requirements; morphological data including volumes and surface areas can be calculated for particular structures; and animation programs can move the individual elements along realistic motion paths to produce working models. A complication often faced when high resolution CT data or synchrotron CT data are gathered is the very large size of the 3D-data set. These data far exceed the memory capacity of the visualization programs so either the data must be subsampled (losing the very data that has been gathered), cropped to a smaller region of interest, or analyzed without visualization. Techniques for calculating volumes and comparing data sets will be explained.

Functional Extremes in Cartilaginous Fish Feeding

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The cartilaginous fishes, sharks, skates and rays, occupy the same functional feeding niches as bony fishes yet their skeletons are constructed of a fundamentally different material. The skeletal specializations that permit functional extremes include innovation at several levels of organization. The mineralized tiles that cover the surface of each skeletal element are composed of at least two different forms of mineral, a globular phase and a prismatic phase. These biphasic blocks, called tesserae, are assembled into a tessellated array that has several advantages over a solid surface. Many of the tesserae are tied together with collagen fibers which allow an applied bending moment to be passed from the tensile surface to the compressive surface. This should decrease the chance of fatigue damage because the stress on the compressive side will be a far smaller fraction of the ultimate stress than on the tensile side. The core of some skeletal elements, notably the jaws of hard prey crushers and extreme protruders is shot through with hollow columns of tesserae. These trabeculae act as reinforcements that decrease strain energy during feeding. Though the feeding apparatus is simple from the point of view of number of elements, cartilaginous fishes have broad dietary habits that include true generalists as well as nearly stenophagous specialists on a variety of diets. In addition to describing the skeletal specializations that allow extreme diets we also present an evolutionary context in which specialist diets evolved and track morphology and diet and their interaction.

Suggestion of an Approach to Morphological Homology—How Data Such as Gene Expression May Provide Information

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Ever since Owen, students of homology have been occupied with sameness. Recently, usage of regulatory gene function in homologization or, alternatively, explanations involving constraints that result in maintainance of homology have been much discussed among developmental biologists and morphologists interested in homology. However, it is recognized that homologous organs may have their identity determined by non-homologous regulatory genes, change their positions through heterotopy, deviate infinitely morphologically and origin from different embryonic primordia. An easily recognized, objective "sameness", sufficient and necessary as a criterion for homology remains elusive, and yields to the arbitress of homology, the criterion of congruence. In phylogenetic systematics, synapomorphy and homology are generally regarded as synonymous. Understood in evolutionary terms, synapomorphy in effect corresponds to a hypothesis of a particular historical event of evolutionary transformation. Different homologizations imply distinct sequences of evolutionary change. Homologization might be understood as the morphological alignment of organisms that demands the fewest ad hoc hypotheses of evolutionary change. Such an alignment can be undertaken within a phylogenetic context assumed to be valid. In the process of evaluating which hypotheses of homology are the most parsimonious, there is no need to ignore change in regulatory gene expression. I wish to stimulate discussion around what I belive may represent valid usage of developmental or molecular data in relation to morphological homologization, something that remains a contentious issue. In doing so, some concrete examples will be presented.

Articular Cartilage Function and Organization: Integrating Dynamic Mechanics With Cryopreservation Effects

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General assumptions regarding the cryopreservation of articular cartilage suggest that its mechanical properties remain unchanged. Protocols have thus allowed freezing for storage convenience. This study investigates freeze-thaw induced property changes for both low frequency (0–12.5 Hz) and high frequency (30–100 Hz) loading in osteochondral dowels (8 mm diameter) stored at: +4, −20, −80, and −196 degrees C. Specimens were hydrated with PBS, brought to storage temperature, then rapidly thawed (35 degrees C) before testing at 22 degrees C. Mechanical testing consisted of non-destructive, low amplitude (0.1MPa) dynamic loading, comprising equal amplitude sine waves periodic in the time record. The full range of physiologic impact loading rates (0–100 Hz) was analyzed via Fast Fourier Transformed storage and loss moduli, from which complex modulus and phase angles were calculated. Preliminary results reveal freeze-thaw treatment to significantly increase the sample stiffness without significantly affecting the fluid flow properties. An explanatory hypothesis recalls the creation and propagation of ice in biological solutions (such as the ECM of cartilage). Ice causes solute effusion away from the ice interface. Freezing from exterior to the centre of the sample (sample frozen in solution), may cause the efflux of positively charged solutes (Na+) towards areas in cartilage that possess the greatest proportion of proteoglycans (middle and deep zones). This may result in an increased interaction with the positive solutes upon thawing, greatly affecting the swelling potential, disturbing equilibration, and possibly resulting in a stiffness increase. Any change in the mechanical properties may cause erroneous results when analyzing cryopreserved samples.

Fluid Dynamics and Kinematics of Feeding in the Little Skate, *Leucoraja erinacea*

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Suction feeding is the most common feeding mode among fishes. This technique involves the rapid expansion of the buccal cavity enabling water to flow into the mouth after a drop in pressure and has been studied in bony fish as well as some elasmobranchs. Digital particle image velocimetry (DPIV) along with high speed video were used to examine suction performance via the fluid dynamics and kinematics employed by *Leucoraja erinacea* during prey capture. Studies of this species are particularly difficult as the skate covers it prey with its body and pectoral fins. Peak flow velocity and vorticity were measured with DPIV below a platform from which the skates fed. Analysis indicates that *L. erinacea* is a weak suction feeder. Other kinematic variables were also examined. Maximum gape during successful and unsuccessful prey captures was significantly different, as was the extent of the water flowing into the mouth (both $P < 0.001$). Gape was wider and smaller fields of flow were produced during missed capture attempts; some suction events produced flow that did not come passed the mouth. Successful prey captures were associated with narrower gape and larger flow fields. There was no significant difference in distance the jaws protruded between captures and misses. Time to peak gape is also analyzed. Often after missed capture attempts, *L. erinacea* forcefully exhales water to excavate prey from substrate. Length, velocity, and vorticity of jets produced by blowing were measured. This is the first study to evaluate the hydrodynamics of feeding performance in this derived elasmobranch.

Non-destructive 3D-investigation of Dental Microstructures and Incremental Features Using X-ray Synchrotron Microtomography, New Interpretation of the Laminations vs. Cross-striations Phenomena

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During growth, teeth record their own development in incremental features at different time scales, from sub-daily features to annual ones. Analyzing these incremental marks, it is possible to obtain precise data about dental development that are well-correlated with important aspects of life history. These aspects have been extensively studied on primate teeth, but up to very recently it implied to cut the teeth to perform histological slices. It is problematic in the case of fossil primate teeth since that kind of material is rare and that it is generally impossible to sacrifice teeth in good state of preservation. Moreover, even if isolated teeth are sometimes sacrificed, it is never the case for teeth in more complete fossils. Here, I will present a non-destructive way to access to internal microstructure and developmental features up to microscopic level in modern and fossil teeth. That technique is based on phase contrast X-ray synchrotron microtomography and would permit to increase substantially our knowledge about development and life history in fossil hominids and hominoids since it is now not always necessary to cut the teeth. In a second part, I will present a new interpretation of the laminations and daily cross-striations phenomena in mammals enamel based on histological observation and 3D synchrotron investigations. These two kinds of structures are not only temporally equivalent but are in fact a single structure. The real incremental daily lines are the laminations, the cross-striations being a special case of laminations due to prismatic enamel with low daily secretion rate.

Conserved Developmental Mechanism of Vertebrate Appendages

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The morphology of appendages (limbs and fins) is strikingly diversified in size, shape, and position along the body axis. Median fins, unpaired appendages in fish, are fundamental locomotory organs that are believed to have evolved before paired lateral appendages in vertebrates. In extant vertebrates, median fins can be seen in agnathans (lampreys and hagfish) as well as gnathostomes, while paired fins/limbs are regarded as the synapomorphy that defines the gnathostomes. It has also been shown that there is a group of ancestral craniates in fossil records that have no paired appendages equipped with a continuous median fin. Thus, the ancestral mechanism of median fin development may have been co-opted for the development of paired appendages. Despite the evolutionary significance, many issues about the mechanisms underlying median fin development, especially the mechanism by which development of the median fin fold in early embryonic stages is initiated, are largely unknown. I report here the developmental process of the median fin fold, focusing on early embryonic stages and the function of FGF in the process. Our findings demonstrate that ectopic median fin fold structure can be induced in the dorsal midline and the lateral trunk in zebrafish embryos, suggesting the existence of continuous stripes of competency for appendage formation. Such a model represents the common developmental program at the root of appendage formation in gnathostomes, which permitted subsequent divergence into various levels of limbs/fins in each animal group.

Modifications of the Locomotor Skeleton During Gait Acquisition in Humans: The Pelvis as a Keystone of Functional Integration

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Gravity is a significant challenge both to the adult and to the child learning to walk bipedally. Drastic changes in loading of the whole locomotor skeleton, including the vertebral column, the pelvis and the lower limbs occur during the process of learning to walk. We test the hypothesis that the pelvis would be the keystone of the locomotor system during postnatal growth. It would play a major role in the formation of the vertebral curves as well as in the modification of the directional axes of the lower limbs from varus to valgus position. We used the software package, "DE-VISU", developed by J. Hecquet and applied it to 90 adult, infant and newborn pelves. From a set of 47 landmarks, we reconstructed the three pelvic joints and the articular parameters controlling the pelvic system. We show how this program differs from standard morphometric geometry. The angle of "sacral incidence", a sagittal pelvic parameter, establishes the functional link between pelvis and vertebral curves. The parameters of three-dimensional orientation of the acetabula establish the functional link between pelvis and lower limbs. We describe the major morphological changes occurring in the different anatomic elements of the locomotor skeleton post-natally. We show that most changes are the opposite of those resulting from intrauterine constraints during prenatal growth. We conclude that functional influences are critical to the development of the locomotor skeleton.

Effects of Maternal Protein Malnutrition and Intrauterine Growth Restriction on Redox State of the Central Nervous System in Offspring Rats

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Nutrition plays a crucial role in the maturation and functional development of the central nervous system (CNS). Both maternal protein malnutrition and intrauterine growth restriction (IUGR) have deleterious effects on brain development, but a comparison of these effects has not been previously reported. The objective of this study was to investigate the effects of these factors on redox status of CNS including spinal cord in offspring rats. We evaluated various parameters of oxidative status, indexes of damage to lipid, and protein damage in addition to antioxidant enzyme activities of superoxide dismutase and catalase in different regions of CNS from rats subjected to pre-postnatal protein malnutrition (middle 12%, low protein 4%) and IUGR. Results were analyzed by one-way ANOVA followed by Tukey's post hoc test. Both, protein malnutrition and IUGR altered various parameters of oxidative status. There was an increase in levels of thiobarbituric acid-reactive substances, the index of lipid peroxidation, in the cerebellum, cerebral cortex and spinal cord ($P < 0.001$) from protein-malnourished rats. Furthermore, IUGR increased lipid peroxidation level in the blood samples ($P < 0.04$) and protein oxidative damage in the cerebellum, and cerebral cortex ($P < 0.005$). The highest decreased in catalase activity was in the cerebellum ($P < 0.001$). In addition, a significant decrease in antioxidant enzyme activities ($P < 0.005$) was observed in the cerebral cortex from protein-malnourished rats. The present data indicated that both protein malnutrition, in different protein contents, and IUGR increased oxidative damage to lipids and proteins from CNS areas.

Taking It to the Edge: Field Studies vs. Museum Studies of Dental Microwear

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Dental microwear analysis takes us into interpretations of how teeth are actually used, rather than focusing solely on what they are capable of doing. As a result, these analyses often raise more questions than they answer, as we begin to grapple with the true complexity and diversity of diet, especially in animals, like primates, with varied diets. Field studies would seem to be the ultimate source of information on diet and dental microwear. Yet such studies are difficult and relatively rare. Meanwhile, analyses of museum material, while more feasible, are often harder to interpret, due to a lack of feeding data on the specimens in question. Still, researchers are pushing analyses to their limits. Recent work with living primates in the wild has begun to sort through the relative effects of exogenous grit and abrasive foods on dental microwear patterns. This raises the hope of gaining new insights into the diet and ecology of prehistoric creatures. Meanwhile, analyses of museum material are using larger and larger sample sizes to begin to document the range of dental microwear exhibited by species found in multiple habitats. This will, at the very least, begin to bracket the extremes of what one might find in fossil assemblages, ultimately leading to insights into intraspecific differences in diet and ecology. By pushing dental microwear analyses to finer levels of resolution, researchers are promoting the development of even better methods of data collection, which, in turn, will make even better interpretations possible.

The Auditory Region in the Cainotheriidae: New Information from CT-scans

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The Cainotheriidae are well known from numerous specimens and their cranial anatomy is well documented from complete, partial and disarticulated cranial material. However, high resolution CT scans can provide additional data to resolve problems in the interpretation of the auditory region. Hürzeler's 1936 (Abh. Schweiz. Paläont. Gesellschaft) description of the auditory region in *Cainotherium* is highly detailed. He depicts a large flange of the periotic overlapping the margin of the basioccipital, and reconstructed the petrobasilar canal as running in a sulcus along the medial part of this flange. Norris (1999, J. Vert. Paleo.) could not find any such sulcus on the specimens he was able to examine, and suggested that the specimen figured may have been broken, because the figure showed a discontinuity in the periotic. A MicroCT scan of YPM 25037 shows the morphology is more complex. Anteriorly, the periotic has a small projection over the basiocciptal. In this region, the periotic bears a shallow sulcus with a slight ridge along the lateral margin, and no medial flange or ridge. The lateral ridge becomes more pronounced posteriorly, and the medial edge of the periotic becomes depressed, forming a deep sulcus in the periotic and restricting the contact between the basicoccipital and the periotic to the ventral portion. The periotic does not completely roof over the petrobasilar canal at any point. Thus, the basioccipital encloses the petrobasilar canal only on the medial side, unlike the condition seen in camelids, *Bunomeryx*, and *Merycoidodon*.

The Virtual Pig Head: Digital Imaging in Cephalic Anatomy

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Domestic pigs are commonly used as biomedical animal models for several human disease states such as in temporomandibular joint (TMJ) disorders and mastoid air cell infections. However, unlikely the highly successful Visible Human project and similar imaging projects for laboratory rodents and other model animals, no digital representations of pig anatomy exist to aid biomedical researchers. To address this problem, the Virtual Pig Project uses digital datasets derived from computed tomography (CT scanning) to construct virtual models for research and education. Multiple specimens of domestic pig were CT scanned at O'Bleness Memorial Hospital, Athens, OH. Moreover, an explant of the TMJ region of an adult pig was subjected to microCT scanning to probe its fine-scale bony and soft-tissue architecture. All data were imported into powerful 3D visualization software (Amira), and anatomical structures such as bones, muscles, brain, air sinuses, and blood vessels were digitally extracted and visualized, rendering a virtual anatomical atlas of the head. The utilization of these data in visual comparisons to CT imagery of key human systems highlights interspecies similarities and differences. The Virtual Pig Head has already provided a series of often dramatic 3D visualizations, including virtual dissection and vascular traces, ultimately to be delivered through an interactive website. These virtual data provide an important new resource for researchers in the biomedical field and beyond.

Exploring the Molecular Basis of Digit Identity

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We are taking two approaches to uncovering genes involved in digit identity. In one approach we are pursuing the idea that the molecular code that specifies the identity of digits in the chick wing may parallel the molecular code that specifies the identity of veins in the fly wing. We have constructed, in the chick wing bud, 3D maps of expression of vertebrate homologs of genes enocoding transcription factors involved in fly venation and traced the fate of cells that express different combinations of transcription factors. We are also carrying out functional analysis in developing chick wings to test whether these genes might contribute to digit identity. In a second approach, we are using microarrays to identify genes expressed in primordia of different digits in the chick wing. This analysis has uncovered a number of genes whose expression is restricted to a particular digit primordium. These not only represent candidates for genes involved in generating digit anatomy but may also provide tools for recognising specific digits.

The Expanded Femur of Tardigrada and Its Morphofunctional Implications

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Among Xenarthra the femur is noticeably expanded mediolaterally, more so than in other mammals of comparable size. Tardigrada (sloths) exhibit the most extreme condition, particularly among the largest forms, such as the giant ground sloths, with femoral expansion always associated with strong anteroposterior compression. Biomechanical indexes show that Tardigrada, among Xenarthra, plotted far from other mammals, except those adapted to peculiar environments and strategies (such as aquatic, semi-aquatic or bipedal habits). The lateromedial expansion of the femoral diaphysis, along with anteroposterior compression, might be due to many factors: the lack of a medullar cavity, the torsion of the hindlimb associated with a complex and relatively rigid pelvic girdle, the rearrangement of the pelvic musculature and the presence of some sacrofemoral ligaments, and an inclined attitude during a bipedal stance (as might occur during feeding or defense). Further, hindlimb torsion probably affected lateromedial expansion more than previously supposed. According to other studies, the expanded and somewhat twisted femoral diaphysis is a morphological response to torsion strains due to the nearly horizontal position of the bone during both locomotion and bipedal standing. On the other hand, the short femoral neck is invariably associated with a well developed greater trochanter, always far from the caput. A better lever arm for the gluteal muscles involved in posture is produced mainly by the displacement of their insertions.

Comparative and Experimental Analysis of Jaw Muscle Morphogenesis in Quail and Duck: A Basis for Understanding Developmental Mechanisms Underlying Evolutionary Change

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Vertebrate jaw morphology is highly diverse and closely linked to species-specific differences in feeding. However, developmental processes that generate such diversity are not well understood. To identify molecular and cellular mechanisms that may have played a role during the evolution of the jaw complex, we conducted a comparative developmental study of avian jaw musculature. We analyzed the pattern of jaw muscle morphogenesis in two species of birds, quail (*Coturnix coturnix japonica*) and duck (*Anas platyrhynchos*), which belong to phylogenetically distinct groups (Orders Galliformes and Anseriformes, respectively), and which show considerable differences in jaw anatomy. We employed histology, immunohistochemistry, and in situ hybridization to follow myogenesis. The spatiotemporal patterns of myogenic gene expression and muscle-specific protein localization during relatively early stages of myogenesis (specification and differentiation) appear equivalent in these two avian species. In contrast, species-specific anatomical differences were observed in later stages of myogenesis (pattern formation). To understand the origins of such species-specific differences in muscle morphology, we generated quail-duck chimeras. Previous data have suggested that patterning of cranial muscles might involve connective tissues derived from cranial neural crest cells. Thus, we exchanged premigratory neural crest cells between quail and duck embryos to test the extent to which donor neural crest cells pattern host jaw muscles. We also performed transplants of jaw muscle precursors between quail and duck. Our results reveal the role of neural crest-derived connective tissues during muscle patterning and suggest that developmental mechanisms have shaped the course of morphological evolution.

Dissociation Between the Axial Myology and Osteology in the Anterior Precloacal Region of Limb-reduced Squamates Including Snakes

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In limb-reduced squamates with an elongated body, various anatomical structures that are usually associated with the cervico-dorsal boundary in tetrapodal squamates tend to be displaced relative to one another. In the present study, characteristics of the adult axial myology and osteology in the anterior precloacal region were examined in limb-reduced squamates including snakes. In forms that still retain a vestigial pectoral girdle such as amphisbaenians and *Dibamus*, features of the axial myology (e.g., appearances of muscles inserting on the skull) and osteology (e.g., emergence of vertebral hypapophyses) tend to be dissociated not only from the position of the pectoral girdle but also from one another, occurring at different vertebral levels. Most notably, cranio-vertebral muscles belonging to both the subvertebral and m. transversospinalis groups tend to extend much more posteriorly well beyond the level of the pectoral girdle. The posterior extents of these cranio-vertebral muscles vary similarly in snakes. In addition, unlike in tetrapodal squamates, the posterior extents of hypapophyses and the subvertebral m. rectus capitis anterior are dissociated from each other in many limb-reduced squamates, with the latter muscle extending much more posteriorly than the former structure in amphisbaenians, *Dibamus*, *Acontias*, and scolecophidian snakes (but vise versa in many alethinophidian snakes). These observations suggest that the regulation of axial patterning may be dissociated between different muscle groups or between the vertebral column and the associated musculature within the primaxial domain in limb-reduced squamates and snakes, thus further blurring the cervico-dorsal boundary in these animals.

The Evolution of the Middle Ear in Parareptilia

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Traditionally, the origin and evolution of the impedance-matching (tympanic) middle ear in amniotes was considered a key innovation of basal tetrapods, only later modified during amniote diversification. Recent investigations, however, have shown that the otic region of early amniotes lacks any indication of impedance matching; consequently, the tympanic middle ear seen in modern taxa must have evolved independently multiple times. When turtles are considered diapsid reptiles, only two of the three major amniote clades, Synapsida and Eureptilia, were known to possess a true tympanic ear, with convincing evidence lacking for the third, Parareptilia. For an unequivocal interpretation of impedance matching in fossil amniotes, several functional requirements must be reflected in the anatomy: a) a modified temporal region indicating the presence of a tympanum; b) firm contact between the skull roof and paroccipital process, freeing the stapes from its bracing function; c) a slender stapes, indicative of mediating airborne sounds via vibrations from the tympanum to the inner ear; d) differentiation of the posterolateral braincase wall into oval and pressure-relief windows, along with ossification of the medial wall to separate the inner ear from the remaining braincase. Basal parareptiles lack these features, suggesting that airborne sounds could not be perceived effectively. However, we present here evidence that within derived parareptiles, a poorly-known clade from the Middle Permian of Russia possesses all anatomical characteristics typical of an impedance-matching middle ear. This represents the first true evidence of a tympanic ear in parareptiles, and the oldest yet found in amniotes.

Current Knowledge of Tooth Development, A Model Mineralized Element System

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The tooth represents a great model of epithelial-mesenchymal interactions and organogenesis, and due to its accessibility it provides a great opportunity for tissue engineering. The signals involved in many of the stages of tooth development have started to be elucidated and provide a wealth of information regarding initiation of a tooth, shape of a tooth, size of a tooth and number of teeth. Using the mouse as a model organism, tooth development will be discussed, looking at each of these processes which together result in the formation of a particular pattern of dentition. How variation in dentition could be generated will be discussed using information learned from gene manipulation in vivo and explant culture. In such studies the basic shape of a tooth, the cusp pattern, the number of teeth, the size of teeth and the pattern of mineralization have all been altered. Our understanding of tooth development can then be utilized to address the question of what is necessary for formation of a tooth. Given this information we can then move onto investigate how to re-create a tooth, with the ultimate aim of providing replacement teeth by tissue engineering.

Structure and Function of European Starling Syringeal Muscles

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The avian vocal organ, the syrinx, has four pairs of intrinsic muscles (ventral and dorsal tracheobronchialis, vTB/dTB; ventral and dorsal syringealis, vS/dS). EMG recordings in singing European Starlings (*Sturnus vulgaris*) showed activity bursts that correlate with amplitude modulation rates of up to 170 Hz, suggesting that these muscles directly control airflow gating and acoustic parameters at such high rates. Myosin ATPase and immunohistochemistry were used to characterize and quantify muscle fiber type composition and individual fiber diameters. A small fiber type (mean diam 14–20 μm for all muscles) comprised roughly 30% of the muscles and reacted like fast oxidative (type IIa) fibers with ATPase and antifast antibody reactions. A larger fiber type (mean diam 31–38 μm for all muscles) comprised about 70% of the muscles and had intermediate reactions to both acidic and alkaline preincubations and lower oxidative capacity. It reacted negatively to both antislow and antifast antibodies. The unusual staining profile and EMG data support the view that these fibers are superfast, as described for rattlesnake tailshaker muscles. Nitric acid digestion, used to measure fiber lengths, revealed fibers 3–4 mm long, spanning the length of vS and dS, but only half the length of vTB and dTB. The latter muscles consisted of two-fiber units arranged serially. Similar patterns of fiber types and sizes were also found in species from 3 other songbird families, indicating that the presence of superfast fibers is likely a common trait of the oscine syrinx. Supported by NIH grant # DC004390 and WSU.

Microwear Texture Analysis: Microwear as Applied to Fossil Primates and Human Ancestors

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We can be confident that patterns of dental microwear reflect material properties of foods eaten by an animal. We do not know, however, the ultimate potential of this approach for reconstructing diets of fossil forms. While SEM analyses of microwear represented a significant advance in the 1970s, this approach is time-consuming and expensive. Quantification of microwear features is prone to measurement error, and results vary with instrument settings and geometric relationships between the electron beam, specimen and collector. It is at times remarkable that any diet signal comes through at all given the "noise" in the system; to say nothing of data loss due to the representation of a 3D surface in two dimensions. In this presentation I describe an inexpensive, rapid, objective, repeatable, 3D approach to characterizing dental microwear textures. A digital elevation model is generated for each microwear surface using a white-light scanning confocal microscope. Attributes including surface complexity, anisotropy, fill volume, and heterogeneity are calculated using scale-sensitive fractal analysis. These attributes together characterize the texture of a surface. Dental microwear texture analysis allows examination of within species variation without the confounding effects of observer error. This provides a way to test some hypotheses concerning the nature of selection for dental functional morphology. For example, does occlusal form reflect material properties of preferred foods or just those of the most mechanically challenging ones (even if infrequently eaten)? Data on platyrrhine (*Alouatta palliata, Cebus apella*) and cercopithecoid (*Lophocebus albigena, Trachypithecus cristatus*) monkeys will be presented as an example.

Response of Regenerating *Ambystoma mexicanum* Tails to Varying Concentrations of Retinoic Acid

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Many studies have investigated the effects of retinoic acid (RA) on the speed and efficiency of limb regeneration, but few have looked at the impact of retinoic acid on tail regeneration. Research on regenerating axolotl limbs has shown that retinoic acid interferes with patterning and causes deformities (Ludolph et al., 1993). This study explores the effects of retinoic acid on tail regeneration in different stages of axolotl development. Axolotls with amputated tails were exposed to either 0.1 μM or 3 μM concentrations of retinoic acid by inserting retinoic acid soaked beads into the regenerating tail blastema. Regenerating tails were measured at 1–3 day intervals and subsequently imaged to document morphological changes. Implanting the highest concentration of RA (3 μM) into regenerating embryonic tails resulted in 100% mortality. In terms of length, amputated tails in both control and RA-treated embryos exhibited parallel patterns of regeneration. The same trend was found for hatchlings and larvae. When compared to their original amputated lengths, regeneration of control and RA-treated (0.1 μM) embryo tails far exceeded the length and rate trends observed for hatchlings and larvae. Initially, the dorsal and ventral fins were the only portions of the tail that elongated posteriorly after amputation. At hatching, the dorsal and ventral fins had merged at the posterior tail tip, but no elongation of neural tube or notochord was apparent. We are currently investigating how RA might be affecting the presence and patterning of various cell types and tissues in regenerating embryonic tails exposed to retinoic acid.

Lumbar Ontogenetic Growth and Sexual Dimorphism in Modern Humans

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A sample of modern humans (601 males and 1117 females) from the urban area of Barcelona was studied. The age ranged from 0 to 21 years. Dual energy X-ray absorptiometry (DXA) was used to analyse the lumbar region (L2-L4) of the individuals. From the DXA results, the measured variables were: average length and width of the segment; posterior projected surface area; bone mineral density. Furthermore, the ratio length/width was calculated. The corresponding growth trajectories of these variables were analysed by means of the Gompertz model. Both in males and females length initial size was significantly higher than width initial size. The same happened with the initial growth rate, although the maximum initial growth rates are those corresponding to surface area and density, in both cases in females. In both sexes width scaled faster than length. These results must be put in relation with the fact that bone growth takes place differently in length than in width. Sexual differences in growth rate accounted only for a small proportion of the variation in lumbar segment length, mineral density, and surface area, but they played an important role in the growth of the length/width ratio. Regarding the age at which a significant percentage (70%–90%) of adult size is attained, length of the lumbar segment presents an intermediate-very late growth, width a late-later timing pattern, and surface area and mineral density present a late-really late growth.

Biting Performance and Skull Shape Variation in Durophagous and Teeth-digging African Mole-rats (*Fukomys*, Bathyergidae, Rodentia)

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Phenotypic variation arises from adaptations to local environments and phylogenetic constraints. The obligatory subterranean African mole-rats of the genus *Fukomys* have been shaped within the context of their underground habitat, posing particular limits on the animals' morphology. Especially the biting apparatus is likely shaped by strong evolutionary constraints, as it is used for feeding on hard geophytes, for digging complex tunnel systems, and for defensive purposes and social interactions in a colony. We studied interspecific differences in bite performance among three taxa, in relation to their skull anatomy and skull shape using landmark based geometric morphometric techniques. Scaling of bite force is positively allometric relative to body weight. Moreover, differences in maximal biting force exist between taxa. These results are interpreted in relation to jaw mechanics, whereby possible spatial tradeoffs with e.g. the brain, the auditory and olfactory systems are considered. Relying on a molecular phylogeny, this study enabled us to analyze the evolutionary pattern behind the variation in structure and performance of the biting apparatus in Fukomys mole-rats.

Causes and Consequences of Sexual Dimorphism in Functional Traits: A Comparative Approach

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Sexual dimorphism in body size and shape is widespread among animals. Although the phenomenon is usually attributed to sexual selection, it may also arise through fecundity selection or competition avoidance.

Discerning between these causes has proved problematical. Part of the difficulty may stem from the fact that the fitness consequences of morphological differences are often not well understood. While dimorphism in morphological features has been documented extensively, data on dimorphism in whole-animal performance traits are still scarce. In this study, we take a comparative approach and investigate whether and how sexual dimorphism in body size and shape correlate with sexual dimorphism in physiological performance. We also examine among-species patterns of performance dimorphism with life history traits. We use lizards (in particular, members of Anolis and Lacertidae) as study animals.

Long in the Tooth: Evolution of Sabertooth Cat Cranial Shape

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The sabertooth ecomorph is one of the most remarkably extreme and convergent feeding morphologies among carnivorous mammals, having arisen independently at least four times during the Cenozoic. Within sabertooth lineages, two distinct morphotypes have been described: dirk-toothed forms with long canines and robust skeletons, and scimitar toothed forms with shorter canines and more gracile skeletons. Previous studies on sabertooth cranial shape have relied on multiple linear measurements and/or ratios, rather than estimates of overall shape. Here, we use geometric morphometric techniques to describe and compare overall cranial shape in feline and machairodontine felids and nimravids. Sabertooth cranial morphologies occupy distinct portions of morphospace, but are found to be extremes of trends in cranial shape present in extant conical toothed cats. In extant felines, body size is strongly correlated with cranial shape with larger cats having more elongate rostra, taller, more vertical occiputs, procumbent incisors and an anteriorly displaced mastoid process. However, in sabertooths, crown height of the upper canines appears to be more important in determining cranial form. Selection for larger canines results in a cascade of morphological changes that are driven by functional demands of gape angle, bite, and cervical musculature. We discuss the various factors that may have driven sabertooth evolution, and the reasons why these forms have been prone to extinction.

Morphological and Functional Determinants of Fighting Capacity in Lizards

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As is the case in most organisms, many lizard species are known to defend resources (e.g., territories, partners, food). Previous studies have shown that morphological traits, such as body and head dimonensions may determine fighting capacity in staged encounters. However, up until recently the functional relationship between the variation in morphology and fighting ability has remained unclear. Here, we quantify different performance traits, such as locomotor ability and bite strength in *Anolis* and lacertid lizards, and test whether either one or both can explain the link between the variation in morphology and aggressive behavior. In addition, we explore whether the evolution of territoriality and aggressive behavior in lizards has been paralelled by the evolution of greater performance capacity. We do so by comparing performance capacity and sexual dimorphism therein among different lizard species known to vary in degree of territoriality.

Functional Morphology and Frequency Perception in Anuran Amphibians' Inner Ear Receptors

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Disposition of the hair cells (HC) in the hearing papillae of the amphibian inner ear on the firm basement makes the tectorium (T) in both cases the principal stimulating element, whose mechanical (resonance) peculiarities determine the frequency band perceived by amphibians. In this case, the "lightened" T of the basilar papilla (BP) provides for the "volley" excitation of HC, reproducing adequately vibrations of relatively high (over 1.0 Hz) frequencies, while the T of the amphibian papilla (AP) with its evident "mass gradient" reacts to low and middle (lower 1.0 Hz) frequencies. As the morphological polarization of HC in AP shows, HC of its rostral part are excited with the longitudinal movements of the T "head", while HC of the caudal part react to the transversal shift of the T "cauda." Hence the mass of the rostral T part determines perception of relatively low frequencies (0.4–0.7 kH), and the thin (light) caudal T part, bent almost at a right angle realizes its elasticity, moving transversally and exciting HC with higher frequencies. But, being "monolith" mechanic structures tectoria of both papillae reproduce mainly temporal pattern of the sound signals in accordance with their enveloping (modulating) frequency. Perception of the carrying frequencies in sound signals of amphibians depends on characteristic frequencies of HC, that is proven by their dependence on the ambient temperatures.

Role of Thyroid Hormones in Skeletal Ontogeny in Anurans

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The role of thyroid hormones (TH) in the development of the bony skull, axial and limb bony skeleton was experimentally studied in the common frog *Rana temporaria* (Ranidae) using exogenous stimulation of larvae by TH (triiodothyronine) and goitrogen. The TH-treatment resulted in the overall acceleration of development, including the precocious ossification of the skull and limb bones and urostyle formation. This effect was dosage-dependent, and the highest concentrations of TH affected not only the timing, but also the sequences of bone formation in comparison with the control tadpoles. In contrast, the stimulation of developing larvae by the goitrogen resulted in the overall skeletal ontogeny retardation on early stages, and some latest skull bones failed to form. The influence of TH excess or deficiency on the vertebrae formation was not found, but the development of urostyle and particularly its hypochordal element is evidently under TH-control. The obtained data concerning the role of TH in the skull development in *R. temporaria* suggest these hormones exerting more likely the regulating effect on the earliest skull bones to form and the obligatory inductive impact to the latest ones. Our findings indicate that in anurans the skeleton development on the whole is much more affected by TH than in urodelans, in which the postcranial skeleton and some cranial bones are free from TH-control, as was shown in our preceding researches.

Geometric Morphometrics of the Skull and Mandible of the Iberian Desman, *Galemys pyrenaicus* (Soricomorpha, Talpidae)

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Sexual dismorphism and post-natal variation in the skull and mandible of the Iberian desman, *Galemys pyrenaicus*, were tested by means of geometric morphometrics. Analyses were based on collection specimens coming from different locations from northern Spain. Desmans were grouped into four relative age classes (0-3) on the basis of the wear of their canine and first premolars. In each specimen, ventral skull, dorsal skull, and mandible shapes were represented by 14, 11, and 15 two-dimensional landmarks respectively. The geometric morphometic analyses were performed using programs of the TPS series (Rohlf, 2003; http://life.bio.sunysb.edu/morph/). Results on centroid sizes revealed that male skull was significantly larger than the female one, probably due to sexual selection. As for shape variables, significant differences were only observed between age classes for the partial warp scores and weight matrices of the ventral skull and mandible. Canonical variate analyses of the corresponding weight matrices furnished three significant functions, which classified correctly 71.1% of ventral skulls and 74.2% of mandibles. In each case, projection of individual scores onto the two first functions revealed a separation between juveniles (class 0) and adults of classes 2 and 3. The non-uniform plots showed that, in comparison with juveniles, adult desmans have a longer anterior part of the upper dental series and a narrower muscular region of the mandible. These shape modifications do not seem to be related to diet changes, but to increased tooth wear, causing a morphological remodelling in adult mandible to provide an optimal mastication.

Sagittal Foot Joint Mechanics During Hylobatid Bipedalism

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The human foot is a hallmark of our habitual bipedal gait, combining flexibility and shock-absorption at touchdown with rigidity and propulsion at push-off. It has evolved from a mobile structure in our early ancestors, related to an arboreal lifestyle, towards a more rigid lever in modern humans. To find out how a flexible foot could affect the bipedal gait kinematics, we have analyzed the foot function of an arboreally-adapted ape during terrestrial bipedalism. High-speed recordings (125 Hz) of the lower leg have been taken during spontaneous hylobatid bipedalism. The sequences were digitized and, followingly, the sagittal plane kinematics of the metatarsophalangeal, midtarsal and ankle joints were analyzed using a 4-linked-segment model in Kwon3D. These data were combined with previously collected kinetics and plantar pressure data to perform an inverse dynamic analysis and work out joint moments and power. The results show that, apart from the large range of motion at the ankle joint, there is also considerable amount of flexion/extension at the midtarsal and metatarsophalangeal joints. Although the movement at the midtarsal joint is highly variable, the main pattern is extension. Coupled with hyperextension of the metatarsophalangeal joint prior to push-off, this stretches the plantar ligaments allowing elastic energy storage. The relaxation of these joints after push-off brings about recoiling of the elastic tissues, thus contributing to energy recovery during bipedalism. This study indicates that flexible feet clearly influence the bipedal gait kinematics; it also suggests that compliant feet could facilitate alternative energy-saving mechanisms during bipedal locomotion.

Comparative Development of Mineralized Integumentary Elements

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Among the most diverse and yet poorly understood components of the dermal skeleton (dermoskeleton) are mineralized investments of the integumentary system. Generally regarded as derivative of the once all-encasing skeleton of structural grade ostracoderms, during the course of evolution these elements have undergone considerable modification as well as a trend towards reduction. Developmental studies at the tissue level have demonstrated an evolutionary link between odontodes and various other organs including teeth and denticles among non-tetrapods ("fish"). For other elements, including elasmoid scales and osteoderms, the relationships are less clear. Ongoing pursuit of these topics includes molecular work, identifying genes and signaling pathways involved in development, as well as additional comparative tissue studies. We begin by reviewing current information on the development of mineralized integumentary elements, highlighting the roles of odontogenic and/or osteogenic cell populations and the frequent requirement for an adjacent or surrounding well-structured foundation. We then turn our focus to amniote osteoderms. Osteoderms demonstrate a sporadic taxonomic distribution, and their homology as skeletal organs has previously been questioned. More recent studies reveal, however, that osteoderms, postcranial dermal plates of teleosts, and other mineralized elements are fundamentally homologous in terms of sharing the integument as a structural foundation and source of (non-cartilaginous) skeletogenic cells.

Geometrics Morphometrics and Fragmented Archaeological Skeleton Remains: Examples, Limits and Perspectives

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Though the use of geometrics morphometrics analysis is wide spread since at least 15 years in the scope of biological and anthropological sciences, the overwhelming majority of archaeologists still investigate the morphology of animal remains by the way of traditional measurements and basic statistical methods. This is at least partly due to the high level of dissociation and fragmentation of the archaeological skeletal remains. In order to estimate more precisely the limitation made by bone fragmentation and to try to take more advantage from the morphology of vertebrates' archaeological bones, we experimented successively more and more sophisticated morphometric methods: Log Shape Ratio analyses applied to traditional length measurements (historical times in Europe; Neolithic equids of Iran), Landmark analyses (Late Glacial Equids of Western Europe), Outline analyses (Mediterranean house mouse). These different examples will be briefly presented, and assessed in terms of efficiency with reference to traditional archaeozoological measurements. General conclusions emphasize the high benefit that archaeozoology can get from a separate analysis of shape and size, especially for interpopulation comparisons and phylogeographic approaches. But it also highlights the true limitations induced by the fragmentation, which may lead to bias simplistic morphological approaches and preclude some investigation such as asymmetry analyses.

A Juvenile Plesiosaur Specimen From the Early Jurassic (Toarcian) of Holzmaden, Germany

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A juvenile plesiosaur discovered in the Posidonien-Schiefer (Toarcian) of Holzmaden, Baden-Württemberg, South-western Germany is described. It includes the almost complete skull and skeleton and is one of the most complete and youngest plesiosaurs ever discovered from the Early Jurassic. The skeleton shows a mosaic of characters (plesiosauroids and pliosauroids) and it is difficult to assign this specimen to a superfamily. It provides new valuable information about the early phases of plesiosaur ontogenetic development. A possible sequence of suture ossification of the skull and a discussion concerning the ontogenetic pattern of post-skeletal ossification are proposed.

A Preliminary Analysis of the Relationship Between Masseter Muscle Strain and Food Properties During Chewing in Tufted Capuchins (*Cebus paella*)

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The recent influx of data on dietary mechanical properties from free-ranging primates has not been matched by corresponding laboratory studies documenting how food properties affect primate chewing mechanics. To better understand masseter mechanics during chewing, we combine electromyography with sonomicrometry to measure masseter strain (i.e., length changes) during muscle activation. By combining technologies, we can determine when the masseters shorten, as might occur while moving the jaw, or contract isometrically, as might occur when creating bite force, and how muscle length changes relate to dietary properties. We surgically implanted pairs of sonomicrometry crystals along individual muscle fascicles in the superficial and deep masseters of two female tufted capuchins. Indwelling electrodes were inserted in these muscles. After recovery from anesthesia, we fed individuals foods with varying elastic moduli (E) and toughnesses (R) while recording masseter activity. We collected data from four experiments per muscle. Masseters typically shortened while active. Shortening of the superficial masseter during activation averaged 5.8% on the working-side and 5.4% on the balancing-side. The balancing-side deep masseter shortened 6.1% on average during activation, while shortening 9.2% as a working-side muscle. Although highly preliminary and varying somewhat by individual, foods with a higher displacement index (R/E)0.5 tended to elicit larger masseter strains. Alternatively, masseter strains during activation tended to be less when chewing foods with a higher stress index (ER)0.5. Clarifying these complex muscle strain patterns during chewing will further our understanding of how diet relates to primate jaw-muscle function and masticatory apparatus evolution. Supported by NSF.

The Masticatory Apparatus of Fossil Xenarthrans

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The masticatory apparatus of fossil and living xenathrans reflects a combination of historical, functional and biomechanical constraints. The hypselodont teeth, usually reduced in size and number, are simple (but may be lobate), separated by short diastemata, and composed of osteodentine. Enamel is absent (except possibly in *Utaetus*), as are the cuspal patterns present in other mammals. However, the great diversity of forms suggests several adaptive possibilities ranging from specialized myrmecophagous species to carrion-feeders or predators among animalivores, selective browsers to bulk grazers among herbivores, and omnivores. Within cingulates, the mandible and teeth of eutatines and pampatheres resemble those of certain ungulates. The elevated mandibular condyle improves the mechanical advantage of the massetericus; its morphology allows considerable lateral and anteroposterior movements. The arrangement of outer and inner hard dentine layers on the flattened distal lobate teeth suggests a strong lateral component. The temporalis was larger, imparting a more prominent vertical component (a pattern typical of carnivorous mammals) in euphractines and peltephilines (though the latter was likely a specialized herbivore). Within pilosans, anteaters, with their edentulous jaws, are apparently highly specialized. Among sloths, the craniomandibular joint and wear facets in mylodontids indicate anteriomedially directed masticatory movements, as in generalized therians; in megatherioids, muscular attachment sites and tooth contact facets indicate strong vertical masticatory movements. Some xenarthrans, without living analogues, evolved mechanical solutions not shared by closely related taxa. Biomechanical analyses of such forms can yield models for investigating and interpreting adaptations in other lineages without living representatives.

The Mechanical Properties of Foods Consumed by Wild Orang-utans (*Pongo pygmaeus wurmbii*) in Central Kalimantan, Indonesia

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Orang-utans (*Pongo spp*.) are characterized as having thick tooth enamel thickness and robust jaw morphology relative to other extant apes. Orang-utans often rely on tough food items, such as bark, seeds, and vegetation, during periods of low fruit abundance, and it is thought that these food items have shaped their masticatory morphology. While it is almost uniformly accepted that variation in enamel thickness and jaw morphology are adaptations to dietary hardness, few relevant data exist to test this conjecture. Here we present the first empirical data on the mechanical properties of foods consumed by wild orang-utans (*Pongo pygmaeus wurmbii*) in Central Kalimantan, Indonesia. We measured Young's modulus and fracture toughness of over eighty species consumed by orang-utans using a portable field tester. There are significant differences in both fracture toughness and Young's modulus among the different parts of the fruits (exocarp, mesocarp, and endosperm), and among different stages of ripeness. Inner bark, seeds and leaves are significantly tougher than fruits. When we compare the parts of the fruits consumed by the orang-utans against the parts they discarded, the former were less tough than the latter. Finally, to examine this data in a broader context, we compare mechanical properties of orang-utan fruits to those consumed by chimpanzees (*Pan troglodytes schweinfurthi*) and discuss the results in terms of the foods they fall back on during periods of low fruit availability. These data help deepen our understanding of why molar enamel thickness, and craniofacial and dental morphology vary across primates.

Evolution of Body Plan Complexity: What Does it Mean?

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When talking about evolution of major groups of organisms the term "complexity" seems to be unavoidable, even though there is no generally accepted metric for it. In this contribution I will suggest a conceptual outline of how to define organismal complexity to be usable in the context of animal body plan evolution. The basic idea is that body plan complexity reflects the number of developmentally individualized body parts, including different cell types. This proposal is consistent with previous proposals but emphasizes that this measure depends on the recognition of what parts of an organism represent developmentally individualized parts. I will discuss the mechanistic basis for this proposal and suggest genetic correlates of this concept. For instance recent work suggests that the origin of novel cell types correlates well with the origin of novel miRNAs, which makes mechanistic sense given the role of miRNAs in gene regulation. In addition, I will discuss the relationship between the evolution of novel body parts and genome duplications with reference to our work on teleost evolution and Hox gene duplications.

Developmental Evolution of Digit Identity in Birds and Skinks

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Digit identity and homology has been controversial ever since the discovery of the bird- dinosaur affinities. The main source of controversy is the discrepancy between phylogenetic and osteological evidence which identifies the finger in the bird wing as digits 1, 2, and 3; and the embryological origin of the bird digits suggesting that they are digits 2, 3, and 4. A similar controversy exists regarding the identity of the three digits of the Italian skink *Chalcides chalcides*. In this contribution we will review new evidence regarding bird and skink digit identity. 1) A detailed examination of the skink fingers and their development confirms that the digits 1, 2, and 3 are developing in the positions 2, 3, 4, making this another case of digit identity frame shift. 2) In mice the knockout of Hoxa-13 leads to a specific loss of digit 1. Using a RCASBP(A)-Hoxa13-Engrailed Repressor strategy to knock down the activity of Hoxa-13 in the chicken wing we obtain a specific loss of the most anterior digit. We conclude that the anteriormost digit in the bird wing has the same developmental dependency on Hoxa-13 as digit 1 in mammals. 3) Expression of HoxD genes in the *Alligator* confirms that, ancestrally, digit 1 differs from the more posterior digits by the absence of Hoxd-11 expression. We conclude that digit identity frame shift is a possible mode of evolution that happened at least once in the birds and once in skinks.

Feeding in Olive Baboons (*Papio anubis*): Sexual Size Dimorphism, Energy Requirements, and Masticatory Mechanics

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The impact of sexual dimorphism in body size, jaw dimensions, and jaw muscle size on feeding mechanics is poorly documented. *Papio anubis* males are twice the size of females and have similar diets. Aggressive biting in males has been proposed to explain sex differences in jaw muscle characteristics. To examine the mechanical consequences of sexual dimorphism for the feeding apparatus, EMG activity during mastication, fiber type, mass, fiber length, and cross-sectional area (PCSA) of the jaw-adductor muscles, and mechanically-relevant jaw dimensions in 2 female and 3 male baboons were measured. Females have more slow-twitch fibers in deep temporalis and superficial masseter, lower PCSA, and lower PCSA-to-load arm ratio. Males have long muscle fibers and more muscle volume. Both sexes have a fast-twitch superficial temporalis that is recruited during resistant-object feeding. Results suggest that fiber-type distribution is not necessarily related to aggressive biting in males, but that fiber length is. A model of feeding behavior is developed that incorporates daily energy requirements, masticatory mechanics, and the consequences of size dimorphism. The model suggests that a functional consequence of small size in females is that a given fiber is recruited more frequently and more fibers are recruited relative to total PCSA to generate bite force necessary to meet energy requirements. This explains the high percentage of slow-twitch fibers in deep temporalis and superficial masseter in females. The model has testable assumptions and predictions concerning the mechanical effects of body and jaw size on the feeding apparatus. Supported by the NSF.

The Correlation Between Structure and Function of the Heart of Snakes and Lizards

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The heart of lizards and snakes (squamates) consists of two separate atria, receiving oxygen-poor systemic venous blood and oxygen-rich blood from the lungs, and a single ventricle. A muscular ridge (MR), however, divides the ventricle into the major compartments (cavum pulmonale and cavum dorsale), assisted by one or more apical septa. The MR arises from the ventricular wall, but has a free lateral opening. However, during ventricular contraction this opening can be effective closed by the MR abutting to the bulbuslamelle on the opposite side of the ventricle. The MR and bulbuslamelle are particularly large and well developed in varanid lizards and pythons, which enable the ventricles of these reptiles to have a high pressure in systemic circulation (approximately 60–100 mmHg), while keeping a low pressure in the pulmonary circulation (around 20 mmHg). Thus, it seems that interspecific differences in the degree of ventricular septation determine the degree of shunting between the pulmonary and systemic circulations. We will present and discuss the ventricular anatomy of different species of snakes and reptiles. Using NMR scanning and ultrasound, we have shown that the atrio-ventricular valves direct blood flows from the left and the right atria into the cavum dorsale and the cavum pulmonale, respectively, which can explain the pronounced blood flow separation that has been documented from measurements of blood gases. These findings will be discussed in relation to measurements of blood flow and shunt patterns during various types of behavior and metabolic states of the relevant species.

Effects of Body Elongation on the Patterning of the Abdominal Viscera in Polypteriformes (Actinopterygii)

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A highly elongate body form has evolved independently multiple times within Actinopterygii. Axial elongation in fishes occurs via the addition of abdominal vertebrae, addition of caudal vertebrae, and/or by lengthening the vertebral centra. Most ray-finned fishes elongate by adding caudal vertebrae, but some groups elongate by the addition of abdominal vertebrae. One example of abdominal addition of vertebrae occurs within Polpyteriformes, where one genus has twice as many abdominal vertebrae as its sister genus. Previously, studies have focused on anteroposterior patterning of the vertebral column. In this study, we examined anterior-posterior patterning of the viscera in *Polypterus senegalensis*, *Polypterus palmas*, and *Erpetoichthys calabaricus*. We recorded the anterior and posterior positions of individual visceral organs relative to percent total length and vertebral number to determine whether organs were relatively longer and covered more segments, or whether organs maintained the same span, but were located at different segment numbers. In addition, we examined whether there were differences between males and females within the same species. We found that abdominal elongation involves both lengthening of some organs, as well as changes in the segmental positions of others. When the span of a given organ was longer, the number of vertebrae spanned doubled. The results of this study provide a basic understanding of the anteroposterior patterning of the viscera in Polypteriformes, and how changes occur when the number of abdominal segments is increased. In the future, this work will be extended to investigations of the visceral topography of other abdominally-elongate lineages of vertebrates.

The Developmental Basis for Adult Craniofacial Variation: A Morphometric Analysis of the "Short-faced" crf4 Mouse Mutant

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Phenotypic shortening of the basicranium and face is a hallmark of human evolution. Congenital facial malformations, notably palatal clefting, occur with high frequency in human populations where studied. The etiology of clefting remains poorly understood, although we now appreciate that the high integration of craniofacial structures may factor into these birth defects. Compared to wild-type, the Crf4 mutant mouse was a previously uncharacterized strain with an apparently shorter head. Thus, this mutant was potentially a valuable model for understanding human craniofacial development and evolution. Here, we investigated Crf4 craniofacial developmental morphology. Our first aim was to statistically quantify craniofacial skeletal variation between Crf4 and wild-type mice. Our second aim was to test the hypothesis that between-strain morphological variation in adults was also manifest in embryos and/or neonates. 3D landmark data taken from micro-CT scanned Crf4 and wild-type embryos, neonates and adults were analyzed using a combination of Euclidean Distance Matrix Analysis, and Generalized Procrustes and Principal Components Analyses. Samples were age and size corrected. The Crf4 phenotype was characterized by shortened face, basicranium and cranial vault lengths, increased neurocranium height and globularity, and increased face and neurocranium widths. Morphological variation was statistically different between strains, comparable across all three age groups, and highly correlated with the allometric variation related to head size. Earlier midline fusion of the Crf4 nasal processes may contribute to the mutant phenotype. We were correct in that the developmental mechanism of the Crf4 phenotype is expressed at the embryonic stage of development.

A Single Ancient IGFL Allele Causes Small Size in Dogs

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The domestic dog exhibits greater diversity in body size than any terrestrial vertebrate. We use a novel three-part strategy to determine the genetic basis for size in dogs. First, through a genome-wide scan, we identified a major QTL on dog chromosome 15 associated with size variation in a single breed. Second, we examined genetic variation in the relevant 15 Mb interval in small and giant dog breeds, finding striking evidence for a selective sweep in a 70 kb region spanning insulin-like growth factor-1 (IGF1). A single IGF1 haplotype is common to all small breeds and nearly absent from giant breeds. Lastly, data from >3,200 dogs representing 143 breeds demonstrates that IGF1 accounts for a majority of the variance in average breed mass. These results suggest that the evolutionary mechanics of size variation in dogs is relatively simple and uniquely dependent on the appearance of a single ancient variant.

Evidence for Bird-like Air Sacs in Sauropods and Other Saurischian Dinosaurs

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The presence of postcranial pneumaticity in sauropod and theropod dinosaurs has been assumed to indicate lung ventilation by air sacs. Pneumatic diverticula are widespread in vertebrates and can develop from any part of the respiratory system. On this basis, some authors have argued that postcranial pneumaticity in extinct archosaurs does not inform us about their lung morphology or mode of ventilation. However, the inference that saurischian dinosaurs had a bird-like respiratory system does not rest on the mere presence of pneumaticity. Rather, the evolutionary pattern of postcranial pneumatization provides strong evidence for bird-like air sacs in saurischians. Early saurischians have pneumatic spaces only in the cervical skeleton. Pneumatization by cervical air sacs is the most parsimonious explanation for this pattern. In more derived sauropods and theropods, pneumatization of the posterior dorsal, sacral, and caudal vertebrae indicates that abdominal air sacs were also present. The presence of abdominal air sacs in saurischians is also indicated by pneumatic hiatuses in a few taxa. Minimally, saurischians had a dorsally attached diverticular lung and air sacs both anterior and posterior to the lung, and thus had all of the pulmonary prerequisites for flow-through lung ventilation like that of birds. In birds, air sac ventilation mitigates the tracheal dead space associated with long necks, averts alkalosis during thermoregulatory panting, and facilitates efficient gas exchange. Sauropods were the largest and longest-necked of all land animals, and these capabilities of a bird-like respiratory system may have been pre-adaptive for the evolution of large body size and long necks.

Dental Microwear in Multituberculate Mammals and Dietary Change Across the K/T Boundary in Eastern Montana

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We examined dental microwear on molars of cimolodontan multituberculate mammals from the Hell Creek and Tullock Formations of Garfield and McCone Counties in Montana, USA. This geological section preserves fossil assemblages crossing the end-Cretaceous extinction at 65.5 mya, an event which some multituberculate species survived. We photomicrographed a consistent wear facet on upper first molars of *Mesodma* and *Cimexomys*. Qualitatively, the most common patterns of wear within each taxon vary between Cretaceous and Paleocene individuals. Microwear on Cretaceous individuals often consists of short scratches and frequent pits, with the anterior edge of individual cusps often chipped to form a ragged edge. Microwear in Paleocene individuals is characterized by longer, parallel scratches, most of which extend beyond the edges of individual cusps, and the cusp edges themselves are sharp. Many fine, parallel scratches are also present. In the species *Mesodma thompsoni*, for which we have the largest sample thus far, differences in feature length and orientation are significant at $P = 0.05$. These results suggest that multituberculate diets changed across the K/T boundary, possibly to include tougher foodstuffs. Available foodstuffs may well have changed, considering the contemporaneous floral turnover in this region, and it has long been hypothesized that generalized diet could have increased likelihood of survivorship. This is the most direct evidence of dietary change in a surviving species reported to date. Alternatively, some of the difference may be attributable to increased ingestion of fine grit, as the Paleocene part of this section includes multiple tonsteins.

The Red Royal Family and Phenogenetic Evolution

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The choreographed dance of development was important evidence for Darwin's ideas on evolution, but after Darwin, competition among adult individuals became the centerpiece of life for much of biology. Resemblances of related embryos were accepted as supporting evidence, but perhaps partly due to Haeckel's recapitulation enthusiasm, the protected embryo was displaced by the armed gladiator. The notion of life-as-competition has been likened to the Red Queen's endless struggle to stay in the same place in the Darwinian arms race. In Lewis Carroll's *Through the Looking Glass* that view is widely accepted and taught as *the* formal theoretical basis of life. Evolutionary theory rests on a few simple assumptions about the processes of history, to account for genes and their variation. But those principles say very little about phenogenetics, that is, what genes actually do to construct the organisms that carry the genes into the battle for survival. Research in developmental genetics has made it possible to formulate a few basic phenogenetic principles that are analogous to those of evolution. These principles concern the role of genes in differentiation within and among organisms, unify broader areas of biology than evolutionary principles alone—and they also contain surprises. Most notably, perhaps, is that life is a royal family, not just a Queen. Cooperation probably explains more about the nature of life than competition, and getting along competes with getting ahead in life.

Morphology of the Jaw Apparatus of *Oryzias latipes* in Comparison to Its Relatives (Teleostei, Atherinomorpha, Beloniformes)

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The taxon Beloniformes represents a heterogeneous group of teleost fishes including distinct forms as ricefishes (Adrianichthyidae), flying fishes (Exocoetidae), halfbeaks (Hemiramphidae), needlefishes (Belonidae), and sauries (Scomberesocidae) which show an extraordinary diversity of their jaw morphology. The rice fish, *Oryzias latipes*, is an important model organism in genetics and developmental biology. Beside the monophyly of Beloniformes, the relationships of its major taxa are disputed resulting in the proposal of several conflicting phylogenetic hypotheses. In order to investigate the contribution of cranial soft tissue elements to this debate the morphology of the jaw apparatus of five representatives of Beloniformes and four related species was analyzed comparatively. Furthermore, a 3D-reconstruction of the cranium of *O. latipes* was performed to identify anatomical details of the complex jaw apparatus. The 37 cranial soft tissue characters described in this study were mapped onto the alternative topologies and supported at best the monophyly of Beloniformes. Although *O. latipes* shows numerous autapomorphic characters, Beloniformes are characterized by a derived reduction of the intramandibular portion of m. adductor mandibulae and the specific course of truncus maxillaris, which separates near the jaw joint. Within Beloniformes a sister group relationship of Adrianichthyidae to a clade consisting of ((Exocoetidae + Hemiramphidae) + (Belonidae + Scomberesocidae)) is supported by the reduction of the external section of m. adductor mandibulae and the shift of the m. levator arcus palatini origin to the sphenotic. These different observed characters could be correlated altogether to the reduced mobility between the elongated beak-like jaw bones evolved within this group.

Tail Autotomy and Regeneration in *Sphenodon* (Reptilia: Rhynchocephalia): Morphological, Functional and Evolutionary Aspects

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Morphology, function and ecology of tail autotomy and regeneration are less known in Sphenodon (Reptilia: Rhynchocephalia) than in lizards. We examined the tails of 188 museum specimens (both species) and 19 wild *Sphenodon punctatus*. Unlike in most Squamata, the relative length of the intact tail was equal in males and females and tail growth was isometric with body length. Sexes had equal frequency of regenerated tails. The autotomous tail usually but irregularly broke by intra-vertebral autotomy. This was usually but irregularly followed by ablation of a variably-sized terminal piece of vertebra, in partial deviation from these processes in lizards. Hypothetically, tail autotomy in *Sphenodon* is imperfect due to its early evolutionary stage. As in lizards and snakes, left-biased asymmetric *S. punctatus* individuals showed more tail injuries. In *Sphenodon*, morphological asymmetry associated with asymmetry in digit injuries at the individual level (from lizards known only at population level). Tail-losing individuals had higher fluctuating asymmetry; they morphologically differed from tail-retainers ("Seligmann effect"), but their exclusion did not facilitate the distinction between the *Sphenodon* species. We tested correlations, heeding developmental constraints by a method derived from phylogenetic contrasts; in *S. punctatus* the extent and direction of sexual morphological dimorphism paralleled the extent and direction of differences between tail-keepers and tail-losers, females resembling tail-losers. The association of morphotype with the occurrence of tail injury was gradual; the variation in the location of tail injury was correlated with the continuum of variation between injured and intact (pholidotic) morphotypes. These last two phenomena remain to be explored in lizards.

Cranial Capacity and Insular Dwarfism: A Case Study of the Extinct Dwarf Hippopotamuses from Madagascar

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The effect of insular dwarfism on the brain size of island mammal species relative to that of their mainland ancestors is a matter of debate. Although it is generally accepted that a reduction in body size within a mammalian species is usually associated with relatively little brain size reduction, reflecting the early completion of brain development, it remains unclear whether the insular dwarfing process follows this trend. Most dwarfed island mammals are extinct and incompletely preserved, accounting for the dearth of empirical data previously known. Measures of cranial capacity have been taken from up to 50 well preserved crania of the Malagasy dwarf subfossil hippopotami, *Hippopotamus lemelei* and *Hippopotamus madagascariensis* and from a complete postnatal ontogenetic series of dry skulls of the probable ancestor, the extant mainland *H. amphibius*. Results from a comparative morphometric analysis of growth in the larger mainland hippopotamus and the two dwarf species are presented. A hypothesis of ontogenetic scaling is evaluated in the

context of the reduction in both brain and overall skull size of these dwarf species. In light of the current controversy over brain size reduction in the putative dwarf hominin *Homo floresiensis*, studies of other mammalian analogues such as the hippos, with larger samples and ontogenetic series, are likely to be informative on mechanisms of dwarfing in mammals.

Toward a Greater Appreciation of Adapiform Biodiversity: A Geometric Morphometric Analysis of Lower Molar Shape

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As we approach the 200th anniversary of what would become recognized as the first adapiform primate discovery by Georges Cuvier, paleoprimatologists continue to struggle with methods to accurately pose hypotheses regarding biodiversity of European, North American, and Asian adapiforms. These questions take on even greater significance as data from embryological studies suggest the determination of relative cusp location and formation is one of the earliest processes in tooth development. This study provides the most current and broadest comparison of lower molar shape between fossil adapiform material from Eocene and Miocene deposits spanning three continents and extant primate (lemurs, lorises, and *Tarsius*) and non-primate outgroup taxa (*Tupaia*). In considering the relative orientation of major molar landmarks (including major cusps and shearing crest intersections), it has been found that North American notharctines (*Notharctus, Smilodectes*, and *Cantius*) differ significantly from their European adapine counterparts (*Adapis, Palaeolemur*, and *Leptadapis*). Whereas North American taxa appear to resemble African and Asian lorisiforms, European adapines exhibit similarities to Malagasy indriids. These results speak to the interpretation of dietary patterns in these fossil taxa and larger patterns of adapiform radiation. As significant (and somewhat surprising), are the results of shape comparisons between extant groups and smaller samples of Miocene Asian sivaladapids and European cercamoniines. Together, these results suggest a much broader perspective of biodiversity must be taken—should adapiforms continue to be categorized as simply "lemur-like primates"? This study suggests, no.

Coupled Locomotion and Ventilation in Mammals: What is the Primitive Condition?

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In this study, we investigated the loss of epipubic bones in eutherian mammals. Previously, we have shown that the epipubic bones and the abdominal musculature of two didelphid marsupials (*Didelphis* and *Monodelphis*) exhibit a "cross-couplet" pattern of activity that provides long-axis support of the body during locomotion employing symmetrical gaits. These same muscles, however, were shown to contribute to the expiratory phase of ventilation. These results were significant because they reveal a potential functional constraint on simultaneous locomotion and ventilation in mammals that retain the primitive condition (i.e., epipubic bones, the pyramidalis, and a linkage to the femora via the pectineus) of the earliest mammals and their cynodont ancestors. Here, we report on the activation patterns of the abdominal musculature in another metatherian (*Philander*) and two eutherians (*Atelerix* and *Rattus*) during resting ventilation and locomotion. Electromyography (EMG) was used to investigate muscle activation during rest and running on a motorized treadmill. Simultaneous high speed video (250 Hz) recorded limb kinematics and gait. Videoflouroscopy was used to correlate muscle activity and diaphragmatic movement. All species tested exhibit bilateral activation of the abdominal muscles during the expiratory phase of resting ventilation with some differences between the metatherian and eutherian taxa. This bilateral activity is superimposed on the cross-couplet activity of locomotion on all observed velocities of locomotion and symmetrical gaits.

Are Cartilage-free Areas at the Canine Ulnar Trochlear Notch Associated with Alterations of Subchondral Bone Geometry?

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Paired grossly normal elbow joints of 12 adult German shepherd dogs were examined in two sagittal slices using a non-contact 3D digitizer to determine, whether the presence of a cartilage-free area in the center of the ulnar trochlear notch denotes the antebrachium to form a deeper socket than in specimens with complete articular cartilage (as previously suggested in literature). The mean inter-observer reproducibility ranged between 0.03 mm and 0.05 mm, left-to-right variability ranged between 0.09 mm and 0.20 mm. Although not statistically proven for all reference points, the socket was slightly deeper in specimens with complete than in specimens with incomplete articular cartilage, whereas only minor differences were noted in the geometry of the corresponding humeri. Subchondral bone of the elbow joint was more congruent in specimens with incomplete articular cartilage. Cartilage-free areas might be required to form synovial reservoirs, whereas these could be redundant in specimens with complete articular cartilage because of a wider joint space.

Evolutionary Divergence in the Suction Feeding Mechanism of Fishes

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Recent studies have increased our understanding of suction generation during feeding in actinopterygian fishes; however, it was unknown whether the more basal sharks and rays use a similar mechanism. Buccal expansion and pressure was quantified during feeding in species from the three main groups of elasmobranchs: *Chiloscyllium plagiosum* (Galea), *Squalus acanthias* (Squalea) and *Leucoraja erinacea* (Batoidea). Gape area to hyoid volume ratios distinguish the strong suction capture mechanism of *Chiloscyllium*, from the moderate suction mechanism of *Squalus* and the predominantly bite mechanism of *Leucoraja*. Surprisingly, *Leucoraja* captures prey primarily by rapid bites coupled with weak suction. Moderate suction is used by all three species to process prey. The suction feeding mechanism in elasmobranchs differs from actinopterygians primarily in hyoid arch movements due to morphological constraints. During suction generation in all three species, the hyoid is depressed ventrally as in actinopterygians; however, at the same time the hyoid is laterally compressed. The jaw suspension of elasmobranchs contains fewer skeletal elements than actinopterygians and constrains the distal hyomandibulae to adduct when the basihyal is depressed. This causes a temporal and magnitude delay in peak pressure in elasmobranchs compared to actinopterygians in which lateral and ventral expansion of the buccal cavity permits a more rapid event. A novel finding is that *Chiloscyllium* is able to generate relatively large suction pressure and *Squalus* and *Leucoraja* generate more moderate suction pressure while paradoxically compressing the mouth cavity laterally. This represents a fundamental difference from the mechanism used to generate suction in elasmobranch and actinopterygian fishes.

Exploring Genotype-phenotype Relationships for Size and Shape Determination in Animal Development

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Despite the enormous progress of developmental genetics in recent decades, the elucidation of genotype-phenotype relationships in animal development has been uneven. Understanding the patterning of early animal embryos, in particular the specification and patterning of tissues and organs, has been the biggest success. In contrast, the genetic-molecular mechanisms that govern changes of size and shape during development have remained obscure. These two proceses, however, along with color patterning changes, are the ones of greatest relevance to morphological microevolutionary events. Thus, for evolutionary studies, getting to grips with the mechanisms that govern size (and proportion) and shape during development is of fundamental importance. In this talk, I will present a genetic network perspective for thinking about the genetic controls of these processes. For questions of size determination, both at the regional and whole body levels, some genetic network information is available for *Drosophila*. However, important differences in network organization for integrating patterning and size regulation between small-embryo and large-embryo (vertebrate) animals must exist. With respect to shape changes, the classical phenomenon of morphogenesis, some clues are provided by recent studies on gastrulation in *Drosophila melanogaster* and *Caenorhabditis elegans*, which may have wide relevance. The final part of the talk will focus on the evolutionary questions about microevolutionary morphological changes that this genetic network perspective raises.

A Preliminary Report on a New System for Recording Jaw-muscle Electromyograms From Free-ranging Primates

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In vivo lab-based studies of primate mastication describing jaw-muscle activity and mandibular bone strain provide the empirical basis for most evolutionary hypotheses linking primate masticatory form to diet. However, testing these hypotheses is problematic because data recorded in the lab often lack the appropriate ecological context for fully understanding masticatory function and performance. For example, rhythmic chewing in these studies is elicited using foods that may not represent the diets of wild primates. Because the textural and mechanical properties of foods influence jaw-muscle activity and the resulting strain patterns, chewing behaviors observed in the lab may not adequately reflect chewing behaviors of primates feeding in their natural habitats. Here, we present recent efforts to address this limitation of lab-based studies of primate mastication. Specifically, we developed a system for recording jaw-muscle electromyograms (EMGs) from free-ranging primates so that in vivo studies of primate jaw-muscle function can be conducted in the field. We used the system to successfully record jaw-muscle EMGs from mantled howling monkeys (*Alouatta palliata*) at La Pacific, Costa Rica. These represent the first EMGs recorded from a non-captive primate in the field. Further refinements of the system will allow long-term EMG data collection so that jaw-muscle function can be correlated with food mechanical properties in primates feeding freely in their natural habitats. In addition to furthering our understanding of primate feeding biology, this work will foster improved adaptive explanations for topics like the evolution of primate jaw form. Supported by NSF.

Skeletal Development of the Embryonic Leopard Gecko (*Eublepharis macularius*): A Real–Time Study of the Genesis of Gross Pattern and Its Correlation with Developmental Stages

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The Gekkota is a major early squamate radiation, with over 1050 described species. Major clades within the Gekkota are the Eublepharidae, Pygopodidae and Gekkonidae, the former generally regarded as a basal assemblage. Phylogenetic studies of the Gekkota based on morphological characters rely heavily on features of the dermatocranium, which has not been well studied from a developmental context, leaving open many questions regarding the homology of individual elements. It has been suggested that pre-hatching development may be a valuable source of phylogenetic information, but for the Gekkota little such information is available. We herein document the pattern and sequence of ossification of the dermatocranial elements of the eublepharid *Eublepharis macularius* (the leopard gecko), and correlate these to an embryonic staging sequence assembled in real time from embryos incubated under standardized and controlled conditions. We correlate this information with that available for other clades of lizards, and compare changes in shape and form to posit predictions about potential onset of skeletogenic pattern, and proportional changes that may be associated with rate changes and growth trajectories. This initial documentation is the first step in the compilation of a comparative data base of gekkotan head skeleton development, the assembly of which is directed towards investigation of variation in skeletogenic pattern that may be clade specific.

Evolving an On-board Flight Computer: Brains, Ears, and Exaptation in the Evolution of Birds and Other Theropod Dinosaurs

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Evolutionary studies of flying groups typically focus more on the aerodynamic components (flight surface, skeleton) than the sensorineural components (brain, senses). We examine the evolution of the brain and inner ear in Theropoda, using CT scanning and 3D-visualization. Specimens of about 100 species of fossil archosaurs and 50 species of extant sauropsids were CT scanned and analyzed, yielding the largest dataset of virtual cranial endocasts and osseous labyrinths. Sampling includes over 30 species of non-neornithine coelurosaurian theropods, spanning the transition to birds. Despite dense sampling, reconstructing this transition in detail is hampered by the lack of critical information on neural wiring in fossils. Nevertheless, many aspects of avian brain and ear structure are present in numerous nonavian coelurosaurs, and many "modern" traits are not encountered until well within the avian radiation. Mechanistically linking particular brain and ear attributes to flight has been problematic, and the reason now seems clear: many of these attributes did not evolve in a flight context, but rather were exapted in birds for the sensorineural control of flight. Controversy about whether some "nonavian" theropods may actually be secondarily flightless birds is relevant in that they display some strikingly avian attributes of the brain and ear. Likewise, the discovery of aerodynamic feathers in some nonavian clades raises questions about the inferred adaptive context. The evolutionary pattern appears complex: early aerodynamic experimentation may have contributed to the evolution of birdlike sensorineural attributes, and these attributes were subsequently exapted and honed during the course of the avian radiation.

Early and Late Vertebral Fusion in Atlantic Salmon (*Salmo salar*): Vertebral Bodies and Arches as Developmental Modules and the Lifelong Role of the Notochord

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Classically, the somitic mesoderm is viewed as the source of segmental patterning of the vertebral bodies. Ablation experiments in amphibians and birds and developmental studies on teleosts challenge this view and show that the notochord directs the segmental patterning of vertebral bodies. Spinal ganglia on the other hand determine the segmentation of neural arches. In fact, the independent segmentation of vertebral bodies and vertebral arches is required to construct the teleost caudal fin. In evolution and in development, fusion of vertebral body anlagen leads to multiple neural and haemal arches which become elements of the caudal fin endoskeleton. Fusion of vertebral bodies in teleosts is not restricted to early caudal fin development. We have followed vertebral fusion in other parts of the salmon spine and conclude that vertebral fusion can be initiated at any time in life. Although later vertebral fusion must be considered as pathological, the process shows remarkable resemblance to early vertebral fusion. Like early normal fusion, late fusion can be fully completed and result in the reconstruction of one regular vertebral body, yet with multiple haemal and neural arches remaining separated. Our results support the idea that vertebral bodies and neural arches are independent developmental modules and suggest a lifelong role of the notochord for keeping vertebral bodies separate in teleosts.

The Influence of Food Material Properties on Jaw Kinematics and EMG Activity in Humans

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Electromyographic and kinematic recordings and analyses of the granulometry of the food bolus are the main methods used to study mastication in man. They allowed to reach the following conclusions: 1) Physiological recordings have shown that the number of cycles, the muscle contraction and the vertical amplitude of the jaw movements are the variables that are the most concerned by adaptation to an increase in either the size, the hardness or a change in other rheological properties of the food mouthful. There is, however, a large variability between subjects in the mastication parameters. With aging, the number of cycles and the total muscle contraction in one masticatory sequence are enhanced but the ability to adapt to an increased hardness is not impaired. 2) The distribution of particle sizes in food boli collected before swallowing are very similar from one subject to another even if physiological parameters recorded during the corresponding mastication are very different. This suggests that subjects with healthy dentition have different strat-

egies to chew, each one being adapted to the individual cases. The goal is to obtain a safe swallow, i.e., that neither hurts the throat nor flows into the upper airways. The distribution of particle size differs, however, from one food to another. 3) The study of these parameters in specific populations such as the edentulous persons, the Down syndromes, the elders or the facial dysmorphoses leads to the distinction between a satisfactory mastication although the masticatory performance is decreased and an impaired mastication.

The Phylogenetic Significance of the Basicranial Articulations of Screamers (Anhimidae, Aves)

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In the last years, controversial discussion regarding the phylogenetic significance of the avian basicranial joints arose. Non-homology of two different kinds of basicranial articulations was proposed based on ontogenetic studies. 1. A diarthrosis formed between the endoskeletal basisphenoid and exoskeletal pterygoid, developing from an early quadratopolar commisure. Among birds, the Palaeognathae and Neoaves have such an articulation, which is probably homologous to the basipterygoid articulation of other amniotes. 2. A more rostral diarthrosis between two exoskeletal bones (parasphenoid and pterygoid) developing through secondary apposition of these bones, without any participation of the endoskeleton. This kind of a secondary diarthrosis, termed "rostropterygoid articulation", is known in Galliformes (fowl) and the anseriform family Anatidae (waterfowl). Based on the character distribution the rostropterygoid articulation was proposed as a synapomorphy of galliforms and anseriforms. However, this conclusion is disputed, because form and location of the basicranial articulations of adult screamers (Anhimidae, Anseriformes) is intermediate between rostropterygoid and basipterygoid articulations. To test for homology we investigated the ontogeny of the basicranium of a screamer (*Chauna sp.*) by using computer-aided 3D-reconstruction, build-up from a histological serial section. As a result, the screamer basicranial articulation develops exactly as in other anseriforms and galliforms by apposition of dermal bones (i.e., pterygoid and parasphenoid) without participation of the neurocranium. Our results confirm the hypothesis that the complex character "rostropterygoid articulation" is a homoplasy-free synapomorphy of Galliformes and Anseriformes, and reject the assumption that this new articulation type arose convergent within the Galloanseres.

Comparative Ontogeny in Mammals

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The use of ontogeny for clarifying systematic-phylogenetic relationships largely depends on the underlying organism concept. Although older authors such as Haeckel, DeBeer and others defined ontogeny as the complete life history, in practice they considered embryonic and adult stages as somehow antinomic: early ontogenetic stages were attributed specific values to clarify morphological issues. The specific quality of early ontogenetic features was addressed as palingenetic and was supposed to be recapitulatory in some way. In fact, such recapitulatory features normally represent plesiomorphic homologies, which may be helpful to design evolutionary scenarios; caenogenetic or apomorphic homologies were considered to be less useful for evolutionary morphology. However, what is plesiomorphic and apomorphic depends on the systematic level of argumentation. Inspite of theoretical incertainties, comparative ontogeny was very successfully applied to mammalian morphology since the 19th century. It was especially helpful in solving the fate of the branchial (including the Reichert-Gaupp-theory) and urogenital systems whose homologies are largely disguised in later ontogentic stages. We assume that all stages of ontogeny have principally the same potential to provide characters for designing phylogenetic hypotheses, and consideration of all ontogenetic stages enhances the chance to procure systematically valid characters. This contribution will discuss some more recent results from ontogenetic studies of mammals that proved to be useful for solving specific systematical problems of this group: Primate placenta, dental lamina and chewing muscles in rodents, epipterygoid-alisphenoid problem, scapular spine of therians and some others.

Limb Bone Loading in Salamanders During Terrestrial Locomotion

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Salamanders are often used as representatives of the basal tetrapod body plan in functional studies. However, little is known about the loads experienced by their limb bones during locomotion; previous studies of bone loading have focused mainly on animals such as mammals and birds with parasagittal limb posture. This study evaluates the loads on the limb bones of the tiger salamander (*Ambystoma tigrinum*) during terrestrial locomotion using three-dimensional measurements of the ground reaction force (GRF) and hindlimb kinematics, as well as anatomical measurements of the femur and hindlimb muscles. Peak GRFs acting on a single limb were about half the body weight of the salamander. The GRF is initially oriented posteriorly but shifts to an anterior direction later in the step, and has very little medio-lateral inclination. At the time of peak stress, the GRF is primarily vertical and perpendicular to the femur. Peak stresses were generally below 15 MPa, which is fairly low compared to observations from other vertebrate lineages. The peak stress was primarily associated with dorso-ventral bending, which may be partially due to a lack of activity in knee extensor muscles that span the length of the femur. Comparisons of stress magnitudes to mechanical property data for salamanders indicate their limb bones may have safety factors as high as 10 or more. Together with data from other amphibian and reptile lineages, these results suggest that low magnitude loading and high limb bone safety factors may have an ancient evolutionary history. Supported by NSF (IOB-0517340).

Using Food Material Properties for Defining Primate Ecomorphological Units

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Primates have faced a vast array of potential dietary resources throughout their evolutionary history and a range of adaptive responses have been the result. By quantifying the mechanical properties of primate diets we are better able to explain dietary niche breadth and morphological adaptation. Studies focusing on a community of six platyrrhine primates in Guyana and on *Cebus libidinosus* in Brazil reveal how food mechanical properties help to segregate species into ecological and morphological units, highlighting what species do best and improving our understanding of feeding niches. Those species that process the most mechanically demanding tissues with either the anterior dentition or cheek teeth also exhibit marked seasonal shifts in diet. These shifts include a higher percentage of tough masticated tissues (*Alouatta seniculus*), extraction of embedded insects and seeds (*C. apella*), palm fruit exploitation (*C. libidinosus*), and extraction and mastication of legume seeds (*Pithecia pithecia*). The importance of seasonal changes in dietary emphasis from weak to tough or stiff plant tissues in *A. seniculus, Cebus,* and *P. pithecia* suggests that masticatory features often identified as "specializations" may actually be niche broadening characters. These features permit the annual exploitation of a broad array of plant tissues that vary widely in mechanical properties, and may also account for larger geographic ranges. Although many factors play a role in the ability of a species to colonize and exploit new habitats, the ability to ingest a wide array of mechanically demanding plant and animal tissues appears to be a critical factor.

Structure and Function in Turtle Heart: What in vivo Imaging Teaches Us About Form and Function

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The turtle heart is grossly similar to that of many other reptiles. A large thin-walled sinus venous overlies the paired atria and large compartmental ventricle. The ventricle contains three compartments through which blood moves before going to systemic or systemic and pulmonary circuits via the three trunks of the great vessels. There is not a one-to-one correspondence between the compartments and the great vessels. While internal physiological probes and anatomical dissection identify potential blood flow and shunting routes, newer noninvasive imaging (fMRI and CT) combined with more traditional methods add additional information on the relationships of shuts (intra-cardiac, great vessels, and pulmonary, and peripheral) to ventilation and on the variation in some shunts. I will discuss the use of fMRI imaging to track real-time flow, perfusion, and

limited shunting from MRI. Newer fast computed tomography (CT) imaging for soft tissue and flow will be compared to fMRI imaging results to better understand the turtle five chambered heart. The results from the combined methodologies support the hypothesis that species that are deep divers differ in how their ventricular compartments function when compared with shallow divers and terrestrial species.

Relationships Among Dietary Diversity, Food Properties, and Masticatory Morphology in Lemurs

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Lemurs are a diverse group of strepsirrhine primates endemic to Madagascar. Their radiation is notable for its great morphological and behavioral diversity. We have examined differences in food properties among sympatric species in a southwestern dry forest site (Beza Mahafaly special reserve) and an eastern rainforest site (Ranomafana National Park). The two dry forest species (*Lemur catta* and *Propithecus verreauxi*) are more folivorous than their rainforest congeners. The three rainforest species examined are congeners (*Hapalemur spp.*) and all are bamboo specialists. At both sites, the species differ in their reliance on specific food parts throughout the year. We report on how food toughness translates into differences in food choice, behavior, and performance. Food toughness tracks subtle differences in diet throughout the year in sympatric species, and these differences appear related to reducing feeding competition. The dry forest species overlap in their mechanical dietary profiles, though *P. verreauxi* has a slightly tougher diet. The tough diet probably presents more of a challenge for *L. catta*, which, though possessing relatively long molar crests, has absolutely shorter crests than *P. verreauxi* with which to process a mechanically similar diet. Where their diets overlap on two bamboo species, the *Hapalemur* species concentrate on different parts. The largest species, *H. simus*, consumes the culm pith of the giant bamboo, which is the hardest, toughest, and stiffest food eaten. This difference in food toughness is correlated with differences in morphology and biting performance among the species.

Functional Bases of the Spatial Dispersal of Venom During Cobra "Spitting"

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Multiple lineages of cobras have evolved the functional and behavioral ability to expel venom streams, or "spit", at the face and/or eyes of vertebrate predators. The functional ecology of this unique defensive behavior presents several challenges to the cobra, including: 1) target distances that can exceed 2 meters; 2) a short (~50 msec) duration which seemingly precludes active correction; 3) a fixed exit orifice (the fang) which minimizes dynamic modulation of the venom stream; and 4) venom that is deleterious to the cornea but not to the surrounding skin or other tissues. Recent studies have shown that spitting cobras are quite accurate at targeting the area immediately around the eyes, but also that the spatial pattern of the spat venom is highly variable even between successive spits from the same cobra. The present study was undertaken to explore the potential relationship(s) between the variation in venom dispersal and the targeting accuracy, particularly within the context of the ecological challenges faced by the cobras. Anatomical examination of the internal morphology of the spitting cobra's fang revealed no obvious source of modulation or control of venom dispersal. Quantitative analysis of the electromyographic signals recorded from the muscle primarily responsible for venom propulsion (the adductor mandibulae externus superficialis) demonstrated no significant relationships with quantified features of venom dispersal. Using high-speed videography we demonstrate that the cobra performs rapid cephalic movements while spitting its venom, and that these movements are the main determinants of the spatial distribution of the spat venom.

Bite Force, Muscle Loading, Mandible Shape, and the Developmental Origins of Adaptation in Shrews

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A central question in evolutionary biology is to understand how complex phenotypes adapt to local conditions. Adaptation of complex traits requires modularity, or compartmentalization of larger traits into smaller integrated subunits, such that these modules are free to vary independently of one another. At the same time, strict patterns of covariation within modules may limit trait versatility in novel environments. Thus, given the requirement of modularity for adaptation, how can species experiencing fluctuating or novel environments adapt to local conditions? Recent theoretical work suggests that the constraining effects of modularity depend on how trait covariation arises through ontogeny, as persistence of modules across contexts should differ if trait covariation results from direct developmental connections (e.g., shared pathways or precursors) versus similar response to a common stimulus (e.g., genetic or environmental). Here, capitalizing on methods developed in studies morphological integration for distinguishing developmental and functional sources of variation in skeletal traits, I investigate the developmental origins of patterns of trait covariation in the shrew mandible by examining the relationship between mandible shape, musculature and function (i.e., bite force) in a species of soricid shrew.

Bicuspid Teeth of a Gecko, *Paroedura pictus*: Ontogeny of Cusp Formation

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Differentiation of teeth cusps is considered an essential factor producing complexity of mammalian dentitions. In mammals, it is linked to signalling activity of the enamel knot. However, little information is available on tooth cusp development in non-mammalian vertebrates where enamel knot of the mammalian type does not appear. We studied it in a gecko, *Paroedura pictus*, in which adult teeth are conspicuous for their bicuspid tips. With different techniques (total staining, histological analysis, SEM, TEM) applied to 60 embryos we examined particular stages of tooth development from its beginning at ED15 to the stage of early adult dentition (ED60). The adult type bicuspid teeth (pleurodontly ankylosed to bones) appeared as the third embryonal teeth generation after those of the 1st generation (superficial small conical teeth incomplete in enamel cover not ankylosed and soon resorbed) and the 2nd generation (small conical teeth with indistinct enamel tubercules instead of true cusps, rarely attaining an acrodont ankylosis). Cusp formation in the 3rd generation teeth begins at early bell stage with specific heterotopic histodifferentiation of IEE at the tooth tip. The cluster of axial cells abbruptly differentiated into mature ameloblasts producing a thin enamel layer. At the late bell stage their secretory activity apparently disappears while the neighboring cells of IEE differentiate into ameloblasts and the enamel they produce overgrows the axial complex in the form of well marked sharp cusps. We did not observe any structure corresponding to the mammalian enamel knot but believe that the axial complex may present a plesiomorphic arrangement functionally homologous to it.

Interactions Between *Hox* and *Gli3* Genes Control the Zone of Polarizing Activity and the Apical Ectodermal Ridge

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Vertebrate limb development depends on two signaling centers, the apical ectodermal ridge (AER), which provides the underlying mesenchyme with essential growth factors, and the zone of polarizing activity (ZPA), the source of the *Sonic hedgehog* (SHH) product. Work involving gain- and loss of function of *HoxD* and *HoxA* clusters in mice has emphasized their impact on both these embryonic structures. In addition, recent genetic evidence indicates that AER function depends on antagonistic interactions between posterior *Hox* genes and *Gli3*, a zinc finger transcription factor, suggesting that the latter product protects the AER from the deleterious effect of the former. In genotypes with increasing posterior *Hoxd* excess antero-posterior digit specification and proximo-distal limb patterning are affected progressively, such that limbs deviate from the standard stylopod, zeugopod, autopod pattern. Together, these data suggest that *Hox* collinear information is mediated by multiple signaling mechanisms to promote appendage growth and patterning.

Variability of Mandibular Form: Variance, Fluctuating Asymmetry and Integration of Deer Mouse Jaws

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One of the central aims of evolutionary developmental biology is to explain the variability of complex morphologies. Variability refers to the ability to vary and is an outcome of interactions between developmental and evolutionary processes. The mandible has emerged as a favored model system for studies of variability because this bone comprises multiple developmental units of both structure and process. It is particularly useful for dissecting the relationship between embryonic and variational modularity, which often differ. To explore the structure of variability we examine variation among individuals, fluctuating asymmetry (FA) and integration among parts in second generation deer mice (*Peromyscus maniculatus bairdii*) reared in the laboratory. We measured mandibles using landmarks plus semilandmarks that capture the curving shape of mandibular processes and alveolar regions. The dominant component of variation spans the entire mandible, relating changes in orientation of the condylar and angular processes to those of the incisor alveolus. Similarly the major component of variation in FA spans jaw processes and incisor alveolus. The spatial patterning of among individual variation and FA are significantly similar, although patterns of covariation are weakly correlated. Not surprisingly, variation shows a higher level of integration than does FA, but not in the alveolar region, where the two are equal in degree of integration. Our preliminary results thus indicate a complex hierarchical structure of variability, with highly integrated dimensions that span the entire jaw and other highly localized, weakly canalized regions. Both patterns are evident in among-individual variation and FA.

Reproductive Patterns in Amniotes with Special Reference to Mammals

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The different extinction and diversification of marsupial and placental mammals at the K/T-boundary can possibly be explained by the differences in their strategies of reproduction evolved in the late Mesozoic. Marsupial neonates are born after a short gestation with immature lungs, which allow only low metabolic abilities in the first weeks. In contrast, the placental neonates have well developed lungs, allowing a high metabolic rate and thermoregulatory capacity early in postnatal development. Hence, placental young are more resistant against environmental stress which means an evolutionary advantage under harsh conditions, e.g., at the K/T-boundary. Because neonates are the result of a feto-maternal metabolism, it is essential to understand which differences between the placental and marsupial type of placentation correspond to the developmental degrees of the neonates. The marsupial morphotype includes a superficial and diffuse placenta formed by the yolk sac. Until shell coat rupture the embryo depends on histiotrophic nutrition by uterine secretion. In late gestation the placenta invades the uterine mucosa in many taxa and hemotrophes become the main source of nutrients. In placentals, however, the stem species had a well developed compact, chorioallantoic, endotheliochorial, definitive placenta with labyrinthine feto-maternal interdigitation (Carter and Mess, 2006, pers. obs.). This type of placentation permits a more intimate contact between fetal and maternal blood system and an effective, hemotrophic nourishment of the embryo throughout pregnancy, which might be accountable for the advanced developmental stage of placental neonates.

Histone Deacetylase Inhibitor, Trichostatin A, Affects Gene Expression Patterns During Morphogenesis of Chick Limb Buds *in vivo*

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Epigenetic controlling and chromatin remodelling are involved in embryonic genesis and tumorigenesis. Acetylation is one of the key modifications to control gene transcription. HDACs inhibitor are considered to be among the most promising targets in drug development for cancer therapy. However, the basic aspects of what kinds of genes are more sensitive to the modification of acetylation *in vivo* are not fully understood. Spatiotemporal expression patterns of developmental genes are implicated in embryonic development. Taking chicken embryonic limb as an experimental model, we have investigated the reaction of a batch of genes in the limbs treated with Trichostatin A (TSA), a histone deacetylase (HDAC)-inhibitor. The results show that TSA (75 μM) changes the expression levels of the genes, which have important functions during limb development. Among then, *BMP4, SF/HGF* and *Twist1* were up-regulated; *BMP2, FGF8, Shh, Scleraxis, Myf5* and *MyoD* were down-regulated. In contrast to that, the *Pax3*, *Paraxis, Msx1*, *CREB,* and *PCNA* were still expressed at the same levels as controls. Increasing the concentration of TSA (>750 μM) can induce apoptosis and embryonic limb malformations. Our results indicate that chicken limb development can serve as a convenient *in vivo* model for studying the effect of HDAC inhibitors on gene expression. It may be useful for improving our understanding of the role of chromatin remodelling and epigenetic control of gene expression patterns and developing the drugs against cancer.

Sequence Heterochronies in Lissamphibia

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Variations in life history traits of lissamphibians is often correlated with modifications of developmental sequences. The larvae of anuran amphibians have undergone major adaptive changes (e.g., in feeding mode) in relation to many aspects of their life history. We analyzed the timing of cranial muscle development in larval lissamphibians from a comparative, phylogenetic perspective to investigate the role of sequence heterochrony in lissamphibian evolution. Three outgroup taxa (*Neoceratodus forsteri* and two salamanders) and seven ingroup taxa were investigated. The developmental timing data was analyzed quantitatively using the Parsimov technique. Parsimov is an event-pair and parsimony based method that can be used to interpret developmental timing data in a phylogenetic framework, and to establish the minimum number of heterochronic events. Our results corroborated previous observations that cranial muscles generally tend to develop from anterior to posterior. Especially the development of eye muscles is characterized by an unexpectedly high degree of heterochrony. Tentative results indicate that anlagen of the eye muscles in anurans develop simultaneously with the anlagen of the mandibular and hyoid arch muscles. However, interesting differences in the timing of eye muscle development occur within the pipidae. In *Xenopus laevis* these muscle anlagen develop earlier and in the closely related *Hymenochirus boettgeri* they develop later than the anlagen of the mandibular and hyoid arch muscles. In general, our results show more heterochronic events than expected, also in cranial muscles other than eye muscles.

On the Unique Deep Plantar Tendons Arrangement in the Foot of Piciformes (Aves): Its Possible Origin and Evolutionary Implications

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The monophyly of Piciformes sensu Wetmore (1960) has often been questioned. A strong argument for monophyly of the Piciformes is a unique arrangement of the deep plantar tendons of m. flexor digitorum longus (FDL) and m. f. hallucis longus (FHL) which occurs in Galbulidae, Bucconidae, Capitonidae, Indicatoridae, Picidae. In this arrangement the tendon of the second muscle supplies digits I, II and IV, while that of the first supplies only digit III. Scenario of the origin of such an important character of piciforms has not been revealed prior to our studies. We show that the best supported hypothesis is a derivation of an arrangement in question from an ancestral one, confined to the pool of ancient birds, ancestors of trogons, coraciiforms and piciforms. The unique piciform arrangement of deep plantar tendons is only partially explained by the acquisition of zygodactyly. It bears ancestral prezygodacyl features and cannot be functionally explained by climbing adaptations.

Characterization of Cow Long Bone Tissue

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Bone presents a specialized supportive tissue. Changes in bone structure leads to different diseases and there is no clear picture about the real health of the skeleton in agricultural animals. Aim of this work was the investigation of bone morphology and factors able to influence bone structure in healthy dairy cows. Materials and Methods. Humerus in five lactating cows was examined for native changes in slides prepared by Cutting-Grinding Technique and for growth factors BMP 2/4, FGFR. TUNEL was performed to detect cell death and for matrix degradation we used MMP2 and MMP9. Results. Bone showed thin trabecules with variable number of osteocytes. Osteones presented different diameter. Proliferation of connective tissue and small capillaries were seen in osteon channels. Regions with granular, basophilic substance demonstrated different density. Articular cartilage seemed not changed in routine sections. Few BMP2/4-containing cells were detected in cartilage of all animals and in main part of bone. Numerous chondrocytes expressed FGFR1, but few osteocytes of spongy bone contained these receptors. Apoptosis affected mainly chondrocytes. Both MMP mainly degraded cartilage. Variable number of osteocytes expressed these collagenases. Conclusions. Bone of healthy dairy cows demonstrates various number of osteocytes and diameter of osteones, different density, proliferation of connective tissue and small capillaries in osteon channels that proves regional osteoporosis. BMPs are expressed in articular cartilage and bone where they stimulate growth. FGFR, apoptosis and MMP more affect the articular cartilage. Apoptosis and degradation by MMP seem to correlate, but increased expression of FGFR indicates compensatory reaction of supportive tissue.

Olfactory Organs of the Mudskipper, *Periophthalmus barberus* (Pisces, Gobiddae)—Preliminary Morphological Study

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The olfactory organs of the mudskipper are located in the short preorbital area of the head. Each organ resembles a tube-like structure, running from the upper lip in an upward direction and widening in front of the orbital cavity into a spacious, rounded chamber. The organs communicate with the external environment by small nostrils located on the upper lip (inlet nostril) and under the eye sockets (outlet nostril). The diameter of the tube-like organ is approximately 0.3 mm in its lower part but is 2-3 times greater in the middle part. The surface of the non-sensory epithelial cells lining the inner walls of the organ is characterized by the presence of microfolds. The sensory olfactory epithelium is presented there in the form of islands located in the medial wall of the tube. In the lower part of a tube the islands are numerous and densely spaced, whereas their numbers gradually decrease in the upper part. The chamber-like widened section of the nasal cavity (near the orbits) lacks an olfactory epithelium, i.e., the olfactory rosette is absent there. The islands of sensory epithelium are small (60–140 μm in diameter). They are round or irregular in shape. The islands consist of flagellar olfactory receptor cells, sporadically cells with a single thick "giant flagella" and also common ciliary cells. The outlets of mucous cells are apparent in the non-sensory lining of the organ. Distinctive features of the anatomy of olfactory organs in the mudskipper include a tube-like shape and lack of an olfactory rosette, which can be perceived as adaptations for temporary forays out of the water environment. Supported by Grant BW/IZ/40/2006.