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 continues to evolve. 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 Natura, 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 huge 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 used in 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 allonemony, 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 thalamic areas 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.
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 model of development is not a single, but a fine picture of how the mosaic 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 Vertebrae: 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 “Baublán”, 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 ‘ostrocodomers’, 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 eurhynchopids. 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 usually reported that the cardiac outflow tract of the chondrichthians 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, ammopteriformes, and in some basal teleosts, an intrapericardial, nonmyocardial chamber, the bulbous 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 bulbous 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 bulbous arteriosus in phylogenetically advanced teleosts. The morphology of the teleosteans conus varies according to the structure of the ventricular myocardium. Nonetheless, the conus displays specific anatomic, histochcmical, and immunohistochemical characteristics that distinguish it from the ventricle. Embryonically, the conus arteriosus appears earlier than the bulbous arteriosus, yet it shows a negative allometric growth with regard to the bulbous. 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 valve.

The cthoptychian bulbous arteriosus is an elastic chamber, whose walls usually contain smooth musculature. In phylogenetically basal taxa, the bulbous 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 variations the bulbous 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 chondrichthians, 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 bulbous arteriosus of sturgeons and teleosts. Therefore, the bulbous 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 chondrichthyan 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 bulbous 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

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

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The heart of chondrichthians 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 usually reported that the cardiac outflow tract of the chondrichthians 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, ammopteriformes, and in some basal teleosts, an intrapericardial, nonmyocardial chamber, the bulbous 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 bulbous 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 bulbous arteriosus in phylogenetically advanced teleosts. The morphology of the teleosteans conus varies according to the structure of the ventricular myocardium. Nonetheless, the conus displays specific anatomic, histochcmical, and immunohistochemical characteristics that distinguish it from the ventricle. Embryonically, the conus arteriosus appears earlier than the bulbous arteriosus, yet it shows a negative allometric growth with regard to the bulbous. 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 valve.

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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 labeled with the fluorescein-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 derivatives are 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 splanchic 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 second heart field. This fact, together with the results of bulbus labelling mentioned above suggests that a second heart field might exist in chondrichthians 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.

II. Abstracts

Gait Analysis During Unsteady Locomotion

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The use of the fractal 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 gait depends from a common basic pattern controlling the coordination of the forelimbs (foreleg, FL), the coordination of the hindlimbs (hindleg, HL) and a relationship between them (pairleg, PL). During locomotion, the limbs are coordinated in time and space, thus three analogouse 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 gait 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 posterior ampulla was absent and the receptor cones of the posterior canals 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 HD46188.

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 up to only a few recent studies in e.g., silurids, PL. In an APS model, cantharid 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 specialization in catfishes: functional morphology of the trophic system in a hematophagous 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 post 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. Horned 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 and skin appendices, 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% identity among 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, play a role in patterning the jaw articulation, the role of the tgf-ß superfamily of signalling molecules in patterning the mammalian jaw articulation.

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

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The evolution of the novel mammalian jaw articulation, the squamosal-dentary or temporalomandibular joint, has resulted in an increased complexity and modularity of the dentary bone, reflecting the multiple roles it now fulfills 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 patterning 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, play a role in patterning the jaw articulation, the role of the tgf-ß superfamily of signalling molecules in patterning the mammalian jaw articulation.

**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 processes: a caudolateral ‘external trochanter’ and a medial ‘internal trochanter.’ This arrangement has been retained with little modification by most members of the Euarchiptilia excepting some of the more derived Archoosauriformes, 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 archosauromorph fourth trochanter has been interpreted as a novel structure characterising a major clade, but this current orthodoxy 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 myological utility of femoral trochanters.

**A New Stem Batrachian (Tetenospondyli: Amphibamidae) from the Lower Permain of Texas**

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The on-going controversy over lissamphibian 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 for the tympanic cartilage, closely approaches the orbital margin. There are 14 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 “3+3-3-4-3.” 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 Amphibamidae (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 branchiosaurids, 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.
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: Zarelyus 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), Zarelyus and Chaetophractus vellerosus have 2 or 3 bands of dehydrocholic acid, while the other species have 1 or 2. Zarelyus 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, C. vellerosus and C. villosus because it has no X2. Priodontes is the unique species without deoxicolic acid and differs from 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 Xenarthra and may have impact on future studies about the conservation and the ecophysiology of the group. This study was supported by UNS, PGI 24/0812, ANPCyT-BID 1728/OC-AR-PICT 074/03 and CINUSAs, 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 in situ hybridization, we demonstrated 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 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 multivertebrae 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 multifidis and the longissimus muscles numerous morphological subunits along the cranio-caudal axis could be identified. The spatio-temporal activation pattern of the multifidis 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 multifidis and rotatores muscles seems to be conservative in consideration with 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 Eremtemum 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 Eremtemum by comparing its skeletal anatomy, particularly that of the auditory region, to that of other afrotherians that are semiaquatic (e.g., potamogaleses), terrestrial (e.g., Tenrec), and semi-arboreal (Echinos). Skeletal adaptations that may correlate with ‘sand-swimming’ are investigated both in extant and fossil insectivoran-grade afrotherians. The well-documented case of the well-known marsupial mole Notoryctes lives in a somewhat similar environment as Eremtemum, 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 is generally conservative in Didelphididae, but within the more diverse Didelphidae, variation is related to a combination of factor A—sexual dimorphism; B—after conspecification of the oocyte envelope, the follicular cells multiply and invaginate the vesicle, thus becoming phagocytic; 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 follicles shrivel and become denser; the follicle cells do not invade the follicle, and finally the follicle collapses. Types II and III were observed mostly in previtellogenic oocytes.

**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, Pau-citucerulata 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, Metachirus, some Monodelphis). Within Didelphidae, relative warps separate Caluromyines, Didelphini and smaller taxa, except for Chironectes scapulae, being more similar to marsomorphs. 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 taxa clustering into similarly shaped scapulac regardless of locomotor preferences.

**Aerodynamic Importance of Variation in Aspect Ratio of Bat Wings**

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Bat wing morphology varies greatly among species. Traditionally, the fusion 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 coracocostal joint contribute the majority (63%) of fore-arm movement; the glenohumeral joint provides only 34%. (2) General kinematic patterns of the coracocostal and glenohumeral joints are similar to those described in the literature for varamid 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 studies attempting to use articular geometry to assess joint ranges of motion in extinct archosaurs.

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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. On extant fishes, however, has shown that dental microwear varies according to how and where individuals feed (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 at different levels of feeding 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 in the area of 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 searched with terms and terms that cover: time period, location, habitat, basic taxonomy, life events and behaviour, each of which can be structured hierarchically. 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 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 vomerofactory behaviors (used for collecting chemicals): Eublepharis macularius (terrestrial) and Pseudemys scripta (arboreal). These gekkotans occupy very different ecological environments, in which water may be either very abundant (rainy season—Pseudemys) 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 hyobranchial are recorded 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 Cuciformes, Columbiformes Picinae and a disparate group of ground birds clearly shows that the radius of curvature scales allometrically (∝ 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 Falco concolor 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 kinematics of jaws and hyobranchial is observed with the time 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 Australolophites Pelvic Morphology (stw 431 and stts 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, Australolophites 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 three species were coexisted with A. africanus in Sterkfontein. Digital models created from CT-images of original fossils allowed us to obtain
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 Iguanidians

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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 dermal membranes, the fascia and musculature 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 transversospleninals 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 cuccularis group to the rectal 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 transversus abdominis fasciculi deriving from the internal abdominal muscles is synapomorphic within Squamata. Several parts of Iguania apomorphically share with Autarchoglossa a portion of the lateralis superficial to the obliquis 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 the high cost 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 hypodont cheek teeth has been caused by rich-in-grass diet. However, high hypodontodonty levels are not necessarily synonyms of grazing habits. Actually,
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Many quadrupedal animals use paddle-like mechanics to exchange kinetic energy (KE) and potential energy (PE), thereby reducing muscular work required for walking. Pendular mechanics are well characterized in cursorial animals, but are poorly understood for less cursorial animals. The "stealthy" walking style of cats provides a good contrast to this paradigm. We collected kinematic and force data for five adult cats. Using these data, we calculated the phase relationship of peaks in KE and PE, 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 cursorial 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 Unguuals in the Astylosternidae

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Many aspects of bone function have the potential to change through evolutionary processes. 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 another 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 distinctly stiff only among their close odontoceline relatives, and generalized least squares reconstructions of ancestral antler modules that show that moose have diverged significantly from their ancestors. Finally, experimental comparisons of functionality 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 digitized 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 (363-360 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 (digital 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 models, 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 most of the mesopodium. Hoxd13 is a gene involved in polarizing the anterior to posterior (thumb to little finger) axis of the developing hand most of the mesopodium. Hoxd13 is a gene involved in polarizing the anterior to posterior (thumb to little finger) axis of the developing hand most of the mesopodium.

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 wayniensis (Pteraspidiformes: Heterotractus). Flow visualization along a generic 23-cm, anatomically exact model of the fish was made in a wind tunnel, tapering colored gas (propylenylc glycol 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-
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 morphologi- cal and molecular studies. In most recent morphological phylogenetic analyses including the higher-order phylogeny of modern birds by LIVE- zey 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 (rhinos) plus Struthionidae (ostrich). In most molecular works the Apterygidae group with the Dromaiidae plus Casuariidae, and the Rheidae and Stra-thionidae 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 paleognathous 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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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, endo- dermal, and mesenchymal epithelia are similar. The main function of kera-tins is the formation of tonofilament bundles of the cytoskeleton in combi-nation with other microfilaments and filament-associated proteins. The ker-atin 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. Keratin genes are 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, paleontol- ogy, and development are poised at the edge of a revolution in our abil- ity 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 resolu-tion of these methods and made them suitable for use with developing embryos as well as larger specimens. Improvements in labeling techni-ques 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 rotoscopy’), 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 particular difficulty 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 = 115; 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 Euphractini. This larger clade then formed an 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 selection 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 Cineradiographic 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 hypotheses 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 thoracic 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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1Mathematical Modelling of Breathing Parameters in Birds and Sauropod Dinosaurs

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Ontogeny and Homology in Fishes
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Instead of using Snout 2, index 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 Snout 2 is inconsistent with a proposed role as a repressor of tooth formation. Instead, Snout 2 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 Rostro-Caudal 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 cranial and vertebral vertebral systems. 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.

Molecular Control of Successional Tooth Formation in Snake
Marcela Buchtolová,1 Gregory Handrigan,2 Town Liam,1 Katherine Fu,1 Molecular Control of Successional Tooth Formation in Snake
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Marcela Buchtolová,1 Gregory Handrigan,1 Town Liam,2 Katherine Fu,1

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 Indotostomus, the phylogenetic position of which depended largely on the correct interpretation of its body armour formed by bony plates. Ontogeny reveals that this armor is formed from two different ontogenetic sources, endoskeleton and exoskeleton, and thus resembles that of gasterosteids, and not synagnathoids 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 EcSox17, 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. 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, mero- blastic 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 snail 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. 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.

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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 salatorial mammals. Therefore, we ask: whether or not particular pathways that connect variation in morphology with variation in performance and also show how these interact to influence fitness. Here, I present 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. In this paper, we present measurements of in vivo strains from femora of turtles (river cooters, Neoremys concinna) have shown moderately high strain magnitudes. To study the evolution 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.

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. Here, we present measurements of hindlimb 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. 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 address this gap by incorporating 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 correlation that characterizes species of Anolis 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 correlated traits, that 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 yawn mediad relative to the proximal end of the tibiotarsus. The yawn 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 yawn 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 the yawn 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 (stygopod, 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 size. A key role for the mouse (Mus musculus) and Mongolian gerbil (Meriones unguiculatus) in the evolution of the limb bone length is suggested by the observation 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 Neoreomyos australis (Rodentia, Caviomorpha, Dasypodidae) from the Miocene of Patagonia
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The postcranial skeleton of the extinct Dasypodidae has not been evaluated from a functional-adaptive perspective. Morphofunctional analy-
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 the 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 cellsGoodrich’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 those paired (later fusing) condensations representing the basibranchials. In the extinct placoderms, paired median elements are preserved in several taxa. New evidence from Coelacanthus melichari (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 NC interpretation. The presence of anual 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, Siharanu tropicalis, Pseud hymenochir us merlini, Hymenochi rus 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 of unipalpids was measured relative to the body as well as the hyoid itself. Some derivatives of the hyoid, but is also affected by flexion of the pectoral girdle. The hyoid is positioned posteriorly further posteriorly in pipids than is typical for anurans, but maintains the same spatial relationship with the posterior buccal expansion. 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 running and economical locomotion differ from the demands of aggressive behavior in ways that may prevent simultane-
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 determined 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 Xerarthra

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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 Xerarthra, nothing is known for sloths and anteaters, but we demonstrated that the armadillo has a haemostatic 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 Xerarthra. 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., the 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 Naturphilosophen 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 guamanensis 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 stimsoni 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. guamanensis would be dominated by fast, white muscle fibers whereas S. stimsoni would exhibit more, slow red muscle fibers. Furthermore 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. guamanensis tail musculature was dominated by white fibers while juvenile S. stimsoni 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 during 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 Axl2/Hox: 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 Approach to Multivariate Ontogenetic Allometry in Birds

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Multivariate 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 characterized with longitudinal measurements of the head (e.g., eyes and beak), body (length, width), and skeletal structures 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 HH 33 and posteriorly. 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. non-cursoriality), and maturity patterns within the allometric-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 anterio-posterior axis into polysonal 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-tomes 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 Ostechthyian Fishes

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Ever since the birth of comparative anatomy, ostechthyian 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 (Chenet et al., 2007, Cybium, 31(suppl.) in press). Consequently, we have experimented using different modern techniques of medical imaging of ostechthyian 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 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 multiclorus*. We examined the plasticity in response to alternative oxygen environments for fishes from three habitats in Uganda that differ in terms of stability and dynamics and genetic admixture. 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.

### 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 multiclorus*. We examined the plasticity in response to alternative oxygen environments for fishes from three habitats in Uganda that differ in terms of stability and dynamics and genetic admixture. 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 developmentally-independent modules allows for somewhat independent evolution of different regions of the cranium. The co-inheritance of 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 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.
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 phenomenon are known from various primates and birds. 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 genera (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. Interindividual 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 used to advanced forms such as Megangerion 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 Ballalones-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 in symphysis, where the symphysis forms a much less inclined angle to the mandibular rami 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 Feline 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, Malayian 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 derived anatomy accompanying the large ecological diversity appear to be a combination of a rather short phylogenetic history, since the Ursine derived anatomy accompanying the large ecological diversity appear to be a combination of a rather short phylogenetic history, since the Ursine derived anatomy accompanying the large ecological diversity appear to be a combination of a rather short phylogenetic history, since the Ursine derived anatomy accompanying the large ecological diversity appear to be a combination of a rather short phylogenetic history, since the Ursine derived anatomy accompanying the large ecological diversity appear to be a combination of a rather short phylogenetic history, since the Ursine
nary abnormality. The patient had prolonged exertional chest pain probably related to myocardial ischemia. The ECG revealed anterolateral dynamic T-wave changes and echocardiographic examination showed severe systolic 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 Microscope Study of the Lingual Dorsal Surface in Dasypodidae

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Filiform, fungiform, and circumvallated papillae are distributed over the dorsal mucosal 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, Chacoerphactus vellerosus and C. villosus, using scanning electron microscopy. The pieces of lingual tissue were fixed in dilute 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, the only living archosaurs, lack the anatomical and functional features characteristic of crocodylians and have fully ossified rather than cartilaginous sternal ribs. The relatively highly constrained skull and 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 occurring 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 groups 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 development stability. Here we explore the divergence in integration patterns between parental populations. The difference in strength of
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 placental. In each of three major lineages (Shima, 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 tyloponds 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 computer programs will be 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.

Comparative Anatomy in Exhibitions
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Comparative anatomy was created by Georges Cuvier in the Natural History Museum, 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 transmitted 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.

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 mastatory system. A composite study of four primate genera 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 mastatory systems relative to the other members of their clade. These trends include a taller mandibular corpus and symphyssis, a taller mandibular rami, 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 evolutionary processes, but also provides a framework for future research on the functional morphology of primate skulls.
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 morphogenetic 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.

**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 oculomotor 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 signaling. It 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 signaling. This has been tested by comparing the spatial arrangement of the extraocular muscles and semicircular canals during ontogeny, but that, in most cases, there is little realignment beyond the fetal period.

**Resting Metabolic Rates, Bone Growth Rates and Bone Tissue Types in Annmotes**
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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 evolutionary differences and metabolic rates 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 anniates. In some species of our sample (Chelonia and Lecitcyclidae), 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 human postures 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 sylvestricat) 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 temporals 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 gap angles and bite points.

**Tooth Attachment Complexity in a Cretaceous Mosasaur**

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Vertebrate teeth are attached to jaws by a variety of mechanisms, including mastication, 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 ICVM-8 ABSTRACTS 1063

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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-0232626 is gratefully acknowledged.

The Musculoskeleton 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 (myoseptum and skin) and of red muscle in *Anguilla rostrata*, focusing on the interactions 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 (myohyphoid 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 compac-
tum perpendicularly. These fiber bundles are evenly distributed along the insertion line of the myoseptum. Red muscles insert into lateral and myohyphoid 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 hori-
zontal septum. We find that based on internal morphology eels are sim-
ilar to subcarangiform swimmers but different from carangiform swimmers.

Enameloid/enamel Transition Through Successive Tooth Replacements in *Pleurodones walli* (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 (posi-
tion 1), from late embryos to young adult *Pleurodones walli*. 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 den-
tin. Enameloid, like enamel, mineralizes and then matures, but amelo-
blast 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 matura-
tion. Our data suggest that there is no enameloid/enamel transition but, rather, an enameloid/dentin transition, which seems to result from a pro-
gressive 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 tooth mor-
onomy, or on functional causes, especially the speed of cortical accretion? The Varanidae, a monophyletic clade (one genus, 9 subgenera, 53 spe-
cies) 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 (frontal and fibula) differing by the absolute growth speed of their dia-
physseal 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 basi-
cally dependent on specific size, not on taxonomic frames; b) vascular density reflects the absolute growth rates of bone cortices; c) the orienta-
tion 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 glypto-
donts, similar to big armadillos, and ground sloths, terrestrial relatives of the extant tree sloths. Recently, palaeobiologists have paid special atten-
tion to their unusual traits. These odd features make it difficult to under-
stand 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, regressions are tautomorph patterns of 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 extinct 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 (Perisodactyla, Artiodactyla and Xenarthra) and size groups (0–20 kg, 20–300 kg and more than 300 kg). Only five equations have a homogenous error among the aforemen-
tioned groups. These were applied to 6 extinct species. A body mass of 80 kg was estimated for *Propalaeeoplophorus australis* (Cingulata: Glyptodontidae); 50 kg for *Barychirus capensis* (Phyllo-
phaga: Mylodontidae), and 3550.7 kg for *Lestodon armatus* (Phyllo-
phaga: Mylodontidae). High scatter in body mass estimates is observed for the remaining species: *Catanus tarjensis* (Phyllophaga: Mylodonti-
daem!), *Thalassomys nutans* (Phyllophaga: Megatheridae) and *Pronotho-
thereus typicus* (Phyllophaga: Megatheridae). This could be due to dif
erent specializations.

The Association Between Mandibular Shape and Habitat in Ungulates Analyzed 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 Procrustes 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: Scelidotheriidae)
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The taxonomy and anatomy of Brazilian scelidotherien 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 scelidotherium species were present during the Pleistocene. Writing early in the 20th century, H. Winge agreed with Lund’s conclusions. However, this view of scelidotherium 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 scelidotherium 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 scelidotherium species was erected on remains from Piauí, Brazil. However, abundant and well preserved material recovered over the past decade leads to a reassessment of Hoffstetter’s opinion and the validity of the Piauí 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 scelidotherien, and belong to one or the other of the scelidotherium species originally recognized by Lund. The species recently described from Piauí is, similarly, a synonym of one of Lund’s species.

On the Status of Megatherium (Pseudomegatherium) tarjiense (Xenarthra: Megatheridae)
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Knowledge of the history and anatomy of megatherian 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 category is Megatherium (Pseudomegatherium) tarjiense Gervais and Ameghino, 1880, which is based on a complete but eroded calcaneum from the Pleistocene of southern Bolivia. Most modern authors of the past century viewed this specimen as a poorly defined and probably a synonym of Megatherium (Megatherium) americanum. Confusion over the status of M. (P.) tarjiense 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.) tarjiense is indeed valid. This material includes abundant remains from the Tarjia 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.) tarjiense 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 application of these methods and 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 mineralization (involving purely physiochemical 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.

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Towards a Classificatory Scheme and Nomenclature of 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 coted or used for abutting structures for centuries. Nomenclature implies stability over time. 2) Bone and bones. Tissue classification/terminology should address their proper hierarchical 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 description allows us to express similarities: study 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 clyclic 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 mineralized layer of 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 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. intertransversalis, 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 protruding 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 an 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 Paleozoological Reconstruction of Procervulus (Artiodactyla, Cervidae)
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Attempts to reconstruct the diet from an incomplete and potentially biased collection reveal insights into the evolution of the diet and 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 assess the dietary preferences of samples from the intramountain basins of the Iberian Chain which cover a temporal interval between 19.3 to 13.75 million 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.

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 its 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 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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Tooth, 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 has 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 these signal molecules which are used repeatedly 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 patterns which 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.

The Amphibian Ancestors Came from Fresh Water – Considerations Based on Renal Development
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Anemone canidens, the desert species of penguins, were analyzed in a phylogenetic context using comparative methods. We found no relationship between...
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 vertebrates 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 fossilremaindersof 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—for some species 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 properties, and we have used these properties to develop a new metric 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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Carnivorous 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 stages of early odontogenesis in 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 ceratobranchial 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 interfaces 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 mediadally 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 paraflex of the superficial masseter. The tendon of the paraflexa 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 dega (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 infra-orbital 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 to 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.biome.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 temporal EMG data were collected and calibrated to masticatory force using a force transducer. Commumination (fragmentation) performance was assessed using particle-size analysis of unswallowed boluses. Results from preliminary experiments indicate that processing affects masticatory performance differently depend-
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 chondrichthyan 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 stylodermum 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 variation in strain magnitude in each species, the correlation 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-montcalliculatus) 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 stridulatory sounds among species were found investigated by models representing 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.

Voxel-based Finite Element Analysis—Working Directly with Microscan 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 involved in biomechanical analysis 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 ecologically 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 luteovenstii Gervais, 1859 from Usclas, Lodeve basin, Southern Massif Central, Southern France. Erected by Gervais (1859) and briefly redescribed by Theyvenin (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 anapsid. Aphelosaurus is documented by a unique but well preserved postcranial skeleton housed in the MNHN collections, Paris. The holotype shows gracile (elongate and narrow) forelimbs and limbs. The ribs are relatively short, slender and curved. The last phalanges 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 aecoselid. A phylogenetic analysis of most of the representatives of the Permian annectes, including Aphelosaurus, tests this hypothesis. Several phylogenetic analyses of this gracile skeleton are also proposed to test different scenarios on the locomotion of Aphelosaurus.

Molecular Insights into Evolution of the Gastrointestinal Tract
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Gasulation 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 endoderm 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 predate 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 americum 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 xerarthans have been viewed, for example, as one of Nature’s oddest anatomical experiments, as climatic indicators, 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 trends have been added to the list, including investigations into their trophic and locomotor 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 xerarthans have been conceptualized and focus on recent research that has altered our interpretations of their palaeobiology. This historical parade passes from the Barón’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 clumping, tank-like doths 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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1Department of Biology, 257 South 1400 East, University of Utah, Salt Lake City, UT 84112, USA (farmer@biology.utah.edu), *1Utah Artificial Heart Institute, 803N 300W, Suite 180, Salt Lake City, UT 84103-1414, USA
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 arterial system in 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 coronaryigenetic process.

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A Peculiar Osseification of the Skull of Neosclerocephalus Paula Couto, 1957 (Mammalia: Cingulata) Juan Carlos Fernicola,1 Néstor Toledo,1 Sergio F. Vizcaíno,2 and M. Susana Barto2, 1Sección Paleontología de Vertebrados, Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”. Buenos Aires, Argentina, 2División Paleontología de Vertebrados, Museo de La Plata, La Plata, Argentina (vizcaino@fcnym.unlp.edu.ar) In glyptodonts many structures of the skull are obliterated during ontogenetic development, hindering the recognition of the different bony elements that compose it. A detailed analysis of skulls assigned to different glyptodonts 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 Neosclerocephalus 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 with the paries nasi projects medially into a fold that expands within the tectum nasi. A longitudinal depression between the latter and 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 following structures are assigned to the cartilago viscerum: the extended turbinal (marginoturbinal?) and medially a plate that possibly represents the processus superioris alaris.

Walking and Climbing on Small Branches: Convergent Solutions in Chameleons, Marsupials, and Primates Martin S. Fischer, Karin E. Lilje, and M. Schmidt, Institut für Spezielle Zoologie und Evolutionbiologie, Friedrich Schiller Universität Jena, Erbstrasse 1, D-07743 Jena, Germany (Martin.Fischer@uni-jena.de) 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 quadrupedism 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 Laura Catherine Finton, University of Liverpool, Liverpool, UK (lcf@liv.ac.uk) 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 skeletal changes in a species tolerant of a varied diet. More than 200 landmarks were chosen to represent craniofacial geome-
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 speciose 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 the allometric growth period concerns each character in attainment 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 tus)
Roland Frey,1 Alban Gebler,2 Kirk A. Olson,3 Daria Odonkhuu,3 Guido Melcher,4 Bruno Fre´de´rich, Orphal Colleye, and Pierre Vandewalle; Laboratoire de Morphologie fonctionnelle et évolutive, Université de Liège, 4000 Liège, Belgium (bruno.frederic@ulg.ac.be)

However, it appears that the largest studied specimens of Dascyllus species have a common ontogenetic trajectory which clearly differs from that of C. viridis. During the allometric growth period concerns each character in attainment 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).

The Evolution of Preaxial Dominance in Tetrapod Limb Development—Implications for the Origins and Relationships of Modern Amphibians
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Limbss 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 zygopodium 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 (Tennispodylida) 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 (Desmostyla, Mammalia). This study focuses on reconstructing elbow joint angle, EJ(A, 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, EJ(A 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 EJ(A. Desmostylus would have had more

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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 smooths 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 biocentric 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 galeaspid remain the most significant outstanding source of information. Although seminal work was conducted by Halstead (1979, Nature, 282: 833–836), Wang (1991, Science, 41–65), the galeaspid brain still remains poorly understood, especially in comparison to osteostracans whose neurocrania were resolved by serial sectioning by Stensiö (1927, “The Devonian and Downtonian vertebrates of Spitzbergen. 1. Family Cephalaspidae.” Skrifter om Svallbard 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 galeaspid matched well the condition in osteostracans. Our studies also speculated an anteri- orly 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 69 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 wetary 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 in osteostematic. 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 scano- rial 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 cranial 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 accelerates 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 that the compensatory development in the later Gosner stages to reach the same cranial shape.

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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, topological 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 fluorescence 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 maintains morphology-based 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 Xenartha 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 disagreement over the proper allocation of the putative anteater Euratomandua 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 megolonychid sloths. This study corroborates the monophyly of the sloth families Nothrotheriidae, Megatheriidae, Megascleroderidae, and Mylodontidae. The latter group unites nothrotheriids and megatheriids in a clade called Mylodontomorpha. Relationships within these latter families, in particular Mylodontidae and Megascleroderidae, 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 approach was to use semi-thin sections of resin-embedded tissues. In this species, the ovulated yolk provides most of the nutrients for development. Our study of placental specializations for secretion and absorption 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 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 Sceloporus 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 FAPEJR

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 archosaur 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 archosaurs was a crucial precondition to their spectacular Middle-Late Triassic adaptive radiation, a time characterized by widespread global drying that would have favored the harder archosaurian egg. However, this adaptation likely canalized archosaurs to obligate oviparity. The occurrence of placental specializations for secretion and absorption in Sceloporus jarrovi suggests that morphological adaptations for placentotrophy can evolve in the absence of an evolutionary reduction in yolk.
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-dependend sex determination, a selectively advantageous strategy in the usually equable climates of the Late Jurassic-Late Cretaceous. Global climatic instability at the end of the Cretaceous may have critically dinned saurian 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 Carangiform 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 resemblance, 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 differences in activity patterns that were discernable in these data. Asynchronous activation.. Due to differences in cranial design, the batoid is more efficient in using fewer muscles. 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 epiplottal movement. The movements were highly stereotyped, but the recorded EMG signals were variable at both the intramuscle and intermuscle 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 pattern 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 batoidea) using electromyography. Electrodes were implanted in three of the jaw adductors: two divisions of the quadratomandibularis and the preorbitals, 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 asynchrony cases, 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 batoide 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 Qeqqertarsuq, 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.

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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 laterals, 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 laterals 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 enameloid 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 holoccephalan). 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 columnar distinct-tube enameloid and basement lamell-leaf transversely-layered enameloid) in Chlamydoselachus anguineus, a basal saural 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 distributed within a mosaic and 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.
Acipenserian Vertebral Characters That Aid in Taxonomic Discrimination
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Vertebræ are arguably the most common diagnostic fish remains recovered from archaeological excavations. The variation present in fish vertebræ makes the task of species identification daunting. Not only do vertebræ 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 dorsoventral 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 coordinate systems of landmarks taken on seven Lepidaptes 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 the 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 weight. First, we develop a quasi-steadyhydrodynamic model of lungefeeding 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 force are severly increased over the course of a lunge. Lastly, we present a phylogenetic analysis of the scaling relationships for the various dimensions of roqual mandibles, which range in length from 1 m (mink 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 lung-feeding model, and compare these allometric trends to non-lunge-feeding baleen whales of similar size.

Redescription of the Carpuses 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 Lovatic 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, Lepidosaurus 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 used laser Doppler vibrometry to record the effects of the foot, the limb, and the torso on the dynamic response to ground contact. The system was controlled by a novel feedback-based approach that allows for a 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 to decrease between the wrist and at the elbow but not in the shoulder. The “limb” retraction as it has been observed in the asymmetrical gaits (gallop, half bound) of different sized mammals is reduced to a speed-dependent duration 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 spatio-temporal 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 dorso-ventral views to identify the times of abduction and adduction relatively in a qualitative way. The second method deals with coordinates issued from lateral and dorso-ventral 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 dorso-ventral 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 ground travel. Although it is generally known to play a visual role, 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 m s⁻¹) using high-speed (250 Hz) videography synchronized with ground reaction force data. The results demonstrate that the head-bobbing cycle can occur at 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 annoiote 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 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 caudal 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 lamina and enhanced odontogenic capacity of P. vitticeps, 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 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.

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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 variables so that our dietary deductions can be applied to fossil taxa. RMA correlations on logged variables show that temporals and masseter (the largest jaw adductors) muscle mass, PCSA and a proxy for adductor force (PCSAforce) 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 temporals 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 temporals and masseter FL is best approximated by a line representing an anterior temporalis fiber (i.e., from the anterior corner of the sagittal crest to the anterior most point on the coronoid temporals scar, just posterior to the caninaul). 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

Pavla Havlevková; Department of Zoology, Faculty of Biological Science, University of South Bohemia, Bransovskí 31, 370 05 České Budejovice, Czech Republic (pavla.havelkova@bf.jcu.cz), Laboratory for Functional Anatomy, Department of Biology, University of Antwerp, Universiteitsplein 1, B-2610 Antwerpen, Belgium, Department of Palaeozoology, Geological Institute, Academy of Sciences, Rozvojova 135, 165 00 Prague 6, Czech Republic (pavla.havelkova@bf.jcu.cz), Department of Zoology, Charles University, Vincenc 7, 128 44 Prague 2, Czech Republic. Unlike extinct Tetranopondylids 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 tail muscles using functional analysis (high speed videotachometry 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 presented by an evolutionary series of neotenic temnospondyls, Triadobatrachus, and Mesozioc anurans.

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

Pavla Havlevková,1 Anthony Herrel,2 Peter Aerts,2 and Zbynek Roces1,3; 1Department of Zoology, Faculty of Biological Science, University of South Bohemia, Bransovskí 31, 370 05 České Budejovice, Czech Republic (pavla.havelkova@bf.jcu.cz), 2Laboratory for Functional Anatomy, Department of Biology, University of Antwerp, Universiteitsplein 1, B-2610 Antwerpen, Belgium, 3Department of Palaeozoology, Geological Institute, Academy of Sciences, Rozvojova 135, 165 00 Prague 6, Czech Republic (pavla.havelkova@bf.jcu.cz). In order to re-examine the origin of jumping in frogs, it is still debated whether these features that appear to characterize jumpers evolved in water or 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 tail muscles using functional analysis (high speed videotachometry 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 presented by an evolutionary series of neotenic temnospondyls, Triadobatrachus, and Mesozioc anurans.

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

Jason J. Head,1 and P. David Polly2,3; 1Department of Biology, University of Toronto at Mississauga, Mississauga, ON L5L 1C6, Canada (jason.head@utoronto.ca), 2Department of Geological Sciences, Indiana University, Bloomington, IN 47405-1405, USA (pdpolly@indiana.edu) 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 intracranial changes in squamation and resultant 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 intracranial 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)

Pavla Havlevková,4 Elena Egon Heiss,5 Hanss Pleenk, Jr.,2 and Josef Weisgrum1; 1Faculty of Life Sciences, Department of Theoretical Biology, Section Morphology, University of Vienna, Austria (heisseg@hotmail.com), 2Bone and Biomaterials Research, Institute for Histology and Embryology, Medical University of Vienna, Austria, 3Department of Biology, Faculty of Biological Science, University of South Bohemia, Bransovskí 31, 370 05 České Budejovice, Czech Republic. 4Department of Zoology, Faculty of Biological Science, University of South Bohemia, Bransovskí 31, 370 05 České Budejovice, Czech Republic. 5Department of Zoology, Faculty of Biological Science, University of South Bohemia, Bransovskí 31, 370 05 České Budejovice, Czech Republic. We examined the histological architecture and microanatomical structures and specializations of the palatal oral mucosa of the Malayan semi-aquatic turtle Cuora amboinensis are described

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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 part of the palatal plate. Keratinization is reflected in the presence of an articular connection between the parasphenoid and the first element of the palatine arch: the basipterygoid articulation. In this study, the ontogenetic differences between the winter skate (Leucoraja ocellata) and previously described Chondrichthys

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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 chondrichthys 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 30 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.), Normenthal zur Entwicklungs geschichte der Wirbeltiere, Vol. 12, pp. 1-140. Gustav Fisher, Jena) and refined by Ballard et al. (1993 J. Exp. Zool. 267: 3-126). 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 spiral ducts 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 its 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 paraprosphene-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 paraprosphene and the symphysial 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 tryptic-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 paraprosphene is later completely replaced by a bent bar. 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 + palatoquadrate), 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, zebrasfish 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 kinetohiod, a rostral ossification associated with premaxillary protraction. As an example of the many 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 kinetohiod, 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 protrusion, the mechanical demands on these systems may vary dramatically. Muscles causing tongue elongation and shortening in nectar feeding birds or bats, 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 morphogenetic and ultrastructure of some of the most extreme tongues in vertebrates (nectar feed-
Dwarving a Giant: Allometry and Ontogeny of Elephant Limb Bones
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Elephants are the largest living terrestrial mammals. They represent the adaptation of extinct elephant species, especially the dwarfed species 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).

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 suture 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 suture growth (and hence cranial morphology) is influenced by mechanisms. Sutural growth in pigs can be studied using vital staining of the neurocranium. Tissue layers analogous to the periosteum line the bone lagenous ligament and bound water. Ligamentous anatomy is thus an important determinant of suture 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 on the vertebral column and thus in different functional demands on the musculature. The paraverterbral 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 paraverterbral 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). Consequently, 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 oligoskeletal 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, oligoskeletal as well as for the superficial, multigemulate muscles.

Effects of an Erect Posture on the Lumbar Paraverterbral Musculature
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As out-group 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 (Cyprinidae) and Pachypanchax (Pimelodidae) were investigated. 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 intra-specific allometry and ontogeny of elephant limb bones has been little studied. This is necessary for 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 (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 intra-specific allometry and ontogeny of elephant limb bones through ontogeny is assessed. These data shed further light on the effects of scaling on morphological and biomechanical adaptation.

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, Atherinomorphs, and Perciformes as out-group 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 (Cyprinidae) and Pachypanchax (Pimelodidae) were investigated. 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 intra-specific allometry and ontogeny of elephant limb bones has been little studied. This is necessary for 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 (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 intra-specific allometry and ontogeny of elephant limb bones through ontogeny is assessed. These data shed further light on the effects of scaling on morphological and biomechanical adaptation.

Turtle Beaks, Bird Beaks, Croc Beaks? Parallel Evolution of Rhamphotheca in Sauropods
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Edentulous beaks appear several times in sauropod evolution. Although both extant examples (turtles and birds) are entirely edentulous, many extinct beaked sauropod clades show substantial maxillary and dentary tooth roots. 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 sauropod taxa were surveyed for the morphology and topology of skin features, dermocranial 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 sauropod taxa were also examined to determine the heuristics. This indicates a stabilizing function for both the deep, oligoskeletal as well as for the superficial, multigemulate muscles.

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Persistent and congruent similarities in sauropod 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) dermatoes. A second border occurs between the dermatoes 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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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 reptilian 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 sauroglossan 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 Ichthyosaurus and, and was retained in both spectacleted 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 Tyrannosaurus (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 thick distal ends. The distal ends of the 13th–15th ribs are directed medially (not anteriorly). These features suggest that these three pairs of ribs primarily articulated with cartilaginous sternal elements, and the sternum rocking seen in extant birds is unlikely in tyrannosaurid dinosaurs 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 vertebral cortex orients relatively dorsoventrally in tyrannosaurid dinosaurs, 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 tyrannosaurid dinosaurs. This interpretation indicates that the basic avian thoracic architecture was incomplete despite the possible presence of airsacs in tyrannosaurid dinosaurs.

From Mice to Monkeys: How Similar Are Their Dental 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 into the appropriateness of broad application of the mouse model, as these analytical methods can be performed on animals that are logistically impractical for developmental 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 Pattern- ing 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 Sauria, Spondylus, 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 advantageous, because permanently energy-consuming, 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 (cur- m. pectoralis) keeps the shoulder joint in equilibrium. Its pull leads to ling. It implies, however, solid biomechanical advantages, which will be discussed.

New Fossil, *Tiktalaik 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 environment. 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 further: The selective advantages for characters affecting 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 powerful manipulatory forces 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 *Egermia 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 (*Egermia 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 Pil- bara; 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 kinetics in non-avian dinosaurs. Intracranial synovial joints and protractor muscle are ubiquitous among dinosaurs including clearly akinetik taxa (e.g., ankylosaurids, 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 kinetics. Moreover, although many extant lizards bear all of the morphological features suggestive of cranial kinetics, 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 kinetics. This bears significance for understanding avian evolutionary as well as general reptilian cranial form and function.

The Microarchitectures 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 demins and its papillary body whose configuration varies depending on its location. The demins is densely supplied with blood vessels, most of which emerge from the proximal half of the cornified sheath. The pappilla 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 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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Ridges are surface structures that juxtapose the 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 Trisphenic Molars: Developmental Background of a Major Mammalian Apomorphy
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Prismatic molar that is morphologically adapted for fossoriality. It presents a phylotypic stage to all mammalian molars. We analyzed architecture of TM enamel coat in several molars, particularly bicuspid, 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 (iii) the 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 perierupational stage, is related to a switch of the secretory activity of ameloblasts from a slow production of large-crystallite prismatic enamel to a rapid production of small-crystallite amorphous enamel and apatocrystalline enamel, supposedly under the mechanical stress of tooth eruption.
locomotion in tunnels, our study may provide some insight into the evolution of the short-limbed and slender morphotype typical of mustelidines 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 vertebræ 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 central axis and neural arch, where the reconstruction deficit makes the originally compact cortex cancellous, and the endochondral spongiaoso 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
Morphster incorporates the security and bookkeeping needed to maintain the identity and separation of each contributor's work including isolation of authoritative contents. Morphster extends the existing ontology. In support of collaborative endeavors Morphster controls keywords drawn from an existing ontology. Morphster is designed 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 non-paleontological perspectives may sometimes differ, our case studies show some common themes as well; both must confront large numbers of hypothesis and understanding.

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 two such 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 non-paleontological 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 among 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, protocanthopterygian 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 an extraordinary tooth replacement. We propose that the mode of tooth replacement in Atlantic salmon displays several ancient characters similar to those observed in chondrichthyes, and that differences between Atlantic salmon and chondrichthyes 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 in-bred sets, 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 from egg to mature-recapture, researchers tried to develop a 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 that 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 these variations. 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 formed 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 development process including the mechanism that causes the morphological variation in the renal vascular system.

Mouse Enamel From Frog Amelogenin
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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 tasks designed for concept exploration, or higher-order inquiry. We have determined that enamel hardness 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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Bivariate plots show sthenurines have a relatively shorter fourth metatarsal than terrestrial macropodines, and thus a shorter foot, resembling 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.
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 evolve several times in mammals. At least primates, bears, and murid 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 the low-level taxonomy, detail 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 vertebral 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 macallichani, 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 dwellers, 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 examine 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 combina-
nation of feeding adaptations not found in any extant taxon, notably: 
large chisel-like premaxillary teeth, an acrodont dentition, and
enlarged palatal teeth 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 pat-
ent 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., premaxilla-
vomer) whereas others have a very close fit (e.g., postfrontal-postori-
tal). 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 cli-
matic conditions. They have been applied successfully in numerous stud-
ies 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 iso-
topic 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 tis-
sues (ortho-, vaso-, and/or osteodentin) as well as of cementum. The
aim of this survey is to check the preservation potential of primary iso-
topic 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. Immedi-
ately 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
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hardness using three model stimuli presented in the form of spheres of
the food’s subsequent processing. In

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 pre-
ceded 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 ana-
tomically 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 intercon-
nections. 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 sepa-
ration 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 under-
standing 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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Kalmar University, Kalmar, Sweden (ola.karlsson@hik.se)
Stable isotope compositions of xenarthran teeth and their
potential for the reconstruction of the diet of fossil xenarthrans.

Explaining the Growth of Craniofacial Skeleton Under Protein
Restriction and Ligation of the Uterine Artery by Principal
Component Analysis (PCA)
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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 UGGR and 24% protein (the offspring of the previous experiments) during pregnancy. To investigate the effect of low, middle protein and UGGR 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 these 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-temporals 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.

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
Anna L. Keyte, Tanveena Imam, and Kathleen K. Smith; Department of Biology, Duke University, Box 90338, Durham, NC 27708, USA (alk2@duke.edu)
Heterochrony, or a shift in developmental timing, is an important source for evolutionary change. Here we utilize Monodelphis domestica (Meta-theria), 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 M. 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 Cretaceous (Cretaceous) of the Middle East
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A new genus and species of a double-armed Ellimichthyiformes (Teleostei: Clupeomorpha) is described from the Cretaceous marine deposit of Ein Yabrud, near Ramallah, West Bank. Thirteen species of Teleostei, as well as a bipped 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 clade of Clupeomorph with a Tethyan geographical distri- bution and they are not well diversified during the late 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 dor- sal fin rays. It shares both the synapomorphies of |Ellimichthyiformes Grande, 1982 and of the family |Paralucipidae Chang and Chow, 1977. I present evidences that the new species is a close relative of the triple-armed |Ellimichthyiformes |Triplomystus Forey et al. 2003. Temperature, Size, Performance and Fitness

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This talk focuses on three related patterns often observed in echothermic 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 Trenda- guru Beds and from the Morrison Formation), basal macronosaurs (Camarasaurus, Brachiosaurus, Europasaurus) and titanosaurus (Phu- wiangosaurus, 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 rela- tively 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 differ- ent 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 (Gymnophionidae (Caudata)), and frogs (Anura). Derived reproductive modes in amphibians comprise oviparity with direct devel-
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 60 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
Robert Knell; School of Biological and Chemical Sciences, Queen Mary, University of London (r.knell@qmul.ac.uk)

Weapons such as horns are widely distributed in the Coleoptera, and exhibit an astonishing diversity. Male beetles of the species Eumecetiscus 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 shown 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 choioalantois and the omphallantoic membrane. The latter is formed from the yolk sac oophalopleure and isolated yolk mass, with the allantois on its inner surface. SEM shows that epithelium lining the choioallantois consists of broad, flattened cells that form a thin, unbroken barrier over the allantoic capillaries. In contrast, epithelium lining the oophalopleure is cuboidal and bears surface ridges suggestive of absorptive capabilities.

Until recently on viviparous snakes has revealed that the choioallantois and oophalopleure 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 Patterned 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 significance. 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.; Knita et al., 2005, Nature 435:1113–1116). Here, we analyzed fin development in embryos of cartilaginous dogfish, Scyliorhinus 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, and 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 head 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 sonar sonography. Electromyography illustrated that activity in the basilihal 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 basilihal 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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Abstract: In all vertebrates, the intramandibular joint (IMJ) is a secondary mandibular joint. The IMJ is typically formed by the mid-mandibular (MMEJ) and bimaxillary (BMEJ) joints and can be interpreted as a secondary mandibular joint formed by a process of synostosis, a process that occurs in many taxa. The IMJ is known to play a role in the functional morphology of many taxa, but its evolutionary history has not been well documented. We use a phylogenetic approach to reconstruct the evolutionary history of the IMJ in the class Actinopterygii. We find that the IMJ is present in all extant species of Actinopterygii and that it has evolved independently in several clades. We also find that the IMJ is associated with the evolution of feeding strategies in many taxa, including coral reef fishes. The IMJ is found in all clades of Actinopterygii, including the Gymnodonts, which are characterized by the evolution of a beak. The IMJ is present in all Gymnodont species, and it is associated with the evolution of a beak. The IMJ is also present in many other clades of Actinopterygii, including the Pomacanthidae, which are characterized by the evolution of a suction feeding mechanism. The IMJ is present in all Pomacanthidae species, and it is associated with the evolution of a suction feeding mechanism. The IMJ is also present in many other clades of Actinopterygii, including the Labridae, which are characterized by the evolution of a predatory feeding mechanism. The IMJ is present in all Labridae species, and it is associated with the evolution of a predatory feeding mechanism.

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 leius, 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 split of membrane bone ensues 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 autopallial sutures tightly with the frontal. In the molida Ranzania the autopallial has a caudal lamina of membrane bone that runs along the paraprosphoid 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 hypomandibular (= infrarostral) and one metapterygoid (= supraroostral) cartilages. The second type is typical for all other anurans, with the anterior part of the skull consisting of a pair of trabecular horns terminated by supraroostral cartilages. Its lower jaw consists of a pair of infraorosals, sometimes interconnectec 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 tennosphondyl scheme by its modified larval jaw to displace stnultipartite, the pipid larval type is basically the same as in ancestral tennosphondyls. 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-pipid 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 abdution of the humerus is caused by an abduction of the scapula. The medio-lateral excursions in the glenohumeral joint are avoided in Microcebus murinus, Saguinus oedipus and Eulemur fulus. 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 measured using a developed method. Size, shape and curvature 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 gelenoid fossa. In addition, terrestrial primates possess a relatively broader gelenoid fossa. 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 have a worldwide distribution and live in very different biotopes, from tropical to arctic climates. Some are 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 pouch over the surface 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. canadenisis*, *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 *Cercopithecus aethiops*, at different ontogenetic stages. The models were subjected to masticatory muscle forces estimated from arrested development of the carapace at the site of electroporation. We found that the dominant negative form of Lef-1 in the CR epithelium resulted in the CR mesenchyme with its specific gene expressions. We also note 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 therefore the CR must 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 falling 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 *Leihteron 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 anomiote 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 luciopeca* (L., 1758), *Cyprinus carpio* (L., 1758) and *Chromis nodosus idella* (Cuv. et Val., 1848). They display significant biodiversity: *S. luciopeca* is a predator, its food consist of other fish or fish juveniles. *Cyprinus 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. Morphofunctional analysis of mandible bones as well as four points in the symphysis (cranial end of Premaxilla, Hyomandibulare concurrence with neurocranium, Quadrate-articular facet, cranial end of Dentale) 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 cusp 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
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 Sandrine Ladervèze, Département Histoire de la Terre, Muséum National d’Histoire Naturelle, USM 0203 - UMR 5143 CNRS, Paléobiodiversité et paléoenvironnements, 8 rue Buffon, CP 38, F-75005 Paris, France (ladervze@mnHN.fr)

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 Itaborai (Brazil) have yielded partial to complete metatherian skulls with associated petrosal bones (assigned to the pucadelphids 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 Itaborai was made by combining parsimony and morphometric methods. Morphometric studies show that molar proportions are correlated with that of petrosals; however, the assignment 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 Astrapotheria. The identification of australidelphian taxa (petrosal Types V and VII) among the Paleocene fauna of Itaborai makes the stratigraphic origin of Astrapotheria older than it was thought.

Mxs Genes Are Important Effectors Downstream of Gli3R in the Shh/Gli3 Pathway Controlling Antero-Posterior Development of the Limb Yvan Lallemant, Vardina Bensoussan, Cécile Saint Clément, Benoît Robert; Génétique moléculaire de la Morphogénèse, CNRS URA 2578, Institut Pasteur, 25 rue du Dr Roux, 75715 Paris, France (yvanlal@pasteur.fr)

Mxs 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 oligodonty 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 an important role in the Shh/Gli3 pathway that controls antero-posterior patterning of the limb. Indeed, Mox gene expression is affected in the Shh and Gli3 mutants, suggesting that Mxs1 and Mxs2 are downstream targets of Gli3R. To analyze the genetic interactions between Mxs and Shh, we produced Shh/Mxs1: Mxs2 compound mutants and showed that diminishing Mxx activity in Shh mutants leads to a partial rescue of the Shh limb phenotype. The precise role of Mxx 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 Tobias Landberg, Jeffrey D. Mailhot, and Elizabeth L. Brainerd; 1 University of Connecticut, Storrs, USA (tobias.landberg@uconn.edu), 2University of Massachusetts, Worcester, Brown University

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 turtle species; either if they breathe during locomotion and when they stop, the locomotor-respiratory coupling. Both species had 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 the proteome 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 Fulcras in a Common Joint—the Mammalian Jaw Joint Stuart O. Landry; Department of Biology, SUNY, Binghamton New York, USA (slandry@binghamton.edu)

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 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 cutting 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 the canine is almost parallel to the sagittal plane of the skull. Just behind the mediolateral fulcrum is a massive post gneid process which braces against the backward push of the mandible when the canine is being plunged.

The Evolutionary Morphology of Lizard Weaponry A.K. Lappin, J.F. Husak, J.M. Macedo, Y. Brandt; 1Biological Sciences Department, California State Polytechnic University, 3801 West Temple Avenue, Pomona, CA 91768-2553, USA (aklappin@csupomona.edu), 2Department of Biology, University of Massachusetts, Amherst, MA 01003, USA, 3School of Life Sciences, Arizona State University, Tempe, AZ 85287, USA, 4Biological Department, University of South Dakota, 414 E. Clark Street, Vermillion, SD 57069, USA

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 autopod 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 reptiles) 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 1990s, that the established consensus was not the most parsimonious tree. All phylogenies published after 1996 indicate that the basal dichotomy between amphibians and reptilemorphs (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 Muroida (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 Murid rodents (Rodentia, Mammalia) shared by Desmostylidae, Chalicotheriidae 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 Potwaranus (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 Potwaranus. 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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Comparing 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 (run-time) and speed (turning) are highly heritable, yet selection for 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. Together, 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 peristeal 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 chelonians, 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 today 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 these museums that will be able to maintain the mutual enlightenment 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.
saur. Uncertainty in growth estimates of dinosaurs exists because no single bone preserves a complete record of cortical deposition. Medul-
lar expansion and cortical remodeling remove or obscure lines of
arrested growth (LAGs), which are measured to estimate ontogenetic sta-
tus. Several models of perosteal 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 depo-
sition 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 rela-
tive 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,
leaves 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 meas-
ured 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 sup-
ported 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 fa-
tigue and vertebral strain. A new sagittal pelvic parameter, the sacral
incidence, is the most significant parameter. This angle (35°–75°) deter-
mines 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 bipedal-
ism. We conclude that adequate correlations between the degree of inci-
dence 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 anatomi-
cal 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
among different species, and embryologists to compare gene expression among embryos of different taxo-
nomic groups. Herein we describe our community-based efforts to de-
velop 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.am-
phibanat.org—which includes discussion boards, links to contacts and
mailing lists, and the user interface for searching, browsing, and navigat-
ing 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 pipe-
fishes and seahorses (Syngnathidae) very remarkable fish. Despite their
exceptional appearance, little is known about their morphology and on-
togeny. The aim of this study is to compare the ontogeny of the head
skeleton in Syngnathus rostellatus (Nilsson’s pipefish) and Hippocampus
capensis (Kensy seahorse). First, a detailed morphological study was
performed using cleared and stained specimens. In addition, serial histo-
logical sections were used to create graphical 3D-reconstructions. Sec-
ond, 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 posi-
tion 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 substan-
tial work on the genetic and epigenetic mechanisms by which develop-
mental integration occurs, we have less of an understanding of the evo-
luutionary relationships between functional and developmental integra-
tion. 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, how-
ever, 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 run-
ning. While the arm and the head interact little during walking, we
have found that, during running, the stance side arm acts as a counter-
balance to the head, stabilizing it against impulsive pitching forces
generated by the heel strike transient. Moreover, the functional proper-
ties of this linkage may have driven several developmental changes in
the proportions of the arm and the anatomy of the shoulder girdle dur-
ing human evolution. Thus, evolutionary changes in arm and head mor-
phology during human evolution may be more integrated than previ-
ously 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, the intralimb proportions are very similar, such that it seems that intralimb proportion escapes selection. Animals were filmed during locomotion using high-speed 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 morphoclone 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 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 morphoclone 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 tend nests 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 to 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 (ten- sion, 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 nimbfish, Narcine bancroftii, the yellow stingray, Urolophus 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 measured the intralimb proportions of the pelvis. The pelvic fin to pectoral fin surface deformation, skeletal morphology, and swimming kinematics, including punting distance (body length (BL)), speed (BL/sec-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

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with the cyclical forces encountered during mastication. Owing to their complex 3-dimensional structure it is difficult to determine which micro-anatomical feature may constitute a functional adaptation, an epigenetic phenomenon or a phylogenetic character. 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 allowed us to make predictions about the function of a specific structure in a certain taxon. The histology of the enamel of the canine teeth of the horse and the allis river otter was examined, and 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 (NERA/S/2003/003472).

Observations on the Turbinal Elements of the Ethmoid Bone of Marsupials

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The skeleton of the horse 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 turbinial elements (maxilloturbinals, nasoturbinals, ectoturbinals, endoturbinals) that coalesce caudally to form the cribiform 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 folds, and are tube-like in form caudally. In contrast, the maxilloturbinal of the Virginia opossum is complex, possessing many branches and folds 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 analyses of these elements to provide evolutionary insights. Histological observations of the ethmoid bone of marsupials, particularly the maxilloturbinal and nasoturbinal elements, 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 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, β-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 calomogenesis (when cells remain adherent producing a tubular calamus). During cortical cell epithelialization in both barbs and rachis, additional β-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 spate 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 species through 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.

**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, palaeontologists, 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 cranial and extremal 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 peristomial 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.
datasets have been generated as part of the National Science Foundation Assembling the Tree of Life project for squames (Deep Scaly). These represent extinct and extant taxa spanning the full spectrum of body size (snout lengths from <1 cm to 0.5 m), lifestyle (fossilous to aquatic to arboreal to gliding), and phylogenetic position within Squamata. Significant differences exist in the relative size of the vestibule and the statocystic mass, the relative diameter of the semicircular canals and their radii of curvature, and the degree of differentiation of the lagena 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 chondrichthyanas. Thus, the articulation in hexanchiforms has been widely considered to be an ancient, conserved feature and became secondarily conscripted among modern elasmobranchs (including xenacanths, 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, Paraarhacodex); paraadoxically, 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 caudal 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 homogeneously, 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 interneuroneuronic 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 gestational ages at differentiation this so-called segmental map of the expression of molecular markers, such as genes coding for transcription factors or enzymes involved in neurotransmitter metabolism. We propose a synthetic neurogenic 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). Based on 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 PCO2 did not decrease drastically during UAV, suggesting that high the COV measured is not due to UAV induced metabolic suppression. Additionally, the COV per unit ventilated was the same in resting and running birds (20.3 ml O2 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 Contribute to 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 across a wide range of lifestyles. Variances and multivariate covariances 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 phenotypically 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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Aerial 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 the ability of 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 adaptive responses 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, Lapinque 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 to 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 by providing food reward. The results of these two groups 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.
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 joint angles, lumbo-sacral, tholaco-lumbar, and cervico thalamic 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 thoraco-cibo-lumbar 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 thoraco-lumbar 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. Seventy-six 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 and cartilaginous 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 basidsorsals 3, 4, 5 and hypural 1 and 2. For fishes longer than 7.5 mm, the efficiency of the undulatory movements become better and better affected 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 Ground Sloths: Does Size Limit Plasticity?
H. Gregory McDonald,1 Gerardo De Iuliis,2 François Pujos,3 and Castor Plasticity?
Hearing Capacity in Extinct Grounds Sloths: Does Size Limit TL. Maximum efficiency in swimming is reached at approximately 13 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.

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Is Iroquois-I 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 identified 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 ~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 ractrack 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 coupled 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.

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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 some character suites associated with successful radiation remain relatively unexplored. We present promising results of this work, however, aspects of bone microstructure in some character suites associated with successful radiation remain relatively unexplored. We present

Sensory 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 characteristic of hammerhead sharks, being important for studies on its origins, evolution and diversity. The cephalofoil shape in Sphyrids changes during its ontogeny, being necessary to establish other taxonomic characters to determine correctly its species. The present work studied the distribution of electrosensory pore regions in ventral surface of the cephalofoil (VSC) in Sphyra lewini, S. tiburo, S. tudes and S. zygaena from the Southwestern Atlantic. Those pores in VSC represent a specialized electrosensory network capable of catching subtle variations of electric field. Electrocception 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 Sphyrids. 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 electrosensory pores on the VSC of the studied hammerhead shark species occurring in Southwestern Atlantic (c.f. S. lewini, Sphryna 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 (Tragopotorax and Miotragocerus) browsed, the dental microwear analysis suggests wider ranges of feeding habits. In fact, the species of Miotragocerus usually have a high bit percentage and especially very few scratches on shearing molar facets. This undoubtably indicates browsing habits. In contrast, the populations belonging to Tragopotorax display a different microwear pattern. Some populations were indisputably more engaged in grazing than others.

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 (Sphyra lewini, S. tiburo, S. tudes and S. zygaena). As in all Sphyrids, these 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 mediobital anterior and posterior constrictus, in its proportions, size and angle in the cephalofoil. It was possible to list characters that will allow future phylogenetic studies, referring 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 mediobital connexion, the presence of the nasal groove, the presence of lateral indentations and the angle of the posterior margin of the head.

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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 in vitro utilizing 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 in vitro utilizing ultrasonic pulse transmission technique 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 in vitro utilizing ultrasonic pulse transmission technique 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 in vitro utilizing ultrasonic pulse transmission technique to determine how humans interact with foods of varied physical properties.
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 humeri 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 humeruses. 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 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 1108 ICVM-8 ABSTRACTS

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 masticatory 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: Echimyoid 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 rami 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.

Musculoskeletal Modelling and Finite Element Analysis of Lizard Skulls

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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 vromerosal 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 cinerhysteroscopy, 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., gaping opening angle and hyale position between snout and esophagus) to compare kinematics of trophic system in scleroglossan and iguanian 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 (Crotalidae 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 before the evolution of rattles, and highly specialized shaker muscles. We are currently testing for relationships among tail morphology, muscle physiology, and mechanical energy output.

Development of the Skull in the Chinese Soft-shelled Turtle, Pelodiscus sinensis (Reptilia: Testudinata: 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 crustose calvarium and movements of the supratemporal and basisphenoid fenestrae. 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-pteranotrichid, 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, urodele and caecilian caecilians, covering all genera for which free-living larva 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. 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 supraspacularis 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 ambisonensis and the yellow-margined box turtle (Cuora flavomarginata).**

This study examines the anatomy and histology of the feeding apparatus of two closely related turtle species, the Malayan box turtle (Cuora ambisonensis) 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 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. ambisonensis only), the prey is captured by a fast forward strike (ram feeding) of the head. Compensatory suction by hyoid prevents the prey from floating away during the head approach. In C. ambisonensis, food transport under water involves intraoral 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 ambisonensis 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 relics 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, its feeding habits have not been described in 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 hypo-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
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 across 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, Agassiz 1835. The most commonly accepted in the literature. This indicates that Plio-Pleistocene hominins were not as speciose as modern humans. It should be, however, noted that hominin specimens cover through just a few species to well over 10 species and several genera. 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 (n = 347) and 33.8 kg/mm2 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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Whole Body Lift and Ground Effect During Pectoral Fin Locomotion in the Northern Spearnose Poacher

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The northern spearnose poacher, Apogonopsis vula, 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. vula overcomes negative buoyancy and generates forward thrust during pectoral fin locomotion. When slowly swimming (0.7 body lengths/second [b/l/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 b/l/s. These results suggest that pitch angle is important in lift generation which allows A. vula 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 b/l/s and 5° at 2 b/l/s (Wells, 1996, JEB 202:2311–2332). In contrast, when poachers swim 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 arboreal marsupials. 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 inclinination 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 gait on inclined (diagonal sequence) and declined substrates (lateral sequence),brushed-tail 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 Baulan: 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 size and structural pneumaticity in the postcranial skeleton. For instance, birds (ostids, 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 diploote 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 diploote oocytes at the beginning of the season, and their number increased to 34,666, and eventually reached 23,440 in three-year-old females. The
sharp decrease was accompanied by massive intrafolllicular 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. temporalis from another population reported by Płytycz 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 newborn’s 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 the feeding might have been exaggerated and comparing 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) bulb 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.

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 so far. 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 skeleton and muscle development, and sequence-heterochronic changes are correlated with both feeding mode and phylogenetic relatedness. Supported by the Deutsche Forschungsgemeinschaft (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 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) bulb 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 activity 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 subfamily 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 said snout.

Morphological Study of the Otic Region and Petrogal 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 basioccipital. 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 posi-
tion. The morphology of the otic region of fossil suids has been studied in
depth by Pearson (1927), but no suids from the subfamily Listriodon-
ini 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 listrio-
donts exhibit various morphologies, triggering the question of the plas-
ticity of the otic region of suids.

Hagfish Embryology Project
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Hagfish and lampreys are the sole members of the extant jawless verte-
brates occupying a critical position on the phylogenetic tree. Since
the 1870s, when the scientific importance of hagfishes was already well rec-
ognized, many embryologists have endeavored to sample hagfish embryos
at various locations including the North Sea and off the Cali-
ifornia coast. Despite abundance of the adult hagfish populations, how-
ever, 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 inac-
cessibility of their deep sea habitat. Even now, although a few modern
scientists try to collect hagfish embryos applying sophisticated techni-
quies, there has not been major success. To obtain hagfish embryos, we
have picked up an inshore hagfish species Eptatretus burgeri, and con-
tacted a local fisherman familiar with the seasonal behavior of these ani-
mals in the Japanese coastal area. We collected adult hagfish individuals
in the candidate spawning season with the fisherman and maintained col-
clected 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.

Insipatory Mechanisms in Reptiles: Primitive or Derived, Primary
or Accessory?
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Costal aspiration is the basal mechanism of lung ventilation in anamniotes.
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 pump-
ing, as a ventilatory mechanism, was first observed in monitor lizards dur-
ing 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 threat/behave and was subse-
quently co-opted as an accessory inspiratory mechanism by larger lizards.
Crocodylians possess a unique diaphragmaticus muscle, which powers the
hepatic piston mechanism. Previous studies have shown the diaphragmati-
cus 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 hyperventi-
lating (during hypercapnia or recovery from exercise). Neither maximum
acrobic 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 suc-
cessfully at lower oxygen levels than embryos of endotherms. Recent mod-
els 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 Permian-Triassic boundary. To investigate the ef-
effect of such an atmospheric change on whole-body morphology of embry-
onic amniotes, we incubated the eggs of a common alligator (Alligator
mississippiensis) under different laboratory conditions: hypoxia (12–13%),
normoxia (20–21%) or hyperoxia (29–30%). All embryos were incubated at
68°F 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-spe-
cific 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 sib-
lings, hypoxic hatchlings showed reduced skeletal growth, indicative of
lower endochondral and periosteal bone formation rates. This suggests Palae-
ozic oxygen levels may have had a profound influence on growth patterns
of extinct amniotes, e.g., as a constraint on growth rates in some Tri-
assic taxa. Thus, attempts to infer growth rates of extinct taxa from their fos-
sil 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 poly-
perid 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 com-
pare movements in each habitat aquatic and terrestrial locomotor trials
of the ropefish were captured using high-speed digital imaging. The mid-
line 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
locomotion of the ropefish. Terrestrial locomotion more closely approxi-
mates 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 anterior ends of the animal. These preliminary results are similar to
results found for eels, suggesting that elongate fishes may move simi-
larly 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,
KLP20, 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 ame-
logenesis 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,
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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 palaeoarchitectological methods (thin-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. chropae. 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. 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 (box) 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/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 a pre-adult “hidden” rhombomeres caudal to r7. The presence of rhombomeres r8 to r11 was originally suggested by Cambronerio and Puelles (J. Comp. Neurol. 427:522, 2000) on the basis of chick-qual 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
Anna Pecio, Dagmara Podkowa and Lucia Goniakowska-Witalinska; Department of Comparative Anatomy, Institute of Zoology, Jagiellonian University, Ingargena 6, 30-060 Krakow, Poland (pecio@zuk.iz.uj.edu.pl)
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 cups 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 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 phenotypic architecture. However, the complexity 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-phenotype mapping in the modularization 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 suggest 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 (box) 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/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 a pre-adult “hidden” rhombomeres caudal to r7. The presence of rhombomeres r8 to r11 was originally suggested by Cambronerio and Puelles (J. Comp. Neurol. 427:522, 2000) on the basis of chick-qual 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
Anna Pecio, Dagmara Podkowa and Lucia Goniakowska-Witalinska; Department of Comparative Anatomy, Institute of Zoology, Jagiellonian University, Ingargena 6, 30-060 Krakow, Poland (pecio@zuk.iz.uj.edu.pl)
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 cups 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 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 phenotypic architecture. However, the complexity 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-phenotype mapping in the modularization 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 suggest rQTL in affecting the traits of interest revealed multiple interaction loci. The effects of these loci upon the allometry are presented.
dorsal part, but single or aggregated melanomeres are observed between
and within the epidermal cells. Ventral skin is almost devoid 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 protu-
berances.

Evidence for Sertoli Cells in the Testes of Bombina variegata
(Anura: Bombinatoridae)
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Zoology, University of Wrocław, H. Stienkiewicza 21, 50-335 Wrocław,
Poland (pecio@ukr.jj.uj.edu.pl). Because Sertoli cells (SCs) are inherent to the germinal epithelium in all
male chordees, 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
the cysts containing 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
spermatogonia were positioned adjacent to the basement membrane,
and within the epidermal cells. Ventral skin is almost devoided of

Non-occlusal Dental Microwear, Enamel Microtopography and
Tooth Crown Morphology in Neanderthals: Evolutionary
Determined or Ecologically Constrained?
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Recent analyses have shown that enamel 3D-topography is highly sensi-
tive 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. How-
ever, 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 mor-
phology between hominin species may be interpreted as biological adap-
tations 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 coevo-
lutionary 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 mod-
ern humans, fought a parallel, never-ending struggle for survival deter-
minant of both cultural and biological adaptations.

Synthesis of Current Data in Growth of Early Jawless Vertebrates
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75 231 Paris cedex 05, France (pernegre@hotmail.com)
Recent published works on the growth of the heterostracans (armored
jawless vertebrates) led us to present a synthesis of current data concern-
ing 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 Pteraspid-
iformes. 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 his-
tory of the dermal plates in adult specimens. Variations of speed in
cyclomorial development and heterochronies can explain some remarka-
table forms such as the huge Gigantoaspis or the aberrant Doryaspis (Pter-
aspidiformes). 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. under-
stand 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 prefer-
ence is poor. However, of the large-bodied strepsirrhines, those that
tough foods (leaves) tend to have greater PCSA than those that eat frag-
tile foods (fruits). Multiplying a muscle's PCSA by its leverage changes
the distribution of data points very little: those strepsirrhines that have
lengthened foot and hand (metapodials, astragalar neck, and cuboid),
and a hoof-like morphology of the dis-
tal phalanges that, among other
features, suggest an overall unguligrade stance. The postcricium 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
early 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. Sagatherium antiquum has a
high number of thoraco-lumbar vertebræ as in other paenungulates,
but a lower number than in extant hyraxes. It therefore illustrates an
intermediate structural pattern between the noticeable derived condi-
tions of modern hyraxes and the more primitive condition of tubuliden-
tates and other paenungulates.

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sugest 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
Steven F. Perry,1,2 Thomas Bresser,1 Nadine Piekarski,1实现了体重估计可能太高。财务
possibly involving the neck and sac-like lung regions, and that the latter
monary diffusing capacity could set the anatomical limit to gigantism.
mechanisms and whether the animal is resting or moving. Thus, the pul-
masses between 10 and 50 tonnes, depending on temperature control
192). Not surprisingly the predicted lung structure was either of such
mammalian model (Gunga et. al., 1995. Naturwissenschaften 82:190–
Not surprisingly the predicted lung structure was either of such low
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Previous attempts to model lungs of giant sauropods (Dinosauria: Sauris-
chial genes) have been based on either a crocodilian (Hengst et al., 1996. In:
In: Keller and McDougall, eds. Cretaceous-Tertiary Mass Extinctions: Biotic 
Environmental Changes. W.W. Norton & Co. NY: 327–347.) or
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Skeletal Derivatives of the Somites in the Mexican Axolotl
( Ambystoma mecaleum) Nadine Piekarski and Lennart Olsson; Institut für Spezielle Zoologie und Evolutionsbiologie mit Phyletischem Museum, Friedrich-Schiller-
Universität, Erbertstr.1, D-07743 Jena, Germany (piekarski@pan.zoo.uni-
jena.de; lennart.olsson@uni-jena.de) The axial skeleton of vertebrates as well as the occipital area 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 experi-
ments in the quail-chick chimera system have revealed that cranial and 
caudal halvex- and somites are lineage restricted and retain their axial 
information while forming single vertebrae. This is in contrast to a less 
strict resegmentation observed in zebras. Further comparative data for 
regeneration modes are needed for a better understanding of this proc-
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-fluo-
rescein in an urodile amphibian, the Mexican axolotl. After 10 to 40 
days of development the marker was detected and amplified by immuno-
fluorescence on paraffin sections. We were able to determine the con-
tributions 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 Mexi-
can 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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street 16, Riga, LV 1007, Latvia, 2University Children’s Hospital, Riga, 
Latvia, Vienibas gatve 45, Riga, Latvia (pilmane@linet.lv) Incidence of esophageal atresia is reported in one case from 3000 new-
borns. The morphopathogenesis of this malformation still is not clear. 
Aim of work was investigation of innervation and growth factors in the esophagus in children with EA. Material was obtained from 15 new-
born infants during plastic surgery. Control material was taken from children who died from non-gastrointestinal diseases. PGP 9.5, VIP, SP, NF, M, 
TGFβ and NGFR were detected by use of immunohistochemistry. Results 
showed vacuolized epithelieytes and hyperplasia of basal cells, disorgan-
ization of muscle, vacuolization of ganglioneytes in Auerbach’s plexus in all 
patients. Esophagus showed weak staining of myelin- and NF-cont-
taining 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 neu-
ropetide-containing nerve fibers in muscle layer, around esophageal 
glands, and in adventitia. NGFR was richly expressed in nerves of 
controls, but varied in patients. FGFR was equally expressed in patients 
and controls, but expression of TGFβ 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 

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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 metallo-proteinsases (MMPs), apoptosis, and genes in tissue around the implants.

Methods: PGP9.5, VIP, SP, TGFβ, FGFR1, BMP2/4, MMP, barx1, mnx2 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 TGFβ, 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 glialolocytes 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.

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 elicits 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 ca-nine 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-sex and multimale species show high levels 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 selection 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 is at a depth, whereas the establishment of the axial-appendicular junction—the morphogenesis of the pelvic girdle—is still a largely 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) (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. (1991) 248: 583–602; 3. Streicher J. et al., Nat. Genet. (2000) 25: 147–152.

Locomotor Energies 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 hominids 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 strain values were evaluated as 440%. In both groups the cryptal alveolus 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 lead to 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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Omnithischian 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 shear surfaces results in a key structural change 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 Elasmobranch 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 and cartilage variations 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 evolutionary tree (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
Emmanuel Pouydebat1, Philippe Gorce1, and Vincent Betéz1; LESP, Université de Toulon et du Var, La Garde, France (pouydebat@mnhn.fr), 1Museum National d’Histoire Naturelle, Paris, France
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 (iii) 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 and 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.

Evolution of Complexity Across the Vertebrate and Teleost Genome Duplication Events
John H. Postlethwait, Angel Amores, Susan Bassham, Cristian Cainestro and Eric L. Nelson; Institute of Neurobiology, University of Oregon, Eugene, OR 97403, USA (jpostle@uoneuro.uoregon.edu)
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 evolutionary tree (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.
Odd Carboniferous Iniopterygian Anatomy Revealed by Synchrotron Radiation Microtomography

David Gaitros, Debbie Paul, and Cynthia Gaitros; 1Department de Terre. USM 0203-UMR 5143, Paleobiodeversité et Paleoenvironnements, 8 rue Buffon, 75005 Paris, France (pradel@premfr.fr) Living chondrichthyanis, 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 skeletons 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

Holger Preuschoft, Bianca Hohn and Ulrich Witzt; Ruhr-Universität Bochum, Germany (holger.preuschoft@rub.de) 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 squamate, crocodile, 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 caudal 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

Albert Prieto-Márquez, Gregory M. Erickson, Katja Selman, Fredrik Ronquist, Gregory A. Riccardi, Carolina Maneva-Jakimova, Neelima Jammingapula, Austin Mast, Steve Winner, Wilfredo Blanco, Andy Deans, David Gattoz, Debbie Paul, and Cynthia Gattoz; Department of Biological Science, Florida State University, Tallahassee, FL 32306-1100, USA (apr@bocgs.fsu.edu), Department of Computer Science, Florida State University, Tallahassee, FL 32306-4120, USA, College of Information, Florida State University, Tallahassee, FL 32306-4530, USA, Department of Computer Science, Florida State University, Tallahassee, FL 32306-4530, USA, and the African bathyergids represent two major clades (the South American hystricognaths and the African bathyergids) of modern mole rats. Data for digging adaptations in the autopods 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 phalanges, 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 Ctenomyos opinus, Spalacopus cyanus and the African bathyergids Heliohippus 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 sesamoids 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 lunar and scaphoid), interpreted as adaptations to fossorial lifestyle to stabilize the carpus during digging.

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

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

Luis Puigues; Dept. Human Anatomy, Medical School, Univ. of Murcia and CIBERER Murcia, Spain (puigues@um.es) 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 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
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 organs and start at 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 column is the columella 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 alar 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 Tinguirinuran 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 Monterhermosan SALMAs, and several indeterminate Monterhermosan SALMA Megatherioidea. These new sloths, in addition to the well known Pseudoglyptodon sallaensis (Deseadan SALMA), Xyophorus villarroelii (Huayquerian SALMA), Megatherium altiplanicum (Monthermosan SALMA), and Eromeritherium sfevi (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 La Venta fauna from the middle Miocene of Colombia.

On the Revision of Octodontotherium: The Oldest Mylodontid 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, allows 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 Triphic 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 on origins and early history of vertebrates, particularly focusing on 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 Oshino’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 evidence 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, inhalatory pressure. The synsacrum and posteriorly directed, laterally open pectoral girdles 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 (Phocoenidae) 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 (Neophocaena 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 Neophocaena 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 quadrupedalism 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 juvenile kinematics through the pendular mechanics of limb motion, and lead to long swing periods, low stride frequencies and long strides. We also examine primates 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 Locomotor 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 convergent 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 = 0.87), 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 based extractions and incorporate fossils, because sampling of vertebrate diversity based on extant evidence alone will inevitably produce biased and unreliable evolutionary patterns.

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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—rampal assemblages—the subject of much functional analysis—extant birds are an obvious candidate for FE-validation. Furthermore 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 grazing 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 < 0.001). A significant relationship between the angle of the central 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 significance 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 family 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 hominin 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 the habitats being “fixed” to hominid 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 interpretative 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 have 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 *Pelodetes 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 previous 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 perceptive anatomical criteria as-developmental units are extracted from. 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 (GABA) which addresses these problems using 3D digital analysis to estimate brain morphology in fossils based on a variety of comparative 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). GABA 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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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 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 Neurormotor 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).

Schmelzmuenter of Alticola stretzovi and Lasiopodomys branditii (Arvicolinae, Rodentia) and Its Evolutionary Polarization

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Enamel Schmelzmuenter offers plenty of information for phylogenetic and mechanical interpretations. Although the arvicoline Schmelzmuenter is taxonomically well known, it remains undetected in some species. In this study, we analyzed the Schmelzmuenter of the first lower molars of two Asiatic arvicolines, Alticola stretzovi and Lasiopodomys branditii, using SEM. In A. stretzovi, 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

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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. (Platyceps) strelzovi could indicate an affinity to the Alticola-subgenus or a common ancestor. We did not notice individual Schmelzmuster-polymermorphism as Koenigswald (1980) did in A. macrotis. In L. brandti, 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 Schelzmuster of L. mandarinus (Koenigswald, 1980) that belongs in Microtus to the more advanced form 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 modestes 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. modestes 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 the Symphagniidae. Symphagnids (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 feature differs from the typical cranial-branchial water intake of most other 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 corpus shear 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 zebrasfish, 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 zebrasfish and chicken a region within N-terminal domain 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 electoreceptors. 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 specifically.
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 peristomal 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 period 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 rate of 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 areas of contact, and any given footfall the load-bearing 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 intrinsically 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 whole organic 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 diaphagous 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 overflies 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 sinuses 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 bony structure of the sinuses 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**

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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 limited by the bone structure (the roof of the oral cavity) and the 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 that 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. In silico simulation 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 for the reconstruction of 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 method 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 batothrichid 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 conflict with the analysis of Lissianhiphyl polyphyly, although other hypotheses (the Tennozyon 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 diorphoid have long been studied. The aim of this work is to address the life history traits of *Apateon* species by bone histology and skeletal chronology. A sample of 22 individuals belonging to *Apateon caducus*, *A. pedestris*, and *Apateon sp.* from the Saar-Nahe Basin, Western Germany (Erdeshach, Odernheim/Pfälz and Niederkirchen/Pfälz, respectively), have been studied and their long bones sectioned at mid-diaphyseal level. Bone histology of *A. caducus* shows juvenile features such as a relatively low 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 Erdeshach 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 stumpy 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 carpal 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 condensation 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 di4 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 *Notonectus laticeps* 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 bone histology and studied 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 indicates 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. Consequently, stressing the ancestral morphotype of the group, be it non-cornuate with developed pectoral and dorsal fins or finless tremataspis. 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 osteostracan intra- and inter-relations 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 tremataspids 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 tremataspids can now be added to the already well char-
etized examples of pectoral fin/limb loss in vertebrates such as snakes, caecilians and eels. What makes the tremataspids exceptional however is that the loss occurs almost immediately after the initial evolution of this crucial character.

Development of the Dermoymotome: 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 meso-
derm and give rise to a variety of derivatives including skeletal muscle, cartilage, endothelia and connective tissue. The dorsal somitic compart-
ment, the epithelial dermoymotome, is patterned by signaling cues from adjacent embryonic structures like neural tube, ectoderm and lateral mesoderm: signalizing the cell fate specification that lead to the various dermoymotomal derivatives. All dermoymotomal cell lineages have to undergo an epithelio-mesenchymal transition and subsequent cell migra-
tion prior to the onset of differentiation. Here, I will discuss our recent results on the molecular regulation of early dermoymotomal differen-
tiation 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 arrange-
tment of the radials as a basis for models of local and whole-wing stiff-
ness 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 stiffness contributions. Stiffness calculations were based on a con-
strained linear spring model minimized for stored energy after perturba-
tion. Direction of passive bending was based on the spatial relationship between neighboring joints. Comparing data from the wings of six spe-
cies 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 oscilla-
tors 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 cap-
ture 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 verticaxis mus-
els. We predict that due to the presence of the extraordinary degree of morphological and functional specialization of the prey capture appa-
ratus, 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 ani-
mal capable of achieving steady speeds of approximately 60 km/h for durations exceeding 20 minutes. This distinction is dependent on numer-
ous 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 ostriches’ leg-segment ratios are optim-
ed for efficient long-endurance locomotion when taking into consid-
eration 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 RScan 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 slaught-
tered specimens. This suggests inherent morphological constraints that passively manage limb positions during locomotion. Our prior examination of ligament function revealed the presence of an “auto-return” mecha-
nism located at the intertarsal joint. This presumably provides the distal limb elements with a rapid forward impetus to re-establish ground con-
tact in the shortest possible timeframe. Ongoing analyses seek to quanti-
tify 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 ha-
bitual 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 sus-
spension behavior are in contrast to the relatively low humeral loading conditions in humans, which occur primarily in connection with manipu-
lation 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 prox-
imal 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 variables 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, has been missing. The developmental and phylogenetic relation between the bone 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 vertebrae form the plate-like spinous processes as part of the carapace. Central questions are whether the development of neural arches and costals of pleurodiran turtles is homologous to cryptodirans, if the costals and neural arches are of endo- or exoskeletal origin, and what ontogenetic causes relate to neural reduction in Pleurodira. The neural arches and costals do not develop as independent ossification centers, but they are initial outgrowths of the periostracal layer 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 neural arches 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 half-bound, the hind limb had 1 intervertebral joints, independent of their adaptations for locomotion 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- or oligossegmental 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 countering gravity enduringly. Superficial, polyssegmental 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.

Eyal 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 promoted both 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 labyrinths were taken, e.g., the height and width of the arc of each semicircular canal. The relative sizes and spatial arrangement 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 changes from arboreality to terrestrialism. In particular, there are differences among diprotodontians in the height of the anterior semicircular
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/upper 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 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 zebrasfish, *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 (2) 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 anniate limb to the three-segmented mammalian limb occurred differentially in forelimbs 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 middle limb is always approximately 38% 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 corre-

**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 lorises 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 and substrate axes (= balance). Large limb excursions and powerful permanent grasping should demand that particular contractile properties of the limb muscles are different from the musculature 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 (Loris tardigradus) using immunohistochemistry. We found that proximal limb muscles that move and stabilize the shoulder, elbow, and knee joints contain 50% or more Type I fibres in the loris, whereas the corre-

**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 accommodate 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, lemur 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 proportion 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 Synapomorph 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 stomiids genera the internal anatomy is a highly variable number of anterior vertebrae reduced or absent. This rare feature among teleost fishes obviously enables extreme dorsal expansion of the gape. The phylogenetic interrelationships 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 box 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 amphiendromous 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 success of climbing ability advantageous to adult gobiids. 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 performance of gobiids, we compared climbing performance and kinematics between adults and juveniles from all three climbing Hawaiian species (Awaous guamensis, Sicyopterus stimpsoni, Lepinotus 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 clench 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 powerbursts in 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 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 deep musculature and to prevent rotation, 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.

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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 project primarily manages morphological images for morphology using MorphBank tools. The system will be used as an active image
Effects of Temperature on Skeletal Growth in Mice

Maria A. Serrat,1 Donna King,2 and C. Owen Lavery3; 1Department of Anthropology and School of Biomedical Sciences, Kent State University, Kent, OH, USA, 2Department of Microbiology, Immunology, and Biochemistry, Northeastern Ohio Universities College of Medicine (NEOUCOM), Rootstown, Ohio, USA (mserrat@kent.edu; mserrat@neoucom) 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 wk) through maturity (12 wk) 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 bone growth. Conclusions: 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 femoral head. In birds, 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 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 prevents 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 maximum/minimum law. This concept in mechanics has explained 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. Results: 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 in 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 continuously optimizes the feather shape to one with constant strength.

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 different lines of evidence: 1) Neocortical cell types are diverse and the distribution of these cell types is limited to different mammalian species. 2) Neocortical cell types are likely to be involved in the evolution of cognitive abilities. This study aims to address these limitations by comparing neocortical cell types in anteaters and sloths. The results of this study will provide insights into the evolution of neocortical cell types and their potential role in the evolution of cognitive abilities.
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 morphologically distinct neuronal proteins, calcium-binding proteins (calbindin, calretinin, parvalbumin), neuropetide Y, and glial fibrillary acidic protein in three species of xenarthrans (Myrmecophaga tridactyla, Tamandua tetradactyla, Choloepus didactylus). Overall, these species share 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 xenarthra 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 descendant 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 LRPS/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 pericocular 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 mesencephyme 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 as to WISE’s described above, and electroporation of Axin and Dishevelled deletion constructs into 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 Dolerops peton and the Anura specifically.

**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 tract, 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, Austra-

**New Features of the Amphibian Dolerops peton (Telmampondyli), and Its Implications for the Origin of Frogs**

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Since it was first described in the late sixties, the Lower Permian (Leon-

**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 tibiofibulae 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 rami (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 strong 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 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 placentaion of Talpa occidentalis strongly resembles this of Talpa europaea (Malassine 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 emuate 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 study examines the pattern and level of integration in the mandible of modern humans and chimpanzees. Before the morphological differentiation 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 Pax2, engrailed, 1, Ephrin A1, and 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 across-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 informal programs and activities, 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 osteichthyans. 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 teeth. Studies on mouse mandibles show that the heterochronies observed in morphological studies extend to shifts in the expression of major genes. In early timed stages of development together with in situ studies of osteichthyan tooth row on the dentary as observed from appropriate phylogenetic map the expression of genes that are important in establishing regional differentiation, including Pax2, engrailed, 1, Ephrin A1, and 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.

Le Moustier 1 Dental Development and Enamel Thickness
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The Carnivorous Mammals (“Creodonta”, Carnivoromorpha) from the Early Eocene (mp7-mp10) of the Paris Basin?

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In Europe, carnassial mammals of the orders “Creodonta” and Carnivoromorpha 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, MP9+9; Grauves, MP10). Current knowledge on the Eocene carnassial faunas from the Paris Basin is based mainly on the works of Rich (1971, 1972) (USP. Cal. 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 MP9+9. Thereafter, during the MP10, they increase in size and show morphological innovations, as exemplified by the first hypercarnivorous Francotherium indigreni. “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 Limmnocyoninae (Prolimmo­cyon) 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 carnivore 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 the surface of the anterior part of this endodermal tube as a “stomodal collar.” Since the ectodermal endoderm are histologically unidentifiable, in search for a role of them in odontogenesis we used orthotopic transplants of oral endoderm 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 a collar 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 the origin of odontosome. Several new intermediate stage between odontosomal and perikymatal layer of odontosome. The evolution of the perikymatal/pattern from endodermal to ectodermal.

What Do We Know About the Carnassial Mammals (“Creodonta”, Carnivoromorpha) From the Early Eocene (mp7-mp10) of the Paris Basin?

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The locality of Le Quesnoy (Oise) has yielded the most diverse continuation of the European carnassial fauna during the early Eocene. This site is situated 20 km north of the megalodontian 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.

The Carnivorous Mammals (“Creodonta”, Carnivoromorpha) from the Early Eocene (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 Hyaenodonta: Arfa gingerichi Smith and Smith, 2001; Promotus mueni Smelik and Smith, 2001; and Promotus girardoti Smith & Smith, 2001; two Oxyaenidae: Palaecionis gigantea de Blainville, 1842; Oxyaena woutersi Lange-Badré and Godinot, 1982; and two ‘Miacidae’: Miacis laticaudus Quiet, 1966; and Miacis sp. Moreover, the enigmatic species Dormaaldon woutersi Lange-Badré, 1987 from Dormaal is shown to be synonymous with P. gigantea. A possible synonymy for the two species of Promotus is proposed based on the generic attribution of O. woutersi, which might be referred to Dipsadiformes. Our cladistic analysis of primitive early Hyaenodontidae roots the Limnocyoninae within the “Provinverriinae.” The European “Provinverriinae” belong to two main lineages. The cladistic analysis supports an African origin for the “Provinverriinae”, 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 composition and paleoecological localization of the Paris Basin.
Functional Morphometry of the Pelvic Joint (Articulatio Coxae) of the Quail (Coturnix coturnix japonica)

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Plate-forme Morphométrie, IFR101 & UMR 5202, ©, Structure, Evolution and Biodiversity Dept., Systematic and Evolution, Museum National d’Histoire Naturelle, CP 55, 57 rue Cuvier, 75231 Paris cedex 05, (baylac@mnhn.fr).

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 birds, and the relevance of reconstructing cartilage in functional anatomy 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 placental, Afrotheria (except some tenrecs) and Xerarthra, do not possess a baculum. So this element appears to be typical for more derived placental mammals (except lago-morphs, tree-shrews, cetartiodactyls, perissodactyls and pangolins and some particular exceptions in bats, carnivores, insectivores and primate). 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 arvalis, M. subterraneus, Sciurus vulgaris, Microtus minutus and Apodemus sp.). The whole glans of penis was dissected, double-stained with alizarin and alcian blue and stored in glycerol. Especially we concentrated on the bacular size and shape (variability). Moreover, in M. arvalis 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 phyleogenetic context. 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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2Faculdade de Filosofia Ciências e Letras-RP Universidade de São Paulo, Brazil, Instituto de Zoologia, Universidade Bonn, Germany. Although echimyrid 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., Clamartys hirumi 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 purpose of this investigation is to detect 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 Cuvum venosum and the Cuvum pulmonale are connected by a wide opening, but, during ventricular systole, are functionally separated by a muscular ridge. The Cuvum pulmonale has no arterial exit ejecting oxygenated blood through the intraventricular canal into the Cuvum venosum and the Cuvum pulmonale. A functional hypothesis suggests that the muscular ridge acts as central shunt that directs oxygenated blood from the Cuvum arterioso into the left and right aorta, and deoxygenated blood from the right atrium through the Cuvum 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 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 methods 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
skeletal changes of the fascicles’ 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 Microwear 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 diet-related 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 has 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 brunnea 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 Lysosomatine Skinks (Squamata: Scleroglossa)
James R. Stewart; Department of Biological Sciences, East Tennessee State University, USA (stewarjr@etsu.edu)

Viviparity and placental nutrient provision have evolved on numerous occasions in squamate reptiles. Five lineages are substantially placentotrophic. For these, the genera Paratroposoma and Niveoscincus, are closely related scincid lizards geographically distributed in the highlands of southeastern Australia. Histological comparison of placental ontogeny of placentotropic 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 omphaloplaenta (yolk sac) and a chorioallantoic placenta. The omphaloplaenta 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 placentotropic 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 placentotropic species have evolved regions or zones that are functionally specialized. Differences in the degree of structural similarity of these regions among placentotropic 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 Tenmospondyl Skulls
J. Sebastien Steyer,1 Christian A. Sidor,2 Ross Damiani,3 Marc Boulay,4 and Jean-Christophe Scheyer5

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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 morphological comparison of placental ontogeny of placentotropic 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 omphaloplaenta (yolk sac) and a chorioallantoic placenta. The omphaloplaenta 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 placentotropic 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 placentotropic species have evolved regions or zones that are functionally specialized. Differences in the degree of structural similarity of these regions among placentotropic species are explicable if selection favors retention of some functional characteristics, in addition to the enhancement of novel functions.

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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 project anteriorly to the forebrain and posteriorly to the spinal cord. This map of all r4-derivatives from their origin to their final locations. We have generated a transgenic line containing the Hoxb1 CRE-recombinase gene expression may provide information about the hierarchy of homology. 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 worsen 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 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 Matt E. Svensson; Uppsala Biocenter, Box 7080, SLU 75007, Uppsala, Sweden (svetman@googlemail.com) Ever since Owen, students of homology have been occupied with same-nomous. Understood in evolutionary terms, synapomorphy in effect is the arbitress of homology, the criterion of congruence. In phylogenetic systematics, synapomorphy and homology are generally regarded as synonymous. Recent usage of regulatory gene function in homologization or, alternatively, explanations involving constraints that result in maintenance 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 believe 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.

Contributions of Rhombomere 4 and Hoxb1 to Hindbrain Sensorimotor Structures Michele Studer,1 Marianna Di Biondo,1 Marta Mancano,1 Anna Maria Franze,2 Luigi Sequino,2 Luis Paules,4 3Telethon Institute of Genetics and Medicine (TIGEM), Naples, Italy v-2GB “A. Buzzati Traverso” CNR, Naples, Italy, 2University of the Stadi di Napoli Federico II, Naples, Italy, 4Faculty of Medicine, University of Murcia, Murcia, Spain (studer@tigem.it)

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 circuits. We have generated a transgenic line containing the Hoxb1 gene expression 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 localizations. 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 axial 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 Adam P. Summers; Univ. California Irvine, Irvine, CA 90278, USA (asummers@uci.edu)

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 used 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 producing 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 Adam P. Summers and Mason N. Dean, University of California Irvine, Irvine, CA 90278, USA (asummers@uci.edu)

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 worsen 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 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.
Articular Cartilage Function and Organization: Integrating Dynamic Mechanics With Cryopreservation Effects
M. Szkarka, and J.E.A. Bertram; University of Calgary, Calgary, Alberta, Canada (mszkarka@ucalgary.ca) 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 equilibrium 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
J.A. Szczepanski, and C.D. Wilga; Department of Biology, University of Rhode Island, 101 Flagg Road, Kingston, RI 02881, USA (jazz@uri.edu) 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 exhalas water to exca- vate 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
Paul Tafforeau, Laboratoire de Géobiologie, Biochronologie et Paléontologie Humaine, UMR CNRS 6064, Poitiers, European Synchrotron Radiation Facility, Grenoble, France (paul.tafforeau@esrf.fr) 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 very rarely 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 preservation. In this paper, 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
Koji Tamura; Graduate School of Life Sciences, Tohoka University, AobaYama Aoba-ku, Sendai 980-8578, Japan (tamj@biology.tohoku.ac.jp) 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
Christine Tardeu, Christophe Boulay, Geneviève Dival-Beaupère, and Jérôme Hecquet; 1 CNRS, Anatomie comparée, MNHN, 55 rue Buffon, 75005 Paris, France; 2 INSERM, C.H.U. Raymond Poincaré, 92380 Garches, 3 Ingénieur informatique, CNRS, MNHN, 55 rue Buffon, 75005 Paris, France 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. Here, it is 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 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, 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 in animals, both typically and otherwise. 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-scanning
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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. Palaent. 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 petrosal 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 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 basioccipital and the periotic to the ventral portion. The periotic does not completely roof over the petrosal canal at any point. Thus, the basioccipital encloses the petrosal canal only on the medial side, unlike the condition seen in camelids, Bunomeryx, and Merycocecidon.

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, unlike 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’Brien 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 imaging 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 encoding 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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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 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 tissue 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 Precaudal 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 tetrapod squamates tend to be displaced relative to one another. In the present study, characteristics of the adult axial myology and osteology in three other precaudal regions 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 each other but also from the level of the pectoral girdle. The posterior extents of these cranio-vertebral muscles vary similarly in snakes. In addition, unlike in tetrapod 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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Morphological changes in the avian vocal organ, the syrinx, have been extensively studied from a functional perspective. The syrinx is a complex organ that allows birds to produce a wide range of sounds, including songs and calls. This study aimed to investigate the structure of the European Starling syrinx and its function in detail.

The avian vocal organ, the syrinx, has four pairs of intrinsic muscles (ventral and dorsal tracheobronchialis, vTB/DTB; ventral and dorsal syringeal, 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 immediate reactions to both acidic and alkaline preincubations and lower oxidative capacity. It reacted negatively to both antifast and antifast antibodies. The unusual staining profile and EMG data suggest the presence of superfascicular superfast fibers, as described for rat-tailed snake 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 specimens from 3 other songbird families, indicating that the presence of superfascicular fibers is likely a common trait of the oscine syrinx.

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Microwave 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 and generating microwear elevation models 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 occusal 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 Amblystoma 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. RA has been shown to induce regeneration of control or RA-treated (0.1 μM) embryo tails far exceed 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 presomatic and somatic regions. The presence 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-early late growth.

Biting Performance and Skull Shape Variation in Durophagous and Teeth-digging African Mole-rats (Fukomys, Bathyrhigidae, 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 trade-offs 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.

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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 to 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 Lactertidae) 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, we explore whether the evolution of sabertooth-like cranial shape with larger canines having more elongate rostra, taller, more vertical occupants, 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 dimorphisms 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 in lizards, of which the postcranial skeleton and some cranial bones are free from sexual selection. As for shape variables, significant differences were only observed between age classes (0-3) on the basis of the wear of their canine and first premolars. In each specimen, ventral skull, dorsal skull, and mandibles 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 morphometric analyses were performed using the statistical shape analysis (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 arborically-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 osteoderms, 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 dermal development as additional components of the dermoskeleton. 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) skeletal 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 Iraq), 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 Posidonienschiefer (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) 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 masseter 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 xenarthrans reflects a combination of historical, functional and biomechanical constraints. The hypsodont 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 Ureutis), 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 amnioliores, selective browsers to bulk grazers among herbivores, and omnivores. Within cingulates, the mandible and teeth of cutiatuses 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 eucharitales and peltodentes (though the latter was likely a specialized herbivore). Within pilosans, anteatere, with their edentulous jaws, are apparently highly specialized. Among sloths, the craniojambidular joint and wear facets in mylotodontes indicate anterio- medially 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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Across primates, molar enamel thickness, and craniofacial and dental morphology vary significantly across primate species, and these differences have been linked to the mechanical consequences of the foods consumed. We sampled the mechanical properties (fracture toughness and Young's modulus) of fresh orangutan fruits to test whether eating hard or soft foods correlates with these morphological adaptations. We found that the mechanical properties of selected orangutan fruit parts (exocarp, mesocarp, and endocarp) were significantly tougher than fruits. When we compare the parts of the fruits among different stages of ripeness. Inner bark, seeds and leaves are significantly tougher than fruits. Finally, to examine this data in a broader context, we compare mechanical properties of orang-utan fruits to those of certain ungulates. The elevated mandibular condyle improves the mechanical advantage of the massetericus; its morphology allows considerable lateral and anteroposterior movements. The mechanical properties of foods consumed by wild orang-utans (Pongo pygmaeus wurmbii) were significant 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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The complexity of major groups of organisms the term “complexity” seems to be unavoidable, even though there is no gener- ally 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 individu- alized parts. I will discuss the mechanistic basis for this proposal and suggest genetic correlates of this concept. For instance recent work sug- gests 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 ante- rior digit. We conclude that the anteriormost digit in the bird wing has the same developmental dependence 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.

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Feeding in baboons is highly energy-intensive, and 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 functional 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 more muscle fibers and more muscle volume. Both sexes have a fast-twitch superficial tempora- lis 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 func- tional 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 tempora- lis and superficial masseter in females. The model has testable assump- tions 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 Head 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 bulbuslacertellum on the opposite side of the ventricle. The MR and bulbusla- certellum 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 seption determine the degree of shunting between the pulmonary and systemic circu- lations. 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 pat- terns during various types of behavior and metabolic states of the relevant species.

Effects of Body Elongation on the Patterning of the Abdominal Viscera in Polypterus Forms (Actinopterygii)

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A highly elongate body form has evolved independently multiple times within the bony fishes. Axial elongation of fishes occurs via the addition of abdominal vertebrae, addition of caudal vertebrae, and/or by lengthening the vertebral column. 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 Actinopterygii. Axial elongation in fishes occurs via the addition of abdominal vertebrae, addition of caudal vertebrae, and/or by lengthening, which 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.

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 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 comparison 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 cor- rected. 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 de- velopmental mechanism of the Crf4 phenotype is expressed at the em- bryonic stage of development.

A Single Ancient IGF1 Allele Causes Small Size in Dogs

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The domestic dog exhibits greater diversity in body size than any ter- restrial vertebrate. We use a novel three-plot 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 Sac in Sauropods and Other Saurischians

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The presence of postcranial pneumatization in sauropods and theropods 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 pneumatization 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 re- spiratory system does not rest on the mere presence of pneumatization. Rather, the evolutionary pattern of postcranial pneumatization pro- vides strong evidence for bird-like air sacs in sauropods. Early sau- rishchians 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, pneumatiza- tion 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 thermoregu- latory 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 Tullibock Formations of Garfield and McConie Counties in Montana, USA. This geological section preserves several 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 Mesodon and Comexomys. 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 Mesodon thompsoni, a genus 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 generalizes diet could have been a key component of the mechanism of survival. 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 tectonic events.

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 hypothesis, 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 place. It is generally accepted that increased ingestion of foodstuffs and the relative length of the intact tail were 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 equal 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. Systematically 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 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 on detailed details of the morphological characters. 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 from the jaw joint. Within Beloniformes a sister group relationship of Adrianichthyidae to a clade consisting of ((Exocoetidae + Hemirampidae) + (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: Rhynchocephalia: Morphological, Functional and Evolutionary Aspects

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Morphology, function and ecology of tail autotomy and regeneration are less known in Sphenodon (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 equal 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.

Journal of Morphology DOI 10.1002/jmor
Coupled Locomotion and Ventilation in Mammals: What is the must be taken—should adapiforms continue to be categorized as simply samples of Miocene Asian sivaladapids and European cercamoniines. To—are the results of shape comparisons between extant groups and smaller patterns of adapiform radiation. As significant (and somewhat surprising), North American taxa appear to resemble African and Asian lorisiforms, (orientation of major molar landmarks (including major cusps and shearing)

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, paleontologists 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—a sampling of three continents and extant primate (lemurs, lorises, and 

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, paleontologists 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—a sampling of three continents and extant primate (lemurs, lorises, and 

Palaeolemur, Adapis, Cantius, Leptadapis, and Nosuchius differ significantly from their Euro-

Adapiforms exhibit significant differences from Malagasy adapiforms. 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 African 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 abdo-

mental 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 pyra-

mids) and their cynodont ancestors. Here, we report on the activation pat- 

terns of the abdominal musculature in another metatherian (Philander) and two eutherians (Atelerix and Rattus) during resting ventilation and locomo-

tion. 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. Videofluoroscopy was used to correlate muscle activity and diaphragmatic movement. All species tested exhibited 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 loco-

mation and symmetrical gains.

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 vitro 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 anterbrachium to form a deeper socket than in specimens with complete articular cartilage (as previously suggested in literature). The mean inter-observer reproducibility ranged from 0.03 mm to 0.05 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 any minor differences were noted in the geometry of the corresponding humeri. Subchondral bone of the elbow joint was more congruent in specimens with complete 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 plagiodum (Galea), Squallus acanthias (Squalidae) and Leucoraja erinacea (Batoidea). Gape area to hyoid volume ratios distinguish the strong suction capture mechanism of Chiloscyllium, from the moderate suction mechanism of Squallus 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 Squallus 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 processes, 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 Droso-

phila. However, important differences in network organization for inte-

grating 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.

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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 textual 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 correlated with 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.


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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 dermocranium, 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 dermocranial 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 post 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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In the laboratory of exaptation, the highest and most rigorous level of Darwinian design, new functions arise from those that are already present in numerous archosaurous lineages, and many of the old traits are untouched until well within the avian radiation. Mechanically 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 experimentations 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.

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 bolus 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-
gies 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 Screammers (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 basi-sphenoid and exoskeletal pterygoid, developing from an early quadratoporal commissure. Among birds, the Palaeognathae and Neognathae 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 basicrania of a scooter (Chauna sp.) by using computer-aided 3D-reconstruction, build-up from a histological serial section. As a result, the scooter 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-fox synapomorphy of Galliformes and Anseriformes, and reject the assumption that this new articulation type arose convergent within the Galloanserae.

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 of the 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 palaeogenetic 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 evolutive purposes. Thus, ontogenetic characters are often used as representatives of the usual 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 and 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).

Limb Bone Loading in Salamanders During Terrestrial Locomotion

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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 platyrhine 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. libidinosa), 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 shunts (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

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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 congeneric (Propithecus 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 which 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 culms 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 spot 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 spot 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 result 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 of 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 E115 to the stage of early adult dentition (ED60). The adult type bicuspid teeth (pleurodontly ankylosed to bones) appeared as the third embryonal tooth 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 abruptly 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 overlaps the axial complex in the form of well marked convexity. Any structure of IEE connected 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 bairdi) 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 hierarchy of structural variation, 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 Marsupials
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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 reproductive evolution involved 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. 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 amniants 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 pipiidae. 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 heterochronous events than expected, also in cranial muscles other than eye muscles.

On the Unique Deep Plantar Tendons Arrangement in the Foot of Picorniformes (Aves): Its Possible Origin and Evolutionary Implications
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The monophyly of Picorniformes sensu Wetmore (1960) has often been questioned. A strong argument for monophyly of the Picorniformes is a unique arrangement of the deep plantar tendons of m. flexor digitorum longus (FDL) and m. hallucis longus (HFL) which occurs in Galbulidae, Buccoida, 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 arrangement and its evolution has been revealed prior to our studies. It seems that the first supply digits I and II, while that of the first supplies only digit II. To explain the origin of such an arrangement we propose the following hypothesis of a derivation of an arrangement in question from an ancestral one, which is a pool of ancient birds, ancestors of trogons, coraciiforms and piciforms. The unique arrangement of the deep plantar tendons is only partially explained by the acquisition of zygodactyly. It bears ancestral prezygodactyl features and cannot be functionally explained by climbing adaptations.
Bone presents a specialized supportive tissue. Changes in bone structure lead 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, Gobidae)—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.