

Post-natal Cerebellar Granule Cells of Rat: A Quantitative Study

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We aimed to verify how granule cells of two post-natal ages (6 and 10 days) modify quantitatively and whether their parameters get close to those of a younger age (2 months) of an adult age spectrum already studied. In semithin sections, we estimated the mean volume (V_N) of the nucleus using the ratio: nuclear volume density (V_N) / nuclear numerical density (N_N). In electron micrographs, we calculated the V_V of cytoplasm, mitochondria, Golgi complex, cytosol, and the surface density (S_V) and absolute surface (S) of rough endoplasmic reticulum (RER). These values permitted the estimation of absolute values (V) and the somatic mean volume (V_N). At 6 days, the nuclear V_N was $196 \mu\text{m}^3$ and at 10 days was $113 \mu\text{m}^3$. At 6 days, the V_N of the soma was $291 \mu\text{m}^3$ and at 10 days was $156 \mu\text{m}^3$. Significant differences were also exhibited by the V of cytoplasmic components, and the S of RER. The comparison 10 days versus 2 months detected no significant differences in the nuclear or somatic V_N , in the V of cytoplasm, of mitochondria, of cytosol and in the S of RER. It was concluded that, under this stereological study, granule cells of 10 days are already similar to the younger adult ones. Supported by the FCT and the Eng. António de Almeida Foundation.

The Studies of Ecomorphs of Different Classes of Hydrobionts

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A complex large scale process of formation of organisms, adapted to concrete habitat conditions and thus belonging to definite ecomorphs, is the main side of biological evolution. Ecomorph is a complete system of inter-conditioned ecological-morphological adaptations, which determines the general body construction of the organism in connection with a species concrete evolution under concrete biotope (Alev, 1986). For more than 40 years in the Department of Theory of Living Forms (now Ecomorphological Laboratory) they have conducted comparative studies of complex adaptations in hydrobionts of Pisces, Amphibia, Reptilia, Aves, Mammalia classes, representatives of which belong to different ecomorphological groups—plankton, benthos, necton. In particular, they have studied morphological peculiarities of the body and coverings form structure, hydrostatic and hydrodynamic adaptations, moving systems and their functioning, etc. The main methods for studies are: functional-morphological analysis, observation of living objects, various experiments on animals. It is established that characteristically similar adaptations systems, adequate or nonadequate by their complexity and effectiveness, are produced in genetically distinct systematic groups of organisms, belonging to one ecomorph, under evolution on the convergent basis. Numerous qualitative and quantitative data, permit one to work out a principle of building up the general ecomorphological system of hydrobionts. Such investigations are problems of biological evolution, functional morphology, hydrobiology.

The Functional-morphological Studies of Water Birds and Semi-water Mammals

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Formation of secondary water vertebra is connected with the basic change of habitat and gradual creation of auxiliaries, providing a possibility of such change; this line is essential in evolutionary and functional morphology of animals. Insufficient knowledge in this question makes it difficult to form a general view of the formative laws for higher vertebra, whose representatives are at the initial stage of their formation as hydrobionts and at the final eunecton stage of nectogenesis as well. In the Laboratory of Ecomorphology they conduct studies of the ways and laws of nection adaptations development in Aves and Mammalia. They study comparatively hydrostatic, hydrodynamic, habitat-morphological adaptations, peculiarities of construction and functioning of water habitat gears. The methods of studies are quite variable, most of them are functional-morphological analysis, experiments with living objects, modelling, film shooting. It was established that with the transfer from nectoxeron ecomorph species to xeronection and eunecton oaves there takes place gradual improvement of hydrostatic and hydrodynamic adaptations of body form water streaming. All this leads to the lowering of energy expenses for movement. The data obtained are important for under-

standing the ways and peculiarities of animals historical development, functional and evolutionary ecomorphology, formative role of habitat, etc.

Ontogeny of the Basicranial Articulation of *Pantodon buchholzi* Peters 1877 (Teleostei, Osteoglossomorpha)

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Osteoglossoids are unique among teleosts in possessing an articulation between a ventrolateral peg of the parasphenoid and the entopterygoid. The development of this basicranial articulation is investigated in the butterflyfish, *Pantodon buchholzi*. Pars metapterygoidea of the hyopalatine arch already develops a prominent medial cartilaginous knob at 7 mm SL. The peg-like process of the parasphenoid is not developed yet. The knob on pars metapterygoidea remains cartilaginous even when the metapterygoidea begins to ossify at around 10 mm SL. Only then, a short lateral process of the parasphenoid is developed, though without immediate contact to the hyopalatine arch. During subsequent development this process elongates and articulates with the metapterygoidea knob. It is only in later ontogenetic stages that the entopterygoid also contributes to the articulation by forming a deep trough-like socket housing the ventrolateral peg of the parasphenoid. This is also the anatomical situation found in the other adult osteoglossoids. The significance of the basicranial articulation in osteoglossoids is reevaluated by comparison with other gnathostomes that possess similar articulations.

Comparative Aspects of Breathing Mechanics

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Among mammalian species, parameters related to pulmonary capacity, including tidal volume and compliances, are directly proportional to the body weight (BW) of the species. On the other hand, parameters related to the timing of breathing or flow rates are not directly proportional to BW. Specifically, the exponent of the relationship between breathing rate and BW is -0.25 and that for airflow resistance is 0.75 . Hence, the tendency of smaller species to breathe faster than larger species is accommodated by a lower BW-specific resistance and by a shorter time constant of the respiratory system. These general rules, in first approximation, apply also to the neonatal period, and could be interpreted as the adequate design to appropriately accommodate systematic differences in metabolic rate and pulmonary ventilation (VE), which, per BW, are higher in smaller species. However, during breathing the respiratory system behaves as if its mechanical properties differed from that measured in passive conditions. In expiration, partial narrowing of the glottis prolongs the expiratory resistance and time constant. In inspiration, the distortion of the chest wall substantially lowers the effective compliance. Hence, priorities other than those of accommodating ventilatory and metabolic needs dictate the mechanical behavior. In newborns, chest distortion due to poor coordination of the inspiratory muscles could pose a limit to VE, and in the most altricial newborns VE is largely substituted by gas exchange through the skin.

Osteoderm Function in the Lizard Family Cordylidae

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In the family Cordylidae, there is considerable variation in the degree of development of osteoderms in the epidermis of the dorsal and ventral body, from their complete absence in some species to well-developed ones in others. To elucidate the significance of this variation, we investigated possible correlations between degree of osteoderm development and running speed, body coloration and altitude. Brightly colored and montane species with extended basking times, lack osteoderms and are fast runners, while lowland, cryptically colored species that spend less time in the open have well-developed osteoderms and are slow runners. We hypothesize that this dichotomy is due to differences in visibility of lizards and the relative roles of birds of prey versus other predators in shaping antipredator devices. Armor is ineffective against birds of prey, a speedy retreat to shelter probably the best means of escape. Armor is, however, highly effective against other predators, especially those that can extract lizards from their shelters during times of inactivity. The observed pattern in degree of osteoderm development in the Cordylidae is, however, confounded by phylogeny,

the forms lacking osteoderms also being closest relatives. We found a way to test our hypothesis by comparing the degree of osteoderm development in melanistic and non-melanistic populations in a few *Cordylus* species, the melanistic populations known to be cold-adapted. The melanistic populations consistently had lesser developed osteoderms than their non-melanistic counterparts.

Heterochrony in the Skull of Lacertid Lizards

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Lacertid lizards generally have a very uniform appearance. Homoplasy and character incongruences affect both the external morphology as the osteology, and hence lacertids are still one of the least understood lizard groups of all. Despite this uniformity, recent investigations have shown that the lacertid skull is the subject of a great influence of intra- and inter-specific heterochrony, which can at best be recognized in the derived African clade, although heterochrony is also present in palaeartic lacertids. Among the different heterochronic traits in the family, paedomorphosis is a very conspicuous phenomenon, causing, for instance, a reduced degree of dermal ossification, a short parietal table, or an enlarged braincase and closed post-temporal openings. Within lacertid lizards, the reasons for heterochrony are different. While the paedomorphic traits in Caucasian Rock lizards appear to be functionally correlated to cranial kinesis, those of many derived African lacertids as well as of palaeartic, xeric-adapted forms result from progenesis in relation to ephemeral, "r-selecting" environments. However, many questions concerning the phenomenon of heterochrony in lacertids still remain unresolved due to the lack of knowledge of interspecific differences in ontogenetic development, which can be illustrated, for example, in the shape and development of the lacrimal bone. If the phenomenon of heterochrony in lacertids is better investigated, it will surely be helpful for understanding the phylogenetic affinities within the family.

The Innervation of the Avian Lingual Apparatus and its Use for Systematics

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In the development of the avian tongue, material of different gill arches was incorporated. Therefore, the muscles of the tongue are innervated by different cranial nerves. This provides an important aid in establishing homologies of some of the avian, lingual muscles, for which otherwise only topographic criteria would be available. It will be shown that paleognathous (tinamous and ostrich-like birds) and neognathous birds have a markedly different functional morphology of the lingual apparatus. It will also be shown that the paleognaths retained the small tongue and its associated plesiomorphic construction, while the neognaths developed apomorphic features as a response to a development of the free part of the tongue and its involvement in food transport.

Gene Expression Patterns and Segmental Plan of the Lamprey Brain

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The vertebrate neural tube contains a series of neuromeres along the anteroposterior axis. The lamprey occupies an important position in the phylogeny for understanding the origin of this segmental pattern. We have isolated cognates of several regulatory genes from the embryonic cDNA library of *Lampetra japonica*, and performed in situ hybridization on the developing brain. Among the genes examined, LjOtxA, LjPax6, LjDlx1/6 were expressed in clearly demarcated domains, implying the presence of developmental compartments. They were also consistent with the prosomeric patterns by comparison with the expression of gnathostome cognates. Together with the morphology of nerve tracts, the lamprey brain seemed to possess a polygonal pattern similar to those in gnathostome brains. In the lamprey telencephalon, however, there was no clear expression domain of LjEmx, the cognate of gnathostome Emx that defines the pallium. Moreover, in the telencephalon of the lamprey, expression do-

main of LjDlx1/6 and LjPax6 widely overlapped, unlike in gnathostomes in which the genes are expressed in a complementary manner. It was concluded that the patterning of the lamprey telencephalon is not based on a tripartite pattern, as seen in gnathostomes.

The Skull Skeleton of Triassic Colobodontidae sensu Andersson 1916 (emended) (Actinopterygii: Perleidiformes)

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The actinopterygian genus *Colobodus*, originally established from a dentition fragment (*Colobodus hogardi* Agassiz, 1833–45, t. II, p. 237), has been known for one and a half centuries from numerous fossils, mainly scales and teeth from the Germanic Triassic (see Browne, 1891; Schultze and Kriwet, 1999). Aside from these fragmentary remains, a number of more completely preserved and thus better documented species have since been added (*Colobodus bassanii* de Alessandri 1910, see Dames, 1888; Stolley, 1920; Oertle, 1927). Several papers have contributed to the knowledge of the osteology of this wide-spread genus (Guttormsen, 1937; Beltan, 1972, 1988; Schultze, 1986, see especially, Andersson, 1916; Stensiö, 1921; Hutchinson, 1973b; Bürgin, 1996), but some questions concerning the composition of the dermal skull elements have persisted. On the basis of a core sample of well preserved specimens the skull morphology of Colobodontidae sensu Andersson 1916 (emended) is briefly reviewed and tentatively restored as a basis for future phylogenetic studies of stem group neopterygii. For most references see: Bürgin T., 1992. Basal ray-finned fishes (Osteichthyes; Actinopterygii) from the Middle Triassic of Monte San Giorgio (Canton Tessin, Switzerland).

The Anatomy, Histology and Contents of the Gastrointestinal Tract of *Schilbe mystus*

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Twelve female *Schilbe mystus* were obtained from Lake Victoria (eutrophied by the water hyacinth) during the rainy season. Gross anatomy and histology of the gut were done using conventional methods (dissection, HE-stain and Masson's Trichrome stain). Gut contents were determined by percentage visual assessment. Grossly, there were two rows of teeth on the upper jaw and two pairs of pharyngeal teeth. The gastrointestinal tract (GIT) consisted of a short esophagus, two-chambered stomach and four coils of the intestine. Histologically, the oral stratified squamous epithelium changed to pseudostratified columnar in the rest of the GIT. Cells resembling alarm cells were present in the esophageal epithelium. The wall consisted of the conventional layers, tunica mucosa, submucosa, muscularis, serosa/adventitia. The gut contents were 80% algae species and 20% insecta. The carnivorous fish were not stunted by the relatively rich vegetarian diet imposed on them by the eutrophication of Lake Victoria by the water hyacinth.

Recapitulation of the Somatic Muscles of Vertebral Animals in Prenatal Ontogenesis

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The study of mechanisms of the morphogenesis of separate tissues during embryogenesis, especially during transformation from one structural level to another, has direct relation to the fulfillment of the morphological variety in evolution. Herein, differentiation of the initial cellular components in first turn, then cellular mutual contacts in the result of which different tissues are formed, act as basic moving force of evolution. Separation of the myoblasts from the myotome and their merging in muscle platelets and myosimplasts is index of the first stage of the gytogenetic differentiation of the somatic muscles of the animals. Owing to complexation of the myofibrillar apparatus in these myogenesial structures first myotubes, then primitive and definitive muscular fibrils are formed. Such consequent morphological reforming is at one side morphofunctional adaptation of the muscular tissue. Besides of that, each next form rejects previous one. In the development of the somatic muscles of the vertebrate animals cenogenesis which exists in definite periods of ontogenesis and disappear afterwards is revealed. In our opinion, it is right to subdivide it on cenogenesis - cellular (early) and symplastic (late). In the limits of these periods striped

muscular fibrils histologically are not differentiated yet, and because of that these periods cannot be called cenogenesis at tissue level. In the development of the somatic muscles of the vertebrate animals there is several histogenetic recapitulation. First of them is forming of the third embryo layer, which is formed either by teloblastical (proto-mouther), or enterocolical (secondary-mouthed) way. Second one is appearance of the somites, third-myotomes, fourth-separation of the myoblasts from myotome, fifth-mergence of myoblasts in muscular platelets, sixth-formation of the myosimplasts, seventh-formation of the muscular tubes and, at last, eighth-formation of muscular fibrils.

The Cranial Morphology of the Ground Sloth Genus *Hapalops*

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Sloths of the genus *Hapalops* (Lower-Middle Miocene of South America) are among the smaller-sized members of the family Megatheriidae, and are often described as part of the basal stock that gave rise to later, larger-bodied animals such as the Pleistocene *Nothrotheriops* and *Megatherium*. There are many cranial similarities supporting this idea; however, *Hapalops* is not merely a smaller version of later genera. Rather, this sloth shows a unique pattern of character distribution, combining retention of characters previously described as both plesiomorphic and apomorphic in other genera. Specifically, *Hapalops* retains anterior caniniform teeth not present in either other genus in this lineage, but also has a temporomandibular joint elevated significantly above the cheektooth row, as seen in the recent genus, *Bradypus*. Other unique character complexes include the elongate ascending process of the zygomatic arch as in *Bradypus*, combined with the the anteroposteriorly elongated skull of *Nothrotheriops*. Previous work has delineated the features and functions of these and other character complexes in megatheriids, and has demonstrated constraints against these character combinations. Nevertheless, *Hapalops* demonstrates that these and other functional complexes can exist simultaneously in a single animal. These characters affirm that these modifications through time mimic a Booksteinian transformation series and define the polarity of changes that occurred in the evolution of the megatheriid lineage. This paper relates these complexes to their functional and evolutionary implications.

The Hubrecht Laboratory Embryological Collection

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"A Collection of Collections," contains embryos from about 600 species either preserved in alcohol, as histological sections or embedded in paraffin ready for sectioning. There is a wealth of accompanying documentation, protocols, field notes and original drawings of whole embryos and sectioned material. The core of the collection is that assembled by Hubrecht in the late 19th and early 20th centuries. He began by accumulating embryos of various developmental stages of local hedgehog and shrew. Thereafter embryos of a variety of species from the former Dutch colony of Indonesia and also Africa and South America were also assembled. Hubrecht's collection is matched in size and diversity by the one of J. P. Hill, a later contemporary. This nicely complements the Hubrecht collection as Hill focussed mainly on Australian species. Equally valuable collections include slides and notebooks of both Mangold and Spemann and serial sections of natural mutant mouse embryos donated by Gruneberg. The collection is therefore a comprehensive assimilation of embryos of various stages ready for study by vertebrate morphologists, embryologists, developmental and evolutionary biologists, comparative anatomists and historians of science. Information about the collection, visits and loans can be obtained from Jenny Narraway e-mail: jenny@niob.knaw.nl

Morphological Specializations of the Lumbo-sacral Vertebral Column of Birds

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The lumbo-sacral vertebral column of birds is unique in that the vertebrae merge to form a synsacrum. Instead of joints recently discovered new struc-

tures have been evolved that together with specializations in the spinal cord have been suggested to function as a sense of equilibrium. Ventral parts of the vertebrae meld to form a continuous bottom of the vertebral canal with one groove on each side. The intervertebral cleft of dorsal parts of vertebrae is modified into bony canals on both sides. These lumbo-sacral canals open in the midline and laterally into the vertebral canal. In the mediolateral course of the canal, there is a bony slit towards the vertebral canal which is, however, closed by the meninges. This allows cerebrospinal fluid to flow transversely in the canals. Such a flow could be demonstrated by perfusion with stained physiological saline. Laterally, the canals open above specializations of the spinal cord that consist of accessory lobes protruding into the vertebral canal. These accessory lobes are made up of neurons and glycogen cells of the same type as those of the glycogen body located in the same region. They are thought to function as mechanosensory sense organs that may be stimulated by the fluid running through the canals. Preliminary embryologic studies show that the canals are present before hatching. Further embryologic studies are needed to show the development of these peculiar structures.

Microphthalmia in Mammals as a Sensory Adaptation: A Case Study

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Microphthalmia has traditionally been looked upon as a result of a global degenerative process. According to this doctrine, negative or non-selective processes have led to an evolutionary regression of the visual system. It has only recently been demonstrated in the blind mole rat that reduction of the visual system is highly selective and could represent an adaptive response to the underground environment (metabolic gain yielded by reduction of "useless" functional subsystems). To verify this novel concept, we studied retinal projections in three model groups of microphthalmic mammals differing both in phylogenetic and ecological respects, namely bathyergid rodents, vespertilionid bats, and soricid insectivores. Quantitative analysis clearly shows that reduction of the visual system is selective in all studied species and concerns different functional subsystems in the different model groups. Such evolutionary "pruning" of the system cannot be explained solely by factors acting in favor of regression. We suggest that factors acting against regression, which can be defined as specific demands placed on the visual system by a specific mode of life, are virtually the most decisive for final design of the system. Thus, microphthalmia is a direct result of the action of antagonistic selective pressures, which ultimately lead to reduction of "useless" and retention of "useful" functional subsystems of the visual system, and should therefore be considered as sensory adaptations.

Structure of the Chiropteran Spinal Cord: Implications for Phylogenetic Systematics

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Conspicuous differences in the spinal cord structure between Mega- and Microchiroptera are believed to provide a strong, indisputable support against monophyly of bats. However, such interpretation should be considered as an uncritical generalization, inasmuch as only very few species were studied so far. To gather more data relevant to this topic, we analyzed gross morphology and cyto-, myelo- and chemoarchitectonic organization of the spinal cord in twelve taxa representing major lineages of bats and in five outgroup taxa (soricid insectivores, murid and bathyergid rodents). Surprisingly, we found that microchiropterans share many traits of the spinal cord organization (often mentioned as unique for them: e.g., wide dorsal horns with prominent substantia gelatinosa; well developed reticular formation; poorly developed ascending and descending pathways) with shrews. Thus, the respective traits can be considered as plesiomorphic (i.e., without heuristic value for phyletic reconstruction). Moreover, the spinal cord of the small Megachiroptera *Cynopterus sphinx* resembles (both in gross morphology and architecture) that of microchiropteran bats rather than that of large-sized megachiropteran ones (the only ones that were examined until now), suggesting that the commonly discussed differences between Mega- and Microchiroptera need not to refer to any disparate qualities or characters with discrete states but to continuous quantitative variables supposedly scaled by body size and the degree of neocortex development.

Morpho-functional Study and Modelization of a Quadrupedally Walking Insectivora

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Insectivora have long been considered as a primitive group among placental mammals. Although this concept is now given up, Insectivora can be considered as non specialized, from a locomotor standpoint. They may be viewed as non cursorial mammals that present a crouched posture, semi-plantigrad feet and paired limbs with equally long segments. Thus, they were chosen to represent an unspecialized mammal from which more specialized locomotor patterns can derive. Four species within the monophyletic Lipotyphla lineage (Insectivora) were considered: the hedgehog, *Erinaceus europaeus*, the shrew *Crocidura russula*, the moonrat *Echinosorex gymmurus* and the tenrec *Tenrec ecaudatus*. Morphology of the limb musculo-skeletal system was studied and the functional incidence emphasized, focusing on bone measurements and joint shapes; muscle weight, insertions, and fiber-type composition. The kinematics of the locomotion of these four genera was analyzed and compared using data obtained with an X-ray high-speed video camera. All these data were compiled to develop a dynamic model of a walking Insectivora using a specific software SDS (Solid Dynamics). This dynamic simulation allows to approximate the mechanical constraints acting on the system during locomotion.

Deuterostome Brains — An Introductory Survey

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The living deuterostomes comprise four monophyletic groups: 1) echinoderms + hemichordates; 2) urochordates; 3) cephalochordates; and 4) craniates, probably interrelated as (((echinoderms + hemichordates) urochordates) cephalochordates) craniates). The group (cephalochordates + craniates) can be called "amphi"-craniates. The morphotype of the craniate CNS comprises a fixed number of histogenetic units, formed by the intersection of transversely oriented neuromeres and longitudinally arranged zones. The classical subdivisions of the craniate CNS: prosencephalon (P), mesencephalon, rhombencephalon (R) and spinal cord are each composed of a number of neuromeres. Microanatomical studies of larval amphioxus and developmental genetic data suggest that the rostral portion of the ancestral "amphi"-craniate CNS showed distinct R and P homologues, but not an olfactory telencephalic region. Morphological and molecular data from urochordates suggest that the latest common ancestor of all chordates possessed a dorsal tubular CNS, developing from a neural plate, and comprising a rostral P-like, primarily sensory brain vesicle, an R-like primarily motor intermediate section and a segmented ganglionated spinal cord. As regards the origin of the chordate CNS and its relationship with that of extant echinoderms and hemichordates, the following theories have been developed: a) the dorsal tubular CNS is a chordate autapomorphy (Northcutt, 1996). b) The chordate neural plate is the product of a dorsal convergence of the lateral ciliary bands of a dipleurula-type larva (Garstang, 1894). c) The phylogenetic primordium of the chordate CNS includes not only the ciliary bands but also the apical plate of the dipleurula larva (Lacalli, 1994). d) Only the ventral postoral loop of the dipleurula ciliated bands gave rise to the chordate neural plate (Nielsen, 1999).

Adaptations in Birds to Climbing in Needles of Conifers

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Morphology and behavior reflect ecology of a species due to adaptive evolution. Moreover, morphology and behavior are two of the factors that determine the fundamental ecological niche of a species. Species can, therefore, be constrained by their morphology, as well as by their behavior, in their ecology for instance in their habitat use. In order to fully comprehend the environmental requirements of a species, it is important to understand the relationships between morphology, behavior and habitat use. I investigate the morphological and behavioral adaptations of birds that forage between needles of conifers or climb on the outermost twigs of conifers during foraging. Applying comparative methods on 89 bird species from 9 genera, I looked for morphological and behavioral convergences, and parallelisms respectively, in this foraging guild. Furthermore, I describe the relationship be-

tween morphology, especially foot sole morphology, and the type of climbing behavior in coniferous foliage.

Scaling of Activity in the Jaw and Tongue Muscles During Feeding in Toads

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Body size changes during the lifetime of an organism as it grows, as well as during evolution. In this study, we asked how activation patterns of jaw and tongue muscles during feeding change with body size in toads. No two muscles showed the same scaling pattern. For mouth opening muscles, duration and rise time increased with body size, whereas decay time was independent of body size. For mouth closing muscles, relative onset and offset, duration and decay time increased with body size, whereas rise time was independent of body size. Overlap in activity of jaw agonists and antagonists was thus independent of body size. For tongue muscles, only the onset of the retractors in relation to the protractors changed with body size. In small toads, the retractors are activated before the protractors, whereas the protractors are activated first in large toads. This occurs because contraction and relaxation times of individual muscles are independent of body size, whereas the duration of activation is directly proportional to linear dimensions. As animals grow, the onset times of muscles change so that peak force develops at the same time during the feeding cycle. In toads, muscle activation patterns are not constant during the lifetime of an individual. Scaling of muscle activity is a function of physiology, movement duration and biomechanics at individual joints.

Genes, Germ Layers, and the Origin of the Chordate Nervous System

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The recent discovery of the conservation of a number of developmental genes in protostomes and deuterostomes that are involved in dorso-ventral patterning has led to a new variation of Geoffroy St. Hilaire's hypothesis of the origin of chordates by inversion of the protostome body plan. Although there appears to be little question regarding the homology of these genes in protostomes and deuterostomes, this does not necessarily mean that either the embryonic or the adult anatomical features in which these genes are involved are homologous. An outgroup analysis of the nervous systems of both groups does not support the claim that their nervous systems are homologous. Furthermore, an outgroup analysis of fate maps and gastrulation in these two groups does not support Arendt and Nübler-Jung's claim that the fate maps and mechanisms involved in gastrulation in the two groups are homologous. Finally, an outgroup analysis of the topography of mesoderm within deuterostome fate maps suggests that the genesis of the chordate nervous system involved a major repatterning event that resulted in a novel nervous system and the loss of the primary larvae.

The Cretaceous Mammals from Mongolia and their Bearing on Eutherian Relationships

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The new discoveries of Late Cretaceous mammals from Mongolia, recovered by the Mongolia Academy of Sciences-American Museum of Natural History Expeditions (MAE) between 1990 and 2000, include a skull and in several cases associated postcranial skeletons of early eutherians. Based on additional information provided by features of the new taxon *Ukhaatherium nessovi*, we recognize a group Asioryctitheria that includes also *Asioryctes* and *Kemallestes*. Although asioryctitheres can be distinguished by derived features in the middle ear, the jaw joint, and other regions of the skull, they retain primitive features, such as the posteriorly inflated nasals, the posterior extension of the jugal, and the presence of epipubic bones. Cladistic analysis of asioryctitheres and other eutherian taxa are consistent with the basal position of the endemic Mongolian clade relative to other groups. This facilitates diagnosis of both Eutheria and its subclade, Placentalia. Another new eutherian taxon from the Late Cretaceous of Mongolia has a very bunodont dentition similar to that of Cretaceous zhelestids and their putative relatives, archaic ungulates. However,

associated skeletal material referable to this taxon suggests close affinities with zalambdalestids, suggesting a zhelestid-zalambdalestid grouping. Contrary to divergence estimates based on gene differences that assume a molecular clock, there is no strong paleontological evidence that extant clades of Placentalia extend farther back than the latest Cretaceous.

Dental Anatomy and Tooth Replacement of *Haldanodon expectatus* (Docodonta, Mammalia) from the Upper Jura of Portugal

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An anatomical and biometrical analysis of 229 upper and lower dentitions of *Haldanodon expectatus* (Docodonta) from the Late Jurassic lignites of the Guimarota coal mine (Portugal) invalidated former assumptions of the presence of two different morphotypes. Only one Docodonta morphospecies lived in the Guimarota ecosystem. The tooth formula of *H. expectatus* is 6I/1C/3P/5M, 4I/1C/3P/6M, including two so called maxillary incisors in the upper jaw. The classification of these teeth, particularly the question whether they have to be considered as maxillary incisors or canines, is discussed in detail. Seventeen jaws (6 upper and 11 lower) of juveniles in various stages of tooth replacement were recognized. *Haldanodon expectatus* had a diphyodont mode of tooth replacement and as usual incisors, canines and premolars were replaced. The milk teeth clearly differ in size and anatomy from their permanent successors. In the lower jaw, dP1 to dP3 are semimolariform; in the upper jaw, dP1 and dP2 are very small and peglike, while dP3 is large and molariform.

The Middle Ear and Hearing of Whales

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The middle ear of terrestrial mammals matches the low characteristic acoustic impedance of air and the high specific acoustic impedance of the cochlea. In whales, the impedance ratio between the outer medium (water) and the inner ear is reversed. In the tympano-periotic complex, which forms the ear region, the ossicles make a bony bridge from the tympanic plate, the lateral wall of the tympanic bone, to the oval window in the periotic bone. In odontocetes, the middle ear is apparently functional in sound transmission. Lever mechanisms and elastic couplings between the ear bones may contribute, by amplifying the particle velocity, when matching the vibration signal to the low specific impedance of the cochlea. Morphometric studies on parameters measured on the tympano-periotic complex reveal roughly isometric scaling in both toothed and baleen whales. These data have been used in constructing models predicting the odontocete middle ear function. Our mechanical four-bone model is based on the middle ear anatomy, and was applied to six odontocetes. It predicts the behavioral audiograms fairly well, as well as the high sensitivity and good acoustic matching (1999, Hear. Res. 133:61–97, and 2000, in press).

On the Comparative Morphology of Avian Lungs

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The lungs of 48 avian species, which represent 11 orders, were studied using light and electron microscopy. Histological structure of the tracheal walls of different diameter was described and compared. It is shown that the bronchial ramification as well as a character of bronchial wall stratification is determined by lung size. Within multiserial ciliary epithelium of the conductive lung compartment of all species examined, basal, ciliary, mucous secretory, and microvillous cells were distinguished. Only a few mixed cells combining the peculiarities of ciliary and microvillous cell organization were recorded. The secretory derivatives of the ciliary epithelium are species specifically differentiated into the mucocytes, mucocyte aggregations located in the mucosal pits, and multicellular alveolar, or tubular, glands with short secretory ducts. Short respiratory bronchioles turning into the blindly closed alveolar sacs with small alveoli have been found running radially from the parabronches. The epithelium of respiratory lung compartment contains type I and type II pneumocytes and macrophages as well. Thus, the following peculiarities of

avian lung could be listed: thin aerohaematic membrane, hypertrophical capability of apical membrane of type I pneumocytes to form a diversity of villi and outgrowths, and relatively weakly-developed type II pneumocytes.

Neuro-Morphological Analysis of the Snake Telencephalon

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One of the most intricate structures in reptile telencephalon is a dorsal ventricular ridge (DVR). Researchers compare it with mammalian neocortex, part of the amygdala or striatum. Study of all versions of its organization in the course of evolution of reptiles may give a good solution to this problem. In this work the DVR structure in some snake species (Serpenta) is analyzed. The following species were studied: *Vipera berus* L., *V. lebetina* L., *V. ursini* L., *Natrix natrix* L., *N. tessellata* L., *Elaphe dione* L., *Ancistrodon halys* L. Both classical methods of neuromorphology and modern methods of TV analysis of microscope preparations were used. The DVR cytoarchitecture shows great interspecific and inter-group variability. In hemisphere DVR can be of different square from 15% in common adder to 30% in mamushi. The internal DVR structure and differentiation on the zones is also very variable. It demonstrates a very high evolutionary variability at different levels of the brain structure. Neurons of the following types were recorded: multipolar spined long-axonal cells, subependymal radial and horizontal neurons, short-axonal stellar neurons (3 types). Neuron-glia complexes of different types are characteristic of DVR of reptiles (these complexes are comparable with neuron modules recorded in different regions of mammal telencephalon). Thus, among reptilian telencephalon areas, the DVR possesses the most complicated organization. This structure and the striatum of mammalian telencephalon are not homologous. This work was supported by Russian University grant N-992718

Postcranial Pneumaticity in Extant Avians: Distinguishing Pulmonary from Nonpulmonary Pneumaticity

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Pneumatic diverticula variably extend throughout the vertebral column, girdles, and proximal limb elements of extant avians. Specifically, certain foramina, fossae, and tracts located on these skeletal elements receive diverticula (i.e., epithelial outpocketings) from pulmonary air sacs. As a result, many features in postcranial skeletons of living birds are typically described as pneumatic. However, the presence of similar, but non-pneumatic foramina in forelimb elements of certain birds (e.g., bucerotids, pelicanids) obscures this association between hard and soft tissues. The goals of this study are twofold. First, I assess morphological variability in the osteological markers of air sac diverticula by surveying extant avian skeletal remains. Second, utilizing both gross anatomical and histological techniques, I attempt to discriminate between the osteological manifestations of pulmonary diverticula and other soft-tissue systems (e.g., vascular). Results from this study indicate that 1) osteological correlates of air-sac diverticula are morphologically diverse and often exhibit intraspecific and even intraindividual (e.g., bilateral asymmetry) variation; and 2) certain soft-tissue structures (e.g., muscles, ligaments) other than pneumatic diverticula can be associated with skeletal markers that are virtually indistinguishable from those described as pneumatic. These findings emphasize the need for a reevaluation of the osteological features used to identify pulmonary pneumaticity in skeletal specimens. This is particularly important when interpreting fossil specimens that lack associated soft tissues.

Rate of Ovary Differentiation with Reference to Somatic Development in Frogs (Amphibia, Anura, Ranidae)

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Two species of brown frogs (*Rana temporaria*, *R. arvalis*) and two species of green frogs (*R. lessonae*, *R. ridibunda*) were investigated. The rate of somatic development is much faster in the brown frogs than in the green frogs: metamorphosis is completed within 9 weeks in the former and 14 weeks in the latter. We were interested to find out whether the rate of gonad differentiation is correlated with the rate of somatic development, or rather with time (from fertilization to sex differentiation and fully developed ovary). The ovary differentiation was divided into 10 stages: 1–3, undifferentiated

gonad; 4, sexual differentiation; 5, first nests of meiocytes; 6, first diplotene oocytes; 7–9, increasing number of diplotene oocytes and decreasing number of oogonia and nests; 10, fully developed ovary composed of early diplotene oocytes with rudimental patches of oogonia. Sexual differentiation is completed in 5 weeks (at stage 28 in green frogs and at stage 31 in brown frogs, according to Gosner, 1960). Fully developed ovary is observed in 12 weeks in the brown frogs and in 10 weeks in the green frogs (4 weeks after metamorphosis and when metamorphosis is completed, respectively). Thus a conclusion can be drawn that the differentiation of gonads has its own timing (“gonadal clock”), independent of the somatic development.

Epigenetic Influences on Skeletal Development in *Hymenochirus* (Anura: Pipidae)

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Hymenochirus, the dwarf African clawed frog, is an ideal taxon for studies in evolutionary developmental biology. *Hymenochirus* is a model developmental organism, and its relation to *Xenopus* and *Silurana*, also model organisms, permits detailed ontogenetic comparisons among three closely related pipid frogs. Tadpoles and adults are highly specialized carnivores and possess many morphological features not present in other pipid frogs. A comparative analysis of skeletal development, including patterns of neural crest cell migration, chondrogenesis, and ossification, revealed that skeletal elements tend to develop in the same ontogenetic sequence across pipids, but that both chondrogenesis and ossification begin earlier in *Hymenochirus*. Epigenetic interactions during development form the basis of many of the differences in larval and adult skeletal morphology between *Hymenochirus* and other pipids, in particular *Xenopus* and *Silurana*. *Hymenochirus* is the smallest member of the family Pipidae; spatial constraints during morphogenesis contribute to both forward rotation of the eyes and reduction of the hyobranchial apparatus. *Hymenochirus* is also unusual (for a frog) in that both tadpoles and adults are suction feeders, and tadpoles feed continuously throughout metamorphosis. This functional continuity has resulted in both the retention of larval characters into the adult stage and the production of unique ossification patterns, including an unusually high number of sesamoids. Such comparative studies elucidate the role of development in morphological evolution and the importance of hierarchical levels of analysis.

Kinetics of burrowing in limbless tetrapods

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Head-first burrowing has evolved convergently among living limbless amphibians and squamates. This ecomorphological syndrome has led to superficially convergent morphological, functional and behavioral characteristics in these groups. Our goal is to quantitatively determine how similar the mechanics of burrowing has converged among unrelated limbless taxa and how much it has diverged within each monophyletic limbless group. By combining three-dimensional force plate measurements and kinematic analyses, the dynamic kinetics of head-first burrow construction can be quantified. The use of artificial burrows that force animals to vary their posture while attempting to burrow from a static position allows us to test hypotheses regarding the mechanics of forward force production. Our results reveal three basic mechanisms of forward force production (vertebral straightening, rectilinear locomotion and hydrostatic elongation). The method of force production that has emerged in each lineage has profound ecological implications as maximum forward force production can vary twenty-fold (N forward force/cm² body cross-sectional area) depending on the mechanical system employed. The stout bodied terrestrial caecilian *Dermophis mexicanus* uses a hydrostatic skeleton to generate forces approximately twice those of similar sized snake *Farancia abacura* which use only vertebral straightening to burrow. The amphibaenian *Geocalamus acutus* produces twenty times the force of *Farancia* using rectilinear locomotion.

Function of the Postpulmonary Septum in *Varanus*

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The postpulmonary septum (PPS) of monitor lizards (genus *Varanus*) partitions the body cavity into distinct pleural and peritoneal compartments, separating the lungs from the viscera in a manner similar to the mammalian condition. Because of its non-muscular nature, the role of PPS in lung ventilation has not been investigated. However, PPS may confer a respiratory advantage to an animal by improving the mechanism of lung ventilation in a number of ways: PPS facilitates even intrapulmonary ventilation of the heterogeneously partitioned lung by fusing to the posterior lung wall; PPS prevents overinflation of the lung when costal aspiration is supplemented by a series of gular (buccal) pumps; PPS, stretched by the antero-lateral rib movement during costal inspiration, allows the animal to develop more negative pleural than peritoneal pressure, thus increasing the effectiveness of the inspiratory muscle effort; PPS, as a physical barrier, minimizes the paradoxical movement of the viscera during inspiration and dampens their impact on the lungs during locomotion. These hypotheses are addressed by experiments on monitor lizards with PPS intact or surgically removed, and compared to the condition of other lizards lacking PPS and of mammals with denervated diaphragms. Though not homologous to the mammalian diaphragm, the PPS of monitor lizards may serve as a useful analogue to elucidate possible physiological benefits of a non-muscular diaphragm and to discover possible selective pressures behind its muscularization.

A reassessment of pelagic specializations in “macrobaenids” and early cheloniid sea turtles and the phylogenetic position of *Osteopygis* Cope 1868

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Osteopygis is an important taxon because it is the only Maastrichtian (Latest Cretaceous) cheloniid that is known from relatively complete cranial and postcranial material. Furthermore, it is the only sea turtle known to cross the Cretaceous-Tertiary boundary and is the first cheloniid to be found outside North America. But instead of bridging the gap between the earliest cheloniids and the more specialized Cenozoic taxa, the postcranial morphology of *Osteopygis* is unlike that of any other sea turtle. A reassessment of “macrobaenid” grade turtles sheds new light on the true affinities of *Osteopygis*. Loosely defined, the “macrobaenid” grade encompasses a poorly known stage in the evolution of cryptodires that ultimately gave rise to the chelydrids (snapping turtles), chelonioids (sea turtles), and possibly other lineages with extant species. Although primarily Asian, “macrobaenids” have a modest (although mostly undescribed) diversity in North America. A detailed comparison of the postcranial morphology and pelagic specializations of “macrobaenids” and early sea turtles reveals that the specimens referred to *Osteopygis* represent at least two different species belonging to separate lineages. While the cranial material is clearly referable to an advanced cheloniid, the postcranial material (including the type specimen) belongs to a large “macrobaenid.” The decapitation of *Osteopygis* results in a much clearer understanding of pelagic specializations and the morphological trends of early cheloniids.

Recordings and Mechanisms of Sound in Three Carapidae Fishes

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Different Carapidae fishes are well known because of their amazing behavior: they are able to enter and to leave an echinoderm host notably. Another particularity lies in the presence of specialized muscles called sonic muscles. Some originate within the orbits and insert on the anterior part of the swimbladder just underneath the third great enlarged epipleural rib. Others insert on the back of the neurocranium and attach to the first rib that is in connection with the anterior part of the swimbladder via a ligament. In this study, sound emissions were recorded from three species (*C. boraborensis*, *C. homei* and *E. gracilis*) that are entering the Holothuroid *Bohadschia argus*. At each experiment, sonic pulses were recorded only when the fish was entering the host or just after. A detailed study of the musculature and the skeleton in relation with the swimbladder is realized. The study of the sound producing mechanism is supplemented by an histological approach to the swimbladder.

Neck Mobility in Long-Necked Vertebrates: From Modern Mammals to Sauropods

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Modern long-necked mammals, and especially giraffes, have often been considered appropriate contemporary analogs for sauropod dinosaurs. As part of our studies on sauropod neck mobility, we have done dissections and osteological manipulations of both llamas and giraffids. Several striking differences are apparent between sauropods and the long-necked mammals. First, both mammalian groups have the plesiomorphic mammalian cervical count of seven rather than the expanded sauropod count of 11–19. Nonetheless, the mammals are capable of far greater flexibility than found in avian and reptilian necks, and presumably greater flexibility than achieved by sauropods. The vertebrae may deflect further when attempting to combine ventriflexion with mediolateral flexion. The large angular deflection in the mammals is achieved as a result of the zygapophyses being large and placed close to the midline. Although sauropods have more vertebral segments than mammals, the fact that their zygapophyses are located further from the midline and are generally obliquely inclined results in less mobility between segments and throughout the neck. Vertical flexion and mediolateral deflection are often functionally decoupled, particularly at the proximal end of the neck.

Tooth Enamel Microstructure of a Late Cretaceous Gondwanatherian Mammal From India

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Hypsodont molars of a sudamericid (Gondwanatheria) from the Late Cretaceous of India were studied for enamel microstructure. The present specimens differ from other hypsodont sudamericids such as *Sudamerica ameghinoi*, *Gondwanatherium patagonicum* and *Lavanify miolaka* in having radial enamel, tangential enamel and a zone of plex. The presence of radial enamel with prisms originating from the enamel dentine junction running apically to meet the occlusal surface and turning perpendicularly towards the outer enamel surface has been inferred as an reinforcement against abrasion. Presence of wave-like inter-row sheets in the inner radial enamel, with interprismatic matrix crystallites oriented at 90 degrees to those of the prisms and difference in the orientation of prisms as we move from enamel dentine junction to the outer enamel surface, were probably related to adaptation against propagation of cracks in these hypsodont teeth as early as in the Late Cretaceous.

Enamel Microstructure of Fossil and Extant Mice (*Mus*, Muridae, Rodentia) of India: Adaptive, Phylogenetic and Taxonomic Significance

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Extant *Mus* incisors exhibit a two-layered radial enamel in contrast to a single layer generally found in rodents. The additional layer appears to be a modification of the outer portion of the radial enamel and consists of dense prisms and interprismatic matrix. A clear differentiation of leading and trailing edges, based on the difference in orientation of prisms, distribution of radial enamel and Hunter-Schreger Bands (HSBs) has been observed in both fossil and extant *Mus* molars. The HSBs in mice molars occupy the entire height of the enamel crown (from base to top). They tend to be horizontal around the base and incline apically around the top. This somewhat 'incisor-like' arrangement has been inferred as functionally beneficial for further cutting down the food material into smaller pieces. Presence of horizontal HSBs at the base of the crown is perhaps a reinforcement against cracks developed due to vertical load and horizontal tension. The presence of HSBs and radial enamel occupying the enamel crown can be traced back to the last 5-million years, which has important connotations in understanding phylogenetic relationships. Mapping of HSBs in the molars of several *Mus* species (both extant and fossil) was undertaken in order to understand inter and intra-specific variations at the microstructure level. The preliminary results indicate that it is almost impossible to distinguish

closely related species with similar dentition and diet behavior at the enamel microstructure level.

Ontogenesis of the Oral Vestibule in the Sheep (*Ovis aries*, Ruminantia)

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The oral vestibule is a part of the oral cavity exterior to the teeth. It represents an evolutionary novelty in mammals that enables the offspring to suck milk and prevents the food from falling out of the mouth during chewing. The oral vestibule is described as originating from the vestibular lamina, an invagination of the oral epithelium labially to the dental lamina. In our presentation, by using serial histological sections of sheep embryos and fetuses and three-dimensional computer-aided reconstruction method, we have demonstrated that only the rostral part of the oral vestibule was a derivative of the vestibular lamina. The caudal part originated from a lateral excavation of the prospective mouth cavity. A similar developmental modus of the oral vestibule has been described also in the mouse. Whether this structure has also a dual origin in other mammals remains to be tested. This study was supported by the Grant Agency of the Czech Academy of Sciences (grant A7039901)

Interspecific Differences of Striated Palatal Muscle in Rodents and Lagomorphs

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Broman (1919) described a striated muscle of the hard palate of Lagomorphs and Rodents. It is located between incisor and molar regions and inserts to the upper lip and the cheeks. We have described interspecific differences of the morphology of this muscle in the rat, the mouse, the degu, the hamster, the guinea pig, and the rabbit. Some of the muscle fibers show in all these species a close relationship to the follicles of tactile hairs. The deep part of the muscle surrounds the ductus incisivus and is probably able to open or close this channel. The superficial part retracts skin folds originating from the upper lip between incisors and cheek teeth to the mouth cavity and protects the aboral part of the mouth from injuries during gnawing by this way. In the hamster, one part of the muscle is located near the external margin of the buccal pouches. The palatal muscle is not listed in the veterinary anatomical nomenclature. It belongs to the mimic muscles because it is innervated by the nervus facialis. This study was supported by the Grant Agency of the Czech Academy of Sciences (grant A7039901).

Spermatozeugmata Formation in *Mimagoniates barberi* (Teleostei, Characidae)

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Mimagoniates barberi is an oviparous species with internal fertilization. Our previous research revealed that males of *M. barberi* produce two types of unencapsulated sperm bundles (spermatozeugmata), one-sided and spindle-shaped. In the present study we showed (using TEM and SEM) that both types are formed within the efferent ducts of the posterior, aspermatogenic part of the testis. In the anterior part, only free, longitudinally aligned spermatozoa are present. In the more posterior part of the testis not fully formed spindle-shaped aggregations are found. One-sided sperm bundles first appear in the most cortical portions of the testis and they seem to detach themselves from larger spindle-shaped aggregations. Within spermatozeugmata, spermatozoa are arranged in stacks. The formation of spermatozeugmata seems to be aided by a secretion of testis epithelial cells. In more proximal ducts the secretion is finely granular, whereas in more distal ducts, groups of coalescing spermatozoa are accompanied by a fibrous secretion. The sperm is aligned along strings of this secretion which is most probably instrumental in sperm packets formation. In the most caudal portion of the testis, where only fully formed spermatozeugmata are present, no secretion is visible, either within the sperm packets or in the lumen of the efferent ducts. The epithelial cells of the testicular tubules of the aspermatogenic portion of *M. barberi* testis show signs of both secretory and phagocytic activity. Apical surfaces of the epithelial cells form long processes of various forms.

Morphology and Function of the Hyoid Apparatus of Fossil Xenarthrans

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The masticatory apparatus of fossil xenarthrans has been the subject of various functional studies. However, these have omitted the hyoid apparatus, despite its importance for tongue movements. Although rarely preserved, some fine specimens of *Paramylodon* and *Scelidotherium* (Mylodontidae), *Megatherium* (Megatheriidae), and *Glyptodon* (Glyptodontidae) are known. This contribution describes and compares these specimens with those of the extant sloths, anteaters (Myrmecophagidae) and armadillos (Dasypodidae). Among the sloths, *Paramylodon* is apparently the most primitive, since only the basi- and thyrohyal are fused. In *Megatherium*, the ceratohyals are reduced or fused to the fused basi- and thyrohyals. The same fusions occur in *Scelidotherium*. They are considered a specialization that restricts movement. Muscular attachments are not well developed. The geniiohyoid of *Megatherium* must have been very short, indicating very limited anteroposterior movements. The hyoid apparatus of *Glyptodon* is characterized by the fusion of the stylo-, epi- and ceratohyals of each side into a vertical, robust rod with muscular insertion sites greatly developed. This modification is a response to the migration of the apparatus below the neurocranium. While other muscles were reduced, the actions of geniiohyoid and ceratohyoid, producing protraction and retraction of the tongue respectively, were enhanced. In forms with more extensive fusions, the tongue would have been more important in reworking food in the oral cavity than in food intake.

The Influences of Body Size and Body Proportions on Locomotor Performances in Primates

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Previous studies of the influences of body size on locomotor kinematics have been conducted using either broad interspecific comparisons across several orders of mammals, or ontogenetic changes within a single species. In both cases, changes in body proportions accompany increased mass, and observed kinematic differences could result from either of these effects. This study attempts to isolate the effects of body size and body proportions in a study of the kinematics and kinetics of terrestrial locomotion in a closely related sample of primates: baboons, patas, and vervet monkeys. Data were collected using a Peak Performance 3D-motion analysis system with synchronous recording of force plate data. Comparisons were made between dimorphic conspecifics with similar body proportions, as well as across taxa with different proportions but similar mass. In the body-proportion comparisons, predicted differences were obtained such that animals with longer limb segments used more extended limb postures and had lower hip and shoulder angular excursions than those with shorter limbs. Predicted postural adjustments for increased body mass were expressed most clearly in the male baboon (the largest animal included in the study) while the patas male exhibited fewer changes. The vervet male showed size-related postural adjustments only in the hindlimb. That body size and proportions influence locomotor postures suggests that both factors should be accounted for in interspecific and ontogenetic comparisons. Sponsors: NSF SBR9803079, BCS9806291, LSB Leakey Foundation.

Morphological Markers for Mammal Populations: Towards a Palaeo-phylogeography

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Phylogeography is a term applied to within-species phylogenetic and geographic divergence. It has been the domain of molecular biology because molecular markers record population structure at a finer level than traditional morphologic traits do. Paleontologic studies have thus been limited to among-species considerations. But advances in morphometrics allow complex morphologies to be quantified and analyzed using methods from molecular phylogenetics. Molar-shape distance appears to accrue with time since divergence, as indicated by significant correlation between molar distance and cytochrome b divergence. Molar-shape distance also appears to have a "saturation point" beyond which it is not useful as a phylogenetic indicator. In shrews, that point is between 1.0 and 5.0 million years. Furthermore, analysis of shape variance indicates that significant differences in mean are detectable among populations of the common shrew, *Sorex araneus*. These

findings suggest that molar-shape distance can be used as a metric to study population-level divergence and migration in both extant and fossil populations. A twin study of *Sorex* and *Marmota* reveals that molar-shape divergence patterns differ among species, conforming to expectations based on biological parameters such as tooth function, individual migration rates, gene flow, and habitat connectivity during the Pleistocene. Divergences among some karyotypic races of *Sorex araneus* may be more than 120,000 years, while others may be as little as 10,000.

Functional Analysis of Peripheral Nerve Regeneration in Rats

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The rat sciatic nerve crush is the most widely used model of peripheral nerve injury. Nerve regeneration is most often assessed using histology, electrophysiology, or an index derived from footprint analysis. Though useful indicators of regeneration, these measures do not necessarily correlate with functional recovery. We used an integrative organismal approach to develop a comprehensive, high-resolution method of analyzing functional recovery after peripheral nerve injury. The techniques used include 1) high-speed videography of rats during treadmill locomotion, 2) force platform analysis, and 3) *in situ* physiological measurements of the medial gastrocnemius (MG). We crushed the sciatic nerve with 500g for 10 minutes and monitored recovery every seven days for 28 days. Posture changes predictably from digitigrade (pre-crush) to plantigrade (post-crush) and back to digitigrade (recovery). This transition was documented during stepping by measuring the maximum angle formed by the foot and the horizontal, and by assessing the location of the foot's center of pressure (COP) during stepping. The mean maximum foot-horizontal angle is 118° prior to crush, 43° on post-operative day (POD) 7, and 116° on POD-28. Pre-crush COP is located 3.1 cm distal to the heel, decreases to 1.6 cm at POD-7, and increases to 2.8 cm at POD-28. These postural changes correlate with reinnervation of the triceps surae complex evidenced by 41.4% recovery of MG tetanic force output at POD-28.

Structural Aspects of Stress Concentration in Mammalian Molar Cusps

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How differences in cusp architecture affect the functional capacities of bunodont teeth was investigated in the pig, *Sus scrofa*, and in humans, *Homo sapiens*. Cusp dimensions and enamel thickness were measured with NIH image, and enamel microstructure was described using SEM. Stress concentration in the cusp tip was investigated through application of continuous compressive load with a uniaxial testing machine (MTS/ Sintech) and simultaneous recording of overall cusp strain and breakage. Enamel strain was further investigated by affixing rosette strain gauges to cusps and by recording strain during compressive tests. Overall, human cusps were stiffer than pig cusps, and human cusps sustained high stresses, whereas pig cusps crumbled at lower stresses. Strain gauge measurements showed that human enamel was stiffer than pig enamel ($p=0.02$), and tensile stress at yield was higher (18.82 N/mm² in humans vs. 10.76 N/mm² in pigs, $p=0.05$). Cusp enamel was thicker in human than in pig, and human enamel microstructure showed inter-rod material densely packed between rods. Pig enamel showed inter-rod material forming partitions between rows of enamel rods with gaps appearing between rod rows and inter-rod material; these gaps suggest planes of shear and correspond with the lower enamel stiffness. Thus, pig and human cusps show differences in enamel thickness and microstructure that may be responsible for differences in cusp stiffness and strength and correspond with phylogenetically different strategies for occlusal function.

The Development of Long Bones in the Embryonic Quail (*Coturnix coturnix japonica*)

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The histogenesis of the long bones in the embryonic quail has been investigated by means of light microscopy. Femurs, tibiae and humerus of fetuses from the 6th day till the 16th day of incubation were decalcified,

embedded in paraffin wax, serially sectioned and stained with HE. In the 6th day of incubation, the cartilage rudiments presented three distinct zones. The central zone of hypertrophic chondrocytes was surrounded by a sheath of mineralized osteoid. The next day, the osteoid ring became more prominent and vasculature appeared between the osteogenic and the fibroblastic layer. During the 8th day of incubation, invasion of the cartilage by vasculature and perivascular elements could be observed. Concurrently a second layer of perichondral bone began to form. By the 9th day, the epiphysis presented three zones of cartilage: the articular, the hyaline and the epiphyseal or growth cartilage. Simultaneously the articular cavities of the long bones were formed. The epiphyseal vascular canals of the femur and tibia appeared in the 10th day of incubation whereas those of the humerus appeared in the 12th day of incubation. The perforating vascular canals of the femur and tibia appeared between the 13th and 14th day of incubation. Endochondral ossification was detected late, in the 16th day of incubation. The pattern of histogenesis of the long bones of the embryonic quail is similar to that of the embryonic fowl, which reflects the close zoological affinity of the two species.

Trophic System and Niche Difference in Indo-Australian Swifts (Aves: Apodidae)

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Swifts (Aves: Apodidae) are aerial feeders, which are able to catch insects on the wing with high velocity. The shape and mobility of the feeding apparatus of the common swift, *Apus apus*, allow for a fast and wide opening and subsequent quick closing of the mouth. In addition its lower-jaw surface can also be enlarged when the beak is opened. A group of smaller swifts, the so-called swiftlets, from the Indo-Australian region occupy different niches. There are taxa that are of almost the same size as *Apus apus*, but many of them are only half its size. Next to catching a prey when they are flying fast, they are also able to enter the canopy of a tree where they slowly maneuver between branches and pick insects from twigs and leaves. It is explained how smaller dimensions and different ecotrophic types require different modifications of the design of the swift's jaw apparatus during opening, closing, catching, and manipulation of a prey.

The Role of the Zygomatic Arch for the Statics of the Skull and its Adaptive Shape

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Most discussions about skull development are focussed on the phylogenetic origin of the individual (bony) elements, but we investigate which role they are playing for the mechanical function of the entire head in biting. This is made possible by a modern finite-element program, which allows the analysis of stress distribution within a three-dimensional, homogeneous body under defined load. With only few a-priori conditions (existence of a nasal cavity, two orbits, and a braincase) and the position of the dental arcade as independent variable, we have computed the stress flow within a volume representing the midface between upper jaw and braincase. After removing all finite elements loaded by less than a threshold value, we arrived at shapes that are remarkably close to a primate skull. In these models all present elements are recruited for stress bearing, and their shapes optimized, no matter from which ossification center they are derived. The "pneumatized spaces" turn out to be "shell structures" in the technical sense. The zygomatic arch fulfils a static requirement, since an arch-like stress flow appears at the sides of the skull under the influence of nothing but the bite forces. Evidently, its existence is not a relic of phylogeny, but rather a functional requirement. The exact form of the zygomatic arch as a consequence of the mechanical conditions is demonstrated for *Homo*, *Pan* and *Gorilla* as examples.

Evolution and Diversity of the Turtle Shell

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Many invertebrate groups are characterized by a rigid external envelope, the mollusc shell, or crustacean carapace. But vertebrate shells are rare, requiring evolutionary ankylosis of the flexible vertebral column, a ki-

netic complex of crucial importance to mobility and profound evolutionary investment. The order Testudines constitutes an exception. Toothless maxillae and imperforate temporal regions are noteworthy, chelonian limbs remarkably diverse, and the turtle neck almost miraculous in its compensatory flexibility, but the shell is truly unique. Seemingly a straitjacket, it has proven remarkably successful in an incredible spectrum of ecological specializations. Not just a covering but, by its incorporation of dorsal vertebrae, ribs, clavicle, interclavicle, and gastralia into its structure, the shell *is* the turtle. The turtle shell has multitudinous parallels with human artifacts, showing familiar classic architectural details including keystones, fan vaulting, drawbridges, and flying buttresses. Holistically it parallels defensive shields, cupolas, even geodesic domes. Massive or delicate shells may compare to designs of fortress, cathedral, or jail, the structure entirely windowless, or portholed, or with elaborate juvenile (or senile) fenestration. Moreover, many show kinetic plastra, carapaces, or bridges to promote defense, respiration, visceral displacement during retraction, or oviposition. These parallel mediaeval armor where visor, gorget, beaver, pauldron, vambrace, poleyn, greave and sabaton must all be kinetic if the wearer is not to become (literally) a pushover.

Investigation of Morphogenesis of Rat Brain Asymmetry in Normal and Experimental Conditions of Development

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The formation of morphological brain asymmetry has great significance in central nervous system evolution. We examined the variety of morphological asymmetry in some rat brain nuclei. The right-side asymmetry was found in 20 days old embryos in the fasciculus habenulae lateralis and medialis as well as in the nuclei colliculi inferior and superior and it changes in the left-side at the moment of birth. It appears that stress and immobilization do not have significant influence on the trends of asymmetry in rat ontogenesis. The development of brain nuclei asymmetry depends on animal morphogenesis in general and may change during ontogenesis. The importance of detailed investigation of vertebrate development in weightlessness is evident. The present study was conducted within the framework of an embryological experiment dedicated to complex morphogenetic study of laboratory rat on the spacecraft "Shuttle." In this article we discuss the influence of 11 days exposition in weightlessness on rat brain development. The adaptive changes in adult animals differ dramatically from those in embryos. The left-side asymmetry in brain structure in controls changes to the right-side in microgravity conditions. Probably, it depends on developmental delay in weightlessness. This experiment demonstrated significant differences in brain development expressed in cell differentiation changes and developmental delay in major analyser systems: visual, acoustic and olfactory.

Muscle Valve in the Avian Heart: Anatomical, Ultrasonographic, and Electrophysiological Study.

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The structure of the atrioventricular junction in avian heart is known to differ somewhat from that in the mammalian heart. In the right atrioventricular orifice of the avian heart there is another type of the valve, namely a monocuspid valve and it looks like a muscle plate. This work is the first attempt of combined morphometrical, ultrasonographic, and electrophysiological study of the muscle valve in the heart of the pigeon (*Columba livia* L.), chicken (*Gallus domesticus*), duck (*Anas crecca* L.; *Anas clypeata* L.), and parrot (*Melopsittacus undulatus*). The structure of the muscle valve is similar in domestic and wild birds. During the cardiac cycle, deviation of the muscle valve was stated to exceed twice that of the anterior cusp of the left atrioventricular valve. The electrical activation of the muscle valve occurs simultaneously with the main mass of myocardium of the right ventricle free wall. The discontinuity between the right atrium and ventricle is created by the fibrous ring tissue and pacemaker cells that are situated on the atrial side of the muscle valve along the entire extent of its base. Based on the results obtained, a hypothesis is advanced that the special construction of the muscle valve, together with the main morphofunctional purpose, closing of the atrioventricular ostium during ventricular contraction, is also used to increase dimensions of the free wall (of which the valve is part) and right ventricle cavity volume.

A Theoretical Framework for Studying the Development and Evolution of Feathers

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Feathers are complex and diverse integumental appendages that grow by a unique mechanism from cylindrical feather follicles. The diversity of feather morphology is the result of detailed control of developmental mechanisms within the follicle collar. The development and evolution of the entire plumage phenotype of an individual can be understood in terms of a hierarchical model with interactions or correlations among sets of follicles across the hierarchy. At the most general level, the model determines the distribution of feather tracts (or pterygiae) over the body and the density and distribution of follicles within pterygiae. Within each follicle, the model specifies the values of growth parameters that determine the overall shape and size of the vane. Within a barb ridge, the model specifies the ultimate shape, size, nanostructure, and pigmentation of each keratinocyte. Many features of the plumage phenotype reflect correlations or associations among parameter variables for functional sets of non-adjacent follicles from different hierarchical partitions (e.g., the common shape of the remiges, or the color of feathers from different tracts within a common plumage patch). The model provides a theoretical framework that identifies the appropriate levels at which to address various questions in developmental and evolutionary biology of feathers. The proposed theoretical model also proposes numerous testable hypotheses that can fuel future empirical research.

A New Large Megatherium From the Latest Pleistocene of Northern Peru

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The subfamily Megatheriinae is known in America from the Friasian to the Lujanian. Two genera are currently recognized in the Pleistocene: the temperate *Megatherium* and the intertropical *Eremotherium*. A new large megatheriine Ground Sloth (probably Lujanian in age), has been recently discovered in the "Santa Rosa" cave, near the city of Celendin (Cajamarca department). The specimen is a partial, non-articulated skeleton, and represents the third megatheriine genus reported in the Pleistocene. The most peculiar characters of the "Santa Rosa" Ground Sloth, are: the post palatine notch open to the anterior part of the M³, the skull which is proportionally larger and lower than in *Megatherium* or *Eremotherium*, a quadrangular shaped scapula, the suprascapular fossa occupying practically all the lateral side of the scapula, the greater tubercle of the humerus strongly reduced, the ectal facet of the astragalus proportionally much more voluminous than in *Megatherium* or *Eremotherium* and whose sulcus tali is practically closed. Therefore, this animal, which could have been evolved endemically in the Peruvian Andes, is morphologically very different from all the other Megatheriinae and presents some characters unknown in the family Megatheriidae. The functional study of this specimen will bring new information about the locomotor behavior of the Ground Sloths.

Constraints and Innovations in Early Vertebrate Evolution: The Fall of Agnathans and the Rise of Jaws

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Today jawless fish constitute a tiny proportion of vertebrate diversity, yet for more than 140 million years they were the dominant form of vertebrate life. Most bore an external covering of bony scales or plates, but by the end of the Devonian Period all these armored jawless vertebrates were extinct, and aquatic environments were dominated, as now, by vertebrates with jaws. This faunal turnover represents a fundamental transition in vertebrate evolution, and explanations of the changing fortunes of the key players draw heavily on hypotheses of constraint and innovation. Without jaws and fins agnathans may have been incapable of anything other than suspension feeding; their morphological disparity, taxonomic diversity and evolutionary potential were limited because they lacked certain key anatomical characters. The gnathostomes, on the other hand, became dominant precisely because they possessed fins and jaws; innovations that allowed them to radiate into niches that were unavailable to jawless fish. Also, the superior feeding abilities of gnathostomes may have led directly, through competition, to the

demise of the agnathans. However, the fossil record of early vertebrates fails to support this tidy but oversimplified version of events. Recent work on feeding mechanisms in extinct agnathans suggests greater trophic diversity than previously thought possible, and the pattern of taxonomic diversity through time is hard to reconcile with the hypothesis that agnathans were driven to extinction by vertebrates with jaws.

The Structure and Function of Connective Tissue in Muscular Systems

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The composition, properties and morphology of striated muscles are adapted to fulfil different functional tasks in the body. Perhaps one of the most striking and easily visualized variations between muscles is the pattern of their internal organization into fascicles and fibers by intramuscular connective tissue (IMCT). However, the functional role of this highly variable component of muscle is poorly understood. IMCT has a number of clearly defined roles. It patterns muscle development and innervation and mechanically integrates the tissue. In developing muscles, proliferation and growth of muscle cells is stimulated and guided by cell-matrix interactions. Recent work has shown that the topography of collagen fibers is an important signal in this. The timing and rates of expression of connective tissue proteins also show clear differences between muscles. Discussion of mechanical roles for IMCT has traditionally been limited to the passive elastic response of muscle. However, it is now clear that IMCT provides a matrix to integrate the contractile function of the whole tissue. Mechanical forces are co-ordinated and passed between adjacent muscle cells via the endomysial connective tissue that links the cells together. We are developing the concept that division of a muscle into fascicles by the perimysial connective tissue is related to the need to accommodate shear strains as muscles change shape during contraction and extension.

Regeneration in Teleost Fins

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The ability of teleost fish to regenerate their fins after injury is restricted to the part containing the dermal skeleton of the rays. The process of fin regeneration is similar to limb regeneration of urodele amphibians. It proceeds through the formation of a blastema (epimorphic regeneration) at the level of each ray stump. Blastemal cells, as shown by bromodeoxyuridine incorporation, present a high proliferative activity. Using Di-I staining, to follow cell movement in the stump, we have shown that amputation triggers the migration of epithelial and intra-ray mesenchymal cells from distant positions relative to the plane of amputation. Gene expression analyses, performed by us and others, indicate that the molecular mechanisms involved during regeneration are a recapitulation of those observed during the growth of the rays in juveniles. However, these differ from molecular mechanisms that take place during embryonic development even though many of the same transcription factors and signaling molecules are used. For example, expression and functional analysis of members of the sonic hedgehog signaling pathway during fin regeneration suggests that this pathway is involved in patterning the fin dermal bones and is necessary for bifurcations to take place. During embryogenesis, this pathway is involved in patterning the antero-posterior axis of the limb/fin bud. The two phases of fin development and the regeneration process offer an example of co-option of developmental mechanisms to achieve distinct functions. Supported by a grant from the CIHR.

Are Protochordates Chordates?

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Comparative embryology shows that neither notochord, nor CNS, can be homologous in protochordates and vertebrates. As confirmed by their immigration direction, either opposite or parallel to that of the muscle mesoderm during gastrulation, the prospective chordal cells are anterior in the former, but posterior in the latter, then, due to the "zootype," cannot be homologous in the two groups. On the other hand, in protochordates their position is coincident with that of the stomatoblasts + ecto-mesenchyme in gastroneurians and the CNS, just as in the latter, forms in the vegetal hemisphere parallel to the lateral lips of the blastopore. In vertebrates, in contrast, the CNS develops in the animal hemisphere quite apart from the blastopore, as typical of notoneurians.

These and other observations lead to conclude that protochordates are gastroneuralians with no close phylogenetic relationship with the vertebrates, but the ventral side of their embryos was mistaken for dorsal. Then, an inversion of the dorso-ventral body axis never occurred in bilaterian evolution. However, the similarities of the pharyngeal region in the lancelets and enteropneusts may illustrate a transition from gastro- to notoneuralians. If so, the CNS of the vertebrates could derive from the ectodermal area that gives origin to secretory or sensory "dorsal organs" in gastroneuralians, but is neuralized on mesodermal induction. The neural crest/placodes could derive from the lateral ectodermal stripes which give origin to the CNS of gastroneuralians, but are shifted dorsally, instead of ventrally, at gastrulation.

Saber and Dagger: Differences in Attack Modes in the Saber-toothed Tigers

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The analysis of strike patterns, possible striking curves and tooth morphology in the sabertooth tigers of Tertiary and Quaternary shows that their skulls were adapted to different attack models. Using a morphospace analysis, and the ratios of the several body parts involved in a possible strike, we present different models for the diverse adaptation found among the sabertooth tigers, which basically can be conducted to two attack patterns: a slashing powerful blow aimed to cut, in a saber-slash style, and a piercing attack, like a dagger blow.

Osteological Differences Between Green and Brown Frogs of Russia

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It is usual to divide Russian representatives of genus *Rana* in two groups: the green frogs (*Rana ridibunda*, *R. lessonae*, *R. nigromaculata*) and the brown frogs (*Rana amurensis*, *R. arvalis*, *R. asiatica*, *R. chensinensis*, *R. macrocnemis*, *R. temporaria*). Some frog skeleton bones have common traits for all the species of one group, distinguishing them from representatives of the other. This traits are: 1. Squamosum has a crest extending along the outer margin of ramus retrozygomaticus as a continuation of the upper margin of ramus zygomaticus in green frogs. The crest can be present at the outer margin of ramus retrozygomaticus ossis squamosi only in its anterior half in brown frogs. 2. Corpus parasphenoidei comparatively wider in brown frogs. 3. Horizontal plates of vertebral neural arch abruptly (by ledge) thicken in the middle part, forming the well developed elevated platform in brown frogs. Horizontal plates of vertebral neural arch gradually thicken without forming the well developed elevated platform, or is very narrow, in green frogs. 4. Crista medialis and c. lateralis in male humeri deviate dorsally in brown frogs and do not deviate in green frogs. 5. Tuber superior on ilium is flattened laterally in green frogs. It is convex and is usually complicated with small tubercles in brown frogs. The presence of these complex traits in the bones has practical importance in palaeontological studies.

Functional Morphology of the Skull of *Allosaurus fragilis*: A Study Using the Finite Element Method

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The large, theropod dinosaur, *Allosaurus fragilis*, is found in relative abundance in Late Jurassic deposits of western North America. Although obviously a carnivore, *Allosaurus*' particular skull morphology raises interesting questions concerning its feeding strategy. Parts of the anterior skull are robust, however posterior sections are surprisingly gracile and reduced to a strut-like morphology. In this study, traditional comparative approaches were used to estimate the size and power of the jaw adductors and to calculate bite and condylar forces. More significantly, a three-dimensional finite element model of the skull and lower jaws of *Allosaurus* has been created. Using this model, biting induced stresses and strains within the skull and jaws were analysed, skull strength was tested and the maximum biting force leading to bone yield recorded. A number of bite positions along the tooth row were tested. It was discovered that the muscular-driven bite force of *Allosaurus* was surprisingly weak. When biting together, the skull and lower jaws were also relatively weak; bone crunching was unlikely. However, when forces were applied only to the skull, it comprises a very strong structure. Certain aspects of skull morphology contribute to its extreme strength. This observation may be explained

by over-design, or, as this paper suggests, by the particular feeding strategy employed by the creature, involving a powerful impact of skull into prey.

Lipofuscin Granules in the Inner Retinal Layer of the Ciliary Body in Owls

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In vertebrates, the inner retinal layer of the ciliary body is normally not pigmented, while the outer retinal layer contains melanin. On the contrary, a light microscopical examination shows a well-marked pigmentation of the inner retinal layer in different species of Strigiformes. The retinal epithelial cells were completely filled with rounded dark brown granules. Their diameter is several times larger than melanin granules in the outer retinal layer. It is not possible to dissolve these granules in acetone, xylene, acids or a concentrated lye. Hydrogen peroxide bleaches the pigments. They react PAS- and Schmorl-positive. Moreover the pigments bind basic dyes. These histochemical properties are characteristic for lipofuscin. Up to now lipofuscin was only described as the dominant fluorophore in the retinal pigment epithelium of the ocular fundus in mammalian eyes, which increases during senescence in the retinal pigment epithelia. In contrast to mammalian eyes, in strigiformes the lipofuscin content of the inner retinal layer is not an age related degenerative alteration but a physiological character. In owls, it must have a specific function, unknown until now. An improved absorption of scattered light in the long tubular eyeball of owls is a possible function. Yet, the autofluorescence of the lipofuscin granules may have a special function, for example light intensification in the nocturnal owls.

Evidence of Thoracic Breathing in *Tyrannosaurus rex*, Based Upon Recent Anatomical and Pathological Evidence From "Sue"

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The recent completion of the preparation and mounting of *Tyrannosaurus rex* specimen FMNH PR2081 at the Field Museum of Natural History in Chicago otherwise known as "Sue" presents a unique opportunity to examine an extremely complete specimen of this elderly individual. The unprecedented completeness of Sue affords the opportunity to examine the gastralia (dermal belly "ribs"). The similarity of two fused cranial gastralia with a fragmentary bone specimen previously identified as a *T. rex* sternum suggests that the earlier identification was in error. Negative evidence may imply the lack of a true sternum in the species *T. rex*. As independent corroboration of this, amongst Sue's many pathological lesions, there is evidence of pseudoarthrosis (non-union) in a series of adjacent healed fractures in the right thoracic ribs. This also suggests considerable movement in the rib cage during healing. Both lines of evidence independently confirm the presence of mobile ribs and may imply thoracic breathing in the adult forms of these very large theropod dinosaurs.

Preorbital Fossae in Mammals: A Re-examination of this Unusual Structure

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The preorbital fossa is a bilateral antorbital structure found in several ungulate mammals. It consists of a pit in the lacrimal bone, overlain by connective tissue and skin. Though variable in deer, the fossa is reduced in sheep and absent in both cows and horses. Few studies have examined the organization of this connective tissue. We dissected a wide variety of ungulates (elk, sheep, cow and horse) and discovered the presence of three features common to all animals, 1) a connective tissue raphe (from orbital rim to supranasal part of fossa), 2) muscles attaching both above and below this raphe and 3) a vein traveling below the raphe, under the muscular layer. Absence of fossae in cow and horse, but continued presence of all three structures, albeit reduced, implies that either a) the preorbital fossa was present ancestrally, but secondarily lost in these derived taxa or b) the raphe and musculature represent the initial (primitive) stage of the evolutionary development (in which case cows and horses may represent the primitive condition). A preorbital fossa may have occurred in early horses.

Locomotor Dynamics of a Semi-erect Posture: Correlates of Kinematics and Kinetics in Walking Alligators

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Ground reaction forces, whole body mechanics, and limb kinematics were quantified for *Alligator mississippiensis* as several subjects walked over a series of three-dimensional force platforms. Kinematic and kinetic analyses of alligator walking will be brought together to describe the dynamic relationship between limb segment movements, whole body mechanics, propulsive forces and the torques produced by individual limbs. Initial results reveal that the semi-erect locomotory posture of alligators exhibits unique biodynamic features compared to studies of other more gracile semi-erect species and erect forms and that semi-erect locomotion is surprisingly expensive in the alligator.

The Phylogeny of Amphibian Metamorphosis

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Living frogs (Anura) display a remarkable metamorphosis from the tadpole to the juvenile stage, involving wholesale remodelling of most organ systems. What are the evolutionary origins of this metamorphic process? Here, I examine this question by analyzing anuran metamorphosis in a phylogenetic context. By comparing individual character ontogenies between frogs, salamanders (Caudata), caecilians (Gymnophiona), and fossil taxa for which ontogenetic data are available (specifically temnospondyls and discosauriscid seymouriamorphs), a reconstruction of the evolution of some of the morphological transformations of anuran metamorphosis is possible. This reconstruction suggests that a relatively extreme metamorphosis may be a derived feature of all lissamphibians, which anurans have modified more than have the other two groups.

Adaptations to Marine Life in a Phytosaur (Reptilia, Archosauria) from the Norian (Late Triassic) of Northern Italy

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Analysis of a nearly complete skeleton of a narrow snouted phytosaur discovered in Norian (Late Triassic) marine deposits (Zorzino Limestone, Lombardy, Northern Italy) revealed an adaptation toward aquatic life previously unknown for this group of archosaurs. Main skeletal features suggesting a stronger adaptation toward aquatic life with respect to other phytosaurs are a greater elongation of the tail, consisting of up to 75 vertebrae, a modification of the morphology of the posterior caudal vertebrae, a reduction of the size of the limbs, accompanied by a change of proportions among different limb sections, and a loss of part of the dermal armor. The trunk section is also more cylindrical and narrower than in other known phytosaurs. The overall morphology suggests an undulatory swimming mode for this reptile which probably lived close to the surface of water feeding upon the abundant fish fauna that thrived in the marine basins in which the Zorzino Limestone was deposited. Preparation and detailed systematic study has yet to be completed; however, affinities with the coeval genus *Mystrisuchus* are feasible and it is possible that this specimen represents a new species more adapted toward marine life than most other phytosaurs.

Factors Affecting the Origination of New Organizations of the Enamel Microstructure During Phyletic Change in Dental Stresses

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Information acquired during the last 20 years has shown that the microstructural architecture of enamel in vertebrate teeth is related to the stress regimes within the teeth during chewing, grasping and biting activities. Anisotropic abrasion resistance and brittleness of hydroxyapatite crystals, differences in directions and magnitudes of dental stresses, and the ability of certain organizations of the microstructure to reduce brittleness in enamel explain much of the variation in enamel structure among major groups of tetrapods. However, in mammalian taxa where high occlusal stresses routinely occur, several fundamentally different architectures have phyletically arisen in response to similar changes in stresses. Comparison of the primi-

tive architectures in lineages in which radically different solutions exist suggest that the nature of the antecedent microstructure is a critical factor in the outcome of selection for fracture resistance. Early members of vertebrate lineages are often unknown or unrecognized due to the fragmentary nature of the fossil record, but the relationship between primitive and derived enamel microstructural architectures in several lineages where rapid change has occurred allows prediction of the stress regime and dietary adaptation in the unknown antecedent taxa.

Ontogeny of Macrophages and Pale-grey Cells in Brown Trout Liver

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The fish liver has inspired many studies on phylogenetic comparisons among vertebrates, and also on toxicology. With respect to ontogenetic studies, there are few on the more rare cellular types of this organ, especially on macrophages. For this reason, and taking into account that we previously identified a new cellular type (pale-grey cells) sharing some similar morphological characteristics of macrophages, the present work focused on the ontogeny of both cells. We looked at the presence vs. absence of pale-grey cells and interhepatocytic macrophages in different ages and tried to detect the moment they made their onset in liver embryology. For this ontogenetic study, liver samples of brown trout (*Salmo trutta f. fario*) were taken at 5 particular ages within a period ranging from 2-weeks to 5-months old post-hatching. The samples were processed for electron microscopy. After analysis, it was concluded that pale-grey cells appeared earlier (at 3-weeks post-hatching) than interhepatocytic macrophages (only at 5-months old). In addition, cells with intermediate morphological characteristics between them were also seen in all ages. In conclusion, this study supports that pale-grey cells belong to the macrophage lineage, being eventual precursors of macrophages residing within the parenchyma. Technical assistance: M.H. Oliveira, M.W. Silva. In collaboration with DRAEDM. Financed by FCT.

Form and Function of Patterns of Skeletal Growth in Turtles

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The growth of bone and cartilage in turtles follows two separate and completely different pathways, which can be understood in the light of the functional significance of different growth rates and other physiological requirements. Nearly all turtles have slow bone growth with non-vascular cartilage. A few large marine turtles have developed rapid bone growth with vascularized cartilages. The leatherback turtle is the only living representative of this second mode of bone growth. The leatherback has also developed a suite of other morphological specializations that make it among the most unique of all living reptiles.

"Did Ernst Haeckel Fraudulently Schematize His Illustrations of Embryos?"

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Haeckel had been charged with supporting his biogenetic law with illustrations that he knew were incorrect and fraudulent. The charges were leveled often enough during his life-time and many contemporary histories repeat this accusation. I investigate the substance of the charge and consider what in the prevailing circumstances might be actually fraudulent. The conclusions are surprising.

Extracellular Matrices of the Inner Ear: Molecular and Structural Diversity

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A variety of extracellular matrices are associated with the apical surfaces of mechanosensory epithelia. A cupula sits above the lateral-line organs and cristae of the semi-circular canals, an otolithic or otoconial membrane covers the vestibular maculae, and a tectorial membrane lies over auditory organs like

the avian basilar papilla or the mammalian organ of Corti. Three matrix molecules uniquely expressed in the inner ear are components of these matrices, alpha-tectorin, beta-tectorin and otogelin. In the avian inner ear, alpha and beta-tectorin are expressed in the basilar papilla and striolar regions of the maculae. Alpha-tectorin, but not beta-tectorin, is also expressed in the extrastriolar regions of the maculae. Alpha-tectorin is not expressed in any of the three cristae, and beta-tectorin is only expressed in two of the cristae. In the mammalian inner ear, otogelin is found in the cupulae, and both the otoconial and tectorial membranes. Alpha and beta-tectorin are not expressed in any of the cristae but are present in the otoconial and tectorial membranes. Collagens type II, V and IX are prominent components of the mammalian tectorial membrane, but not of the otoconial membranes or cupulae of birds or mice, nor of the avian tectorial membrane. The appearance of collagens in the tectorial membrane of higher vertebrates may have been one of the major steps in auditory organ evolution. Supported by The Wellcome Trust.

Haeckel and Modern Biology

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The evolutionary studies of Ernst Haeckel have been the subject of lively debate for a century and a half. Haeckel's work addressed fundamental scientific questions, and many of these remain unanswered today. Furthermore, his methods and opinions were often controversial. Molecular studies of development have reawakened interest in issues such as the conservation of development mechanisms — and these issues are informed by Haeckel's work in phylogenetic embryology. We discuss how modern computer-based techniques of phylogeny reconstruction can exploit embryonic characters. We also examine Haeckel's work in terms of the evolution of developmental mechanisms. We discuss Haeckel's influence in fields beyond science, and show how his biology can be viewed in terms of historical theory. Finally we will consider allegations that Haeckel faked his embryo drawings, and show how these allegations were exploited for propaganda purposes by anti-Darwinians.

The Development of the Urinary System in a Frog Without a Tadpole (*Eleutherodactylus coqui*, Anura, Amphibia)

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The excretory system in anurans with free-living aquatic larvae is composed of three distinct organs, pronephros, intermediate and definitive trunk kidney, which appear successively in a regular temporospatial order. Their formation, function and degeneration are supposed to depend on whole body organogenesis and physiological condition during larval life. Hormonal control seems to be one of the main regulators in ontogeny. The organogenesis of the urinary system of the direct developing *Eleutherodactylus coqui* was examined in order to get more information on kidney development in anurans. The development of the pronephros follows the scheme found in anurans with free-living larvae. An intermediate degenerating kidney is missing; the number of the nephrons of the definitive trunk kidney is reduced. Pronephros degenerates and opisthonephric activity starts shortly after the beginning of thyroid function. The present results help to support the hypothesis that the evolution of direct development in anurans is associated with precocious development and activity of thyroid axis. As metamorphosis initiated by thyroid hormone is lacking, extensive remodelling of the opisthonephros is not necessary. Like in other organs (e.g., cranial ontogeny), the trunk kidney exhibits the direct embryonic formation of adult features. Besides, analysis of the anuran kidney organogenesis in alternated developmental modes, such as direct development, probably provides insights into the evolutionary concept of urogenital development in vertebrates.

Parallels of Maldevelopment of the Craniofacial Skeleton in Down Syndrome and in Two Segmentally Trisomic Mouse Models

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Two genetic mouse models for Down syndrome (DS) are currently available for study. The Ts65Dn mouse is at dosage imbalance for a region of

mouse chromosome 16 whose human chromosome 21 counterpart includes 118 genes, while the Ts1Cje mouse has a smaller portion of the same segment at dosage imbalance corresponding to 81 genes from the Chr21 gene catalog. We examined the craniofacial skeleton of these two mouse models for Down syndrome to determine whether they could be used to establish the influence of particular genes on the development of the craniofacial complex. Three-dimensional coordinates of biological landmarks were collected from the skulls of segmentally trisomic mice and their normal littermates. Statistical comparisons of craniofacial shape showed that Ts1Cje mice differ from euploid littermates in ways very similar to the patterns that define the differences between Ts65Dn mice and their littermates. Both mouse models displayed patterns of craniofacial dysmorphology noted in DS. Developmental studies of the two mouse models provides the opportunity to examine the developmental genetic program that underlies mammalian skull morphology by examining parallels in mouse and human craniofacial phenotypes caused by aneuploidy of the same genes. This work was supported by grants PHS F33DE05706 and HD24605

The Phylogenetic Relationships of Turtles

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The analysis of amniote relationships, as expressed in amniote classification, historically placed much emphasis on the configuration of the dermatocranium in the temporal region of the skull. The importance of this character complex was reduced by the advent of computer assisted cladistic analyses of large numbers of equally weighted morphological characters, and by the use of molecular data in the analysis of amniote relationships. This paper focuses on the relationships of turtles, for which three alternative hypotheses have recently been proposed. The application of reverse successive weighting shows the paleontological-osteological data to include two subsets of characters that support conflicting hierarchies. The stronger signal places turtles as sister-group of Sauropterygia at the base of the lepidosauromorph lineage of diapsids; the weaker signal places turtles as sister-group of pareiasaurs among parareptiles. By contrast, molecular analyses show a high degree of congruence in relating turtles to the archosauromorph lineage of diapsids. Neontological characters that have previously been proposed in support of archosaurian affinities of turtles do not stand up against critical scrutiny. On the other hand, it is the Sauropterygia that pull the turtles to the base of the lepidosauromorph clade, while as yet unpublished data place Sauropterygia at the base of the archosauromorph lineage. The resolution of turtle relationships will require additional data, but may also change dramatically with the collection of new fossils, both of early fossil turtles, as well as of Triassic parareptiles such as procolophonids.

The Ethmoidal Region of the Skull in Amphibia

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The structure of the vertebrate skull cannot be properly understood without considering developmental, comparative anatomical, and palaeontological data. Basically, the amphibian skull consists of the otico-occipital braincase that originates from the somitic mesoderm (sclerotom), and the viscerocranial part (including the preotic braincase) that is a neural crest derivative (i.e., neuroectoderm). Three pairs of capsules (otic, optic, ethmoidal) are, to varying degrees, of ectomesenchymal (placodal) origin. It follows from this review that the ethmoidal region of the amphibian skull, which involves axial structures (trabecular horns, i.e., anterior parts of the trabeculae), ethmoidal capsules, and adjacent parts of the viscerocranium (i.e., postnasal wall) are exclusively of ectodermal origin. Studies on temnospondyl amphibians (ancestors of modern amphibians) revealed that they lacked trabecular horns and possessed an internasal plate separating the nasal organs from one another, similar to contemporary pipids. A review of evidence is given for possible derivation of the trabecular horns of non-pipid anurans from this ancestral condition. Non-pipid anurans, in contrast to other amphibians, developed a larval jaw apparatus which is fixed to the ethmoidal endocranium; it consists of the suprarostal and infrarostal cartilages. Both lose their original function and undergo profound transformations in metamorphosis, but partly persist in the ethmoidal endocranium of adults. Some isolated cartilages of the larval nasal region become incorporated into the postnasal wall.

A Stereological Approach of Seasonal Changes in Trout Hepatocytes

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 Studies on the microanatomy of fish liver date from the 18th century. The acquisition of a thorough knowledge of normal liver structure has been shown important for a proper evaluation of pathological processes, and to more effectively understand the relationship between morphology and function. The use of stereology for the quantification of liver structure had its debut for mammals in the past sixties, but only in the eighties was it used in fishes. With this study, using design-based stereology, we wanted to verify whether hepatocytes of brown trout (*Salmo trutta f. fario*) vary their number and size during the breeding cycle and whether gender differences exist. The organellar content was also assessed by unbiased stereology at electron microscopy. Three-year-old specimens were examined in May (pre-vitellogenesis), September (vitellogenesis), and February (post-spawning). It is suggested for the first time that changes in cell number rather than size cause the shifts of relative liver weight that is observed during breeding in trout, and possibly in other species. We hypothesized that seasonal alternating cycles of mitosis and apoptosis occur under the influence of steroids, being most striking in females. We further propose a new process by which females may increase the amount of RER throughout vitellogenesis; constancy of total volume per cell with an increasing number of hepatocytes. Financed by FCT. In collaboration with DRAEDM.

Seasonal Morpho-Functional Plasticity of Fish Liver Peroxisomes

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Peroxisomes appear in most eukariotic cells and are typically abundant in hepatocytes. They are involved in pathways of the metabolism of free radicals, the catabolism of very long chain fatty acids, the synthesis of cholesterol and ether lipids, bile acid formation, and the catabolism of purines, prostaglandins, and leucotrienes. Studies are mainly limited to mammals, but it is known in fishes that several chemicals, including water pollutants, induce morphological and biochemical disturbances in peroxisomes. Moreover, seasonal and gender differences can occur in fish, as we have shown for brown trout (*Salmo trutta f. fario*). In this study, we give a correlation between the seasonal morphological changes and the peroxisomal function, evaluated by enzymatic activities (of catalase, urate oxidase, glycolate oxidase, D-alanine oxidase, and palmitoyl-CoA oxidase). We also correlate the morphological and enzymatic changes with gonadal development and the levels of estradiol and of testosterone. Animals were collected in February (post-spawning), May (pre-vitellogenesis), September (vitellogenesis), and December (spawning). It is concluded that the decrease in dimensions (volume and surface) of female hepatocytic peroxisomes, whereas the ovary matured under the influence of steroid levels, was accompanied by a reduction in enzymatic activity (the changes in males were much subtler.) The study supports our hypothesis that estradiol modulates peroxisomal morphology and function. Financed by FCT, in collaboration with DRAEDM.

How to Tell When Your Fish is Going Steady: Harmonic Analysis of Undulatory Swimming Kinematics

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It is commonly assumed that a steadily swimming fish produces a traveling wave with a caudally increasing amplitude. By digitally processing high-speed video of swimming fish, we present a means of 1) quantifying the accuracy of this assumption, and 2) applying this insight to analyze the kinematics and neural control of swimming fish. We offer evidence that lamprey are quantitatively less steady when swimming backward than forward, and consider the implications in terms of energetic efficiency and coordination of neural control. By examining the phase lag of the fundamental mode and of first and

higher harmonics along the length of the lamprey, we identify characteristics supporting the notion that steadily swimming fish tune their body stiffness to propel themselves with an accelerating wave of curvature.

Biomechanics of the Skull in *Proterosuchus* (Reptilia, Archosauria)

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Proterosuchus was a carnivorous thecodontian three meters in length from the Lower Triassic of South Africa and China. Its main skull characteristic is the downward sloping premaxilla, well known also from other vertebrates as the Recent gar (*Lepisosteus*), the extinct phytosaurs, and a few fossil crocodiles (*Bretesuchus*, *Bergisuchus*). We simulated load on a 2-dimensional and a 3-dimensional model of the *Proterosuchus* skull. Using the Finite-Element-Method (FEM) with ANSYS 5.5 we have got a lot of different developing stages showing a process from a single homogenous and easily structured element into a complex one. The latter resemble the natural construction in many aspects, for example in the presence of an antorbital fenestra, as well as in a nasal aperture, the premaxilla-maxilla-gap and an interpterygoid slit. Amount and direction of forces lead to hypotheses of presence and mechanical characteristics of hard and soft part structures in the snout of *Proterosuchus*. The models allowed us to speculate on the maximum load of the premaxilla-maxilla region due to its functional options.

New Specimens of *Deltatheridium*: Their Bearing on Basal Metatherian Phylogeny

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The discovery in 1993 of the Late Cretaceous locality Ukhaa Tolgod in the Nemegt valley, Mongolia, by the Joint expedition of the American Museum of Natural History and the Mongolian Academy of Sciences has resulted in the world's largest collection of skulls and skeletons of Mesozoic mammals. Therians, including the basal metatherian *Deltatheridium*, form a small percentage in a fauna dominated by multituberculates. We report here on a group of juveniles of *Deltatheridium* retaining deciduous dentition, partial skulls, and postcrania, and on an incomplete skeleton of an adult. These specimens include substantial postcranial elements and portions of the skull previously unknown. The juveniles studied by traditional methods and by the use of high-resolution CT represent a younger stage of *Deltatheridium* than that reported previously by us. The new fossils confirm the predicted molariform morphology for upper and lower dp3, and provide evidence of retained primitive features in the orbital area of the skull such as an optic foramen. The new morphological information on *Deltatheridium* and that on other metatherians described since our last phylogenetic analysis of Metatheria in 1998 are evaluated within the basic framework provided by that study.

High-Resolution X-ray Computed Tomography in Vertebrate Morphology

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High-resolution CT scanners are industrial descendants of medical diagnostic scanners, and can achieve 1-2 orders of magnitude higher resolution, with better penetration of dense materials. For small objects, they can achieve slice thicknesses on the scale of tens of microns, and are now being used to image even the smallest vertebrates. CT detects contrasts in X-ray attenuation properties, including differences between mineralized or experimentally modified structures and soft tissues in recent specimens, and generally between fossilized material and matrix. Because it is non-destructive, CT is increasingly important in studying rare and unique specimens that are too precious to mechanically section. Our

workshop will cover the design and capabilities of these new scanners, image processing using free and off-the-shelf software, and 3-D digital rendering and printing of physical models from CT data. We will describe applications of high-resolution CT, including quantifying trabecular bone architecture, detecting repaired or forged specimens, constructing digital endocasts, imaging skeletal structure in pickled specimens, and imaging extra-skeletal structures such as the endolymphatic system. Examples used to illustrate these techniques will include *Sphenodon*, *Lanthanotus*, and an extant amphisbaenian (*Loveridgea*); *Ornithorhynchus* and an ontogenetic series of *Monodelphis*; and a variety of exceptional fossils. We will also discuss the publication and dissemination of CT imagery via the Web and CD-ROM.

Leave No Stone Unturned; Motor Patterns, Fulcrums, and Feeding Mechanics in *Arenaria interpres*

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As part of a broad-scale analysis of the evolution of feeding mechanisms in shorebirds we analyzed the rock-turning behavior of *Arenaria interpres*, the ruddy turnstone. Turnstones obtain prey in the wild by flipping over rocks to locate invertebrates hiding underneath, but their diets are broad, and they have been considered "generalist" feeders. Turnstones were hatched in the laboratory from wild-collected eggs and, when fully grown, were presented with both stones and artificial targets, such as wooden blocks, both with and without prey underneath. Kinematics of rock turning and prey handling were elucidated by frame-by-frame analysis of high-speed (250 fps) video footage. Object turning is innate; naïve captive birds turned both rocks and artificial targets, and did so prior to having ever found prey beneath the objects turned. Surprisingly, the initial levering of rocks or objects off the substrate is accomplished by jaw spreading, especially by rotating the upper jaw dorsally around the craniofacial hinge (cranial kinesis). The motor pattern used is apparently the same used by a wide variety of other shorebirds in different feeding contexts, including in surface-tension feeding, and suggests that a single initial feeding mechanism may have given rise to a variety of feeding strategies in shorebirds.

Feathered Dinosaurs And Other Myths: A Cold, Hard Look At Reality

John Ruben*¹ and Terry Jones², 1 Zoology Dept., Oregon State University, Corvallis, Oregon 97331, 2 Biology Dept., Stephen F. Austin University, U.S.A. Recently, it has become almost axiomatic that theropod dinosaurs were, to some degree or another, feathered. However, empirical evidence for feathered dinosaurs is far less compelling than is generally acknowledged. So-called "protofeathers" in some taxa (e.g., *Sinosauropteryx*, *Sinornithosaurus*) are completely devoid of feather structure and are often indistinguishable from collagen fibers in extant taxa. The only supposed theropods that possessed integumentary structures clearly identifiable as feathers were *Caudipteryx* and the poorly-preserved *Protarchaeopteryx*. However, there is little reason to believe that *Protarchaeopteryx* was anything but an early Cretaceous, fully-flighted bird. Similarly, *Caudipteryx*' "Bauplan" is consistent only with it having been an early flightless bird. Significantly, the best preserved integument from an undoubted theropod (*Pelecanimimus*) clearly demonstrates that these animals were scaled, not feathered. Other, non-dinosaurian taxa (e.g., *Longisquama*) may reveal far more about feather origins than do theropods.

Morphogenetic Analysis of the Chondrocranium of Muroidea with Special Emphasis on the Ethmoidal Region

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The craniogenesis of Muroidea, by far the richest group of rodents in terms of number of species, is still mostly unknown. Yet, studies of the craniogenesis can provide numerous characters useful to elucidate the phylogenetic relationships of this group. Previous craniological investigations in rodents were mostly restricted to relative young embryonic stages. In this study especially late fetal to juvenile stages of *Rattus norvegicus*, *Peromyscus maniculatus* and 16 other muroid rodent species were examined using histological sections and plate reconstructions. Focal point of these investigations is the ethmoidal region because of its complexity and good documentation in relevant outgroups. For the first time structures that only

occur late in ontogeny are described, e.g., a Fenestra internasalis posterior and one or two Processus caudales of the Processus alaris superior. The Grundplan of the muroid ethmoidal region is hypothesized to include, e.g., a Septoturbinale associated with a Fenestra internasalis posterior and a Processus anterior of the Lamina infraconchalis.

Fidelity of Convergence in Saurian Digital Adhesive Systems: Gekkotans and Anolines

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Among lizards, geckos and anoline polychrotids ("American chameleons") are well known for their possession of subdigital adhesive pads and marked climbing and clinging abilities. The ultimate agents of adhesion are the setae (fine, hair-like outgrowths of the epidermis) that operate at a molecular level to create the bonding force. In order for these setae to effect and break these bonds stereotypical patterns of pedal movement are brought about, mediated through a constellation of morphological systems. The organism-environment interface, in terms of the adhesive bond, constrains the morphological systems to operate in particular ways. Employing the gekkotan adhesive system and its pattern of morphology, predictions were made about the behavior patterns and morphological configurations of anoline polychrotids. These are at least partially interdependent and predict that anolines will display: (a) digital hyperextension during locomotion; (b) skeletal morphology consistent with hyperextension; (c) muscular modifications that promote hyperextension; (d) compliance mechanisms that promote maximal setal contact with the substratum; (e) mechanoreceptor distribution consistent with monitoring surface contact and degree of hyperextension. Individual components and the integrated "assembly" of these is considered in the context of the evolution and operation of a subdigital adhesive system based upon setal elaboration.

A Phylogenetic Framework for the Study of a Behavior-Morphology Complex in Beavers

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The fossil record of beavers spans 38 million years, and contains roughly 20 genera (50 species). Fossil beavers are morphologically diverse and span at least a 6-fold range of size. They also exhibit diverse incisal morphologies, suggesting varied incisor functions. It is usually difficult to study the relationship between morphology and behavior in extinct taxa, however, in fossil beavers two types of associated fossilized behavioral artifacts provide evidence as to how fossil beavers used their incisors: 1) incisor marks in burrows and 2) cut marks on wood. These behavioral indications correspond with different incisor morphologies, and as a result it is possible to study the evolution of this incisor morphology-behavior complex. In beavers the incisors are used in at least two distinct functions: tooth-digging and tree predation. Tree predation is of particular interest because in the living genus, *Castor*, it is associated with dam building, a behavior that is known to exert immense ecological impact. In this study a new cladistic analysis of fossil beavers is presented and used to map the evolution of morphological and behavioral traits. The purpose of the cladistic analysis described here is to reconstruct the evolutionary relationships of the major clades of castorids and thereby provide a framework for the study of the evolutionary relationship between incisor shape, function and behavior in beavers.

On the Development of Some Character Complexes in Marsupial Mammals: Does Ontogeny Recapitulate Phylogeny?

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In spite of the extensive literature about the relationship between ontogeny and phylogeny, few studies have examined this topic empirically, analytically and in an explicit phylogenetic framework. I present new developmental data of several character complexes of marsupials, and I compare changes with the phylogenetic transformations suggested by a parsimony-based reconstruction of them in a consensus tree. Series of animals of different ages, representing all the major clades of Marsupialia, were examined using serial histological sections. In many cases, 3-D reconstructions of the structures of interest were made using the computer softwares Surfdrive and Cinema4D.

Character complexes examined include ear ossicles, vomeronasal complex, petrosal bone, upper molars, and shoulder girdle. How these complexes are partitioned affects the percentages that we obtain for evolutionary transformations with recapitulation. In spite of this caveat, conservative generalizations can be made. As exemplified by studies of ear ossicles, development mirrors the evolutionary transformation. Structures that have appeared later in phylogeny appear also later in ontogeny. However, this 'recapitulation' is imperfect. The spatial relations of the structures in question and their relative sizes are similar but never like those of their purported ancestors. This is also true for features of the shoulder girdle, stapedia artery, stapes form, venous prootic canal, among other character complexes.

Ontogenesis of the Shoulder Girdle in Didelphid Marsupials

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Therian mammals have evolved a mobile breast-shoulder apparatus and a reduction in the size and number of elements that is correlated with more parasagittal limb movements. Broom and Klima had shown that in embryonic and pouch-young specimens of several Australasian marsupials some of the elements that are absent in adult therians persist in a cartilaginous state, which we have confirmed for specimens of the dasyurid *Sminthopsis virginiae*. We documented the anatomy of the shoulder girdle in ontogenetic series of embryonic to juvenile didelphids (*Monodelphis domestica*, *Didelphis virginiana*, *Caluromys philander*) and several Australian taxa by using serial histological sections and 3-D reconstructions. Didelphids show no continuity between the scapula and the sternum prenatally and at birth, in contrast to all other marsupials studied to date except peramelids. At birth the scapular spine has not yet fully formed, and in contrast to adults, the supraspinous fossa is proportionally smaller than the infraspinous one. Only the acromial portion of the scapular spine is preformed in cartilage, the rest is formed through a muscular aponeurosis that becomes ossified during ontogeny. The shoulder joint is at birth in a ventro-medial position, possibly correlated with the climbing activity in the altricial neonate.

Heterochrony in Sauropodomorph Dinosaur Evolution as Deduced From Bone Histology

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Bone histology is a powerful tool for deducing life history parameters in extinct tetrapods. Applied to sauropod dinosaurs such as those from the Upper Jurassic Tendaguru Beds, it appears that these animals grew at mammalian rates and reached maximum size in less than about 30 years. However, as opposed to mammalian growth strategies, sexual maturity was reached considerably earlier. Sauropod life history thus showed the typical reptilian trait of prolonged growth after sexual maturity. Growth lines are rarely and irregularly developed in the long bones, indicating that their growth was uninterrupted. Growth was determinate as documented by the development of an external fundamental system. Sauropods are unique among terrestrial tetrapods in generally having attained >10 t to <100 t adult body weight. How did this gigantism evolve? A comparison between the life history strategies of the plesiomorphic sister group, the prosauropods, and the sauropods addresses the possible role of heterochrony in this evolutionary transition. Among prosauropods, the well known Norian genus *Plateosaurus* was sampled from growth series of various long bones and girdle bones. This taxon is characterized by rapid but cyclical growth as evidenced by fibrolamellar bone interrupted by regularly spaced lines of arrested growth. In the evolution of sauropods from prosauropods, the heterochronic process of acceleration (increased growth rate) thus played a significant role. Other heterochronies may also have been of importance.

Kinematics of a Novel Feeding Mechanism in the Brook Trout *Salvelinus fontinalis*

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The salmon and trout (family Salmonidae) possess a functional novelty, the tongue-bite apparatus, located between the mandibular jaw apparatus anteriorly and the pharyngeal jaw apparatus posteriorly. A similar, but non-ho-

mologous tongue bite is also found in the osteoglossomorph (bony tongue) fishes. Using high-speed video (250 fields s⁻¹) and stop-frame kinematic analysis of feeding behavior in the brook trout (*Salvelinus fontinalis*) I have established that salmonids, like osteoglossomorphs, use their tongue bite as a novel feeding mechanism. Salmonid 'raking' behavior is similar to that of osteoglossomorphs involving extensive neurocranial elevation and pectoral girdle retraction.

Confusing Fossil Vertebrate Hard Tissues and Topologies from the Lower Paleozoic of China

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The early fossil record of vertebrates is characterized by notable plasticity in the development of biomineralized exoskeletal tissues. The presence of cellular and acellular bone, tubular and atubular dentines and enamel and enameloid in the dermal armor of Cambro-Ordovician vertebrates has been well documented. The bewildering array of tissues seen in Lower Silurian vertebrates from China is, if anything, more extreme. Galeaspid are one of the more common components of Chinese Siluro-Devonian vertebrate faunas, and appear to have occupied similar ecological niches to the contemporaneous heterostracans. Previous studies have described their histology, suggesting that the former lack dentine and may include enamel/enameloid. Sinacanthids are only known from ornamented spines that occur in many Silurian localities in China, but nowhere else. New material from Tarim, Xinjiang Province and South China has demonstrated the presence of novel tissues and tissue topologies in galeaspid headshields and sinacanthid spines, as have studies of the scales and teeth of a number of "chondrichthyan-like" taxa, such as the mongolepids. In the absence of detailed data on the morphology of sinacanthids and mongolepids, histology should provide valuable data for their taxonomic assignment, but the tissues are so novel that they tend to confuse, rather than clarify, their phylogenetic position.

Effect of Hypoxia on Histology and Fine Structure of the Rat Lungs

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Histological and ultrastructural changes in rat lungs subjected 30 days influence of high temperature (36°C) and hypoxia were examined. Histological investigation revealed an uneven plethora and edema of interstitial tissue, dysteletease and emphysema locuses and extensive growth of connective tissue around the bronchi and in lung parenchyma. Ultrastructural examination detected compensatory-adaptive alterations of all cellular components in respiratory compartment. Only a few type I pneumocytes were found in a state of hydropical dystrophy and partial necrosis. An expulsion of disintegrating epithelial cells from the basal membrane was followed by recovery of epithelial lining by means of encroaching flattened cytoplasmic extensions from adjacent cells. An appearance of type II pneumocytes with initial signs of differentiation indicated their definite proliferation. Both types of pneumocytes were found in a state of working hypertrophy with tissue-specific and secretory synthesis intensification. Except for a few untwisted lamellate bodies, surfactant complex was missed that was obviously determined by hypoxia. Effusive proliferation of myofibroblasts and their close contact to epithelial cell surfaces were probably directed to optimal stabilization of alveolar fluctuating surfaces. Abrupt intensification of micropinocytosis processes accompanying by thickening of endothelial stratum of aerohaematic barrier prevented an edematization of epithelial and interstitial strata of the last. Fibro-generating function of fibroblasts was replaced by active fibroclazy of redundant collagen fibers. We consider that the morphological changes described as resulted from hypoxia.

Ontogenetic Scaling of Poison Glands in *Dendrobates pumilio*

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Growth related changes in granular (poison) gland size and density were examined in an ontogenetic series of the strawberry dart-poison frog, *Dendrobates pumilio*. Specimens used in this study were collected from the

La Selva Biological Station in northeastern Costa Rica. Patches of skin from the dorsal surface of ten frogs, ranging in size from 11 to 23 mm snout-vent length (SVL), were fixed and embedded in paraffin for histological sectioning. Poison gland size and density were quantified microscopically in these sections. Poison glands are uniformly distributed across the skin and during ontogeny mean poison gland diameter increases at a rate faster than snout-vent length from 42.5 mm at SVL 11 mm to 120.0 mm at SVL 23 mm. Conversely, gland density decreases with body size from 71.9 glands/mm² to 33.2 glands/mm². Due to the positive allometric growth of the poison glands, the percentage of skin surface occupied by poison glands increases from 10.1–22.1% in small frogs (SVL < 18 mm) to 50.0–65.2% in large frogs (SVL < 19 mm), resulting in more toxin per mm² in the larger animals. The largest increase in toxicity is correlated chronologically with the onset of sexual maturity rather than with changes in aposomatic coloring.

Analysis of Tooth Enamel Ultrastructure of Mammalian Fauna From the Quaternary Period of India: Taxonomic, Structural and Dietary Implications

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The tooth enamel ultrastructure of extinct and living species of bovids and proboscideans from geological and archaeological deposits of India is discussed. Quantitative and qualitative analyses of prismatic enamel of living cattle and buffaloes have made taxonomic determination possible in these closely related taxa. This is a significant contribution to archaeozoology since the close similarities in skeletal morphology of cattle and buffaloes makes completeness of their bones a pre-requisite for precise identification. Microstructural adaptations in the enamel of primitive and true elephants demonstrate the relationship between tooth morphology and enamel microstructure. Hunter-Schreger Bands in proboscideans became more complex and individual prism size and prism shape underwent considerable change, suggesting biomechanical adaptations against abrasion and hypsodonty. Three species of cattle from Pleistocene and Holocene deposits of India were examined to see whether in a short time span of nearly two million years and changing conditions on account of the process of domestication have caused any microstructural changes in their enamel. Hunter-Schreger Bands cover more of enamel towards Holocene, indicating adaptation against abrasive diet. The paper gives a detail account of enamel ultrastructure studies carried out on the genera mentioned above and highlights the promises it holds for palaeontological studies in India.

Evolutionary Theory and Concepts: Walter J. Bock's Contribution

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Beginning with the publication of his first scientific paper in 1956, Walter Bock has had an active scholarly career spanning 44 years and continuing unabated in the 68th year of his life. Although there is a broad zone of overlap between them Walter Bock's research can be divided into two major topics: functional and evolutionary morphology and theory development. Since the publication of his seminal paper on "Pre-adaptation and multiple evolutionary pathways" he published approximately 30 important contributions to evolutionary theory. His theoretical analyses center on the question of adaptation and major evolutionary change. Therefore, the aim of the present paper is to appreciate Walter Bock's contribution to evolutionary theory. Here, the sagacity of his theoretical analyses can be demonstrated exemplary, only. One of the most controversial topics in evolutionary biology during the past couple of decades is species selection, the suggestion that possibly entire species are selected in the same sense that individuals are. This debate has raged on the ontological status of species, whether they represent individuals or classes. Most scientists who have commented on this topic have claimed that species are individuals. From this point of view, some authors have argued that evolutionary theory is hierarchical with the same causes acting on each of the several levels of hierarchy. However, as Walter Bock indicates, it has been essential to include ideas from the philosophy of science in the evolutionary theory, as, for example types of explanations. From this position he is one of the few scientists who contradict the concept of species selection indicating that it has resulted from confusion over the nature of explanation in science. Based on the concept of "family resemblance essences" (Aristotle) Walter Bock succeeded in indicating that biological populations are a prime example of classes.

The empirical morphological work provides Walter Bock the basis for his theoretical contributions.

Structural Diversity of the Temporal Region of Catfishes: Convergence in Functional Integration of Sensory Systems

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Morphology of the temporal skull and postotic laterosensory canal was surveyed across loricarioid and outgroup catfishes to resolve conflicting statements regarding homology and significance of intrinsic variation. Higher loricarioids differ from *Nematogenys*, other trichomycterids, and outgroups in having a reduced number of primitively separate temporal region bones. A pterotic branch is common and synapomorphic for catfishes, but its presence in loricarioids has been disputed. Presence of a pterotic branch in *Nematogenys inermis* and other loricarioids is confirmed; the pterotic branch is secondarily absent in scoloplacids and astrolepids. Loricariids share with astrolepids and some trichomycterids direct contact between trunk lateral line and swimbladder capsule chamber, however, only loricariids have the lateralis canal in direct contact with the swimbladder membrane, resulting in an additional laterophysic connection. Higher trichomycterids share with amphiliids, plotosids and sisoriids a cranial exit of the posterior lateral line nerve separate from that of the vagus nerve, while callichthyids share with scoloplacids and loricariids a nerve pathway within the swimbladder capsule. Loricariids are further specialized in having a modified, double-layered pterotic bone, the postotic canal associated with the ventral layer, and dorsal layer posteriorly expanded to enclose the lateral opening of the swimbladder capsule and form an expanded capsule chamber. The phylogenetic distribution of temporal region specializations among loricarioids suggests independent convergence toward increased functional integration of primitively separate sensory structures within the octavolateralis system.

Morphometric Analysis of Anomalurid Rodents

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We used geometric and traditional morphometric techniques to quantify patterns of shape variation associated with feeding and locomotion in anomalurid rodents (African scaly-tailed flying squirrels). A Relative Warp Analysis and UPGMA clustering was used to map cranial and jaw shape on a phenetic tree. Residual shape variation was then interpreted in light of feeding mechanics. The analysis revealed shape variation at both local and global scales that tracked closely the classification of the group. Phenetic clustering based on shape coordinates revealed greater similarity between anomalurids and graphiurids (dormice) than between anomalurids and the Pedetidae (spring hares). Multivariate regression of shape on size revealed significant allometry across the Anomaluridae. The locomotor apparatus was explored in two ways. First, we regressed pelvic girdle shape against girdle size in an effort to study the effect of size on ability to employ a leaping launch. Second, we assessed allometry in the limbs of gliding forms, in an effort to explore size effects on the aerodynamics and quadrupedal locomotion of the group.

The Excavation of the Cardiac Semilunar Valves in a Teleostean Fish

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The morphogenetic mechanism by which the leaflets of the cardiac outflow tract valves acquire their semilunar morphology has only been studied in birds and mammals. The aim here was to elucidate how the excavation of the leaflets of the ventriculobulbar (conal) valves takes place in the sea-bream, *Sparus aurata*. Thirty-five larvae, ranging from 6 to 10 days post-eclosion, were examined by means of serial semithin sections for light microscopy. In addition, 18 adult specimens were studied using scanning electron microscopy and histological techniques for light microscopy to assess the anatomical and histological features of the mature valvular system, which consists of two major valves, right and left. Sometimes, one or two minor valves are located in the dorsal and/or ventral positions. The present observations indicate that the hollowing of the valve leaflets takes place between day 7.5 and day 10 post-eclosion. During this period, the distoproximal length of the valve sinuses gradually increases, whereas the total (distoproximal) length of the valve cush-

ions remains constant. This strongly suggests that the valve leaflets acquire their typical semilunar morphology by means of a true excavation mechanism that presumably relies on a migratory process of mesenchymal cells, from the core of the valve cushions to the sinus walls.

Postnatal Development of Muscles in Small Mammals

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The ontogenetic development of locomotion and of the locomotor apparatus of two species of small mammals with different life history strategies were investigated. Forelimb muscle histology was studied and correlated with ontogenetic changes in kinematic parameters. Distribution and diameter of slow (type-I) and fast (type-II) muscle fibers in forelimb muscles of five developmental stages of *Tupaia glis* (altricial) and *Galea musteloides* (precocial) were analyzed. Fiber type distribution is comparable between all stages. In *M. triceps brachii* cp. medialis, a predominantly slow muscle, an increase in the proportion of slow muscle fibers takes place in both species. During postnatal development the increase in fiber diameter depends on the fiber type distribution, the fiber type, the life period and on the position of fibers in the muscle belly. Fiber diameter increases more in muscles with an intramuscular region of type-I fibers (*M. supraspinatus*, *M. triceps brachii* cp. longum) than in muscles with a nearly homogenous distribution (*M. infraspinatus*, *M. brachialis*). In younger animals, the muscle fibers are round in cross-section. The endomysium has not yet formed the honeycomb structure characteristic for muscle cross-section of adults. In the early stages the collagen fibers are irregularly oriented and form a loose network. During further development the fibers become more and more aligned in a regular pattern, forming a distinct sheath that surrounds the muscle fibers.

Development and Evolution of Neurogenic Placodes in Amphibians

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Placodes are thickenings of the embryonic ectoderm that originated with the evolution of craniates and give rise to several specialized structures of the craniate head. With the exception of the lens and adenohypophyseal placode all placodes are neurogenic, i.e., they include neurons among their derivative cell types. Here, the development and evolution of different types of neurogenic placodes (olfactory, profundal, trigeminal, otic, lateral line, epibranchial, and hypobranchial placodes) in urodeles and anurans will be reviewed. The discussion of placode development will address the following questions: (1) What is the fate of different types of neurogenic placodes? (2) During which time window are placodes induced? (3) Are all types of neurogenic placodes separately induced in a single step or does induction proceed in two or more steps, initially specifying a common placodal precursor, which is secondarily subdivided into different types of placodes? (4) What are the molecular signals involved in placode induction? (5) How is neurogenesis in placodes regulated? Comparative studies of placode development have shown that placodes have been very plastic in amphibian evolution and several of those evolutionary changes in placode development will be discussed. Particular emphasis will be placed on the loss of lateral line placodes in direct-developing frogs, which has been shown to be due to the specific loss of ectodermal competence for lateral line placode induction.

Experimental Evaluation of the Avian Digital Arch Hypothesis and Digit Number Pattern in the Avian Hand

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Shubin and Alberch (1986, *Evolutionary Biology* 20, 319) proposed that tetrapod limbs develop largely through a conserved pathway, with the digits developing from an ulnarly derived digital arch, permitting the homologizing of skeletal elements across taxa. Such apparent invariances have led several investigators to counter paleontological and cladistic conclusions regarding avian and theropod affinity (Hinchliffe, 1997, *Science* 278, 596; Burke and Feduccia, 1997, *Science* 278, 666; Feduccia, 1999, *PNAS* 96, 4740; Wagner and Gauthier, 1999, *PNAS* 96, 5111–5116), all of whom

agree that the digits of the avian hand are II-III-IV. However, all of these previous studies have been descriptive and lack the certitude of experimentation. We have attempted to experimentally test the digital arch hypothesis and the digit number pattern in avian embryos. Following Stephens and McNulty (1981, *JEEM* 61, 191) we evaluated the chick hand digit pattern through use of foil barriers, which can inhibit the formation of the radius or ulna. We conclude there is contribution to the digits from both the radial and ulnar side of the limb, rather than from just the ulnar side as proposed by the digital arch hypothesis. For at least some digits there appears to be bimodal proximal contributions; therefore, specific digit numbers may be ambiguous.

Shoulder Movements During Locomotion in Primates

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One of the most comprehensive changes in primate evolution concerns the exclusion of the shoulder blade from the locomotory active forelimb in favor of an increasing mobility of the shoulder joint. Cineradiographic studies of shoulder movements in arboreal-quadrupedal primates indicate that this reorganization of the forelimb, known from brachiators and hominoid primates, is not a common trait of primates in general. Scapular movements of arboreal quadrupeds consist of cranial- and caudalrotation about the proximal pivot and contribute mainly to propulsion. In mouse lemurs, a slight scapular abduction and medial rotation, caused by the clavicle, can be observed at the beginning of stance phase of the forelimb. Shoulder joint excursions are limited to flexion and extension only. Shoulder movements of the mouse lemur correspond with those of other small therian mammals (e.g., tree shrews or rats), and it seems probable that they represent the ancestral condition for primates. The degree of scapular abduction and scapula medial rotation increase in the brown lemur, the cotton-top tamarin, and the squirrel monkey, but a medio-lateral mobility in the shoulder joint exists only in squirrel monkeys. Despite the pronounced three-dimensional scapular excursion the humerus moves nearly parasagittally in this primate whereas, in the mouse lemur, the brown lemur, and the cotton-top tamarin, a scapular abduction leads to a humeral abduction without any medio-lateral excursions in the shoulder joint.

Ultrastructure and Function of Notochord Vacuole Cells in Fishes

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Cylindrical unconstricted notochords are found in lampreys, sturgeons and lungfishes, and constricted notochord tissue is found in the intervertebral joints of teleosts and amphibians. The cellular medulla of the notochord primarily consists of vacuole cells and is surrounded by an acellular fibrous sheath. The vacuole cells are connected by desmosomes, and are designed to function as cellular hydrostats as each vacuole is enclosed by a dense cytoplasmic mesh of keratin-like intermediate filaments. Intermediate filaments mesh thickness and vacuole size are variable from group to group. Peripheral basal cells typically contain an extensive rough endoplasmic reticulum (RER) and numerous mitochondria and appear to transform into vacuolated cells as they lose contact with the fibrous sheath. During transformation, the basal cells lose their RER network and develop numerous membrane-bound vesicles that, in many electron micrographs, appear to coalesce into a single vacuole. The presence of numerous cavaeolae in the plasma membrane of the vacuole cells suggest that the fluid in vacuoles is maintained by pinocytosis. The presence of RER in the basal cells of the lamprey and sturgeon suggests that these cells synthesize the components of the fibrous sheath. In teleosts, many notochord cells lack a vacuole and surround an extracellular fluid chamber that also is maintained by pinocytosis. This study suggests that as the notochord evolved and became constricted by a vertebral column, the ultrastructure and function of the notochord cells also changed.

Kinematics of Vertical Climbing in Hawaiian Freshwater Gobies

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The Hawaiian ecosystem includes three species of waterfall-climbing gobies. Larvae are washed into the ocean upon hatching, return to freshwater 3 to 6 months posthatching, and climb waterfalls (up to 350 m) to reach adult habitats. We used high-speed video to contrast climbing kinematics of

Sicyopterus stimpsoni (20–24 mm total length) with *Awaous guamensis* and *Lentipes concolor* (both 12–16 mm TL) on a Plexiglas waterfall. *Lentipes* and *Awaous* climb using bursts of axial-based swimming. Bursts last 0.07 ± 0.02 sec at 10.3 ± 4.2 TL/sec (190 ± 80 mm/sec). The pectoral fins extend perpendicularly between bursts, but adduct as climbing resumes (contributing to thrust initiation). *Sicyopterus* climb by alternately attaching oral or pelvic sucking discs to surfaces and ‘inching’ upwards with little axial undulation. As the oral disc attaches its size doubles, then the posterior body is pulled upwards; once the pelvic disc attaches, the oral disc releases and the anterior body advances. Climbing bouts include multiple cycles and last several seconds at 0.25 ± 0.04 TL/sec (6 ± 1 mm/sec). Power-burst climbing may be impeded in *Sicyopterus* as this species loses 15% weight during the metamorphosis preceding climbing. While climbing, *Sicyopterus* always remain attached to substrate by suction. ONR N000149910184 (Westneat); Hawaii Fish Restoration F-14-R-18 (Fitzsimons).

Bringing Fossils Back to Life: The Locomotion of the Messel Horse, *Palaeotherium parvulum*

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Propalaeotherium parvulum was a small horse known from the Eocene deposits of the Grube Messel (Germany). One specimen is only 55 cm in head-trunk-length. The small size of the animals suggests that the kinematics of its locomotion were different from those of the large extant horses. The question arises how the locomotion of this fossil horse might have looked like. Based on available descriptions and photographs of original fossil material we reconstructed the skeleton of *P. parvulum* three-dimensionally using surface subdivision modelling procedures implemented in 3D Studio Max software. Previous results of our working group on the locomotion of mammals of various sizes, indicated that the descriptive parameters of the kinematics of a mammal are size related. Thus, the locomotion of *P. parvulum* can be approximated based on data from extant forms of comparable size and proportions (*Hyrax*, *Tragulus*). These parameters were applied to the virtual *P. parvulum* skeleton and it was animated accordingly.

What is Evolutionary Constraint?

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It is now widely acknowledged that organisms reflect the duality of adaptation to current environmental demands and the inherited tendency to remain the same, or historical contingency. Adaptation is the province of environmental selection whereas contingency is assumed to reflect intrinsic, organismal attributes that somehow resist or bias the effects of that selection. As such, contingency is viewed as a ‘force’ that somehow limits the efficacy of selection to create an adapted phenotype and is therefore termed “evolutionary constraint.” However, uncritical usage of constraint terminology has led to its dilution as a critical concept in evolutionary theory. In particular, ambiguity and conflict in the relationship of constraint to selection has been problematic. This treatment attempts to delineate the factors necessary to operationalize a moribund constraint concept by making explicit the relationship between constraint and selection. Several factors are considered essential: 1) specification of a null model, usually adaptive evolution by environmental selection (different null models lead to different definitions of constraint); 2) application to characters, not organisms or lineages; 3) specification of a clade; 3) specification of a focal life-stage; 4) recognition of both internal and external components of natural selection; 5) recognition that selection operates on all life-stages, including early development. If these criteria are met, evolutionary constraints can be defined mechanistically and with explicit reference to selection, eliminating ambiguity. Greater precision in usage should lead to a more useful constraint concept.

Analysis of Metric and Kinematic Parameters of the Locomotion in African Elephants (*Loxodonta africana*)

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The limbs of elephants are characterized by a pillar-like arrangement and straightened joints. Little is known about metrics, kinematics, dynamics and

energetics of the locomotion of Proboscidea. Obviously the largest extant terrestrial animals are not able to gallop but move quite smoothly. As a first attempt to understand the locomotory principles of African elephants and its ontogenetic development we measured metrics and kinematics of two juvenile animals (0, 2) at Thüringer Zoopark Erfurt. The locomotion was analyzed by an infrared motion analysis system (Qualisys) at 240 Hz, which recorded the light reflexions of markers stuck on the skin above the joints and the vertebral column and calculated their locations in the space. The angle-time-courses of limb joints (shoulder-, elbow-, wrist-, hip-, knee- and talo-crural-joint) at different speeds were calculated. At all speeds the animals used a lateral sequence walk. The fore- and hindlimb kinematics will be compared to that of small- and medium-sized animals (which have more flexed limbs).

Homology and Evolution of Cephalic Vasculature in Archosauria

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Cephalic vasculature is an integral component of the vertebrate head, but very little is known about it in Archosauria, and its functional role in the biology of these organisms has never been assessed. We sought to address this deficit in anatomical knowledge by documenting the anatomy of the head vessels of extant Archosauria (birds and crocodylians), testing hypotheses on the homologies and evolutionary history of the head vascular system, and reconstructing vascular structures in extinct archosaurs using the extant phylogenetic bracket methodology. The task of assessing homology was made difficult by the highly apomorphic head morphologies found in both extant archosaurian clades. However, results of this research project have identified a surprising level of similarity in vascular structure and patterning between birds and crocodylians. A higher level of plasticity was found at more general branching patterns, but even these are highly phylogenetically conserved. Many vascular structures have been found to leave clear osteological correlates which has allowed us to discern and reconstruct vascular structures and patterns in extinct archosaurs such as dinosaurs, to test hypotheses of homology, and to add to a comparative understanding of cephalic vasculature in all amniotes. Some of the reconstructed vascular structures appear to be correlated with important physiological mechanisms and behaviors, such as selective brain temperature regulation.

Relation Between the Ultrastructural Changes of Myofilaments and Neuromuscular Junctions During Altered Functional Demands

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Skeletal muscle fibers exist as dynamic structures and are capable of adapting to altered functional demands. Altered functional demands like exercise cause destruction of thin and thick myofilaments mostly located in the peripheral myofibrils. This process is accompanied by destruction of neuromuscular junctions. The aim of the study was to determine the relation between the changes of the myofilaments renewal, their ultrastructure and ultrastructural response of neuromuscular junctions to the altered functional demand of skeletal muscle. The signs of focal denervation were one of the ultrastructural features of the exercised rats myofibers. Simultaneously signs of intracellular regeneration processes appeared in the muscle fibers of the exercised rats. During the exercise myosin and actin had slower turnover rate than in the pre-exercise period, but 24 hrs after the last exercise, myosin and actin turned over faster than in the control rats. Exercise causes an about 3-fold increase in the number of satellite cells as well as intensification of protein synthesis in the muscle fibers. In conclusion, changes in the turnover rate of muscle contractile proteins in muscle fibers clearly reflect the physiological conditions of myofibrillar apparatus, have good correlations with the activation of satellite cells and reorganization of neuromuscular junctions and can be regarded as a manifestation of the functionally determined adaptive process caused by an increase in muscular activity.

Cronology of the Skeletal Ossification in *Capra pyrenaica* (Mammalia: Artiodactyla)

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The degree of skeletal ossification of the pelvic and scapular waists of 30 skeletons of *Capra pyrenaica* (15 males and 15 females) of well-known age (< 1 to 12 years), is studied. Three types of epiphyses, according to their orientation concerning the longitudinal axis of the bone, were considered: A) perpendicular epiphyses to the axis bone, B) oblique epiphyses to the axis and C) epiphyses outside of the axis bone. The ossification sequence observed for both sexes was similar and is described as follows: Anterior extremity: Epiphyses-A: proximal of the metacarpus > distal of the humerus > proximal of the medial and proximal phalanges > distal of the metacarpus > distal of the radius > proximal of the humerus Epiphyses-B: tuberculum majus Epiphyses-C: tuber scapulae > distal and proximal of the ulna Posterior extremity: Epiphyses-A: proximal of the medial phalanx > proximal of the proximal phalanx and distal of the metatarsus > distal of the tibia > proximal and distal of the femur > proximal of the tibia Epiphyses-B: femur trochanter > tuberositas tibiae Epiphyses-C: pelvis acetabulum > calcaneus tuberositas Different biological implications of these ossification sequences are discussed.

Seasonal Variation in the Ultrastructure of the Sexual Segment of the Kidney in a Natricine Snake

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In mature male snakes and lizards, a distal portion of the nephron is hypertrophied in relation to its appearance in females and immature males. This sexual segment of the male kidney apparently provides secretions that are mixed with sperm and released into the female cloaca during copulation. This study is the first one to provide an ultrastructural description of seasonal variation in the sexual segment of any squamate, using the natricine snake *Seminatrix pygaea*. Previous workers have indicated that the sexual segment is secretory only when the testes are spermatogenically active. The sexual segment of the kidney in *S. pygaea* does not go through an extended period of inactivity but does show a cycle of synthesis and secretion that can be related to the spermatogenic cycle and mating activity. We show that synthesis of secretory product is initiated with the onset of spermatogenic activity in the spring and culminates with completion of spermiation in the fall. Secretion of the product, however, occurs in a pre-mating period in March when the testes are inactive. Secretion during this pre-mating period is probably necessary to provide time for the passage of the products down the ureter in order to mix with sperm during mating later in spring.

Muscular Mechanisms of an Elastically Operating Segmented Leg

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In this study the origin of spring-like leg behavior in long jump is addressed. Therefore, a forward dynamic model of the human musculoskeletal system was used to study the interaction between segment dynamics and muscle dynamics. The model consists of four rigid segments representing the upper body (head, both arms, trunk and swing leg: HATL) and the stance leg (foot, shank and thigh) and six major muscle-tendon complexes (MTCs) acting on the intersegmental hinge joints. Muscle stimulation STIM(t) was optimized for maximum jumping distance whereas each muscle was allowed to switch on only once. This allowed us to investigate the following aspects: (1) To what extent is spring-like operation supported by inherent MTC properties? (2) How is spring-like operation supported by segmental arrangement during leg loading? (3) Which effects are contributing to the passive force peak? It was found that: (1) Optimizing jumping performance leads to spring-like leg behavior. (2) Thereby, synchronous and quasi-elastic ankle and knee joint loading occurred. (3) Leg stiffness is an overall behavior of the whole body and originates from a synchronized, quasi-elastic muscle operation reducing intermuscular and interarticular energy losses. (4) Highly activated MTCs show quasi-elastic behavior at fast loading speeds due to intrinsic muscle properties (force-length, force-velocity, activation dynamics) and loading of serial elements. (5) During passive peak, elastic leg operation was superimposed by distal mass deceleration.

Evolutionary Digit Loss in an Australian Skink: Developmental Morphology and Sonic Hedgehog Expression

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Digit loss is a common theme in tetrapod evolution that may involve changes in several developmental processes. The skink *Hemiergis* provides an ideal model to study these processes in closely related taxa: within three Western Australian *Hemiergis* species, digit quantity ranges between two and five. A comparative study of skeletal condensation patterns in *Hemiergis* spp. did not implicate terminal deletions of an ancestral limb development program in the evolutionary loss of digits. Rather, localized differences in cartilage condensations, possibly due to differential cell proliferation, characterize skeletal reductions. Digit loss may also result from minor regulatory variations in molecular signals that pattern the early limb bud. For example, the gene Sonic hedgehog (Shh) is critical for promoting limb mesenchyme proliferation, establishing the anteroposterior limb axis, and specifying digit identity. To investigate the role of this gene in evolutionary digit loss, Shh protein expression was examined in the embryonic limb buds of *Hemiergis* spp. Immunohistochemical assays revealed that temporal differences in Shh protein expression were correlated with adult digit quantities. These phylogenetic differences in gene expression and skeletal condensation patterns are difficult to characterize in the traditional terminology of heterochrony, broadly defined as evolutionary changes in ontogenetic timing.

Light and Scanning Electron Microscopy of the Lingual Epithelium of the Common Moorhen, *Gallinula chloropus meridionalis* (Gruiformes, Rallidae)

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This paper describes the histological features and surface structures of the lingual epithelium and its associated structures of the common moorhen, *Gallinula chloropus meridionalis*. This study was performed to clarify the correlation between structure and function and how they are adapted to its feeding habits. The study concentrated on the epithelial structures of the free portion of the tongue. Also, the epithelium of the oropharynx is included. Macroscopic investigation, light microscopy, and scanning electron microscopy were used. The macroscopic investigation has shown that the tongue is elongated with a dorso-median sulcus, anterior lingual hairs on the lingual nail, and the most posterior edge of the tongue carries a transverse row of eight posteriorly directed conical papillae. The epithelium under investigation was studied from the following aspects: (1) Structure and thickness, (2) Presence and appearance of keratinization, (3) Surface structures, and (4) Mucosal-submucosal junction. Three advantages of the dorsal epithelium of the free portion of the tongue were found to be well adapted for the large amount of frictional forces: (1) Well developed, thick epithelium, (2) The presence of deciduous epithelia and other protrusions, both with microridges, and (3) High power of adhesion between mucosa and submucosa. The present investigation was performed to elucidate the mechanisms of avian feeding and to be the basis for further investigations.

Amniote Phylogeny Inferred from the Largest Set of Morphological Data

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The evolutionary history of Amniota is among the most contentious topics in systematic biology, and recent publications have brought renewed attention to this field of research. Herein, more than 540 new and previously used characters (osteological, behavioral, physiological, and soft anatomical) are analyzed to determine relationships among extant and fossil amniotes. Taxon sampling includes representatives of six extant (birds, crocodylians, mammals, rhynchocephalians, squamates, and turtles) and several major extinct (non-turtle anapsids, early diapsids and non-mammalian synapsids) lineages of amniotes. The effects of taxon and character partitioning, missing data, and a priori assumptions of character transformation in supporting resulting hypotheses are discussed.

Bone Marrow of Vertebrates

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Morphology of developing bone marrow has been studied in the femur of vertebrates (amphibia, reptilia, aves, and mammal) by the means of histology, histochemistry, and fluorescent microscopy, transmission and scanning electron microscopy. Primary attention was given to morphological peculiarities of differentiating hemopoietic cells, their localization, and intercellular contacts. Development of bone marrow is associated with osteogenesis of the femur. Myeloid cells appear in separate, successive stages, which have specific morphological, and histochemical criteria. These stages are very distinct in mammals: appearance of initial sites of myelogenesis, development of the granulocyte line, development of the erythroid cell line, and formation of multinuclear cells. The most prominent lymphoid cell lines have been found in the bone marrow of Amphibia and Aves. Labile contacts among cells have been identified in developing bone marrow of the vertebrate femur. We have noted contacts among reticulum cells, lymphocytes, and granulocytes. In our view, such labile contacts possibly participate in a signal pathway, and in regulation of differentiation. Observed contacts between macrophages and blood vessels can promote the process of utilization. Labile intercellular contacts in developing bone marrow are influenced in a certain way by the cells of the hemopoietic microenvironment.

Development and Evolution of the Vertebrate Jaw

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The vertebrate jaw is patterned through hierarchically organized epigenetic events. Before immigration of neural crest cells, the perioral ectoderm of the early chick embryo expresses Fgf8 gene in the future mandibular arch. Rostral and caudal to this expression domain, another growth factor-coding gene, Bmp4, is expressed. In the ectomesenchyme of the older embryo, Dlx1, the target gene of FGF8, and Msx1, the target of BMP4, are expressed in corresponding patterns. By implantation of FGF8-soaked beads, the ectomesenchymal expression of Dlx1 is expanded followed by expansion of the mandibular arch domain. Dlx injection has showed that this is due to the transformation of the ectomesenchyme. Distribution of FGF8 and BMP4 thus serves as a prepattern to define the mandibular and premandibular domains in the crest cells in the earliest phase of jaw patterning. Similar expression pattern of growth factors also appears in other gnathostome vertebrates. In the developing lamprey, which possesses upper and lower lips instead of jaws, a cognate of Bmp4 gene is expressed in the distal ectoderm of the lips, consistent with the expression of LjDlx1/6 in the mesenchyme of both the lips. Dlx injection experiments, however, show that the lamprey upper lip is more like the nasal (premandibular) region of gnathostomes. Thus, the tissue interaction is likely to have shifted in the agnathans to gnathostome transition.

The Patterns of Evolution and Ontogeny of the Cervical Vertebrae in Temnospondyl Amphibians: Phylogenetic Implications

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The evolution of the multipartite atlas and axis toward solid ossifications, observable in a number of temnospondyl lineages, proceeded in them at different rates and showed various trends that all have spread to a decreasing degree over the next following vertebrae. These trends include: (a) downward expansion of the cervical neural arches to contribute to the formation of their respective centra; (b) integration of the cervical arches with the intercentra, culminating in their fusion; (c) ontogenetic retardation, or even cessation, of median fusion of the cervical intercentral antimeres; and (d) fusion of the pleurocenter (unless it went reduced) with the intercenter and then with the neural arch. The formation of the intracervical "ball and socket" joint between the atlas and axis rather than between the atlantal hemicentra distinguishes the temnospondyls from other apsidospondylous lineages including the early amniotes. A loss, or reduction, of the parapophyses on the anterior post-atlantal vertebrae, combined with strengthening of their diapophyses and invasion of the neural arch into the center area (the characters best expressed in eryopoids and related forms) make the typical temnospondyl condition similar to that of modern anurans, and seem to preclude both groups from being closely related to the non-anuran "lissamphibian" lineages. The evolution toward the anuran

pattern obviously was preceded by cervicalization of the trunk vertebrae that occurred with their phylogenetic reduction in number.

Ovarian Cycle of Nepalese Snow Trout *Schizothorax plagiostomus* (Haeckel) in Relation to the Environment and Spawning Activity

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Fish living in snowfed mountain streams of the Himalayas display wide variation in their reproductive habit and behavior. Only a few reports are available on seasonal cycles in the ovary of the fishes living in the fast flowing mountain streams of Nepal. The seasonal ovarian cycle of *Schizothorax plagiostomus*, inhabiting the snow-fed hill streams of Nepal can be divided into eight phases. Histological studies of the ovary indicate two spawning periods of the fish, one extending from mid September to October, and the other from February to March. A short relaxation phase and an interspawning dormant phase intervene the spawning periods. During the dormant phase, the fish carries histologically mature as well as maturing ova that are ovulated on second spawning assembly in March. The expulsion of ripe ova takes place in installments. Various maturation stages of the oocyte have been described. The ovarian cycle is in conformity with GSI and the volume of the ovary. Yolk nucleus appears to be associated with vitellogenesis, and the yolk is deposited in the form of granules, which later fill the entire ooplasm to form a non-continuous mass of yolk. The spawning is intermittent and takes place twice in a year and depends on the external factors of the environment. Double spawning in *S. plagiostomus* shows higher reproductive potential and is related to intermittent hillstreams.

Muscle Properties of M. triceps brachii of Small Mammals

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This study examines the muscle properties of the triceps brachii (*Rattus norvegicus*, *Galea musteloides*) in locomotion-like conditions. Different fiber types, different activation, and different alignment of the three heads indicate a strong functional partition in different motion tasks (stand, trab, gallop). The experimental setup allows the static and dynamic investigation of torques and angles generated by the whole muscle at the elbow joint with and without supramaximal neural stimulation. Torques produced by the m. triceps are measured at the separated olecranon driven by a motor aligned with the rotational axis of the elbow joint. In the experiment the shoulder joint angle and the elbow joint angle cover the range of motion occurring during locomotion. Passive force in stance phase do not exceed 1% of maximum force. In the swing phase negative passive forces occur. Passive viscoelastic forces strongly depend on cycle frequency. During locomotion (trab) about 1/4 of the maximum isometric forces are produced. For a shoulder joint angle of 90° and an elbow joint angle of 72° the isometric forces of the three heads were estimated from geometry. Caput longum, laterale, and mediale, contribute to 85%, 8%, and 7% to the total isometrical force of F = 56.6 N (*Rattus*; 460 g). This should lead to a better understanding of the design and adaptation of complex muscle-skeletal systems.

The Use of Rigid Tails and Grasping Claws in Dromaeosauridae and Troodontidae (Theropoda, Dinosauria)

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The evolution of an automatic resupination mechanism associated with several other morphological adaptations in the forelimbs of Dromaeosauridae and Troodontidae (Theropoda, Dinosauria) allowed the construction of a new possible model of predation in those dinosaurs. The forelimbs were used as the main attacking weapon to bring in position the deadly pedal claws. The rigid tail in the two maniraptoran groups would have been a mechanical aid to the killing blows of the pedal claws. This model takes into account all the derived characters associated with predation in both Dromaeosauridae and Troodontidae, also showing how the characters already present in Tetanurae were further "developed" into the most advanced maniraptoran groups.