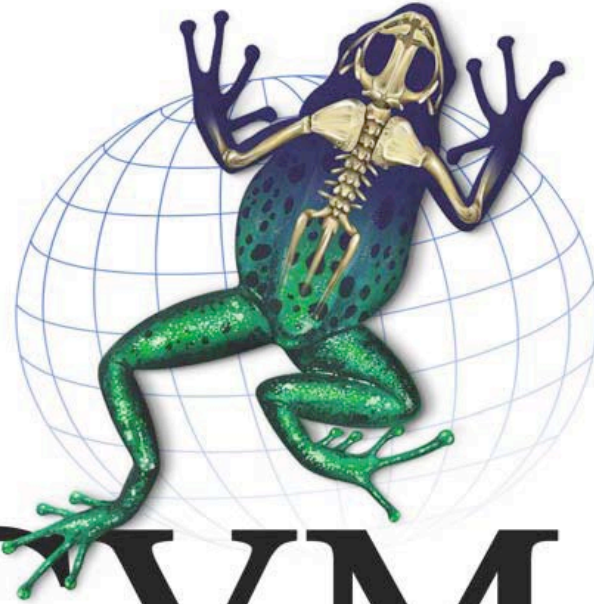


# Additional Abstracts



# ICVVM-7

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**7<sup>th</sup> International Congress of Vertebrate Morphology  
Florida Atlantic University  
27 July to August 1 2004**

## **FROM SYMMETRICAL TO ASYMMETRICAL GAITS, A NEW WAY OF ANALYZING THE INTER-LIMB COORDINATION IN QUADRUPEDS**

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Quadrupeds use two kinds of gaits. Symmetrical gaits (e.g. pace, walk or trot) occur when the footfalls of two feet of the fore pair and those of the hind pair are evenly spaced in time. Asymmetrical, or in-phase, gaits (e.g. gallop and bound) occur when the actions of at least one pair are unevenly spaced in time. Classical methods do not allow the comparison of symmetrical and asymmetrical gaits because most of the parameters used for the gait analyses are different. The aim of the new method is to give a tool allowing analyzing both kind of gaits with the same parameters in order to encompass the inter-limb coordination phenomena as a whole. An approach is proposed, according to the obviousness that in all vertebrates there is a total morphological and functional similarity between both limbs of a pair, fore or hind. Thus, the method analyses all the gaits using a sequence of movements beginning by the action of the two forelimbs followed by the action of the two hindlimbs. It allows to identified all the gaits using only three parameters.

## **ROBOCOQ, FROM AVIAN WALK TO A BIPEDAL ROBOT**

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The RoboCoq project consists in designing a prototype of autonomous biped robot with stabilized vision based on the avian model. The idea of the project comes from the observation of two main applied features of birds: their terrestrial locomotion skill and their peculiar mode of gaze stabilization, the head-bobbing. The dynamics and kinematics features of walking quails are analysed. The force exchanged between the bird and the ground as well as the movements of the centre of mass during locomotion are studied using force plates. The kinematics data, especially the displacements of skeletal segments, are collected using X-ray analyses. This study allows us to measure the amplitude and the phase shift in movements of each leg, to determine the mechanisms allowing the animal balance. Avian head-bobbing reflex is triggered by visual stimuli and its properties as well as the mechanisms allowing synchronization between walking and head bobbing are studied using a treadmill with an optical system permitting the synchronization between the treadmill velocity and the visual stimulation velocity. The biological features are used to determine the kinematics and mechanical characteristics of the powered segments of the robot. Then we test them in simulation. The various loads and physical parameters related to the mechanics of the segments are used to calculate the dimensioning of the joints, actuators, masses and inertias. The geometrical placement of the various elements including proprio- and exteroceptive sensors will be adapted to the robot structure.

## **EXPRESSION OF BETA-KERATIN AND ITS MRNA IN DIFFERENTIATING LIZARD EPIDERMIS**

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

## **SIGNED ASYMMETRY OF VESTIGIAL PELVIC PHENOTYPES IN THREESPINE STICKLEBACK**

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The pelvis of the threespine stickleback (*Gasterosteus aculeatus*) is primitively robust and functions in defense. Vestigial pelvic phenotypes have evolved independently in several populations. Asymmetrical specimens usually have a larger vestige on the left side. Absence of the pelvis in one stickleback population resulted from lack of expression of the *Pitx1* gene during pelvic development. In mice that do not express *Pitx1*, *Pitx2* partly compensates for its absence. However, *Pitx2* expression is stronger in the left hind limb of mice. Consequently, the right hind limb is more strongly affected in individuals without *Pitx1* expression. Although *Pitx2* was not expressed during development of the stickleback pelvis, signed asymmetry of stickleback pelvic vestiges may reflect asymmetrical expression of other genes. We examined 22 populations of *G. aculeatus* with pelvic reduction from Cook Inlet, Alaska. In 19 populations, specimens with asymmetrical pelvic vestiges usually (61-100%) have larger vestiges on the left side, confirming previous results. Pelvic vestiges are equally likely to be larger on either side in one population. However, two populations tend (65%) to have larger vestiges on the right side in asymmetrical specimens. Loss of *Pitx1* expression may explain pelvic reduction in most populations that tend to have larger left pelvic vestiges, but other genes probably cause pelvic reduction in populations in which the right vestige tends to be larger.

## **A COMPARISON OF THE FELINE CLAW AND THE PSITTACINE UPPER BILL: A NATURAL EXPERIMENT**

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The cat claw and the parrot upper bill are similar in shape, basic function, tissue composition, basic tissue properties, and constraints emerging from physical and biological principles. They also differ in their biological roles, mechanosensitivity, skeletomuscular apparatus, and evolutionary origin. Both the claw and upper bill are composed of a bony core, a cornified epidermal sheath, and an interposed soft dermis and living epidermis. The dermal papillary body influences the microarchitecture of the cornified sheath. It also absorbs or resists shear forces that are generated between the two layers of hard tissue when forces act on the cornified sheath. Our results show that the microarchitectures of the cornified external plates of both the claw and upper parrot bill are similar and, hence, reflect similar external forces, as in catching prey or digging out nest cavities. In contrast, the sole plate of the claw and the oral plate of the bill differ in their growth pattern and microarchitecture. These differences can be attributed to differences in biological roles. The sole plate of the claw consists of friable horn ensuring a sharp tip and blade-like ridges. The oral plate of the parrot bill consists of obliquely oriented, alternating layers of hard and friable horn creating a surface that prevents seeds from slipping when they are cut open by the lower bill.

## **APPLICATION OF SKELETOCHRONOLOGY IN AGE DETERMINATION OF LARVAE OF SALAMANDERS OF THE GENERA *GYRINOPHILUS* AND *PSEUDOTRITON* (AMPHIBIA: PLETHODONTIDAE)**

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In an attempt to determine individual age using skeletochronology, we examined femurs of 24 larvae each of the salamanders *Gyrinophilus porphyriticus* and *Pseudotriton ruber*. The larvae were collected from syntopic populations in the southern Blue Ridge Mountains, USA. In *G. porphyriticus*, diaphyseal cortices are made of parallel-fibered bone or lamellar bone. In the latter case, lines of arrested growth (LAGs) are difficult to distinguish from bone lamellae; consequently, age could be estimated in fewer than half the individuals in our sample. In *P. ruber*, parallel-fibered tissue is predominant, and LAGs could be identified in 75% of the specimens. Formation of lamellar bone in salamanders is correlated with low rates of osteogenesis, whereas parallel-fibered bone is associated with higher rates of bone deposition. The differences in bone histology between *G. porphyriticus* and *P. ruber* may be related to microhabitat differences. The correlation between LAG number and snout-vent length in our sample of *P. ruber* agreed with the results of earlier studies of age structure based on size distributions, confirming the estimate of a 2.5 year modal larval period. The larval period of *G. porphyriticus* remains largely unresolved; nevertheless, smaller individuals had 0-2 LAGs and larger larvae 3-4 LAGs, providing a provisional estimate of a 4-5 year larval period.

## **EFFECTS OF REPRODUCTION IN RUNNING PERFORMANCE AND STABILITY IN *IGUANA IGUANA***

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Reproduction is a vulnerable time for females. Since many terrestrial vertebrate taxa run to escape from predators it is paradoxical that many of these same taxa are still able to carry a large reproductive mass. Surprisingly few studies have examined the physical effects of reproduction on female performance, and those have compared only maximal velocity. In this study, I compared gravid vs. post-gravid running kinematics of *Iguana iguana*. Using a 6m trackway, I filmed the initial run at a rate of 250 m/sec using 2 camera views to reconstruct motion in 3D. Iguanas have reduced performance both pre- and post-oviposition. Pre-oviposition, iguanas have a pronounced slower start (significantly longer first stride duration), and require more steps to reach preferred velocity. Post-oviposition, iguanas are slightly slower in all steps, gradually reaching preferred velocity. The recovery from gravidity is gradual, indicating that the main impairment is not a simple load effect. I will also describe changes in stability indicated by the angular kinematics of the pelvis, kinematics of the hind limb, and probability of crashing and falling before and after oviposition. I also investigated morphological changes during reproduction using CT-scan, focusing on changes in lung and body volume. This study is the first part in a larger study considering physiological impacts of reproduction on locomotion.

## **THE WRIST AND MANUS OF ARCHAEOPTERYGIANS: AVIAN, NOT MANIRAPTORAN**

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Recent confirmation that the digits of the avian manus are II, III, and IV, and not I, II, and III as in theropods, brings into question the purported homologies recognized by many as existing between the wrist and manus of birds and those of theropods. A close examination of the wrist and manus of five archaeopterygians confirms the presence of numerous previously recognized, as well as unrecognized, derived avian characters. These include, but are not limited to, metacarpal II very short, "affixed" to, and slightly wrapping under, metacarpal III for most of length; metacarpal II with small Processus extensorius for attachment of *M. extensor metacarpi radialis*; metacarpal IV with proximal end lying well distal to proximal ends of metacarpals II and III, wrapping under and "affixed" to "palmar" surface of metacarpal III; joint between metacarpal II and phalanx 1 typically avian, very restricted; joints between metacarpals III and IV and their respective phalanges relatively immobile; and "palmar" surfaces of all distal phalanges facing anteroventrad when wing extended. None of the above features are found in maniraptoran theropods, but their more highly derived counterparts are found in all modern birds with wings. The avian structure of the wrist and manus of archaeopterygians indicates significant functional differences compared to that of theropods, which is not surprising given that different digits are involved.

## **MORPHOLOGY OF THE UNCINATE PROCESSES IN BIRDS: PHYLOGENETIC APPROACHES**

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Uncinate processes (UP) are bony projections which extend from the posterior surface of the dorsal ribs. They are present in nearly all extant birds but are also reported in Sphenodon, some Crocodylia and also in Theropod dinosaurs. The function of UP may be to increase the efficiency of inspiration, as suggested by Zimmer (1935), based on a 2-dimensional model reconstruction. Here we investigate the morphology of the uncinata processes in birds with different locomotor modes (walking, swimming, flying and diving) using sister groups comparisons. Uncinate morphology was found not to vary phylogenetically within the birds but rather with locomotor mode. The UP are the longest in the diving birds, intermediate in the flying and swimming birds and were the shortest in the walking birds. Uncinate morphology is likely to be important in relation to uncinata function due to their favourable lever arm action on the ribs. While not precluding the putative respiratory function, the long uncينات may function in the diving birds to stabilize the thorax during diving.

## **ABNORMALITIES IN MORPHOGENESIS ASSOCIATED WITH EARLY EXPOSURE TO GROUND-BASED MICROGRAVITY CONDITIONS IN *RIVULUS MARMORATUS* (TELEOSTEI)**

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Ground-based analogues for micro-gravity have been used extensively to study the effects of vector-averaged gravitational forces on cellular functions. One such analogue is the rotating cell culture system (RCCS) in which cells and cell aggregates are supported in a rotating fluid medium. These ground-based studies have been instrumental in elucidating physiological abnormalities exhibited following exposure to space conditions. However, the effect of space conditions on vertebrate development has been limited. To address this issue, *Rivulus marmoratus* embryos of similar age (1-14 days post-fertilization) were placed either in a static container (Control) or RCCS, and maintained until hatching (approximately 21 d after fertilization). Control post-hatchlings exhibited normal morphology, swimming movements, responsivity to tactile stimuli, visual tracking and live prey capture. In contrast, experimental fish placed under RCCS conditions within 24 h of fertilization and maintained through to hatching exhibited a variety of developmental abnormalities. These included: extensive torsion of the axial skeleton; a marked post-ocular cranial depression; atypical CNS organization; and aberrant eye structure. All such fish exhibited no feeding behavior and died within 7 d of hatching, presumably following depletion of yolk reserves. These findings indicate that vertebrate ontogenetic processes require vectored gravitation forces for normal development, at least during the early stages. (Supported by NASA: NAG 2-1600; NASA-LEQSF-LASPACE: R122349; and NASA(2000-01)-DGAP-13 to KSC).

## **TONGUE PROJECTION IN PLETHODONTID SALAMANDERS: A HIGH-POWER BALLISTIC SYSTEM**

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Plethodontid salamanders have evolved, twice independently, the ability to project the tongue and its supporting skeleton ballistically from the mouth such that the skeleton evacuates the projector (subarcualis rectus) muscles entirely. Three genera of plethodontids (*Bolitoglossa*, *Hydromantes*, and *Eurycea*) from two clades with ballistic tongue projection were videotaped at 1000-2000 Hz to examine tongue projection dynamics. Videos were analyzed kinematically to determine the instantaneous velocity and instantaneous acceleration of the tongue, and peak mass-specific power of the projector muscles. All three genera produce extremely high mass-specific power output (in excess of 5000 W/kg) during tongue projection. The hypothesis that high power output is required to strike a distant target accurately was tested by a Newtonian computer model of tongue projection. Power output of the subarcualis rectus muscles vastly exceeds mass-specific power values yet reported for other vertebrate muscles, raising the possibility that high-power projection is accomplished with the aid of an elastic power amplifier.

## **THE IMPACT OF CRANIAL DIFFERENCES ON JAW MUSCLES IN *TRICHIURUS LEPTURUS* AND *APHANOPUS CARBO* (TELEOSTEI, TRICHIURIDAE)**

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Some African catfishes of the Clariidae family have undergone an evolution towards an extreme anguilliformity. Here, the morphological evolution is constrained by at least four factors: 1) elongation of the body, 2) hypertrophy of jaw muscles, 3) miniaturization of skull bones and 4) adaptations to a fossorial way of life. The impact of each of these specific intricately linked characteristics on the "Bauplan" in these clariids remains obscure. In order to analyse the possible impact of each of these components on the Bauplan, species of other teleosts were studied. To investigate the possible impact of jaw muscle hypertrophy, the head morphology of two closely related, anguilliform species of the Trichiuridae family were studied (*Trichiurus lepturus* and *Aphanopus carbo*). Both trichiurid species have a comparable "Bauplan". However in contrast to *Aphanopus carbo*, the ethmo-frontal region is elevated and the posterior confluence of the frontal ridge forms a sagittal crest in *Trichiurus lepturus*. Furthermore, differences in relative size and position of the eye are substantial. These differences in cranial features have imposed spatial constraints on the form and thus the function of the adductor mandibulae complex.

## **HOLOTYPE SKELETAL MORPHOLOGY OF *GYMNALLABES NOPS* (ROBERTS & STEWART, 1976), USING MICRO CT-SCAN**

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One of the biggest systematic problems within the anguilliform Clariidae is the validity and the position of *Gymnallabes nops*. This vagueness is largely due to the fact that the description of this species is based on the holotype only. This also means that the study of this holotype is limited to non-invasive research, such as external morphology and x-rays. For phylogenetic research, however, this approach does not yield many valuable characters. In this study a high-resolution desktop X-ray microtomography instrument (CT-scan) was used. This enables us to confirm the results of the radiographies but also to perform a detailed osteological study. The osteological survey showed similarities with *Platyallabes tihoni* and *Gymnallabes typus*. Besides these traits, *G. nops* shows a unique set of characters, such as a reduction of the infraorbital bones in number and size, a large anterior outgrowth of the opercular and the typical positioning of entopterygoid and metapterygoid bone. These extra results help to clarify the phylogenetic position of *G. nops*.

## **ENDOTHELIOCHORIAL PLACENTAL ARRANGEMENT IN A PLACENTOTROPHIC AFRICAN SKINK**

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Extraembryonic membranes (such as the chorioallantois and yolk sac) are essential to embryonic development and have contributed importantly to the evolutionary and ecological diversity of terrestrial vertebrates. Extraembryonic ectoderm is a component of virtually all known placental organisations in amniotes. In mammals, some extraembryonic ectoderm cell populations (= from trophoblast) display remarkable invasive mechanisms. These cells are often unusually large and multinucleated (so-called giant cells). Curiously, one encounters giant cells of extraembryonic ectoderm origin also in highly matrotrophic scincid lizards. Giant cells mediate close proximity of maternal and fetal tissues in at least three types of placental organs found in matrotrophic skinks. In one type, giant cells process large quantities of uterine secretion. In another, they form an absorptive placentome and in the third type they eliminate the uterine epithelium. The latter represents the only known example of an endotheliochorial placental arrangement recorded in any non-mammalian amniote.

## **MORPHOLOGY AND FUNCTION OF THE POSTCRANIA OF SELECTED GENERA OF THEROCEPHALIA (AMNIOTA: THERAPSIDA)**

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The postcranial morphology of three genera of Therocephalia, *Glanosuchus* from the Tapinocephalus Assemblage Zone, *Ictidosuchops* from the Lystrosaurus Assemblage Zone, and *Bauria* from the Cynognathus Assemblage Zone is described in detail. A comparison is made of the bone morphology of the three genera in relation to each other, and to that of other Therocephalia. Differences in anatomy of the three genera are described and their potential use in identifying the biostratigraphic zone in which they are found is assessed. *Glanosuchus* has robust bones which are easily distinguishable from those of *Ictidosuchops* and *Bauria*. The bones of *Ictidosuchops* are more delicate and have distinctive features, and can be distinguished from those of *Bauria* by the very graceful nature of the latter. Individual bones differ in their diagnostic features. The scapulae of *Bauria* and *Ictidosuchops* are easily distinguishable, that of the former having a prominent ridge and depression, whereas tibiae are indistinguishable except on relative size. The muscles of the three forms are reconstructed and the pattern of locomotion is inferred. Differing patterns of locomotion between the three forms are not apparent, although *Bauria* being a more graceful form might be expected to be agile. All three forms show evidence of a sprawling front limb and a semi-sprawling hind limb. Morphological trends in locomotion in the Therocephalia are briefly discussed. Therocephalians are compared to cynodonts and gorgonopsians and the major differences in morphology are summarised.

## **COMPARATIVE HISTOLOGICAL STUDY OF HARDERIAN GLANDS IN THREE SPECIES OF SQUAMATE**

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Enlarged Harderian glands are known to be present in numerous fossorial squamates. Functional hypotheses and detailed histological descriptions are lacking for many species of squamate, in particular the Scolecophidians. Additionally, enlarged Harderian glands have been observed in the non-burrowing egg specialist, *Dasypeltis*. One functional hypothesis of Harderian gland secretions proposes lubricative properties associated with the eye orbit. We compared microstructure and secretory products in *Ramphotyphlops braminus*, *Dasypeltis atra*, and *Elaphe (Pantherophis) guttata* with emphasis on histological and functional convergence of Harderian gland structure. We made histological comparisons of gland structure and gland secretions by staining alternate sections of Harderian glands for general histological structure, lipids, and mucopolysaccharides. Initial results show no structural differences in microstructure and secretion in the three species of snake.

## **MORPHOLOGY AND ONTOGENY OF HEAD STRUCTURES IN *ANCISTRUS* (PISCES: LORICARIIDAE): TRACKING THE DEVELOPMENT OF A HIGHLY SPECIALIZED FEEDING APPARATUS**

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The catfish superfamily Loricarioidea is characterized by an evolution from a general, omnivorous feeding type towards a highly specialized feeding type. This specialization is most pronounced in the family of Loricariidae or armored suckermouth catfish, i.e. feeding by scraping of algae from substrates, while the animals are able to attach themselves to the substrate by means of their suckermouth.

Little is known, however, about the evolution of the functional design of this feeding type, and about how such a specialized feeding and breathing apparatus can arise during development. In order to clarify these issues, the ontogeny of the head structures of a representative of the *Loricariidae* has been studied. After breeding *Ancistrus* cf. *triradiatus* in the laboratory, different ontogenetic stages were examined, revealing the nature of many structures from small larvae to adults. Cleared and stained specimens have been examined, as well as serial sections (2-5 µm thick).

In a first phase of this research the ontogeny of the cartilaginous and bony skeleton has been described. The specialized, typical loricariid morphology, including the suckermouth and associated structures, is found in adult *Ancistrus* specimens, while the general morphology of hatchlings appears to differ from the adult configuration. The larval morphology suggests the presence of adaptations for the specific needs of the young larvae.

## **DEVELOPMENT OF ANTERIOR-POSTERIOR PATTERN IN THE LAMPREY INNER EAR**

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The inner ear of the adult lamprey (an agnathan) is relatively symmetric about the anterior-posterior (AP) axis compared to the highly asymmetric gnathostome ear. These more symmetric agnathan ears superficially resemble the ears of zebrafish (a gnathostome) in which Hedgehog signaling has been abolished. We therefore suggest that the evolution of a new role for Hedgehog signaling may have been instrumental in the acquisition of otic AP asymmetries in the gnathostome lineage. Before we can address this question we must first establish how symmetrical the developing lamprey inner ear actually is both molecularly and morphologically. To this end we are examining the development of *L. planeri* and *P. marinus* ears histologically and using phalloidin to reveal the sensory hair cells. In addition we are comparing expression of genes which are known to be expressed in an AP asymmetric manner in the zebrafish otic vesicle, such as *ptc1*, *nkx5.1* and follistatin, with that of their lamprey homologues. This should also prove informative in its own right since differences in expression may reveal important differences in otic AP patterning mechanisms between the two species.

## UV BIASED COLOUR VISION IN PISCIVOROUS DIP AND PLUNGE DIVING BIRDS

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UV signals may be useful in private communication between fish of the same species. Because UV scatters more than longer wavelengths of light these signals are only effective at short distances and reduce the risk of detection by swimming predators. However, underwater scattering will be insignificant for dip or plunge diving birds, which prey on fish just below the water surface. One could therefore expect to find adaptations in the eyes of dip or plunge diving birds that increase UV sensitivity or tune colour receptors to UV signals. To clarify how widespread true UV vision is within piscivorous birds, we used a molecular method to survey the colour vision tuning of four families of dip or plunge divers (Laridae, Sternidae, Procellariidae and Sulidae) and compared the results with both related and unrelated taxa of other foraging methods. We found true UV vision in gulls but not in other groups with similar foraging tactics, indicating that the trait is closely associated with phylogeny and not foraging method.

## THE BIOMECHANICS OF BOUNDING CROCODILES

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Aside from some mammals, crocodylians are the only major extant tetrapod group known to routinely use the bound and similar gaits such as galloping. Larger crocodiles do not bound or gallop; their fastest gaits are trots or high walks. To understand the biomechanics of bounding gaits, and how size limits crocodylian speed and gait, we measured joint kinematics and ground-reaction forces (GRFs) in a diversity of crocodylians (*Alligator mississippiensis*, *Crocodylus cataphractus*, *C. niloticus*, *C. johnsoni*, *C. rhombifer*, and *Osteolaemus tetraspis*; the latter four of which used bounding gaits). These crocodiles had a ten-fold range of size (3.9-43.2 kg); 85 trials from 15 individuals moving at various speeds were sampled.

Our data show that the bound was twice as fast as the trot (2.0 m/s vs. 1.0 m/s). The crocodiles typically used half-bound gaits, although we also recorded some rapid trots and transverse gallops. The GRFs demonstrated that the animals used their forelimbs to brake and their hindlimbs to accelerate. The peak GRFs were very high: up to 1.9x and 2.8x body weight for each pair of fore- and hindlimbs respectively. The positive external mechanical power output at these speeds was a surprisingly high 10-20 W/kg body mass. These data reveal some of the biomechanical requirements for fast terrestrial locomotion in crocodylians.

## **THE CRANIAL MORPHOLOGY OF *CORYDORAS AENEUS***

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The Neotropical fauna is one of the most diverse, but also one of the least known fauna's. The understanding of this and of the specific processes of speciation and radiation, is one of the greatest challenges in modern biology. In this context the Amazon-basin houses the most biodiverse ichthyofauna in the world (over 2000 known - 20 000 estimated species). Approximately half of all these known species make up the superfamily of the Loricarioidea. Radiation within this superfamily, has led to the highly adapted head in Loricariidae, which is suited for algae-scraping. To investigate this, it is essential that in a first phase the building plan within less adapted loricarioids, such as *Corydoras*-species, is studied and fully understood. For this purpose the adult morphology of the head in *Corydoras aeneus* was studied, focussing on the osteology and the myology. Already, in these fish, the mouth is situated in more ventrally, allowing a bottom-dwelling feeding habit. Some structural modifications of the head can be related to this feeding habit. These are, for instance: a differentiation of the musculus adductor mandibulae complex, a decoupling of the premaxillary, a shift in insertion of the musculus retractor tentaculi etc. This full knowledge of the adult configuration clears the way for future research at an ontogenetic level, thus supporting a better understanding of the phylogeny of this diverse group of fishes.

## **DIFFERENCES IN BIPEDAL LOCOMOTION BETWEEN TWO SPECIES OF KANGAROO MICE IN THE LABORATORY**

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Two Great Basin Desert kangaroo mice (9-13 g), *Microdipodops pallidus* and *M. megacephalus* are closely related to the bipedal kangaroo rat and have been shown to also move bipedally. However previous attempts using standard techniques of light motion picture or x-ray motion picture failed to show a sustained bipedal hop by either species. This is an observational study of bipedal locomotion in *M. pallidus* (N=4), and *M. megacephalus* (N=5) using videotape with an infrared camera (PC-5ex Microvideo Cam, Supercircuits, Austin, Texas) and Canon videocam at 23 fps in the laboratory. Locomotion took place inside a rectangular, enclosed, sand-paper lined arena (152 cm-l x 47 cm-h x 42 cm-d). The arena had a backdrop with gridlines marked off with glitter and reflective markers and a camera-facing wall of mosquito netting. The animals were induced to hop bipedally with encouragement by an assistant and by putting a small piece of chicken on the other side of the arena. Results showed slight differences between the two species in stride length, angle of projection, jump height and velocity as well as tendency toward bipedal locomotion. Some differences can be explained by habitat differences for the two species as shown in sandiness and presence of gravel in the substrate, density and height of vegetation. More important may be differences between these species and kangaroo rats.

## THE SHAPE OF A SPECIES: MORPHOMETRIC ANALYSIS OF THE CONODONT SKELETON

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As with other fossil vertebrates, a sound understanding of skeletal morphology underlies most facets of research into conodonts, a clade of stem-group gnathostomes. Whilst traditional, qualitative description provides the foundation upon which the current understanding of this morphology rests, there are many examples where the complexity and variability of skeletal elements confounds analysis. Here, quantitative morphometric analysis may be the only means of rigorously evaluating element morphology. The importance of conodonts, arising from their key phylogenetic position within the vertebrate clade and their exceptional fossil record, further increases the value of acquiring accurate morphological knowledge. First, a methodology must be developed to evaluate the robustness of morphometric techniques; this will be achieved using the conodont species *Ozarkodina excavata*, which provides a good example of the uncertainties that can arise in traditional morphological analysis. The taxon displays unusually extensive morphological variability for a single species; morphometric analysis of the skeleton of *O. excavata* has constrained this "intraspecific" variation, which is then quantitatively compared with variation in elements from other parts of the *O. excavata* spatiotemporal range to determine the nature and significance of any trends and differences present, also testing the monospecificity of the hypodigm. Ultimately this will clarify the taxonomy of the species, further elucidate conodont palaeobiology and allow testing of evolutionary models.

## HIERARCHICAL LEVELS OF VARIATION IN ONTOGENY

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Historically, morphometric studies of ontogenetic series have focused on the central values of growth parameters: rates, durations, time of onset and offset. Despite the obvious existence of variation in these parameters, it remains a largely understudied component of growth. The issue of biological hierarchy is critical to studies of variation, but also complicates any analyses. While growth is a property of an individual, measurements of growth, and the variation in those measurements, exist at several obvious levels of organization: within individual and among individuals, as well as between/among whatever biological groups constitute the hypothesis being tested. We have examined variation on each of these levels during the growth of male and female craniofacial regions of *Rattus norvegicus italics*, an animal purposely inbred for reduced variation. Surprisingly, a single mechanism (protein malnutrition) affects variation differently at each of the hierarchical levels. For within individual variation (a measure of developmental disparity), variation was not significantly different between the sexes or diet. However, for most growth parameters, with the exception of initial relative size, all between individual comparisons of variation were different between diets.

## **THE HYPOGLOSSO-CERVICAL NERVE COMPLEX IN A BORNEAN ORANGUTAN (*PONGO PYGMAEUS PYGMAEUS*) AND AN ANUBIS BABOON (*PAPIO ANUBIS*)**

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The hypoglossal nerve represents the fused ventral roots of the cranio-spinal nerves and can be regarded as the most cranial cervical nerves. The descending branch of the hypoglossal nerve usually forms a loop (cervical ansa) with the ventral branches of the upper cervical nerves and is distributed to the infrahyoid muscles. The cervical ansa and the infrahyoid muscles form the hypoglossal-cervical complex and have the transitional characteristics between the cranial and cervical regions. In human, the hypoglossal and cervical nerve of the cervical ansa were observed minutely by tracing nerve fibers into the infrahyoid muscles (Kikuchi, 1970). Bolk (1902) examined the spinal segments and the form of the cervical ansa (*Plexus hypoglossal-cervicalis*) in many species of the primates. However, the precise nerve fiber constitution and the intramuscular distribution of the cervical ansa were not clarified. In this study, we observed the cervical ansa in a baboon and an orangutan. After stripping off the epineurium under a stereomicroscope, we traced the nerve fibers forming the cervical ansa and examined the distribution into the infrahyoid muscles. This study clarified that in both species the hypoglossal nerve fibers contributed to all branches innervating each of the infrahyoid muscles and had the wider distribution than in human. We will discuss the phylogenetic differences of the cervical ansa among primates including human.

## **PATTERNS OF THRUST GENERATION USED BY LIZARDS ACCELERATING ON SAND**

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Despite an increase in our understanding of the mechanisms underlying terrestrial locomotion in the last few decades, little attention has been given to the study of animals as they move over their natural, often compliant, substrates. Lizards running on sand provide an interesting system to study animal locomotion because life on sand presents unique biomechanical obstacles that may influence evolutionary trajectories. Using digital high-speed imaging (500 fps) in the field, I studied the instantaneous accelerations of members of the sand-lizard family (*Callisaurus draconoides crinitus*-Viscaino Desert, Baja California, Mexico; *Callisaurus draconoides* and *Uma scoparia*-Mojave Desert, California) as well as representative taxa of other lizard families. Lizards have two unique locomotor patterns while accelerating: the normal diagonal gait and a laterally symmetrical dual-propulsive gait. The intra-familial comparison represents a morphological series of toe fringes (laterally-projecting scales) that are thought to aid in locomotion on sand, while the inter-familial work investigates the universality of these locomotor patterns. Given the propensity of granular materials like sand to fluidize when rapidly sheared, it appears that lizards utilize a dual-propulsive gait to increase thrust generation using their feet as paddles during the initial impulse when high accelerations are needed and sand behaves more like a fluid, then transition to a standard diagonal gait when the sand behaves more like a solid.

## **HOMOLOGY OF THE TRABECULA IN THE VERTEBRATE CRANIUM**

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Rostral to the mandibular arch skeleton, a pair of rod-like cartilages, called trabecula, have been recognized in the early gnathostome chondrocrania. These cartilages fuse in the middle during development to form the interorbital- and internasal septa in many amniotes. Chick-quail chimera studies have elucidated that this part of the gnathostome neurocranium, or the prechordal cranium, originates from neural crest-derived ectomesenchyme that lies rostral to the notochord, standing in contrast to the mesoderm-derived chordal cranium that requires the presence of notochord to chondrify (Couly et al., 1993). In the lamprey, a similar premandibular ectomesenchyme has been found to be incorporated into the upper lip formation, as a part of the oral apparatus (Kuratani et al., 2001). However, there are also a pair of rod-like cartilages called 'trabecula' in this animal. In the present study, by comparative embryological- and labeling analyses, I show that this rod-like cartilage in the lamprey actually develops from the mandibular mesoderm, not from the neural crest, and therefore it is most likely to represent the parachordal cartilage homologue in the gnathostomes. This finding is also consistent with the heterotopic origin of the gnathostome jaw by Shigetani et al. (2002).

## **DORSALLY RECEDING PREMAXILLAE; CHARACTERISTIC OF THERIA**

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In living Therian mammals (Marsupials and Placentals) the rostrum terminates in a series of cartilages extending beyond the ends of the premaxillae, capped by the rhinarium through which the nostrils open at or near the anteriormost end of the rostrum. The dorsal sides of the premaxillae end some distance behind the ventral. On cleaned skulls (where the cartilages have been removed) the rostrum has a characteristic profile; the dorsal edge of the premaxilla sweeping back to end beneath the anterior end of the nasals, often forming a notch. The opening to the bony nasal cavity faces forward. The side wall of the anterior nasal cavity is made up of lateral extensions of the septal cartilage, the dorsal and ventral lateral nasal cartilages. In monotremes (both platypuses and echidnas), by contrast, the dorsal side of the premaxilla extends to the front end of the rostrum, enclosing a nasopremaxillary fenestra through which the nostrils open dorsally. In advanced mammal-like reptiles (Cynodonts. *sensu latissimo*) the dorsal side of the premaxilla extends to the anterior end of the rostrum (as in most tetrapods); the nostrils opening to either side. This form of rostrum characterizes all non-Therian mammals. Reconstructions of the skulls of such mammals showing the Therian rostrum profile (e.g. Simpson's reconstruction of *Ptilodus* ; Simpson, 1937) are erroneous.

## **THE EVOLUTION OF CONSTRICTION IN SNAKES**

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Constriction as a prey-handling method was associated with the adaptive radiation of snakes and is a behavioral homology for most alethinophidian snakes. Constriction postures vary among lineages, but phylogenetic variation in the epaxial motor patterns underlying constriction remains unknown. We are studying the postures and epaxial muscle activity patterns of constriction in a basal snake and an intermediate snake. With our results, and those published previously for a more derived snake, we can reconstruct the evolution and test the homology of constriction and its underlying motor patterns. In our experiments, five individuals of used lateral bends to coil around mice, as was reported for, whereas two individuals of used mainly ventral bends. These results suggest that the ancestral pattern of constriction involved lateral bending and that pythons use a derived posture. In all three lineages the epaxial muscles fire during coil formation and intermittently during sustained constriction; the bursts of activity appear to be associated with high pressures (to over 300 mm Hg) applied to the prey. We are currently examining how unilateral and bilateral muscle firing patterns relate to the constriction postures and how pressure patterns relate quantitatively to muscle firing patterns. These indicate that constriction postures and motor patterns are homologous in these diverse lineages.

#### **DEVELOPMENT OF THE LAMPREY RETICULOSPINAL- AND BRANCHIOMOTOR-NEURONS; WITH SPECIAL REFERENCE TO THE EVOLUTION OF THE VERTEBRATE HINDBRAIN**

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The vertebrate hindbrain consists of the segmental structure called rhombomeres. In gnathostomes, rhombomeres serve as the unit to produce specific neurons, and Hox genes are involved in the establishment of rhombomere boundaries. In the amphioxus, the bona-fide rhombomeres could not be observed. Therefore, lamprey, the agnathan animal, stands on the important phylogenetic position to understand the vertebrate hindbrain evolution. To identify the neuronal organization in the Japanese lamprey, *Lethenteron japonicum*, we studied the developmental positions of reticulospinal and branchial motor neurons in relation to the expression domains of neuromere marker genes including *LjKrox20*, *LjPax6*, *LjEphC*, and *LjHox3*. We found that the reticulospinal neurons develop corresponding to the rhombomere segments, similar to those in the zebrafish. By contrast, the boundary between trigeminal and facial motor nuclei is not in register with rhombomere boundaries, rather it corresponds to the *LjHox3* expression boundary in the middle of rhombomere4. Exogenous application of retinoic acid induces the anterior shift of branchial motoneurons with no obvious repatterning of the reticulospinal neurons. We thus hypothesized that the rhombomere-dependent and Hox-code-dependent neurodevelopmental mechanisms might have been established independently in the vertebrate evolution, and might be secondary integrated in the gnathostome lineage.

## **MASS SETS FOR INTERACTIVE COMPUTATION OF BODY SEGMENT DIMENSIONS AND BIOMECHANICAL ANALYSIS OF ANIMAL LOCOMOTION**

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We designed interactive software that uses three-dimensional B-spline solids to visualize and estimate biomechanically important parameters for body segments. Although the tool is most useful for assessing unknowns in extinct animals, such as body contours, muscle bulk, or inertial parameters, it is also useful for non-invasive measurement of segmental dimensions in extant animals. Points measured directly from bodies or skeletons are entered and visualized, and then the B-spline solid is fitted to enclose these points, allowing quantification of segment dimensions. The model has a click-and-drag interface that allows body segment dimensions to be either interactively deformed (by warping the solid) or specified quantitatively (e.g., expanding the solid boundary beyond measured skeletal coordinates). It then displays any resulting changes of segment mass, center of mass, and moments of inertia. Objects representing volumes of reduced density can be embedded to represent lungs or air sacs within body segments. The tool was validated by reconstructing an ostrich body from a defleshed skeleton and comparing the estimated dimensions to measured values from the original carcass. We then calculated the segmental masses, centers of mass, and moments of inertia for a Tyrannosaurus with measurements taken from a skeleton, and compared these results to other estimates. We used the model in a sensitivity analysis of unknown parameter values and in a biomechanical analysis of standing mechanics.

## **THE ORIGIN OF THE PARATHYROID**

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It is believed that the parathyroid glands evolved with the emergence of the tetrapods, reflecting a need for new controls on calcium homeostasis in terrestrial rather than aquatic environments. Developmentally, the parathyroid is derived from the pharyngeal pouch endoderm, and, studies in mice, have shown its formation is under the control of a key regulatory gene, *Gcm-2*. We have used a phylogenetic analysis of *Gcm-2* to probe the evolutionary origins of the parathyroid. We find that *Gcm-2* is not only present in the tetrapods but also in teleosts and chondrichthyans, and is expressed within the endodermal pharyngeal pouches, and the gills that derive from them, in zebrafish (*Danio rerio*) a teleost, and dogfish (*Scyliorhinus canicula*), a chondrichthyan. We further demonstrate that *Gcm-2* function is required for the formation of the gills in zebrafish. We have also identified a putative Parathyroid Hormone encoding gene in fish, and we show that this gene is expressed by the gills. These results indicate that the tetrapod parathyroid came into being as a result of the internalisation of the gills during tetrapod evolution.

## **LINKING GENES TO NOVEL MORPHOLOGIES IN FEATHERS**

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Feathers are hierarchically complex integumentary appendages. Feathers have been used for decades in developmental biology to study mesenchyme-epithelial interactions. But few studies have examined the developmental basis of the tubular organization and branched structures that are unique to feathers. Experimental and comparative studies indicate that complex feathers evolved through the repeated evolutionary cooption, or reutilization, of a plesiomorphic molecular signaling module including the Sonic hedgehog (Shh) and Bone morphogenetic protein 2 (Bmp2) genes. Shh acts to foster cell proliferation, while Bmp2 supports cell maturation and differentiation. The Shh-Bmp2 signaling module is primitively present in archosaur scale and feather placodes, but is expressed in novel patterns in each of the first three subsequent developmental stages of feather development. The Shh-Bmp2 module exhibits conserved function of creating spatial polarization and controlled morphogenesis. At different times in feather development, the Shh-Bmp2 signaling is necessary and sufficient for the development of the feather placode, the short bud, barb ridges, branched barb ridge morphology, and the polarized organization of the barbules within the barb ridges. The organization of each subsequent stage in feather development appears as a new emergent property of the Shh-Bmp2 module, which contributes to a mechanistic understanding of why evolutionary cooption of the gene signaling is so frequent.

## **ONTOGENETIC RELATIONSHIP BETWEEN MORPHOLOGY AND PERFORMANCE IN RELATION TO DIFFERENTIAL MORTALITIES IN TWO CLOSELY RELATED SCOLOPORINE LIZARDS**

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For many organisms, varying selective pressures exist throughout ontogeny. This is often observed as different mortality rates along some gradient of age or size. Different mortality rates may be observed because of different predator-prey relationships or, when predator-prey relationships are similar, because changes in morphology and/or performance through ontogeny mediate differences in predator vulnerability. Additionally, in squamates, ontogenetic variation in morphology and performance should be ecologically relevant because parental care is essentially absent. When mortality rates are similar among age classes, juveniles may be expected to respond similar to adults to their environment. Ontogenetic changes in mortality rates should correspond with changes in morphology and performance if any adaptive significance exists. We chose to test whether changes in morphology and/or performance are related to differences in mortality rates through ontogeny within and between two lizard species, *Sceloporus undulatus* and *Sceloporus woodi*. We used lab-reared individuals from field-caught gravid females in an attempt to control for both environmental and genetic factors affecting juvenile morphology and performance. Additionally, lab reared juveniles would presumably reflect a wider range of phenotypes as no post-natal selection has occurred. The results of this study will be discussed in terms of intraspecific variation in morphology and performance and a comparison of two closely related species with different life history strategies.

## **THE ONTOGENY OF FEEDING PERFORMANCE IN DIVERGENT STICKLEBACK POPULATIONS**

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The role of ontogeny in producing interpopulation variation is often overlooked. Hundreds of independent freshwater populations of threespine stickleback in Cook Inlet, Alaska, have been derived from an anadromous ancestor within the last 20,000 years. These populations vary along a phenotypic and trophic continuum between benthic (benthivorous) and limnetic (planktivorous) extremes. The position of any given lacustrine population along this continuum is thought to be primarily a consequence of the food available to it. Benthic fish live in vegetated, shallow water and eat relatively large invertebrates from the substrata of lakes, while limnetics live in open water and eat relatively small planktonic prey. Each type of population appears to be differentially adapted for its characteristic prey. Benthics have a head shape expected of a suction feeder and limnetics have a head shape expected of a ram feeder. However, early in ontogeny, both types are required by size constraints to eat plankton. Using high speed video and geometric morphometrics to analyze differences in trophic morphology and kinematics of feeding, I examine the role of ontogeny in the development of interpopulation variation among divergent stickleback populations.

## **IS IT A DRAG TO BE SMALL? WHY FISH LARVAE CHANGE GAIT DURING DEVELOPMENT**

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Newly-hatched zebrafish larvae swim mainly cyclically. Three days later, larvae prefer to burst and coast. Both age groups have a similar body length ( $\approx 4$  mm), swimming speed and body mass, suggesting that flow regime and inertial effects cannot explain the gait change. However, in the intermediate flow regime, both shear and pressure drag vary substantially with surface area and frontal area. These drag forces might impede coasting until the bulky yolk sac is nearly absorbed three days after hatching. Furthermore, under-developed pectoral fins, the lack of a swimbladder and possibly a net pitching moment on the body cause hatchlings to nose-dive when they cease active swimming. This loss of trim might further increase the hatchling's drag. To investigate in how far the changing body morphology might explain the observed gait switch, we recorded larval burst and coast performance as well as the flow patterns generated by coasting larvae at age 0 to 3 days after hatching. We also computed 2- and 3-dimensional flow fields around two developmental stages of zebrafish. During coasting, the larva entrains a rapidly growing body of water. The areas of high shear and high vorticity in this boundary layer move away from the larva over the duration of the coasting phase, and a new area of elevated vorticity develops near the fish. Our results indicate that the drag on a hatchling is higher than on a 3-days old larva, suggesting that drag is an important factor in the gait change.

## **HUMAN SHOULDER DEVELOPMENT AND COMPARISON WITH BI- AND QUADRUPEDS**

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In orthopaedic interventions, knowledge of the nerves supplying the glenohumeral joint is essential. The aim is to describe the development of the human shoulder and the glenohumeral joint and to compare the anatomy of the shoulder joint in bi- and quadrupedals. Cadaveric fetuses were dissected to examine the course of the suprascapular and axillary nerves. For comparison the shoulders of *Panthera pardus*, *Felis caracal* and *Cercopithecus aethiops* were dissected. In the fetuses both suprascapular and axillary nerves give off branches running to the shoulder capsule. The axillary nerve is responsible for innervation of the anterior/inferior part, while the suprascapular nerve supplies the superior part of the shoulder capsule. In the leopard and caracal the axillary nerve differs in having three main branches to the lateral shoulder muscles. The suprascapular nerve runs more freely over the scapula without a suprascapular notch and -ligament. In the vervet monkey the suprascapular nerve innervates the subclavian, subscapular, supraspinatus and infraspinatus muscles. The suprascapular notch is differently shaped in what a suprascapular notch is absent. The innervation of the shoulder capsule is already fully developed in 20-22 week old fetuses. In the leopard, caracal and vervet monkey injury or entrapment of the suprascapular nerve is less likely due to the osteology and musculature.

## **COMPARATIVE ANATOMY OF THE INTERNAL VERTEBRAL VENOUS PLEXUS (IVVP) - DIFFERENT FORM DIFFERENT FUNCTION**

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The IVVP is a voluminous venous structure of the body. Its shape shows large differences between various vertebrate species and therefore suggests species-specific functional differences. The functions suggested, are thermoregulation and mechanical protection of the spinal cord. Comparing the position of the IVVP in a variety of animals, living under different conditions, might elucidate its function. Penguins, cormorants, dolphins, monkeys and human fetuses were perfused venously with saline, embalmed with glutaraldehyde and injected with coloured latex. The morphology of the IVVP was then compared. The penguin has a double, well-developed dorsal IVVP, while the cormorant has a single slender, dorsal IVVP. A well-developed ventral plexus is found in the vervet monkey, while the human fetus has longitudinal ventro- and dorsolaterally situated networks. In the dolphin, large single or double ventral veins are present. The penguin and cormorant uses the superficial dorsal IVVP to absorb heat by exposing its back to the sun. In the land mammals the ventro- or dorsolaterally situated IVVP is positioned to conserve heat or prevent overheating. The dolphin has a large, deeply situated IVVP, which is conducive to heat conservation. Interspecies adaptations of the position of the IVVP from dorsal to ventral in the vertebral canal reflect their different heat preservation, production and control methods and requirements.

## **MECHANICS OF SUCTION GENERATION DURING FEEDING IN BAMBOO SHARKS**

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Although recent studies have increased our understanding of suction generation during feeding in teleosts, similar studies on elasmobranchs are lacking. The kinematics of selected internal head and hypobranchial structures in an ontogenetic series of bamboo sharks, *Chiloscyllium plagiosum*, are measured using sonomicrometry to quantify elements that are directly responsible for internal expansion of the orobranchial cavity, and therefore the generation of suction inflow. Simultaneous pressure recordings inside the orobranchial cavity and externally at the prey item were used to assess pressure flow at strategically important locations during feeding. Anterior to posterior progression of expansion occurs during suction feeding in bamboo sharks. Pressure in the hyoid region decreases rapidly as the mouth opens and peak subambient pressure is reached well before peak lower jaw and hyoid depression are achieved. Peak subambient pharyngeal pressure is lower and occurs well after peak subambient pressure in the buccal cavity. Hyoid depression appears to be a dominant feature of generating suction in sharks. Pressure is rapidly attenuated with distance outside the mouth. Pressure readings at the prey site, in front of the mouth reach only a fraction of the pressure inside the orobranchial chamber. Sonomicrometry reveals that interhyal distance decreases and the hyoid arch is drawn anteriorly during feeding. A compressive preparatory phase occurs prior to the expansive phase in half of the capture events.

## **EVOLUTION OF MORPHOLOGICAL INTEGRATION: INTERSPECIFIC PATTERNS OF INTEGRATION IN THE SHREW MANIBLE**

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Understanding the evolution of complex morphological phenotypes is a fundamental question in evolutionary biology. Central to this question is the role of functional integration, or the interrelationships among morphological components involved in the same function. Functional interdependencies among components can result from stabilizing selection for organism-wide functionality. Such selection is an internal property of the organism and is therefore independent of the environment. Thus, long term stabilizing selection across environments for organism-wide functionality should lead to the correlated evolution of these functionally integrated components. Alternatively, functional integration can result from external selection for locally appropriate function. Such selection is likely to vary across environments. We examined ecological and evolutionary patterns of functional integration in the shrew (*Sorex*) mandibles. Long term stabilizing selection for organism-wide functionality resulted in the historical persistence of integrated complexes across species, while short-term directional selection for locally appropriate function resulted in variation across species in non-integrated complexes of traits.

## **REVISED ABSTRACTS**

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### **EGG-SHELL MORPHOLOGY AND CALCIUM LOGISTICS IN BIRD**

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Egg-shell composition and structure is widely published on in literature. Few studies, however, consider them in the broader context of the breeding biology of birds. It has long been recognized that the shell of eggs contributes to successful embryogenesis in many ways, such as in protection, respiration and water exchange. It is also well established that egg-shell is the major source of calcium for skeletal development in the embryo. Recent studies suggest, moreover, that growth rate may play a fundamental role in the pattern of skeletal development in birds: the faster the growth the less the skeleton becomes ossified. We predicted, therefore, that fast- and slow- growing bird species should lay eggs with shells designed to support different rates of calcium removal to compensate. We tested this prediction by comparing the structural composition of egg-shells from birds displaying a wide range of growth rates and modes of development (e.g. from Struthinoformes to Passeriformes). Using scanning electron microscopy we examined the fine structure of the inner shell surface (mammillary layer) of both pre- and post- incubated eggs, i.e. before and after embryonic development/calcium removal, and obtained results in agreement with the prediction. The number of mammillary tips per unit of surface area was (1) inversely correlated with the growth rate and (2) directly correlated with the degree of precociality of the chick.

### **HOMOLOGUES OF VERTEBRATES PLACODES IN *CIONA INTESTINALIS***

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

## **THE MECHANICS OF LOCOMOTION IN LIZARDS**

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

## **MECHANISMS OF DEVELOPMENT OF THE NEURAL CREST-DERIVED SKELETON IN *HYMENOCHIRUS BOETTGERI***

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A wealth of information has been collected regarding the mapping and development of the larval cartilaginous skeleton of anurans (frogs and toads). However, little is known about the mapping of the adult bony skeleton, or the mechanisms mediating replacement of the cartilaginous skeleton by the bony skeleton during metamorphosis. Of particular interest is the development of the skull, which is largely derived from neural crest, a secondary germ layer arising from neural ectoderm during neurulation. Sonic hedgehog (Shh) is known to play a role in pattern formation in many vertebrate systems, including the neural tube, limbs and pharyngeal cartilages. The current study utilized the steroidal alkaloid cyclopamine, a potent, specific inhibitor of Shh, to assess the role Shh plays in the development of the skull during metamorphosis of the dwarf African clawed frog, *Hymenochirus boettgeri*. Tadpoles at various stages of embryonic and metamorphic development were immersed in different concentrations of cyclopamine for 24h to 3 days. These tadpoles were then allowed to complete metamorphosis, after which they were examined for abnormalities in the skull, focusing on the mandibular region. Preliminary results discuss stage sensitivity, survival, growth and the effects of cyclopamine, and therefore Shh, on mandibular development. This approach should provide important information regarding the mechanisms by the adult bony skeleton develops in anurans.