tibia length, foot length, ventral color, and first toe length for females. Principle component analysis, when applied on bioacoustic data, revealed that three groups of mating calls were discernible: The first group involving Thrace populations, the second the Lakes District populations, and the third made up of the rest of the populations. In general, the results of morphometric and bioacoustic analyses revealed the presence of three equally distant taxa belonging to the water frog complex in Turkey. In Thrace (European Turkey) *Rana ridibunda* (*s. str*.) occurs, while the greater part of Anatolia (Asiatic Turkey) except for the Lakes District and surrounding parts is inhabited by *Rana bedriagae* Camerano, 1882 (syn.=*R. levantina* Schnieder. Sinch and Nevo, 1992). Finally, *Rana caralitana* Ankan, 1988 inhabits the southwestern part of Anatolia ranging trom the Konya Plain to Denizli and centers on the Lakes District.

The Early Fossil History of the Chordate Nervous System

Richard P.S. Jefferies, The Natural History Museum, Cromwell Rd., London, SW7 5BD, U.K.

The Palaeozoic chordate fossils with a calcite skeleton of echinoderm type ("calcichordates") allow a history of the early nervous system to be partly reconstructed. It begins in the chordate stem group with the solute *Dendrocystoides* that had a brain just anterior to the tail and a left trigeminal ganglion. Next, also in the chordate stem group, comes the cornute *Ceratocystis*, with a brain, left and right trigeminal ganglia, a left ear, a dorsal median eye etc.. In more crownward cornutes, such as *Cothurnocystis*, the median eye was lost and the left ear became conflated with the gonopore-anus. At the base of the chordate crown group, in the mitrates, the left ear was duplicated on the right, and both ears were included in ectodermal atria (= otic capsules). Also the brain became divided into prosencephalon (olfactory, optic and hypophyseal in function) and deuterencephalon (trigeminal, acoustic and probably branchial in function). The mitrates also show that the spinal cord and paired spinal ganglia already existed, that the stem-group acraniates had bigger brains than extant lancelets, that the extant craniate hind brain arose in part from mitrate spinal cord and that the lateral line arose in the right posterior part of the mitrate head. The mitrate brain was probably situated at the anterior boundary of *Hox* gene expression.

Heterochrony in Amniote Evolution

J.E. Jeffery[1], O.R.P. Bininda-Emonds[2], M.I. Coates[1] and M.K. Richardson[2], 1 Department of Biology, University College London, U.K., 2 Institute of Evolutionary and Ecological Sciences, University of Leiden, The Netherlands*

Haeckel pioneered the mapping of developmental characters onto phylogenetic trees. Mapping characters can identify changes in the timing of their appearance in different organisms (heterochrony). Such heterochronies are of particular importance during organogenesis. Within vertebrates, this is the mid-embryonic period when the body plan is specified under the control of regulatory genes, and when major organ primordia develop. However, these heterochronies have never been quantified or tracked systematically across evolutionary history. In part, this is due to the difficulties inherent in analyzing comparative developmental data. A century after Haeckel, we have developed a new protocol, based on 'event-pairing,' for quantifying heterochrony and mapping it across the evolution of different animal groups. It improves upon earlier event-pairing methods by adding an *en bloc* comparison of the shifts at each node of a phylogenetic tree. This can determine the shifts of individual events relative to all other developmental events surveyed, and can identify the stronger trends. Using data from vertebrates, we track timing shifts in embryonic organ development. These include delayed eye development in mammals and advanced heart development within the amniotes. We also subject the data to parsimony analysis, to highlight instances of convergent evolution (homoplasy). In the future, our approach may be adapted to analyze other forms of comparative dynamic data.

Finite Element Modelling Approaches to Morphology in Vertebrate Paleobiology

Ian Jenkins, Department of Earth Sciences, University of Bristol, Bristol, U.K.

Analysis of craniodental anatomy and function in therapsids across the Permo-Triassic boundary has demonstrated novel skull mechanisms in some of these very ancient specialized carnivores. A multidisciplinary approach utilizing modern experimental and engineering techniques demonstrates that the carnivore trophic niches—based on models of skull function—that were occupied by the highly successful gorgonopsids of the Latest Permian, were filled after their disappearance by the Moschorhinidae (=Akidnognathidae), members of the therocephalians. Use of modern anatomical data from various fields allows a rigorous appraisal of cranial function in these animals. Hypotheses of function generated by this modern anatomical information are tested, and corroborated by the application of Finite Element Analysis (FEA). The patterns of osteological remodelling, suture morphology and location, cross-sectional geometry and dental anatomy are found to be consistent with the stress distributions generated by a finite element model of the moschorhinid rostrum. Permian therocephalians show subtly different skull mechanisms to those of contemporaneous gorgonopsids, but the 'gorgonopsid ecomorph' niche, vacated after the P-Tr extinction was filled by moschorhinid therocephalians in an unrecognized example of convergent evolution. Some aspects of moschorhinid cranial function are entirely unique, but they also exhibit features seen in Permian carnivorous therocephalians such as lycosuchids and scylacosaurids. Biomechanical models of this type are dependant upon a synthesis of engineering principles and rigorous experimental anatomical techniques familiar to neontological vertebrate morphologists.

Kinematics of Underwater Flight in Diving Atlantic Puffins (*Fratercula arctica*)

L. Christoffer Johansson and Björn S. Wetterholm Aldrin, Department of Zoology, Göteborg University, Box 463, SE-405 30 Göteborg, Sweden*

We conducted a kinematic study of the underwater flight of Atlantic puffins (*Fratercula arctica*), diving in a 1-meter deep pool, to examine if the puffin (Alcidae) uses an active upstroke while swimming under water. The results show that the wing, which is partly folded, goes through an oscillating movement with the wrist leading the movement. The wing tip is trailing behind the wrist and starts moving up/downwards with a time delay compared to the wrist. The body of the bird also oscillates in depth throughout the wing stroke with the body accelerating downwards during the upstroke. The analysis further suggests that the bird might accelerate forwards during both the down-stroke and up-stroke, at least when increasing the average swimming speed. At larger depth, the buoyancy is less, which might allow the birds to produce more thrust and less downwards directed force during the upstroke. We conclude that at least one member of the Alcidae, the Atlantic puffin, might use an active upstroke during underwater swimming.

Disparity of Skull Morphology in Dogs: Geometrical Morphometry Approach

Stéphane Jouve, Frédéric Courant and Didier Marchand*, Université de Bourgogne, UMR/CNRS 5561Biogéosciences 6, Bd Gabriel, F 21100 Dijon, France*

The species *Canis familiaris* presents a spectacular intraspecific polymorphism (from Yorkshire to Doberman). Opposite to cats, the dog genome can generate various ontogenies. So, an analysis of skull morphology has been realized on 14 complete crania : 10 specimens of *C. familiaris* and 4 specimens belonging to *C. lupus*, *Vulpes vulpes* and *Urocyon cinereocugentus*, for comparison. The method used is that of geometrical morphometry (Landmarks methods) allowing shape differences between specimens to be quantified and displayed (centroid size = 1). The morphological trees, obtained on different views, show that there is an important disparity of skull shape regrouped in three major types : brachycephal, mesocephal and dolichocephal skulls. The analysis of vectorial fields shows i) brachycephal forms, with reduced face, have a palate highly raised in front, zygomatic apophysis very arched and orbits oriented in front and ii) dolichocephal forms have an elongated palate moved downwards, zygomatic apophysis slightly arched and orbits more laterally oriented. Moreover, the relative importance of braincase, compared to face, is much more marked in brachycephal skulls. Finally, their morphological proximity with some juvenile individuals of wolf shows that these adult brachycephal forms have a skull that retained some juvenile characters (paedomorphic morphology).