

ity after acetaminophen, allyl formate, or carbon tetrachloride; repair from partial hepatectomy and bile duct ligation and chronic toxicity (diethylnitrosamine - induced hepatocellular carcinogenesis). Stereologic, 3D reconstructive, immunochemical and enzyme histo- and cytochemical findings have been used as a basis for comparison and a summary of these approaches will be included. The tubular architecture of the livers of fishes must be considered when interpreting alterations associated with potentially toxic agents.

Positions of the Promontory and Acetabulum Center in the Japanese Male Pelvis in the Standing Posture

Yoshisuke Hiramoto, Kitasato University, School of Allied Health Sciences, Sagami-hara, Japan

The portions of the promontory and acetabulum center may be stable in the bipedal standing posture when aligned vertically or with the gravity line. The pelvis in the standing posture is considered to be situated so that three points of the right and left anterior superior iliac spines and pubic tubercle are in contact with the same vertical frontal plane. To confirm the positions of the acetabulum center, promontory and auricular surface of the pelvis in the bipedal posture, the following three measurements from a lateral view were made: (A) perpendicular distance from the vertical frontal plane to promontory, (B) distance from this plane to acetabular center and (C) that from this plane to the anterior edge of the auricular surface. Twenty-five pelvises of modern Japanese males preserved at the Department of Medicine, University of Tokyo University Museum were used in this study. The mean distance was (A) 51.0 millimeters, (B) 56.7 and (C) 63.6. Difference between mean distances was tested by paired t-test. Mean differences with the acetabulum center were not statistically significant. The acetabulum center was found situated more to the rear compared to the promontory and in front of the anterior edge of the auricular surface. The three positions may be contributing factors to stability in the bipedal standing posture.

Origin and Evolution of Turtles

Ren Hirayama, Teikyo Heisei University Uruido 2289-23, Ichihara, Chiba 290-0193, Japan

The origin and relationships of turtles have been under serious debate especially during the 1990's. Many of the recent phylogenetic analyses based on morphology seemed to be reaching a consensus that turtles belong to the Parareptilia such as *Pareiasauria* and *Procolophonia*, in spite of some disagreement over the details. Rieppel and De Braga (1996), however, proposed that turtles are diapsids by studying more characters and taxa than in previous studies, although it was concluded that the available data set would not prove sufficient to resolve the relationships of turtles convincingly by later review. Recent molecular studies among extant amniotes seemed to support the conclusion that turtles are more closely related to extant archosauromorph (crocodiles and birds) than to squamates and *Sphenodon*. Some neontologists reached the same conclusion already before WWII, based on cranial development data. Another derived character shared between living crocodiles, birds, and turtles might be found in their egg structures. The distinct albumen is present only in the eggs of turtles, crocodiles, and birds among amniotes. Eggshell with calcareous layer is found in crocodiles, birds, turtles, and gekkos, but absent in the other squamates, *Sphenodon*, and mammals (monotremes) as well as in non-amniotes. Both the distinct albumen and the eggshell with a calcareous layer would be considered adaptations to arid terrestrial environments. This might be the main reason why dinosaurs, crocodiles, and turtles survived the mass extinction at the end of the Triassic and became dominant vertebrates during the Jurassic and Cretaceous.

The Development of the Avian Claw. A Comparative Morphological Approach

Ruth Hirschberg*, Hermann Bragulla and Marietta von Stüßkind, Dept. of Veterinary Anatomy, Freie Universität Berlin, Koserstr. 20, 14195 Berlin, Germany

Assuming that the avian claw stands between the reptile and mammalian claws in the phylogenetic order, this study focused on the prenatal development and morphology of the avian claw in order to elucidate homologies between avian and mammalian claws. The important criteria for homology of the different regions of the mammalian digital organ are the formation of a subcutis, the conformation of the dermal papillary body and the formation of epidermal

granular layers. Light and scanning electron microscopic techniques were used on the hind feet of different developmental stages of cockatiel, duck and chicken. In the avian claw, the distal scales were contributing to the claw capsule formation. A subcutis was found in the distal scales, but not in the different regions of the claw. A separate desmal ossification of the tip of the distal phalanx was detected. In the epidermis of either scales or claw, no granular layer was detected. Therefore, a direct comparison and attempt to homologize avian and mammalian claws on the above mentioned criteria remained difficult. An additional investigation of the morphology of the reptile claw using the same methods on claws of the green lizard was therefore added to the original scope of the study. The results gained on avian and reptile claws were then compared to related data on the mammalian claw from the literature.

Ontogeny of the Anterior Vertebrae in Cypriniforms and Characiforms (Teleostei, Ostariophysi)

Matthias Hoffmann* and Ralf Britz, Universität Tübingen, Lehrstuhl für Spezielle Zoologie, Germany

The anterior vertebrae in members of the evolutionarily highly successful taxon Otophysi are modified into a sound transmitting system that forms part of the Weberian apparatus. The ontogeny of the anterior vertebrae in the cypriniforms *Myxocyprinus asiaticus*, *Cyprinus carpio*, *Puntius* sp., *Danio* cf. *aequipinnatus*, and in the characiforms *Hoplias malabaricus*, *Ctenolucius hujeta* and *Rhabdalestes septentrionalis* was investigated based on dozens of specimens in each series. In cypriniforms and characiforms basidorsals of vertebra 1 develop into scaphia, basidorsals of vertebra 2 form intercalaria, parapophyses and ribs of vertebra 3 build up the tripus, parapophyses and ribs of vertebra 4 form the ossa suspensoria, and the cartilaginous supradorsals of the first vertebra develop into the claustra. In cypriniforms autogenous supradorsals of vertebrae 3-4 and supraneurals of vertebrae 2-3 build up the neural complex. In characiforms this complex consists of autogenous supradorsals of vertebrae 3-4 and supraneural 3 only. The claustra have cartilaginous precursors in cypriniforms but ossify as membrane bones in characiforms. In characiforms (+ siluriforms and gymnotiforms) the tripus incorporates the *anlage* of a lateral process on vertebra 3. Our ontogenetic results are compared to those of recent developmental studies on the Weberian apparatus and the homologies of the different parts are discussed.

Cranial and Postcranial Perspectives on the Phylogeny of Perissodactyls (Mammalia)

Luke Holbrook*, Department of Biological Sciences, Rowan University, 201 Mullica Hill Rd., Glassboro, NJ 08028-1701, U.S.A.

Previous studies of perissodactyl phylogeny have focused on the dentition as a source of character information. In contrast, little information from the skull and postcranial skeleton has been incorporated into phylogenetic studies of perissodactyls. This study utilizes the substantial amount of cranial and postcranial data that are available for a large number of perissodactyl taxa. The results presented here represent part of an ongoing study of cranial and postcranial evolution in early perissodactyls. Cranial, postcranial, and dental characters were scored for a broad sampling of perissodactyl taxa. The results of a phylogenetic analysis include the following. Unequivocal members of the Tapiromorpha include a monophyletic Tapiroidea, monophyletic Rhinocerotioidea, *Isectolophus*, and Lophiodontidae. Several non-dental characters unite *Palaeotherium* and *Plagiolophus* in a monophyletic Palaeotheriidae. Tapiromorpha and Palaeotheriidae are part of an unresolved polytomy that also includes Chalicotherioidea, *Homogalax*, *Cardiolophus*, *Hyracotherium*, and *Eotitanops*. This lack of unequivocal resolution of the basal relationships of perissodactyls prevents any definite statement about biogeographic origins of the order. Cranial and postcranial data, however, do provide new insights into relationships within Tapiroidea and Rhinocerotioidea as well as additional support for clades supported by dental evidence, such as Palaeotheriidae.

The Articular Cartilage of Extant Archosaur Long Bones: Implications for Dinosaur Functional Morphology and Allometry

Casey M. Holliday*¹, Jayc C. Sedlmayr¹, Ryan C. Ridgely¹ and Lawrence M. Witmer², ¹ Department of Biological Sciences, Ohio University, Athens, OH 45701, U.S.A., ² Department of Biomedical Sciences, Ohio University, Athens, OH 45701, U.S.A.

Extinct archosaur lineages show variably ossified limb bones implying differing amounts of unpreserved articular cartilage. This "lost anatomy" potentially has a major impact on dinosaur functional morphology. Using the extant phylogenetic bracket approach, limbs of alligators and birds were used to establish an objective basis for inferences about cartilaginous articular structures in extinct clades. Limbs of alligator and quail were dissected, disarticulated, and defleshed. Length and shape measurements with intact articular cartilage were taken. Certain individuals were molded and cast. The limbs were subsequently fully skeletonized and the measurements repeated. In alligators, the radius, ulna, and fibula showed the greatest change in length whereas the humerus and femur changed somewhat less. Condylar regions showed marked shape change in all elements. Many structures (e.g., greatly expanded femoral and humeral articular regions; a large, soft process on the proximal ulna; a cartilaginous trochanter on the lateral femur) were found only in the intact elements and were absent when fully skeletonized. Birds showed less dramatic changes. This disparity in the amounts of articular tissue implies changes in degrees of limb ossification within Archosauria. This missing cartilaginous information has important bearing on the systematics, functional morphology, and allometry of extinct archosaurs.

Materials Towards an Intellectual Biography of Walter J. Bock

Dominique G. Homberger, Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803-1715, U.S.A.

Walter J. Bock, born in New York City in 1933, earned a B.S. from Cornell University in 1955 and a Ph.D. from Harvard University in 1959, spent two years at the University of Frankfurt in Germany, and taught briefly at the University of Illinois in Urbana-Champaign before assuming an assistant professorship at Columbia University in 1966, where he quickly rose through the ranks. Walter Bock sees himself primarily as an evolutionary biologist with a focus in basic theory and philosophy. This and his straightforward career, however, stand in stark contrast to his multifaceted research interests and contributions in ornithology, systematics, functional, ecological and evolutionary morphology, biomechanics, the evolution of higher taxa, the theory of evolution, and the history and philosophy of biology and science. Furthermore, in each research area, his influence has reached a large number of students and associates through his world-wide publications, collaborative efforts, personal associations, and activities in professional organizations. His intellectual biography traces the development and diversification of his thinking, as well as the roles that his empirical research and professional contacts have played in the evolution of his work.

Theoretical and Empirical Underpinnings of Functional Morphology

*Dominique G. Homberger¹, J. Matthias Starck^{*2} and Gert A. Zveers³, 1 Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803-1715, U.S.A., 2 Institute of Systematic Zoology and Evolutionary Biology, Friedrich-Schiller-Universität Jena, Erbertstrasse 1, D-07743 Jena, Germany, 3 Institute of Evolutionary and Ecological Sciences, University of Leiden, P.O. Box 9516, NL-2300 RA Leiden, Netherlands*

The concept of the form-function complex lies at the core of Walter Bock's thinking and work in functional morphology. According to this concept, which he developed with Gerd von Wahlert in the 1960s, every structural part of an organism, from molecules to organ systems, inherently possesses a functional aspect, from chemical properties to physiological processes. Consequently, a full explanation of a biological system or process needs to incorporate both its structural and functional aspects. Furthermore, both aspects of an organism and its parts have to be observed and studied because neither aspect can be derived or extrapolated from the other. In the course of his career, Walter Bock has developed various theoretical and methodological tools for the study of functional morphology, such as the free-body force analysis of muscle-bone systems, and the differential staining of muscle and collagenous tissues for dissections. Walter Bock's functional-morphological studies formed the basis for his work on various problems and issues in systematics, ecological morphology, the theory of evolution, and the philosophy and history of science. Therefore, these studies represent the key to understanding his approach to biology in general.

Symposium: Synthetic Evolutionary Morphology — The Contributions of Walter J. Bock

Dominique G. Homberger¹, Gert A. Zveers² and J. Matthias Starck³, 1 Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803-1715, U.S.A., 2 Institute of Evolutionary and Ecological Sciences, University of Leiden, Kaiserstraat 63, P.O. Box 9516, NL-2300 RA Leiden, Netherlands, 3 Institute of Systematic Zoology and Evolutionary Biology, Friedrich-Schiller-Universität Jena, Erbertstrasse 1, D-07743 Jena, Germany

With his first publication in 1956, Walter J. Bock embarked upon a scientific career that has contributed to and influenced several areas of evolutionary biology either through his numerous publications or through his personal interactions with students and colleagues around the world. One of the defining attributes of his work is its firm grounding on clearly defined theoretical concepts. In this symposium the various interests and contributions of Walter J. Bock will be analyzed, and their historical and intellectual relationships to past and present work in evolutionary biology will be demonstrated. The six symposium contributions will comprise: Materials towards an intellectual biography of Walter J. Bock (Dominique G. Homberger); Evolutionary theory and concepts (Klaus Peter Sauer); Morpho-functional concepts in the evolutionary context (Peter Beurton); Theoretical and empirical underpinnings of functional morphology (Dominique G. Homberger, J. Matthias Starck, and Gert A. Zveers); Ecomorphology and the form-function complex (Hans Winkler); The origin and systematics of birds (Andrzej Elzanowski and Richard Schodde). These and other contributions will be published in a Festschrift issue of "Der Zoologische Anzeiger."

The Evolution of the Avian Integument: A Model Exemplifying the Process of Macroevolutionary Transformation

Dominique G. Homberger, Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803-1715, U.S.A.

The skeleto-muscular apparatus of feathers consists of a dermo-subcutaneous hydrostatic skeleton of fat tissue and a complex musculature of striated cutaneous muscles and smooth dermal feather muscles. The latter occur in a variety of types depending on their location on the body, but consistently comprise at least erector and depressor muscles for contour feathers. This condition in birds contrasts with that in mammals and reptiles, in which the smooth dermal musculature consists only of erector muscles of hair (i.e., *Mm. arrectores pilorum*) or of scales (e.g., in snakes), with the resilience of the connective tissue of the dermis acting as antagonist. Since the antagonistic force for the erector feather muscles in birds is also provided by the resilience of the surrounding dermo-subcutaneous hydrostatic skeleton, the depressor feather muscles must have been evolved secondarily as a uniquely avian structure, probably in connection with maintaining the aerodynamically streamlined body contours and surfaces during flight. It can be shown how the depressor feather muscles may have evolved from erector muscles or less differentiated precursor muscles through minor shifts of their attachments within the dermis or on follicles of contour feathers. This model illustrates how minimal structural modifications of individual elements in a complex organ can result in major changes in the functions and biological roles of that organ and place it onto a new evolutionary trajectory.

Early Vascular Morphogenesis Within Rat Metanephros

M. Horiguchi-Izumiyama, S. Isogai and M. Horiguchi, Department of Anatomy, Iwate Medical University School of Medicine, Morioka, Japan*

Despite the importance of the early vascular morphogenesis of the metanephros as a highly vascularized organ, little is known about its fine and complex process of three dimensional change. We applied the corrosive casting method using acryl-resin and the dye injection method using Berlin blue for rat embryos and revealed three dimensionally the early vascular morphogenesis within the metanephric anlage from E-13.0 to E-15.0. The results were confirmed by observations of serial sections. Until E-14.0, a coarse vascular plexus appeared within the metanephric anlage situated ventro-lateral to the dorsal aorta, dorsal to the mesonephros and cranial to the umbilical artery. The plexus supplied by a few arteries from the umbilical artery drained into the subcardinal vein via the mesonephric sinusoid. At about E-14.3, the cranially shifted anlage was supplied by a few arteries from the dorsal aorta. At E-15.0 in the vicinity of the border between the primordial cortex and medulla regions, arcuate vessels developed and anastomosed to