Program and Abstracts of the

10th International Congress of Vertebrate Morphology

Fira Palace Hotel, Barcelona, Spain

8–12 July 2013

Note from *The Anatomical Record*

The Anatomical Record (***AR***) – a flagship journal of the American Association of Anatomists – is proud to host the program and abstracts for the 10th International Congress of Vertebrate Morphology (ICVM 2013) in Barcelona, Spain this month. Hosting is done on the Wiley Online Library for ***AR*** web page. The full URL address is at the end of this welcome message. Please copy and paste the URL to explore the science that will be presented and discussed at the ICVM 2013 meeting.

Our pride in hosting the program and abstracts is based on the Journal's rich history in publishing landmark studies in all areas of vertebrate morphology. Among these top-tier studies are many incomparable ***AR*** Special Issues that have become classics in the field, including: "Many Faces of Somatosensory Cortex: From Molecules to Maps" (2006), "Anatomical Adaptation of Aquatic Mammals" (2007), "The Paranasal Sinuses: The Last Frontier in Craniofacial Biology" (2008), "Unearthing the Anatomy of Dinosaurs" (2009), "From Head to Tail: New Models and Approaches in Primate Functional Anatomy and Biomechanics" (2010), and "Evolutionary and Functional Morphology of New World Monkeys" (2011).

We anticipate discovering more fantastic state-of-the-art science at the ICVM 2013 meeting in Barcelona! And we look forward to receiving your manuscripts for consideration for publication in **AR,** and to continuing the tradition of advancing the best science in vertebrate morphology in our journal.

Kurt H. Albertine, Ph.D.
Editor-in-Chief, *The Anatomical Record*

Jeffrey T. Laitman, Ph.D.
Associate Editor, *The Anatomical Record*
Past-President, American Association of Anatomists

http://onlinelibrary.wiley.com/store/10.1002/%28ISSN%291932-8494/asset/homepages/ICVM_2013.pdf?v=1&s=8e8d03ff9d6f37a123328c338aa097c3b97af10f&isAguDoi=false

model organism mouse, will help to elucidate differences in molecular mechanisms and developmental pathways involved in morphological modification.

Symposium 5 – Evolution of Locomotion: Reciprocal Illumination from a Diversity of Approaches
Organizers: Timothy Higham & Theodore Garland

S-019

LOCOMOTOR ONTOGENY AND THE EVOLUTION OF AVIAN FLIGHT

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Transitional fossils are the record of evolutionary transformations, key to deciphering the origins of major clades and organismal diversification. Bringing these fossils 'to life' to better understand evolutionary transitions involves reconstructing the function(s) of their anatomical features, by investigating how comparable features function in living organisms. Yet, extant adult forms and extinct fossils are often very different and thus difficult to compare. Here, I use theropod dinosaurs and their avian descendants to show how postnatal developmental transformations can help elucidate evolutionary transitions. Though juveniles are not often discussed in extinct-extant comparisons, developing birds share a number of similarities with the extinct theropods whose transitional skeletons and protowings record the origin of avian flight. Many immature birds rely on dinosaur-like, transitional skeletons and protowings to navigate habitats and reach refugia. Though not yet capable of flight, these juveniles use developing anatomies for intermediate locomotor behaviors like flap-running or steaming over water, where wings and legs are used cooperatively. Developing birds can thus elucidate potential locomotor capabilities of extinct theropods with similar anatomies, by actualizing form-function relationships through behaviors that bridge obligately bipedal to flight-capable transitions. To document feather and skeletal ontogeny in the precocial chukar (*Alectoris chukar*), I (i) used a propeller apparatus to measure aerodynamic forces generated by dried wings, and (ii) used high resolution CT scans and biplanar x-ray videos of different aged birds to quantify skeletal kinematics during various behaviors. My results show that juveniles and adults with highly disparate anatomies employ very similar skeletal kinematics, possibly due to differences in aerodynamic force production by protowings versus wings. Locomotor performance improves through ontogeny, but even young birds generate useful aerodynamic forces. This suggests that extinct theropods might also have been capable of more bird-like wingstrokes and greater aerodynamic force production than implied by their transitional morphologies.

S-020

SELECTION EXPERIMENTS AS AN APPROACH TO STUDY THE EVOLUTION OF VERTEBRATE LOCOMOTION

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The evolution of vertebrate locomotion is commonly studied via comparisons among living species or through examination of fossils. These approaches are highly informative, but are limited for various reasons, including common confounding of independent variables (e.g., diet and activity level), an inability to observe transitional forms (the evolutionary process), and because they can provide only correlational evidence. Selection experiments and experimental evolution approaches can overcome each of these limitations, but are rarely applied to the study of vertebrate morphology. However, several experiments with rodents have targeted aspects of locomotor behavior and/or performance, and are providing new insights concerning the evolution of locomotion. Examples will be reviewed, with emphasis on a long-term, replicated selection experiment with outbred laboratory house mice that has targeted voluntary exercise on wheels. The rodent selection experiments have yielded a range of interesting results, including information about the neural mechanisms that underlie voluntary locomotion (e.g., alterations in the reward system of the brain); skeletal, muscular, endocrine, and immune-system alterations associated with endurance running; "multiple solutions" (alternate adaptive responses) that permit high levels of sustained, aerobically supported locomotion; apparent trade-offs and other negative consequences associated with selection for high (or low) locomotor abilities; genetic correlations between maximal and basal metabolic rates; and the genetic and physiological basis of limits to the evolution of locomotor performance. These results and others encourage a broader use of selection experiments to study vertebrate evolutionary morphology and biomechanics, and could be combined with those from comparative studies to elucidate the interface between micro- and macroevolution. In addition, some limitations of selection experiments will be discussed, from the perspective that, as with all models of complicated phenomena, selection experiments are simplified abstractions of reality (i.e., evolution under natural conditions) that can provide us with important insights if interpreted with due caution.

S-021

WHAT SHOULD WE EXPECT FROM STUDIES OF SELECTION ON LOCOMOTION IN THE WILD?

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Several studies have quantified selection on locomotor performance in natural populations, typically by examining how maximal sprint speed or endurance capacity predicts survival. Whereas there is evidence that maximal locomotor capacity explains survival or other aspects of fitness in some species, this is not a universal finding. Furthermore, the limited data available for locomotor capacity use in nature do not consistently show that animals use maximal abilities in every, or in some cases in any, context. This lack of consistency across studies, combined with the existence of locomotor tradeoffs, questions whether selection does or even should operate on maximal locomotor capacity. I review studies of selection on locomotor performance in nature, field use of locomotion, and tradeoffs among speed and accuracy in performance. These types of studies had a brief flourish of popularity, but there has been little new data or theoretical development on these aspects of locomotor performance in recent years. I synthesize these studies to suggest that instead of expecting animals to typically use maximal capacity, and expecting selection to usually act on maximal locomotor performance, perhaps we should consider the role of mistakes, or failure at a task, in the evolution of locomotion. Understanding the costs and benefits of making mistakes, as well as the probability of being able learn from mistakes in different contexts, may be key to elucidating how locomotion is modulated in nature and how selection shapes it over evolutionary time. This approach may allow investigators to better focus their resources on what can be very time- and labor-intensive studies of selection on locomotion in the wild.

S-022

DIVERGENCE AND NOVELTY IN LOCOMOTOR EVOLUTION: INSIGHTS FROM STUDIES OF WATERFALL-CLIMBING GOBIID FISHES

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Many gobiid fish species living on oceanic islands exhibit amphidromous life cycles, in which larvae are swept to the ocean after hatching, and return to streams as postlarvae that climb waterfalls to reach adult habitats. This distinctive life history found among species living in many island systems, and in streams with different characteristics, has facilitated diverse studies of the evolution of locomotor systems and performance. High-speed videography identified two distinct climbing styles across species: powerbursting, involving pectoral fin adduction followed by axial undulation; and inching, involving alternating advancement of oral and pelvic suckers. How might evolution act on these two styles? Using selection analyses, we found a higher failure rate and stronger predominance of correlational selection in powerburst climbers, as might be predicted for a climbing style that requires more integrated fin and body axis movement. Inching is likely restricted to a single goby genus, suggesting it is a derived trait; moreover, the similarity of oral movements between feeding and climbing among inching climbers suggests that one of these behaviors may have evolved from the other via exaptation. In the Hawaiian Islands, the single inching species penetrates streams with different features: nearshore waterfalls on Hawai'i emphasize climbing performance, but long meandering streams below waterfalls on Kaua'i emphasize predator evasion. We found that climbing and predation impose selection favoring contrasting body shapes (streamlined for climbing, tall for predator evasion), and that fish returning to each island have shapes advantageous for the main pressure they encounter. These shape differences also correlate with performance differences that could form the basis for natural selection. Net climbing speeds are similar for fish from both islands, but only because fish from Kaua'i rest less between bouts. Such differences may contribute to the lower climbing success of Kaua'i versus Hawai'i fish over long distances. NSF IOS-0817794, IOS-0817911.

S-023

HOW TRANSITIONS IN MODE OF LOCOMOTION HAVE SHAPED MACROEVOLUTIONARY PATTERNS IN VERTEBRATES

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Vertebrates occupy nearly all of Earth's major habitats, in large part due to the evolution of a rich diversity of locomotor adaptations. Recent phylogenetic and paleontological studies have helped map most major evolutionary transitions in locomotion onto the vertebrate phylogeny, although debate continues to surround the placement of a few. By combining a phylogenetic perspective with new information about the

development and functional morphology of key locomotor innovations, we may begin to answer longstanding questions about the pattern and process of macroevolution. Using a comparative approach, I first review the evidence for consistent trends in locomotor evolution: Does the evolution of new modes of locomotion follow a predictable sequence? I then ask whether evolutionary locomotor transitions are reversible. Certain types of reversals have occurred numerous times (e.g., evolution of walking or running locomotion from a predominantly flying ancestor), but reversals tend to leave an evolutionary signature. Flightless birds, for example, have never re-evolved the quadrupedality of their distant archosaurian ancestors. Locomotor "reversals" frequently do not involve reversion to ancestral morphologies, and are sometimes associated with novel innovations. I outline how past locomotor adaptations and major locomotor transitions have may have promoted, or in some cases constrained, subsequent adaptive diversification, highlighting several interesting patterns for future research.

S-024

MAKING WAVES: SELF-PROPELLED ROBOTS TEST HYPOTHESES ABOUT THE FUNCTIONAL AND EVOLUTIONARY MECHANISMS OF SWIMMING

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For biologists, physically-embodied robots are gaining traction as powerful tools for modeling complex systems. Because they interact directly with the world, embodied robots do not require physics to be modeled. Instead, biologists can focus on the decisions central to modeling the body and its behavior in the world: what hypothesis is the model testing? Which features of anatomy and physiology to include and which to omit? How abstract or simple should the model be? What elements of behavior of the model and the target need to be matched? What makes for a good model? We offer a number of examples of robotic models used to test biological hypotheses related to how fish swim and how they evolve.

S-025

PHENOTYPIC DIVERGENCE IN LACERTID LIZARDS: A COMPARISON OF EVOLUTIONARY RATES BETWEEN CLADES

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The Lacertidae form a speciose (>300 species) family of Old World small- to medium-sized lizards. Phylogenetically, the family comprises two main clades that reflect the distributional range of the species, i.e. the African and the Eurasian clade. Although the pattern and timing of radiation events within the family are still debated, the out-of-Europe hypothesis, positing that lacertids originated in Europe 65 MYA and colonized Africa around 17-19 MYA, seems most feasible. Whereas the European clade has been suggested to have radiated approximately 14MYA, the age of the African clade remains unclear, although recent studies have suggested it to be similar.

Lacertid lizards have been used extensively to test whether and how they are adapted to their environment. The majority of these studies have included European species, leaving African species underrepresented. However, preliminary analyses on external morphology and performance suggest the variation thereof among African lacertids is greater than that found among Eurasian lizards. Also, lacertid lizard communities on the African continent are more complex than the ones in Europe (i.e. comprising 7-8 species *versus* 2-3 species). We will compare evolutionary rates of locomotion-related phenotypic traits between the two lacertid clades and link them to the ecological diversification found within each clade.

S-026

USE IT OR LOSE IT: THE EVOLUTION OF LOCOMOTION ASSOCIATED WITH THE GAIN AND LOSS OF ADHESIVE CAPACITY IN GECKOS

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Geckos are known for their remarkable ability to adhere to smooth and/or inclined surfaces. They do so with adhesive toe pads, which are morphologically diverse and have evolved multiple times within geckos. In addition to the acquisition of adhesive capabilities, there are several documented cases of loss of the morphological modifications associated with adhesion. The *Pachydactylus* clade is a group that exhibits two unequivocal losses of the adhesive apparatus (*Chondrodactylus angulifer* and *Pachydactylus rangei*). This clade occupies both sandy and rocky habitats in southern Africa, and the secondary loss of adhesion appears linked to shifts in habitat use from climbing to ground dwelling. Although the gain and loss of adhesion has been documented, little is known about the functional consequences of using or losing adhesion. Utilizing the *Pachydactylus* clade, we examined the morphometric, integumentary, skeletal and muscular changes associated with the loss of adhesion. In association, we examined the high-speed three-dimensional kinematics of locomotion on level and 30-degree inclines of pad-bearing and secondarily padless taxa to determine the functional consequences of the presence and reduction of the adhesive apparatus. We examined 8 species spanning the clade, including representatives of *Rhoptropus, Pachydactylus, Colopus,* and *Chondrodactylus*. Kinematics included three-dimensional angles of the hip, knee, ankle, and third metatarsal. In addition, we calculated femur rotation, retraction, and depression. Finally, we assessed patterns of digital hyperextension in relation to incline. To examine morphology and kinematics in a phylogenetic framework, we pruned a published phylogeny that was developed using DNA sequence data consisting of fragments of five nuclear protein-coding genes and one mitochondrial gene. With this, we examined whether traits associated with locomotion become more evolutionarily labile when adhesion is lost. Finally, several mechanistic hypotheses regarding the use of adhesion during locomotion were tested using this system.

S-027

MORPHOLOGICAL INTEGRATION AND EVOLVABILITY IN THE VERTEBRATE LOCOMOTOR SKELETON

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Morphological integration (MI) refers to the inter-dependence between phenotypic traits. This inter-dependence in some cases reflects the traits' shared developmental origins, while in others it reflects their shared function. At the population level, MI is observable as increased covariation among phenotypic traits. MI influences the direction and magnitude of phenotypic (co)variation among traits, and thus bears directly on the evolvability of complex organisms, such as the ability of some traits to evolve independently of others in response to selection. The vertebrate locomotor skeleton illustrates this relationship between MI, evolvability and functional diversification. In the limb skeleton, both developmental and functional factors interact to determine the degree of MI within and among limb bones. For example, tetrapod fore- and hind limbs share a common genetic basis, which is known to increase phenotypic covariation between serially homologous fore- and hind limb elements. This strong covariation can impact the rate and direction of evolutionary change in locomotor function. In cases where fore- and hind limbs share common locomotor functions, for example in terrestrial and/or arboreal quadrupedalism, increased MI may actually facilitate joint evolutionary changes in limbs, by coordinating phenotypic changes between limb bones. However, when new ecological niches or locomotor functions promote morphological divergence between the limbs, such as bipedalism, brachiation or flight, strong covariation may initially act as an evolutionary constraint. Here, using data from the literature, and simulations, I illustrate how the pattern and magnitude of MI in the limb skeleton influences the evolution of tetrapod locomotion. I also present preliminary data from a selection experiment in mice targeting increases in relative tibia length. These data confirm that MI is itself an evolvable property of the tetrapod skeleton, with important consequences for the evolution of locomotion among vertebrates.

S-028

INTEGRATION OF METHODS TO RECONSTRUCT THE LOCOMOTOR EVOLUTION OF ARCHOSAURS

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The evolution of archosaurs (Crocodylia, Aves and extinct relatives such as non-avian dinosaurs) famously includes major changes in locomotor function, including shifts from quadrupedalism to bipedalism, more adducted limbs, alterations of muscle function, and shifts of centre of mass. What was the pattern of change- how reliably can we reconstruct when and how changes occurred? Here we consolidate evidence from a multidisciplinary analysis of morphological change, experimental analyses of extant archosaurs (Crocodylia, Aves) and biomechanical computer modelling to answer these questions. First, we present a basic overview of how extant archosaurs walk, synthesizing prior studies' findings and some new experimental data. Second, we show major findings from two computational studies of the evolution of morphology on the archosaur line to birds: changes in body centre of mass and its linkages with segmental masses and proportions, and changes in muscle moment arms and architecture. Our synthesis points out areas where we need more data from extant animals (in particular) but also fossil taxa in order to make further progress. Yet while there is relative consensus on overall changes in locomotor function (e.g. early changes in muscle function with bipedalism; relationship of posture and centre of mass position), some surprising new insights into the timing of functional changes emerge from our analysis, putting many major shifts in bipedal locomotor function close to the presumed origin of flight. We discuss whether this concordance is coincidence, evidence of a functional link between bipedalism and flight dynamics/constraints, or uncertain.

S-029

SWING PHASE MECHANICS AS A DETERMINANT OF LOCOMOTOR BEHAVIOR IN MAMMALS

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Mammal limbs display remarkable diversity in length, mass, and weight distribution, presumably reflecting different functional demands. To understand this variation, most biomechanical studies have focused on stance phase mechanics, while swing phase is relatively understudied. The rate of swing and the muscular effort required, which is determined by pendulum length and mass, can influence velocity and energetic costs. It is claimed that as animals move faster stance time shortens, but swing time stays relatively constant, suggesting that mechanical qualities of the limb constrain swing time. Although swing phase may be constant for each species, the time it takes to swing the limb forward should vary as a function of anatomical differences between mammalian species. For example, primates that have relatively more distal weight distribution associated with prehensile hands and feet may experience longer swing times than other mammals. By calculating swing time in a range of mammals including humans, cats, kinkajous, coatis, lemurs, squirrel monkeys and several Old World monkeys, we test the hypotheses that (1) swing phase is constant in relation to speed in a wide range of mammals and (2) primates have relatively long swing durations. In every group within our sample stance duration decreases with increasing speed and swing duration remains nearly constant. However, regardless of body size or anatomy, there were no significant interspecific differences in swing duration. These data are interpreted in the context of variation in angular excursion across species, and suggest that swing phase duration is a limiting factor in locomotor performance in terms of speed, angular excursion, and limb angle at touchdown. Data on swing phase mechanics are critical to understanding the inherent trade-offs in limb design, and improve interpretations of limb anatomy and locomotor behavior in both living and fossil mammals.

Symposium 6A – Quantifying Evolutionary Development Using Non-model Organisms: Integrating Metrical Frameworks, Gene Expression, and Morphology
Organizers: Laura Wilson & Ingmar Werneburg

S-030

HETEROCHRONY ANALYSIS: FROM EVENT PAIRING TO CONTINUOUS ANALYSIS

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With the rise in interest in sequence heterochrony, phylogenies have come to play a more important role than ever in evo-devo. The first method that successfully integrated the phylogeny into the analysis of reasonably large (i.e. with more than ten taxa) comparative datasets of ontogenetic sequences is event pairing. This method requires transforming ontogenetic sequences into event pairs that represent the relative order between two events. However, this approach has drawbacks that have been recognized soon after the method was proposed. Namely, transforming sequences into event pairs discards information that is hard to recover after the analysis, it generates a large number of characters (proportional to the square of the number of events in sequences), which restricts its analysis to simple datasets, it can lead to impossible ancestral state inferences, and it is impossible to select statistically significant events using an explicit probability threshold. Recently, one of the initial justifications of this method was questioned; the lack of universal ontogenetic time markers does not necessarily imply that time must be discarded from the analyses, or that sequences need to be converted into event pairs. The recently-proposed method called “continuous analysis” rests on a simple standardization of ontogenetic timing or sequence position. The data are analyzed through square-change parsimony to infer ancestral (nodal) values and phylogenetic independent contrasts to provide confidence intervals for these values. Simulations have shown that this new method outperforms event pairing with Parsimov (the latest implementation of the method), at least in the tested parameter space. In addition to covering the history of these methods and explaining the underlying assumptions, this presentation will present further refinements of the continuous analysis.

S-031

ANALYZING DEVELOPMENTAL SEQUENCES WITH PARSIMOV

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Since its publication in 2005 Parsimov was used by several researchers to investigate timing of developmental events in various species groups, including amphibians, turtles and snails. Parsimov is a parsimony-based method that identifies sequence heterochronies in all branches of an existing cladogram.