

ing bats, salamanders and chameleons) were examined. Our data show marked differences in gross morphology and ultrastructure that appear tightly linked to the mechanical demands imposed on the functioning of these systems and show remarkable convergence (e.g., use of helically arranged muscles) in some aspects, but striking divergence in others (e.g., presence or absence of supercontractile muscle).

**Dwarfing a Giant: Allometry and Ontogeny of Elephant Limb Bones**  
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Elephants are the largest living terrestrial mammals. They represent the endpoint taxa for our current understanding of many inter-specific allometric relationships and the constraints imposed by large body size, particularly in locomotion. Despite ranging from just over 100kg at birth to 7,000kg in full-grown males, recent research suggests that juvenile elephants do not differ from their adult conspecifics in their kinematics. The highly derived, graviportal skeletal morphology of elephants has been closely linked with elephant locomotor abilities, and yet the intraspecific allometry and ontogeny of elephant limb bones has been little studied. This is necessary to our understanding of the morphology and adaptation of extinct elephant species, especially the dwarfed species of elephant found on islands 800,000–10,000 years ago. The smallest of these dwarf elephants, *Palaeoloxodon falconeri*, is estimated to have had an adult body mass of just 150kg (equivalent in size to a neonate African elephant), compared to its 10,000kg ancestor, *P. antiquus*. Biometric data have been collected from growth series of African elephant (*Loxodonta africana*) and fossil dwarf elephant limb bones, as well as from fossil *P. antiquus* material, to assess how dwarf elephant limb bone morphology compares with elephants of similar size. Additionally, the intraspecific allometry of extant elephant limb bones through ontogeny is assessed. These data shed further light on the effects of scaling on morphological and biomechanical adaptation.

#### Functional Mechanics of Cranial Sutures

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Sutures are viscoelastic joints that unite the dermal bones of the skull and provide locations for bony growth. The load-bearing elements are the collagenous ligament and bound water. Ligamentous anatomy is thus an important determinant of sutural mechanical properties. Sutures are far more compliant than the bones they join. In vivo, sutures receive quasi-static loads from soft tissue growth, cyclic loads from function, and impact loads from activities such as head-butting. Cyclic chewing strains recorded in pigs (*Sus scrofa*) demonstrate that different sutures are compressed or tensed to different levels. A plethora of experimental evidence suggests that sutural growth (and hence cranial morphology) is influenced by mechanics. Sutural growth in pigs can be studied using vital staining of replicating cells and newly mineralized matrix. Braincase and facial sutures are similar in both their in vivo strains and in their growth, despite a somewhat different development and the presence of dura mater only in the neurocranium. Tissue layers analogous to the periosteum line the bone fronts, providing a continuously renewing source of cells with osteogenic potential. In growing sagittal sutures, cell replication becomes increasingly confined to the ectocranial region, along with a general tendency for growth cessation on the dural surface of the bones and acceleration on the ectocranial surface. Exuberant ectocranial osteogenesis ultimately bridges the suture. Although there is no evidence that sutural strain causes fusion, after fusion is initiated, strain levels drop to those typical for adjacent bones. Supported by DE8513 from NIDCR.

#### A Comparative Study on the Functional Morphology of the Jaw Apparatus in Cyprinodontiformes (Teleostei, Atherinomorpha)

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Cyprinodontiformes represent a heterogeneous taxon of teleost fishes regarding their diverse trophic strategies. In a comparative study, the anatomy of nerves, muscles, and ligaments of the complex jaw apparatus were investigated. Examinations of 95 species including representatives of the related Beloniformes, Atheriniformes, and *Perca fluviatilis* as out-

group enabled the conceptualization of 78 soft tissue characters, most of them described for the first time. Following the new hypothesis regarding the early phylogeny of Cyprinodontiformes, the genera *Aplocheilichthys* from India and *Pachypanchax* from Madagascar are sister groups of all the remaining species. Additionally, the distribution of fiber types in four large muscles of the jaw apparatus of Cyprinodontiformes were studied in eleven species. The histochemical characterization (Glycogen, SDH, mATPases, NADH) resulted in the identification of four different fiber types, arranged in distinct regions within these muscles. Previous functional studies have shown that red fibers are responsible for slow breathing movements, while fast contracting fibers are activated exclusively during ingestion. The distribution pattern of red fibers is highly conserved and consists of small, sharply delimited zones surrounded by a single layer of intermediate alkali-stable fibers. In contrast, the proportions of fast-contracting fibers (white respectively intermediate alkali-labile) varies clearly among the species depending directly on trophic strategies. Fast-contracting fibers, therefore, are responsible for observed differences in the configuration of jaw muscles within Cyprinodontiformes. On the basis of the phylogenetic analysis these results show that jaw muscle characters reflect historical evolutionary adaptations correlated to changes in feeding behavior.

#### Effects of an Erect Posture on the Lumbar Paravertebral Musculature

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Compared to the horizontal posture in quadrupedal mammals, the erect posture of the trunk in human bipedality results in completely different loads on the vertebral column and thus in different functional demands on the musculature. The paravertebral muscles have to counteract gravitational forces acting in parallel to the body axis rather than orthogonally as in other mammals. Surprisingly, the topography of the back muscles in humans is very similar to that found in other mammals. Therefore, we investigated further characteristics of the lumbar muscles to find adaptations to the differing functional demands. We examined the ratio of the anatomical cross-sectional areas of all paravertebral muscles using CT data of a donated cadaver and compared them to data of other mammals. The results showed that the ventral musculature comprised a higher proportion of the entire cross-sectional area of all muscles (1:1 with respect to the dorsal muscle group) in comparison to quadrupedal mammals (1:3). Furthermore, the three-dimensional muscle fiber type distribution was examined in serial sections of the epaxial muscles as an indicator of a muscle's function. In contrast to other mammals, which have high percentages of slow contracting, fatigue-resistant fibers in deep, mono- or oligosegmental muscles only, a high proportion of slow fibers was found throughout all epaxial muscles in humans. This indicates a stabilizing function for both the deep, oligosegmental as well as for the superficial, multisegmental muscles.

#### Turtle Beaks, Bird Beaks, Croc Beaks? Parallel Evolution of Rhamphothecae in Sauropsida

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Edentulous beaks appear several times in sauropsid evolution. Although both extant examples (turtles and birds) are entirely edentulous, many extinct beaked sauropsid clades show substantial maxillary and dentary tooth rows. This results in a great deal of variability in beak form, but the number of parallel occurrences (between twelve and fifteen, depending upon topology) raises the possibility of underlying similarity driving beak evolution. In this study, specimens from 20 extant sauropsid taxa were surveyed for the morphology and topology of skin features, dermatocranial skeletal elements, and trigeminal innervation on the maxillary rostrum, using such anatomical techniques as dissection, microCT, and histological sectioning. Skeletal specimens from over 200 additional extant and extinct sauropsid taxa were also examined to (1) determine the accuracy and extent of bony correlates for these features, and (2) test for congruence between "similar" morphologies in distantly related clades.

Persistent and congruent similarities in sauropsid facial skin include the retention of a fold between the integumentary derivatives of the embryonic maxillary and frontonasal processes, which corresponds in many taxa to the separation between the ophthalmic (CN V1) and maxillary (CN V2) dermatomes. A second border occurs between the dermatomes of medial and lateral rami of the ophthalmic nerve. In cases where skin morphology varies across the maxillary rostrum, the sharpest gradients in morphology generally occur across one of these borders. Separate frontonasal and maxillary skin regions may thus vary as partially independent “modules” of integument, facilitating the parallel evolution of beak plates on the premaxilla and mandibular symphysis.

#### One Gland, Two Lobes: Organogenesis of the Harderian and Nictitans Glands in Deer

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Traditionally, the nictitans and Harderian glands of mammals have been considered to be two fundamentally distinct structures. However, a consistent, unambiguous distinction between these orbital glands, whether based on gross anatomical, histological or histochemical criteria, has remained elusive. The Harderian gland was originally described, and first distinguished from the nictitans gland, in adult deer, and cervine deer are still regarded as paradigmatic for the “dual gland” condition. Yet the developmental origins of their glands have never been investigated. We examined the organogenesis and histochemical development of the anterior orbital glandular mass in a total of 30 fetal specimens of two species of deer (*Muntiacus reevesi* and *Dama dama*). Four stages of glandular organogenesis were observed. Most notably, the two glandular portions developed from the same inception point, but the deep lobe developed faster than the superficial lobe. The common inception point, and the relationship of the collecting ducts clearly show that this is a single glandular mass that differentiates into two lobes, rather than two distinct glands. The histochemical profiles of the two lobes differ slightly, but both produce lipids. We propose that the terms nictitans and Harderian glands, as separate entities, be discontinued, and that the entire complex be referred to as the anterior orbital gland (glandula orbitalis anterior), with superior and deep lobes (pars superficialis and pars profundus, respectively).

#### Animating the Feather: A Four-dimensional Teaching Tool

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Feather development and replacement involve a bewildering series of gross morphological, histogenetic and cytogenetic events and processes taking place in three-dimensional as well as temporal space. Simultaneous and consecutive productions of different types of keratinocytes—some in continuous sheets, others subject to precisely patterned, programmed separation—are one of the most magnificent and unique manifestations of epidermal activity in sauropsids. Consideration of the processes involved demands continual change of mental perspective from anatomical to molecular levels: these processes are a challenge to scholars of development and evolution, and a pedagogic nightmare when trying to communicate them to students. Conventional two-dimensional diagrams, even at their most detailed and complete, are inadequate for illustrating the four-dimensional intricacies of feather genesis: they usually fail to generate a level of comprehension among students beyond “... and then some complicated stuff happens.” Indeed, most available accounts of these processes in the primary literature, let alone secondary and tertiary texts, all suffer from these shortcomings. In an attempt to better illustrate the fundamentals of feather replacement, and on the premise that explaining four-dimensional processes requires four-dimensional illustrations, we have initiated the creation of a series of computer animations about these topics. Drafts of these animated shorts will be presented for evaluation.

#### On the Evolution of the Eyelids and Eye-licking Behaviour in Reptiles

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The reptilian eye is protected from the environment by many different structures, including a pair of eyelids (upper and lower), a nictitating membrane and a variety of orbital glands. This protective system is observed in many extant reptiles, including representatives of turtles, crocodiles, rhynchocephalians and squamates. It thus presumably is the primitive stage. Most commonly this system closes off the eye by using both a large mobile lower eyelid (often containing a translucent window), and a nictitating membrane. However, there are two alternative modifications: (1) In assorted scleroglossan lizards (including most gekkotans and also all snakes) the lower eyelid is transparent and covers the eye temporarily as a framed window or permanently as an entire spectacle. (2) In assorted Iguania (peaking in the Chamaeleonidae) and in eublepharid gekkotans, the upper and lower eyelids are both enlarged. Thus, the half-closed eyelids still permit the lizard full vision. However, within *Anolis* (Iguanidae), all three variations are observed in different species. The role of the nictitating membrane also changes with the modifications in eyelid morphology: In lizards with mobile eyelids, it wipes the cornea and conjunctiva; in lizards with immobile eyelids, and in snakes, it is reduced and finally lost. In contrast, the tongue, which in eublepharid gekkotans also plays a role in cleaning the eye (eye-licking), likewise cleans the keratinized spectacle in all other gekkotans. Thus, the eye-licking behavior probably evolved in the common ancestor of the Gekkota, and was retained in both spectacled geckos (where its function appears obvious) and eublepharids.

#### The Ribcage of Tyrannosaurid Dinosaurs and an Interpretation of Potential Breathing Mechanisms

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Fossil skeletons of Tyrannosauridae (Late Cretaceous theropod dinosaurs) are well suited for a study of costal aspiration breathing, due to the generally good preservation. In this study, I investigated the detailed morphology of the ribcage in tyrannosaurid fossils, in order to develop inferences regarding potential ventilatory mechanisms. Data about the anatomy of the ribcage were collected from specimens housed in the Royal Tyrrell Museum of Palaeontology and other institutes. These observations demonstrate that the tyrannosaurid ribcage extends from the 11th–23rd presacral vertebrae. Throughout the series, the 13th–15th presacral ribs are much longer than other ribs, and possess especially blunt distal ends. The distal ends of the 13th–15th presacral ribs are oriented medially (not anteriorly). These features suggest that these three pairs of ribs primarily articulated with cartilaginous sternal elements, and the sternal rocking seen in extant birds is unlikely in tyrannosaurids because the vertebral rib articulated with the cartilaginous sternal rib at an extremely obtuse angle. In addition, the rotational axis for the rib on the vertebra orientates relatively dorsoventrally in tyrannosaurids, indicating that the mediolateral component was larger than the dorsoventral component in the rib rotation. Taken together, these lines of evidence suggest that dorsoventral movements of the sternum were likely limited, and lateral excursions of the thoracic wall being more integral to costal aspiration in tyrannosaurids. This interpretation indicates that the basic avian thoracic architecture was incomplete despite the possible presence of air sacs in tyrannosaurids.

#### From Mice to Monkeys: How Similar Are Their Dental Genetic Architectures?

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Mice are a powerful model for studying the genetics of odontogenesis. From an evolutionary perspective though, how characteristic of other mammalian taxa is mouse tooth development? Quantitative genetic analyses can be used to gain some insight to the appropriateness of broad application of the mouse model, as these analytical methods can be performed on animals that are logistically impractical for developmental genetics research. We used quantitative genetic analyses to study variation in incisor and molar size in out-bred populations of mice and