SKELETAL ANATOMY AND FUNCTION IN REPTILES

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ABSTRACT

For veterinarians, vertebrate biologists, and paleontologists, the reptile musculoskeletal system serves as a system of landmarks; organ system(s) and bones are a source of key characteristics. Through its formation, the skeleton acts as a reservoir for key minerals. Bones act as levers, provide protection, and in some cases, form bony armor. The architecture of reptilian bone tissue reflects the influences of phylogenetic history, development (ontogeny), the environment, and health status. Bone is a tough and resilient material yet is vulnerable to injury or disease.

The skeleton is described by region and function (cranial, axial, appendicular). Its parts serve as a system of levers; bones and cartilages may move via synovial joints and are stabilized by fibrous joints that restrict movement. Bones directly interact with muscles via their tendons and through their combined functions skeletal form has reciprocal interactions with the environment. Muscles develop as major groups associated with skeletal regions. Those muscle masses share innervation across taxa, and in closely related taxa may share function.

Bone and cartilage, as tissues and as skeletal elements, are shaped by ontogeny, phylogeny, mechanics and the environment in which the animal lives or lived. Here bone is the focus. The ontogeny of bone is reflected in composition of the mineral and fibrous components as well as the architecture of the tissue. In young rapidly growing reptiles often there are many more vascular channels in the bone than in the bone forming mature skeletons. The phylogenetic perspective on bone is simply that linages of reptiles that are more closely related tend to have more similar bone types simply because of shared genetic instruction and similar metabolic features, all else being equal.

The mechanical characteristics of bone as a tissue and as skeletal elements reflect the composite properties provided by the fibrous (collagen), mineral, and living bone cells (osteocyte, osteoclast, etc.) In general, bone form is shaped by genetic instruction and refined by mechanical forces (Wolff’s Law). For example, heavy bodied animals tend to have more compact bone that light-bodied species. Aquatic species tend to have heavier bones than their terrestrial counterparts and may lack a medullary cavity. Species that undergo torsion may have laminar bone form that reflects the mechanical resistance to twisting.

The impact of the environment, both natural and artificially constructed, can profoundly impact bone growth and metabolism. It is common to find thick layers of rapid bone growth and mineral deposition followed by lines of arrested growth when bone is sectioned. In some species this tissue level of organization can be a proxy for aging the reptile. In addition to impacts of
temperature (which generally slows bone growth or repair), other factors such as available sunlight, calcium availability, nutritional state and hydration influence bone as a tissue and skeletal form.\(^9,11,12\) Disease, injury and aging also are reflected in skeletal structure and bone tissue organization.

Cartilage is the other major skeletal tissue. It forms significant parts of the skeletons of hatchling lizards and turtles and lines all mobile joints. Snakes tend to have cartilage between vertebrae as joint surfaces, and those may serve as areas of elongation. The jaws may form as cartilage that is replaced by bone.

**Components of the Skeleton**

The skeleton can be described from a number of perspectives, including (i) the tissues that form its elements, (ii) origins and embryologic development, (iii) the distribution of its elements in the body and (iv) evolutionary history. The evolutionary history is both fascinating and of biologic importance but much is beyond the scope of this discussion.

**Tissues**

The skeleton is composed of bones and cartilages, which are composite mineralized tissues. Bone is described as having a *matrix*, which is defined as water and the soft organic material, mostly collagen fibers, several kinds of cells, and the minerals associated with the fibers.\(^9\) Most bony minerals are calcium phosphate with a lesser proportion of calcium carbonate. The bones may form by endochondral processes (cartilage replacement) or several intramembranous processes (the most familiar are sesamoid or dermal bone formations). Several other kinds of non-endochondral bone are described by the location of formation, including, subdermal, perichordal, and perichondrial.\(^9\) Reptilian bone is formed by several mechanisms: cartilage replacement, deposition of periosteal bone around the cortical compact bone, and by intramembranous condensations of bone.\(^6\)

Cartilage tends to contain more water than bone and its matrix is glycoprotein-based. Young reptiles tend to possess much hyaline cartilage, which is a resilient tissue. Most species retain cartilage throughout life as articular surfaces, at the bases of the great vessels, and supporting the medial aspect of the eye’s sclera. Fibrous cartilage is found at the intervertebral junctions in reptiles and in the intermandibular symphysis of most lizards, but not geckos and iguanine species.\(^10\) Elastic cartilage is rare and is noted in the snout of soft-shelled turtles (*Amyda* and *Trionyx* spp.) and in the articulations of ribs to the sternum of crocodilians.

In reptiles, fish, and amphibians there is the potential for bone growth at the chondro-osseus junction throughout life as there is no secondary bony plate separating articular cartilage from bone.\(^9\) Robust chondro-osseus bone growth found in the leatherback turtle *Dermochelys* is supported by extensive articular cartilages and subchondral bony processes that are rich in blood vessels\(^19\); this differs from the less vascular structure of developing bone in other reptiles.
Cortical bone is located at the periphery of bones, adjacent to the periosteum and is compact. It is often laminar in organization. Endosteal bone is deep to cortical bone and can be tightly spongy (cancellous), form strut-like trabeculae (trabecular bone). Diploë is a form of trabecular bone that is sandwiched between two plates of compact dermal bone. It is found in the carapace of turtles. Medullary bone, such as is found in reproductively active birds, has not been identified in reptiles.

**Divisions of the Skeleton**

Typically the skeleton is described by the embryonic and evolutionary origins of its main bone groups: skull and hyoid apparatus, axial skeleton and appendicular skeleton as well as by the ways bones form. Each of the bone groups is a composite of several structures. While the developmental and evolutionary origins of bony groups may be of little clinical relevance, much of the terminology used to identify bones has its basis in these fields.

The **Skull**

The skull is often envisioned as a single unit, yet it is composed of three parts that have different phylogenetic, positional and developmental origins: chondrocranium, dermatocranium, and splanchnocranium. The skull includes the cranium (often termed the “braincase”), jaws, and hyoid apparatus. The braincase is a composite of parts of the chondrocranium roofed by dermatocranial bones. Chondrocranial bones are endochondral in origin. They encase much of the brain and form the posterior skull including the parietal bones. Most of the endochondral skull bones are deep within the skull housing the brain and inner ear. Bones of the back of the cranium are endochondral, including the occipital condyles, the occipital series, and supraoccipital.

Most reptiles have a ring of endochondral bones in each eye (scleral ossicles) and hyaline cartilage within the sclera supporting the back of each eyeball. The exceptions are snakes and crocodilians.

The dermatocranial (dermal) bones cover many of the chondrocranial and splanchnocranial bones and cartilages. Bones of the dermatocranium form as intramembranous bone; often they arise from neural crest rather than ectoderm or mesoderm; they are often flat and make up the outer casing and roof of the skull.

Most of the superficial bones of the face are dermatocranial bones: premaxillae, maxillae, postorbitals, prefrontals, parietals, jugals, quadratojugals, and squamosals. The bones of the lower jaw (mandible) are dermatocranial. These include the large dentary, surangular, angular, and splenial. The bones of the palate are also dermatocranial, including the buccal surfaces of the premaxillae and maxillae, the vomer, palatines and pterygoids. These composites that make up the palate are important in species identification; they form the partial secondary palate and primary palate adjacent to the braincase.

The hyoid apparatus (the hyoid body and paired ceratohyal bones and cartilages) is attached to the lower jaw, tongue and throat muscles and is located between the two rami of the lower jaw. Part of the hyoid may be modified, particularly in lizards) to support dewlaps for display or as part of the tongue projections system of chameleons.
The bones of the splanchnocranium tend to be similar with families. However, their specific form differs slightly with age and among species. They include the cartilaginous part of the mandible (Meckel’s cartilage). The splanchnocranium forms the jaws (both the mandibles) and skeletal housing of the sense organs. By the time of hatching or birth, upper and lower jaws are composites of several dermatocranial bones and the splanchnocranial elements are reduced. The hyoid, which has both bony and cartilaginous parts, serves as a site for muscle attachments in the jaws, throat, and tongue. Each ear has one bone, a stapes (= columella), which is also part of the splanchnocranium.

The Axial Skeleton

The axial skeleton is composed of the vertebrae (cervical, trunk, sacral, and caudal), ribs and their derivatives, and the sternum. The sternum is mostly cartilaginous in reptiles and is overlain by the interclavical (and appendicular bone). Abdominal ribs (gastralia) of lizards and crocodilians are part of the axial skeleton.

Turtles have several unique axial elements. The cheloniid carapace includes a nuchal bone, marginals, pleurals, neurals, and a suprapygal bone that may be a single structure or divided as two. The ribs are modified as pleural bones; plastron bones are considered to be novel axial elements. The neural bones are ankylosed to dorsal surfaces of the vertebral bodies (vertebrals) and together they enclose the spinal cord in the trunk region. In the posterior carapace, the vertebrae are free from the neurals starting in the sacral region. The sacral and proximal caudal vertebrae are within the carapace. Posterior to the suprapygal bone, the caudal vertebrae form the tail.

Most reptiles have seven mobile cervical vertebrae including a three-part atlas and axis. The number of cervical vertebrae in snakes remains unresolved with some authors identifying just two (atlas and axis) vertebrae, others identify three, other investigators claim seven or eight, and yet other authors claim as many as 18 cervical. Turtles have an 8th vertebra that transitions between cervical and trunk as it articulates with a convex articular surface on the ventral side of the nuchal, the most anterior vertebra of the carapace. Crocodilians have eight cervical vertebrae.

Reptiles have 8-50 trunk (or dorsal) vertebrae that articulate with ribs with long-bodied species having the most. Some authors refer to thoracic and lumbar regions in some lizards and crocodilians; however, Romer (1956) explicitly argues that the presacral vertebrae of reptiles are not differentiated into thoracic and lumbar groups. In snakes and legless lizards the vertebrae are often designated as precaudal (anterior to the vent) and caudal (posterior to the vent) vertebrae.

Reptiles vary in whether they have single or two-headed ribs. Chelonians appear to have single-headed ribs that align at the junction of two vertebral bodies.

Reptiles have two to three sacral vertebrae with long lateral processes (sometime termed sacral ribs) that articulate with the medial ilium. In most taxa, 12 or more caudal vertebrae follow. In chelonians the caudal vertebrae of females are short and decrease in size distally; the caudal vertebrae of males grow in depth, width and length during puberty.
The Appendicular Skeleton

The appendicular skeleton, is defined as the limbs and their supporting structures (limb girdles.) Appendicular bones of the forelimbs are the phalanges, metacarpals, carpals, radius, ulna, humerus, procoracoid (coracoid), interclavicle, clavicle and scapula. Hind limb bones include the phalanges, metatarsal, tarsals, tibia, fibula, femur, ilium, ischium and pubis. In turtles, uniquely, the pectoral and pelvic girdles are located within the shell, an arrangement that is characteristic of all turtles. The forelimbs of some species are modified as flippers (sea turtles and Carettochelys). Chameleons have novel carpal and tarsal organization that is associated with zygodactyl foot form. Snakes have lost all appendages and the pectoral girdle. Most species lack any vestige of the pelvic girdle except for some pythons and boids that retain remnants of the ilium and/or femur.11

Joints

Reptilian mobile joints (diarthroses) such as knee and elbow joints are synovial joints. All reptiles have synovial joints, however their form is considered to be primitive. For example, Crocodilians, Sphenodon, and lizards have a single joint cavity that is shared by the femur, tibia and fibula.8 Motion-limiting joints (synchondroses and synostoses) such as between cranial bones or between plural bones of the turtle carapace are fibrous.10 Many chelonians have an amphiarthrosis (fibrous cartilage) between the radius and ulna that allows restricted mobility.20,22

Epiphyses

Reptiles form epiphyses that may persist through life; consequently bone growth may continue throughout life.7,8 Some reptilian epiphyses receive tendon fibers into the hyaline articular cartilage. In some lizard species, much of the epiphysis is occupied by thick hyaline cartilage; this morphology can persist in mature lizards. In reptiles, break down of calcified cartilage and resorption of bone and calcified cartilage during endochondral ossification is slow.7

Tail Autotomy and Regeneration

Caudal autotomy (ability to shed the tail), usually in response to attack, occurs in a number of reptilian taxa including many lizards2,3 including iguanid, gekkonid, and lacertids, Sphenodon spp. and a few snakes. Autotomy takes place at morphologically distinct areas of tail weakness. Lizards have two main autotomy patterns: (i) intravertebral autotomy, where transverse fracture planes cross each vertebra of the central portion of the tail, (ii) breaks between vertebrae (intervertebral autotomy). Species with intervertebral autotomy do not show any obvious caudal modifications relative to non-autotomizing.2 The autotomous tail has structural adaptations that minimize blood loss and trauma to adjacent tissues. The early phase of wound healing involves a leukocytic response but limited inflammation. Re-epithelialization via a specialized wound epithelium is not only critical for scar-free healing but also necessary for subsequent tissue patterning and outgrowth or the replacement tail.5

Musculoskeletal Systems
Muscles act as stabilizers across joints and as prime movers in location, feeding, display and defense. Muscle positions are conservative as they form as “modules” in early embryos but can vary greatly as specific form arises. Their attachments can be to bones, other muscles or skin. When attached to skin, the skin may be stabilized such that it acts like a skeletal component.

The relationships of muscles to their skeleton are represented by an extensive and rich literature. Briefly muscles form from major groups that develop conservatively. Cranial muscles form three major groups. Jaw muscles are formed of (i) hypobranchial muscles that are innervated by spinal nerves and (ii) branchiomeric muscles that are innervated by cranial nerves (primarily nerves V and VII). (iii) Extrinsic eye muscles arise within the orbital periosteum and insert on the eyeball. Postcranial muscles include the axial muscles, which grossly are divided into epaxial muscles that form dorsal and lateral the vertebral arches, lateral processes, and ribs and the hypaxial muscle groups that are located more laterally and ventrally along the body. Appendicular muscles arise as dorsal and ventral muscle masses that split into complex groups. In general, the dorsal muscles tend to be extensors and retractors and the ventral muscles flexors and abductors.\textsuperscript{11}

**LITERATURE CITED**


Figure 1. How we classify bone.

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<th>Location &amp; Structure</th>
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Bone types