

Emerging Model Organism

The Veiled Chameleon (*Chamaeleo calyptratus* Duméril and Duméril 1851): A Model for Studying Reptile Body Plan Development and Evolution

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Vertebrate model organisms have facilitated the discovery and exploration of morphogenetic events and developmental pathways that underpin normal and pathological embryological events. In contrast to amniotes such as *Mus musculus* (Mammalia) and *Gallus gallus* (Aves), our understanding of early patterning and developmental events in reptiles (particularly nonavians) remains weak. Squamate reptiles (lizards, snakes, and amphisbaenians) comprise approximately one-third of all living amniotes. But studies of early squamate development have been limited because, in most members of this lineage, embryo development at the time of oviposition is very advanced (limb bud stages and older). In many cases, squamates give birth to fully developed offspring. However, in the veiled chameleon (*Chamaeleo calyptratus*), embryos have progressed only to a primitive pregastrula stage at the time of oviposition. Furthermore, the body plan of the veiled chameleon is highly specialized for climbing in an arboreal environment. It possesses an entire suite of skeletal and soft anatomical modifications, including cranioskeletal ornamentation, lingual anatomy and biomechanics for projection, autopodial clefting for grasping, adaptations for rapid integumental color changes, a prehensile tail with a lack of caudal autotomy, the loss of the tympanum in the middle ear, and the acquisition of turreted eyes. Thus, *C. calyptratus* is an important model organism for studying the role of ecological niche specialization, as well as genetic and morphological evolution within an adaptive framework. More importantly, this species is easily bred in captivity, with only a small colony (<10 individuals) needed to obtain hundreds of embryos every year.

BACKGROUND INFORMATION

Chameleons are a group of lizards that are highly specialized for a life of climbing. They show stereotypical characteristics of fast and complex color changes, independently moveable turreted eyes, split hands and feet with differential syndactyly between these serially homologous elements, a highly modified cranium with a ballistic projectile tongue used for prey capture, and a prehensile tail (see Tolley and Herrel 2014). Although these aspects of the chameleon body plan are widely known,

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the family is quite diverse, with multiple genera that show a less rapid and complex color change repertoire, and a more reduced or highly modified tail, which is often not prehensile. Despite the species diversity within this group (Uetz and Hošek 2014), very little attention has focused on this clade with respect to the development and evolution of their body plans (Niswander 1997; Wilkie 2003). Here we describe the veiled chameleon (*Chamaeleo calypttratus*) as an emerging model system to not only begin to understand the evolution and divergence of chameleons, but also to use this squamate reptile as a new model system by which to approach the origin and evolution of the amniote body plan.

Currently 12 genera and ~200 species are recognized within the family Chamaeleonidae (Glaw et al. 2013; Tolley et al. 2013; Tolley and Herrel 2014), with members of this family distributed across Africa into the Middle East, southern Europe, India, and across a few small islands in the Indian Ocean. An out-of-Africa origin of the family, with two rounds of oceanic dispersal to Madagascar, is supported by recent time-calibrated phylogenetic studies, and is consistent with palaeogeographic reconstructions and the fossil record (Tolley et al. 2013; Townsend et al. 2011). The genus *Chamaeleo* is broadly distributed across Africa, Socotra, India, and southern Europe (Macey et al. 2008). *Chamaeleo calypttratus* Duméril and Duméril 1851, the veiled or Yemen Chameleon, is a habitat generalist distributed in the Arabian Peninsula along south and southwestern Yemen as well as in southwestern Saudi Arabia (Tilbury 2010; Hillenius and Gasperetti 1984). The species has recently been introduced into Hawaii and Florida (Krysko et al. 2004), where it thrives and appears to be flourishing.

Chamaeleo calypttratus are large-bodied lizards with males reaching up to 62 cm total length (TL) (or 20–30 cm snout-vent length, SVL) whereas females reach 45 cm TL (10–20 cm SVL) on average (Schmidt 2001). Males develop enlarged cranial casques (vertically projecting cranial vault complex of the parietal and squamosal bones) relative to females and also retain tarsal “spurs” on their hindlimbs as sexually dimorphic traits used during courtship (Fig. 1A,B). In captivity, individuals may attain larger sizes because of increased protein and supplementary nutrition in the diet, as well as captive selective breeding for larger body sizes and other associated traits (casque height; RE Diaz, Jr., personal observation). Sexual maturity in this species can be reached in as early as 4–6 mo (Schmidt 2001), and life spans average 2 and 5 yr for females and males, respectively. Although this species shows a relatively seasonal breeding cycle (September–October) in their native range (Schmidt 2001), captive and introduced populations readily oviposit year round, with an average clutch size of ~40–50 eggs and a maximum of 91 (our unpublished results) to 97 eggs (Nečas 2004). Females place eggs in nests that they construct by digging into the soil. Eggs hatch at ~120–210 d (Nečas 2004), depending on the thermal environment of incubation with temperatures between 26°C and 30°C. In our laboratory, eggs are incubated at 26°C and hatch at ~200 d (see **Captive Care, Raising, and Breeding of the Veiled Chameleon (*Chamaeleo calypttratus*)** [Diaz et al. 2015]).

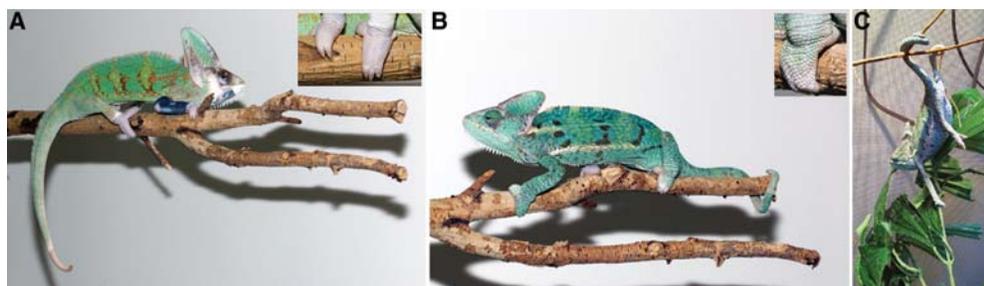


FIGURE 1. (A) Male veiled chameleons are larger in body size, have a significantly taller cranial casque, and have broader color combinations with bold vertical yellow bars. The tarsus of males also presents a posterior tubercle (“spur”), which is a posteromedial projection of the “hooked 5th metatarsal” (inset). (B) Female chameleons are smaller in size, have a shorter casque, and lack the tarsal tubercle (inset). This female is showing the robin-blue spotting coloration indicative of mating receptivity. (C) Chameleons have extremely derived wrist skeletons that allow for a “ball-and-socket” articulation for increased flexion and torsion, giving them incredible maneuverability in their complex arboreal habitat along with the use of their prehensile tail.

SOURCES AND HUSBANDRY

Veiled chameleons were first imported into the United States in 1990, with the first captive matings occurring later that year and the first clutch hatching in 1991 (Tremper 1995) at the San Diego Zoo. *Chamaeleo calyptratus* have since become very common with little to no additional importation (Carpenter et al. 2004). Although obtaining specimens may be as easy as a short drive or online order away, we strongly suggest purchasing only from specialized breeders (e.g., FL Chams or LLL Reptile). Although most chameleons in captivity appear to retain their “wild-type” (or “typical”) characteristics, new strains have become available such as “translucent,” which has a defect in pigment formation because of a codominant trait (CV Anderson, personal observation) (males and females of Fig. 1). In our accompanying protocol, we describe how to establish and maintain a colony of veiled chameleons (see *Captive Care, Raising, and Breeding of the Veiled Chameleon (Chamaeleo calyptratus)* [Diaz et al. 2015]).

RELATED SPECIES

Taxa closely related to *C. calyptratus* (such as the Flap-necked *C. dilepis*, Senegal, *C. senegalensis*, and the Common Chameleon, *C. chamaeleon*) are not as commonly bred in captivity and most are collected from the wild. Other species of chameleons may be found in the pet trade, but few, such as the Jackson’s (*Trioceros jacksonii*) and Panther (*Furcifer pardalis*) Chameleons are bred in captivity with regularity. Chameleons show a very broad range of life history modes, including oviparity and viviparity. Viviparous (“live bearing”) species require sacrificing gravid females to obtain embryos. We and others (Andrews 2004; Andrews and Karsten 2010) have noted that there is considerable variation in the stage of morphogenesis at the time of egg deposition and collection in oviparous species, a variable more prevalent in high clutch number species whose origin may be due to eggs further down the oviduct also having had more time to progress through embryogenesis.

USES OF THE VEILED CHAMELEON MODEL SYSTEM

Chamaeleo calyptratus has served as a model system for studying locomotion (Herrel et al. 2013; Fischer et al. 2009; Spinner et al. 2013; Khannoon et al. 2013), coloration and communication (Ballen et al. 2014; Ligon and McGraw 2013; Ligon 2014), captive reproduction (Kummrow et al. 2010a,b; Hoby et al. 2010, 2011; Haxhiu et al. 2014), feeding mechanics (Anderson and Deban 2010, 2012; Herrel et al. 2014), and various aspects of their morphology, morphogenesis, and development (Diaz 2012). These studies, and those involving other species of chameleon, have recently been summarized in a seminal volume (Tolley and Herrel 2014), which highlights the comparative morphology and diversity seen across this family. With over 25 yr of captive breeding experience for *C. calyptratus*, this spectacular species can be easily reared in the laboratory environment (see de Vosjoli and Ferguson [1995] and *Captive Care, Raising, and Breeding of the Veiled Chameleon (Chamaeleo calyptratus)* [Diaz et al. 2015]) for broadly exploring functional developmental evolutionary questions encompassing cellular, molecular, and genetic data within the comparative framework of our knowledge of other amniotic models such as the chick (Bronner-Fraser 2011) and the mouse (Behringer et al. 2014). To date, few developmental studies have been undertaken in chameleons, with prior studies focusing primarily on the formation of extraembryonic membranes during early embryogenesis (Pasteels 1953, 1957; Peter 1934, 1935), early stages of gastrulation (reviewed in Gilland and Burke 2004), and embryogenesis (Blanc 1974). However, interest in chameleon development has recently been rekindled by the suggestion that *C. calyptratus* and *C. chamaeleon* undergo an extended period of embryonic diapause (Andrews 2007, 2008; Andrews et al. 2008; Andrews and Donoghue 2004). Definitive demonstration of this phenomenon in chameleons still requires rigorous testing, but has the potential

to provide valuable insight into cell-cycle dynamics and the comparative development and evolution of amniotes. In contrast to reptiles in general, chameleon embryos are easily obtainable from early pregastrulation and preneurulation stages through hatching, which provides a phylogenetically intermediate model within amniota through which we can compare morphogenesis of the terrestrial reptilian body plan of lizards with murine and the highly derived avian reptile body plan. Chameleons can therefore serve as a unique model system for studying various events leading to the origin of amniotes. *Chamaeleo calypttratus* also provides an avenue for studying the cellular, genetic, and regulatory networks governing several derived features of chameleons, such as the split autopodia, and the modification of conserved features of vertebrates such as the cranium, tongue, tail, lungs, and eyes (Stower et al. 2015).

Interestingly, chameleons have highly modified wrist elements that allow them to perform complex flexion and rotation of the manus and pes in their arboreal environment (Fig. 1C). Evolution of their distal limb skeletons is evident in the form of highly variable and modified mesopodial (wrist) skeletal elements (number, size, and stage of skeletogenesis) in this clade, which may provide insights into the “black-box” of how carpals and tarsals developed and evolved in tetrapods. The development and evolution of these anatomical elements have been the focus of very few developmental genetic studies.

While the current model species for studying squamates is the Green Anole (*Anolis carolinensis*), which has recently been fully sequenced (Alföldi et al. 2011), the use of this species for studying early embryonic development is limited and hampered by the relatively late developmental stage of embryos at the time of egg laying. The necessity to kill adult females to obtain prelimb bud stage embryos has constrained detailed analyses of morphogenesis and patterning of the squamate body plan. The veiled chameleon overcomes this limitation with the added benefit of strength in numbers. While *Anolis* are quite prolific in the laboratory (Sanger et al. 2008; Sanger 2012), producing an egg every 1–2 wk, female *C. calypttratus* produce a significantly larger number of eggs for study, ovipositing 50–90 eggs every 3–4 mo. With the use of comparatively few females and staggered breeding, it is possible to maintain a collection of incubating eggs covering all stages of development throughout the year. In our experience, a colony of eight females and four males provided almost 1500 eggs during a single year.

Although a transcriptome for *C. chamaeleo* has been produced (Bar Yaacov et al. 2012; Bar-Yaacov et al. 2013) there are currently no sequenced and annotated genomic resources for *C. calypttratus*. Genetic tools such as degenerate primers can be developed through aligning sequences in GenBank (Benson et al. 2013) of *Mus musculus*, *Homo sapiens*, *Gallus gallus*, *Anolis carolinensis*, and *Python sebae*. However, it is important to recognize the divergence between these taxa and the veiled chameleon are rather large (an estimated 180 million years between *Anolis* and *Chamaeleo*, 296 between *Chamaeleo* and *Mus*, 276 between *Chamaeleo* and *Gallus*; Hedges et al. 2006).

A transcriptome for the veiled chameleon, was generated at the Stowers Institute for Medical Research (Kansas City, MO) using a pooled series of early gastrula through early limb bud stage embryos and is currently in the process of being annotated. This has facilitated the cloning of veiled chameleon-specific genes for in situ hybridization and other functional studies. The diploid (2N) karyotype of *C. calypttratus* is 24 in both males and females, with no heteromorphic sex chromosomes despite a genotypic mode of sex determination being hypothesized in this group based on captive breeding (Pokorná et al. 2011).

TECHNICAL APPROACHES

Standard protocols for whole-mount in situ hybridization with RNA probes for mRNA expression (Gomez et al. 2008) and whole-mount immunohistochemistry for protein activity (Ahnfelt-Rønne et al. 2007) have both proven successful in veiled chameleons. Unfortunately, unlike avian eggs, the soft “leathery” eggs of chameleons (as for other squamates, with the exception of sphaerodactylid, phyllodactylid, and gekkonid geckos) are not stable enough to support in ovo windowing and culture.

However, it is possible to ex ovo culture early and late gastrulae (while still in the developing amnion), as well as whole neurulation and early organogenesis stage embryos (enclosed within and out of the amniotic membrane). Furthermore, explants of organs, limbs and other body parts and tissues have been successfully culture on filter supports in appropriate media (Diaz et al. unpublished). Collectively these resources and techniques establish the veiled chameleon as a model system not only for static analyses, but also for real time investigation of evolution and development, through gain- and loss-of-function studies, cell and tissue transplantation, time-lapse imaging of morphogenesis, and more.

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