The Biology of Chameleons

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Edited by KRYSTAL A. TOLLEY and ANTHONY HERREL

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FOREWORD

In putting together this book, we stand on the shoulders of others. The extensive bibliography presented here spans centuries, and the resulting body of literature is based on the work of researchers who dedicated their minds to a deeper understanding of chameleons. We have taken pieces of this great puzzle and have made a start at constructing the whole picture, but there are many glaring gaps. In some respects, it seems there are too many pieces missing and the emerging picture is only a hazy nebula of unclear, scattered, and fragmented bits. But the excitement that comes with the challenge of scientific thought, of asking the questions "why" and "how," is what compels us to keep looking for the missing pieces. For chameleons, the many missing pieces are the why and how of their remarkable evolutionary radiation, and we must keep questioning, even if we never complete the puzzle.

Although this book is built on the works of others, putting together this volume has been a group effort of the authors, all of whom enthusiastically came to the party. Each author brought their own expertise, and together we have made something more than any one of us could have done alone. It has been an extraordinary experience working with this team. As editors, we expected to be herding cats, but on the contrary, the process was surprisingly smooth. Of course, each of the chapters was reviewed by our peers, all of whom invariably provided positive and constructive criticism on the content. It is surprising how many things we missed initially, and we owe much to our colleagues for taking time to review and comment on these chapters: Salvidor Bailon, Bill Branch, Angus Carpenter, Jack Conrad, Frank Glaw, Rob James, Charles Klaver, Lance McBrayer, John Poynton, Phil Stark, Andrew Turner, James Vonesh, Bieke Vanhooydonck, and Martin Whiting. We are grateful to several friends and colleagues who permitted complimentary use of their photos, including Bill Branch, Marius Burger, Tania Fouche, Adnan Moussalli, Devi Stuart-Fox, and Michele Menegon. We also owe much to Chuck Crumly for eagerly taking on the initial responsibility of producing this book, as well as the National Research Foundation of South Africa and Centre National de la Recherche Scientifique and Groupement de Recherche

International for providing the funds that allowed the editors of this volume to collaborate and to aspire. The follow-up production team at UC Press (Lynn Meinhardt, Ruth Weinberg, Kate Hoffman, Blake Edgar, and Deepti Agarwal) were excellent in providing advice and assistance throughout the process. In all, this has been a brilliant experience, despite initial reservations in taking on such a big project. It's clear that the ease of putting this together was due to an outstanding team of authors, all of whom are passionate about their subject and have not forgotten how to ask "why."

ONE

Biology of the Chameleons

An Introduction

KRYSTAL A. TOLLEY and ANTHONY HERREL

Chameleons so easily capture the imagination, and have done so for centuries. In scientific writings, they first appear with Aristotle (350 BC), and although they were recognized as being similar to lizards in some ways, he also likened them to fish, baboons, and crocodiles. Since then, they have since been the subject of strange myths, amusing tales, and nature documentaries and have even taken the form of popular cartoon characters. But what makes them so fascinating that they have infiltrated the common psyche more than other reptiles? Indeed, they are set apart to such a degree that many people are unaware they are even lizards at all. They are simply, "chameleons." In this book, we draw together and review the body of literature that covers chameleons over several centuries by exploring and summarizing our knowledge on this intriguing group of lizards.

Chameleons are highly specialized animals characterized by a suite of morphological, physiological and functional adaptations. Much of what makes chameleons immediately identifiable as such are these morphological specializations. Among these, the laterally compressed body, the prehensile feet and tail, the independently moveable eyes (Figs. 1.1 and 1.2 in color insert), and a long tongue capable of being projected from the mouth are the most striking. As detailed in Chapters 2 (Chameleon Anatomy) and 3 (Chameleon Physiology), many of these features are intimately related to the unique behavior and lifestyle of chameleons as highly specialized arboreal predators. The sensory system of chameleons, for example, is highly tuned toward visual stimuli, as chameleons rely on visual signals in both a social and a feeding-related context. As part of the specialization of the visual system, chameleons have a negatively powered lens and use accommodation cues to judge distance, features unique among lizards (Fig. 1.3 in color insert). Because of their visual specialization, the auditory system is less developed and shows lower sensitivity as compared with that of other lizards. Little is known about the olfactory (smell), vomerolfactory, and gustatory (taste) systems in chameleons, but all appear reduced as compared with other lizards.

Associated with the predominantly arboreal habitat of chameleons comes a number of functional specializations such as their prehensile feet and tails. Chapter 4, Function and Adaptation of Chameleons, examines how these specializations allow chameleons to effectively explore the three-dimensional (mostly) arboreal habitat. However, as a consequence of their specializations, chameleons are the slowest of all lizards, with sprint speeds about 10 times slower than those of other lizards. The slow locomotion of chameleons is a result of the contractile capacities of the locomotor muscles, changes in limb posture that allows them to move effectively on narrow substrates, and a lower overall muscle mass. In contrast to the limb muscles, the tongue muscles of chameleons are anything but slow; they produce high forces for their cross-sectional area. These unusually fast, ballistic tongues permit them to capture a wide variety of prey. The supercontractile tongue-retractor muscles are unique among vertebrates and allow them to reel in even large vertebrate prey.

Chameleons are found among widely varying thermal regimes and climatic conditions, including hot and dry desert habitats, tropical rainforests, Mediterranean climates, and high-altitude environments. Similar to other lizards, however, chameleons carefully regulate body temperatures using behavioral thermoregulation and color change to maintain temperatures close to their preferred temperature of around 30 to 32°C. The preferred temperatures of chameleons are low as compared with those of most other diurnal lizards. The temperature invariant function of the ballistic tongue protraction and their low preferred temperatures may consequently have allowed chameleons to invade high mountain habitats rarely accessible to other lizards.

Ecologically, chameleons have taken control of the arboreal niche across Africa and Madagascar. No other reptile (aside from their avian cousins) dominates to such a degree. Walk through any montane forest in Africa or Madagascar with a spotlight at night, and you are sure to see a sleeping chameleon perched on a branch or twig. Although they are best known for their arboreal lifestyle, a number of species, indeed entire genera, are mainly terrestrial (Fig. 1.4 in color insert). While chameleons are primarily associated with forests, multiple species have capitalized on emerging habitats (grasslands and heathlands). In fact, in some places, they occupy the entire strata from ground to high canopy. Chapter 5, Ecology and Life History of Chameleons, summarizes the considerable body of studies on the interactions of chameleons with their environment. Here, we learn not only the more recognizable aspects of chameleon ecology, but are introduced to the lesser-known details. We are provided with an overview of their reproductive traits, which range from seasonal to year-round reproduction plus entire clades that are viviparous rather than oviparous. We find that although they are primarily insectivorous, their diet can be wide and may on occasion include their own kind. Even their foraging mode is thought to be exceptional among reptiles, being a combination of active foraging with sit-and-wait, termed "cruise foraging," which allows them to remain cryptic, while actively in pursuit of prey.

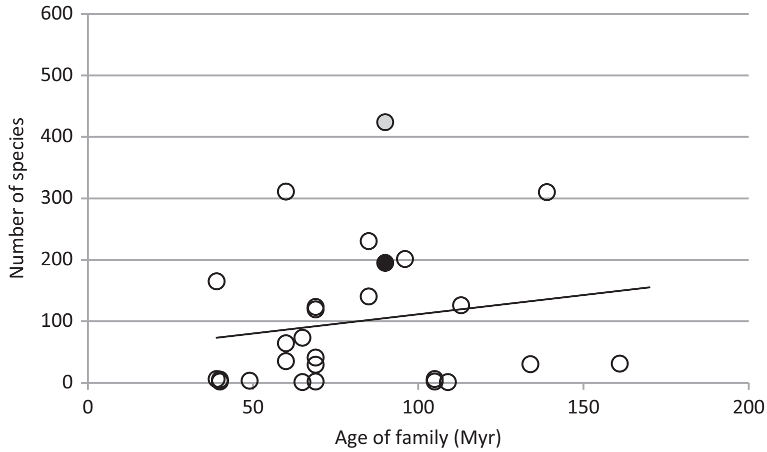

FIGURE 1.8. Age (millions of years) of most squamate families with number of species in that family. The Chamaeleonidae is shown as a black circle, and Agamidae as a gray circle. Scincidae, Gekkonidae, and Colubridae are not shown because of the large number of species in these families (1553, 917, and 1772, respectively). Based on data from Hedges and Vidal (2009) and Uetz (2012).

Despite their intensely cryptic lifestyle (Fig. 1.5 in color insert), chameleons have evolved some interesting behavioral traits. Indeed, chameleons are famous for their sometimes flamboyant ornamentation and their ability to change color. Chapter 6, Chameleon Behavior and Color Change, dispels the popular myths about chameleons and examines the how and why of their behavior. We are introduced to the physiological aspects of color change, and find that it is related to communication, camouflage, and thermoregulation (Fig. 1.6 in color insert). We also discover how ornaments are involved in sexual selection through display and aggression (Fig. 1.7 in color insert). Chameleon behavior is not limited to conspecific interactions, and includes some tricks for predator avoidance that go beyond crypsis, including free-falling from perches to avoid predation.

Moving from the individual level to the landscape level, chameleons have an interesting history and are an unusually diverse group of lizards. They are, in fact, a young clade of lizards, dating back only to the beginning of the Cenozoic, whereas most other lizard families are much older (Chapter 7, Evolution and Biogeography of Chameleons). Despite their young age, there are over 190 described species, and most experts agree that there are multiple species awaiting discovery and description (Chapter 8, Overview of the Systematics of the Chamaeleonidae). Actually, if the age of the clade is considered, the number of chameleon species is relatively high as compared with other many other squamate families (Fig. 1.8), which suggests a history of rapid lineage diversification. Chameleons are exceeded in this respect by their relatives, the Agamidae, but also Gekkonidae, Lacertidae, Scincidae, Colubrid snakes (Colubridae), and vipers (Viperidae). It appears that chameleon diversification

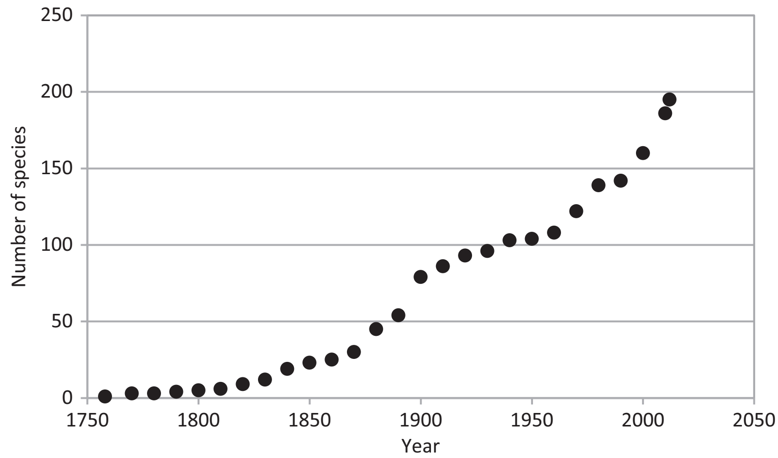

FIGURE 1.9. The cumulative number of chameleon species described, starting with the first description of *Chamaeleo chameleon* in 1758 by Linneaus.

is linked to their invasion of the arboreal habitat some 45 million years ago. Today, there are distinct centers of diversity, particularly in East Africa and Madagascar, that have elevated species richness and endemism. Although the fossil record is scarce, the clues provided by fossils that lead up to chameleons is rich, giving us insight to the early history of the group and ancestors. Chapter 9, Fossil History of Chameleons, takes us on a journey through time, beginning in the Cretaceous with the ancestors of chameleons, the priscagamids, and ends in the Holocene with fossils of extant species from Africa, Madagascar, Europe, and the Middle East.

Chapter 10, Chameleon Conservation, provides a comprehensive and up-to-date examination on the state of these lizards in our modern world. The conservation status and major threat categories are quantified and species are examined for their vulnerability. An alarming statistic that emerges, is that two thirds of chameleons already assessed by the International Union for Conservation of Nature (IUCN) are considered Threatened or Near Threatened, a figure that is much higher than that for other groups of reptiles. Of the tangible threats, habitat alteration appears to be the most prevalent, with a disproportionate impact on narrow-range endemics. Chameleons are also popular in the pet trade, and the more than 30 years of trade statistics have been summarized in this chapter. The majority of exported chameleons are harvested from wild populations, rather than through captive breeding programs, and the largest importer of chameleons is the United States, which is responsible for two thirds of the market.

The scientific literature available is surprisingly large and has filled this volume. Despite this, there is still much to learn about these intriguing animals. Even simple facts about their anatomy, physiology, and function remain unknown. Because of their cryptic nature, we know little of their daytime activities, and our impressions of their interactions with conspecifics and other animals are based on precious few studies. Aspects of their life history appear to be the most well known, yet for most species we have no understanding of their reproductive cycles, diets, home range sizes, and dispersal ability. Poorly explored forests in Africa and Madagascar reveal new species with every survey. The number of species described every year continues to rise (Fig. 1.9), and this is certainly not the end of a trend, given molecular phylogenies that show numerous undescribed lineages. There are huge gaps in the fossil record, particularly early in the history of this family, and new finds would certainly shed light on the morphology of early arboreal chameleon lineages. In exploring what we do know about chameleons, it seems we have succeeded in bringing to light the vast gap of what we do not know. But these are exciting times in the world of chameleons, and with the tools we have at our disposal today, it is clear that it will not take several more centuries to uncover many of these mysteries.

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