The Biology of Chameleons

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Edited by KRYSTAL A. TOLLEY and ANTHONY HERREL

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Cover illustration: *Trioceros johnstoni* from the Rwenzori Mountains, Uganda. Photo by Michele Menegon.

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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."

FOUR

Function and Adaptation of Chameleons

TIMOTHY E. HIGHAM and CHRISTOPHER V. ANDERSON

Lizards have often been noted for their ability to move and capture prey in complex three-dimensional habitats (Huey and Pianka, 1981; Higham et al., 2001; Vanhooydonck et al., 2002; Mattingly and Jayne, 2004; Russell and Johnson, 2007; Montuelle et al., 2008). Given this, it is not surprising that many lizards are specialized for a particular type of locomotion and/or feeding. Chameleons, however, exhibit specialized feeding *and* locomotor behaviors. Their locomotor system has garnered substantial attention, given their purported upright limb posture and ability to perform complex maneuvers within their habitat. Their feeding apparatus is equally elaborate; they have the ability to project the tongue a considerable distance in order to latch onto prey (Zoond, 1933; Wainwright et al., 1991; Wainwright and Bennett, 1992a,b; Herrel et al., 2000; Anderson and Deban, 2010). Despite their unique and somewhat flamboyant characteristics, it is surprising that we are far from uncovering the functional mechanisms underlying their unique behaviors. However, there has been a recent surge of research that is exposing some aspects of chameleon function in relation to both ecology and morphology.

Chameleons are a diverse group of lizards found in Africa, Madagascar, southern Europe, Asia Minor, India, Sri Lanka, the Seychelles and Comoro Islands of the Indian Ocean, and via introduction, areas of North America (Ferguson et al., 2004; Tolley and Burger, 2007; Tilbury, 2010; Chapter 7). They can be fairly small (*Rhampholeon, Rieppeleon,* and *Brookesia*) or quite large (*Calumma, Furcifer,* and *Trioceros*) and may inhabit a wide range of habitats, including fynbos, forest, sandy desert, and grass (Bickel and Losos, 2002; Hofer et al., 2003; Tolley et al., 2006; Herrel et al., 2011; Chapter 5). Although most are arboreal, some species live predominantly on the ground and others frequently move on the ground between clumps of arboreal substrate. The diet of chameleons consists primarily of insects, but it can include small vertebrates such as lizards, mammals, and birds. Given the incredible diversity within chameleons and their specialized behavior, they are an attractive group for studying the functional consequences of phenotypic diversity. The goals of this chapter are: (1) to integrate the current literature that exists for chameleon locomotion and feeding, and (2) to indicate areas for future studies of biomechanics and functional morphology of chameleons.

4.1 LOCOMOTION

Lizards exhibit many types of specialization for locomotion, such as adhesive systems for climbing (Irschick et al., 1996; Russell and Higham, 2009), toe fringes for enhanced traction in sandy environments (Carothers, 1986), and claws for gripping (Zani, 2000). Chameleons, in particular, are specialized for slow arboreal locomotion (Mivart, 1870; Peterson, 1973, 1984; Abu-Ghalyun et al., 1988; Abu-Ghalyun, 1990; Mutungi, 1992; Losos et al., 1993; Bickel and Losos, 2002; Higham and Jayne, 2004b; Tolley and Burger, 2007; Boistel et al., 2010; Fischer et al., 2010; Herrel et al., 2011). Given that chameleons often live in arboreal habitats, where perches are small, gripping tightly with their feet, hands, and tail is critical for maintaining stability. Effective and stable progression is vital because of the limited and narrow base of support (Fig. 4.1) (Peterson, 1973; Cartmill, 1985; Foster and Higham, 2012). This is increasingly important for larger chameleons given that larger animals tend to experience greater toppling moments when moving on a branch (Cartmill, 1985). Chameleons have solved this problem by having prehensile (also termed "zygodactylous" by some authors) hands and feet in which the metacarpals and metatarsals are grouped into two opposing bundles (Fig. 4.1) (Gasc, 1963; Gans, 1967; Peterson, 1984; Losos et al., 1993; Russell and Bauer, 2008). In the forelimb, the first three digits form one group (mesial) and the fourth and fifth form the second group (lateral). However, the hindfoot contains a different pattern. In this case, the first and second metatarsals are bundled, and the third, fourth, and fifth metatarsal form the opposing group (Rieppel, 1993). These opposing bundles, having skin fused together between digits, are effective for grasping, as they are able to exert an adduction force on a branch with a circular cross section. This adduction force essentially squeezes the branch and generates friction. In addition to increasing stability during regular locomotion, grasping onto thin branches in this fashion is well suited for maneuvers because it increases control of pitching and rolling motions (Cartmill, 1985). It is the integration of multiple specializations that permit the effective movement of chameleons. The tail of chameleons is prehensile and can act like a fifth limb, gripping perches and aiding in stability (Zippel et al., 1999; Boistel et al., 2010; Herrel et al., 2012). This, coupled with their specialized hands and feet, extremely mobile pectoral girdle, and laterally compressed body, is ideal for an animal that moves in an arboreal habitat.

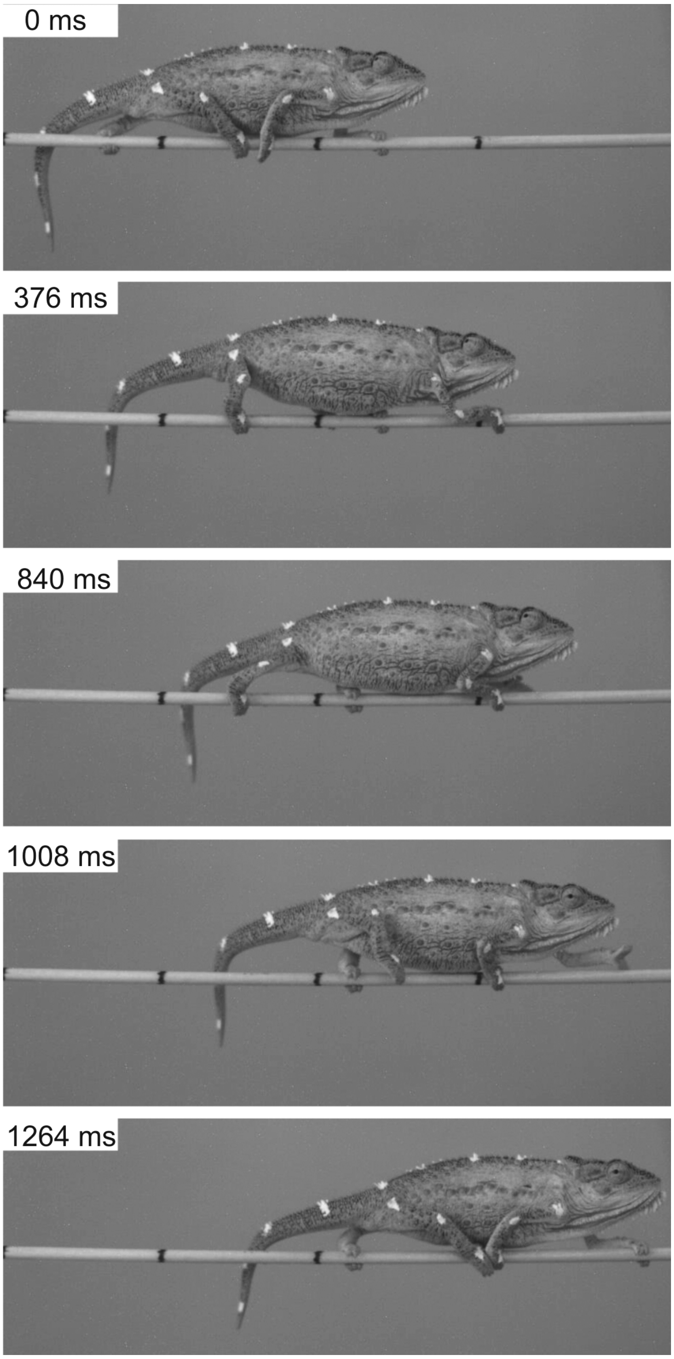

FIGURE 4.1. Lateral images of *Bradypodion occidentale* moving on a level, 3.2-mm-diameter wooden dowel at approximately 5 cm/sec. The black lines on the dowel are at 4-cm intervals. From top to bottom, the images indicate hindlimb footfall, midstance of the hindlimb, end stance of the hindlimb, midswing of the hindlimb, and the subsequent footfall of the hindlimb. Note the extreme forward reach of the hindlimb at footfall. These video stills are from unpublished data collected by Timothy Higham, John Measey, Krystal Tolley, and Anthony Herrel using a Photron APX RS camera operating at 250 Hz.

Limb Kinematics

Forelimb and hindlimb kinematics during locomotion in chameleons have been examined in several studies spanning over 30 years (Peterson, 1984; Higham and Jayne, 2004b; Fischer et al., 2010; Krause and Fischer, 2013). The techniques used to assess limb movements range from biplanar X-ray imaging, to regular video (25 frames per second), to high-speed video (250 frames per second). In all cases, the three-dimensional patterns of limb movement were determined.

Peterson (1984) conducted the first kinematic study of chameleons, although she focused solely on the forelimb. From this study and others, it is evident that *Chamaeleo* moves slowly relative to most other lizards and exhibits a slow trot-like walk. Peterson (1984) found that *Chamaeleo* (one species is now in the genus *Trioceros*) exhibited substantially less lateral undulation of the body as compared with a generalized, yet closely related, lizard species, *Agama*. Specifically, only 6% of the step was accounted for by undulation in *Chamaeleo,* as compared to 24% in *Agama*. One of the key observations in this study is the extreme pectoral girdle movement relative to the body wall. The displacement at the shoulder joint can increase the excursion arc by as much as 33 degrees to create an additional 28% of the step length (Peterson, 1984). This facilitates the long excursion arcs that are important for chameleons during arboreal acrobatic maneuvers (e.g., bridging gaps). Another benefit of substituting lateral body undulation with girdle excursion is that the center of mass displacement relative to the perch is reduced. This likely contributes to stability by minimizing toppling moments. As discussed below, the conclusions about overall chameleon locomotion in this study were based solely on the forelimb, and it turns out that the hindlimbs and pelvic girdle are not functioning like the anterior locomotor structures.

The three-dimensional movements of the hindlimbs during locomotion in chameleons was examined by Higham and Jayne (2004b). Again, this study examined *Chamaeleo,* which is currently the only genus for which kinematic data exist. In addition to the forward reach of the forelimb, which was studied by Peterson (1984), chameleons also appear to have extensive forward reach of their hindlimbs. Rather than stemming from excursion at their hip joint, hindlimb protraction appears to be increased by large amounts of femur protraction and knee extension (Figs 4.1 and 4.2a) (Higham and Jayne, 2004b). This increased reach, coupled with the knee flexion that is observed early in the stance phase (Fig. 4.2a), suggests that the hindlimb acts to pull the body forward early and then push the body forward later in stance. This is unlike the action in other terrestrial lizards, which exhibit minimal knee flexion early in stance. How are chameleons able to pull with their hindlimbs? The gripping feet secure the limb to the perch, facilitating the effective propulsion that arises from pulling the body forward. For a lizard that does not grasp (or adhere) to the substrate, knee flexion early in stance would tend to pull the foot away from the ground. Another key result from Higham and Jayne (2004b) is that pelvic rotation, unlike pectoral rotation, is rather large in chameleons as compared with terrestrial lizards. This conflicts with the results of Peterson (1984), who suggested that lateral undulation is not a major contributor to locomotion in chameleons.

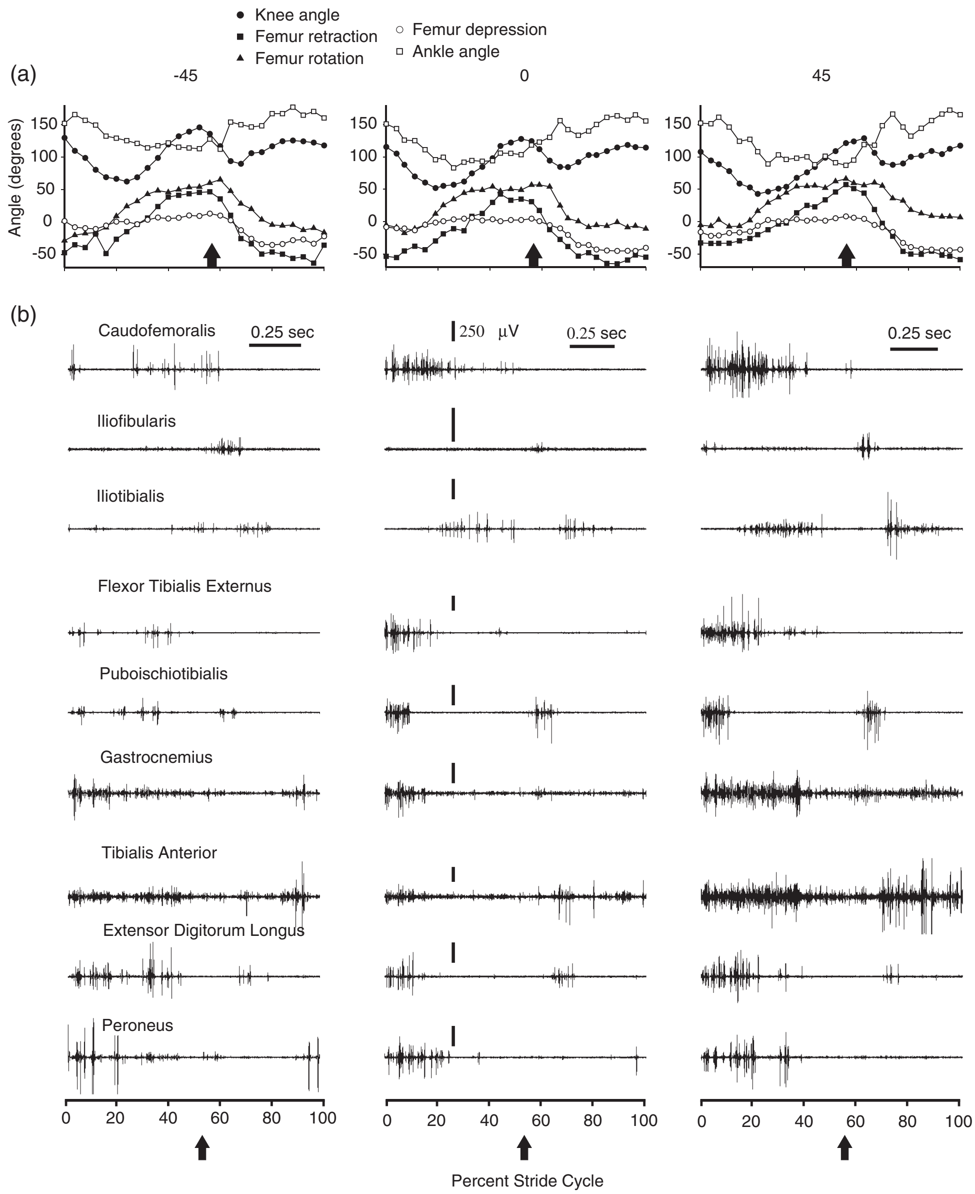

FIGURE 4.2. (a) Kinematics of the hindlimb; (b) Electromyograms versus time (as a percentage of stride cycle) for one stride from a single individual of *Chamaeleo calyptratus* on inclines of −45 degrees (left), 0 degrees (middle), and 45 degrees (right). The arrows indicate the end of stance, and footfall occurs at time 0%. The vertical bars indicate the voltage scales (250 µV), which are constant between all panels within a row. Originally published in Higham and Jayne (2004a).

Utilizing a motor-driven rope-mill (treadmill for arboreal animals) and X-ray motion analysis, Fischer and colleagues (2010) examined the kinematics of the whole body of chameleons (*Chamaeleo calyptratus*) during locomotion (see Fig. 4.3). They discovered that, unlike most lizards, chameleons exhibit a unique mode of axial undulation. Lateral bending of the vertebral column is limited to the lower spine. The anterior part of the spine remains fairly rigid, indicating that the spine does not contribute to pectoral translation but does contribute to pelvic translation (Fischer et al., 2010). This supports the conclusions of Higham and Jayne (2004b). Thus, lateral undulation is important for chameleons but is not driven by the entire spine, as is the case with other lizards. Pectoral girdle mobility compensates for the decreased anterior undulation, whereas pelvic girdle mobility is limited and posterior undulation is higher.

It is clear that understanding the three-dimensional movements of the body and limbs of chameleons is a key to linking their unique morphology and ecology with function. However, we must be circumspect when generalizing about all chameleons using the existing data. Chameleons are very diverse, yet almost all studies have focused on *Chamaeleo calyptratus* (e.g., Higham and Jayne, 2004a,b; Fischer et al., 2010). This is likely a result of their manageable size, ability to be kept in captivity, and availability in the pet trade. However, future work should explore the diversity within chameleons, and even between populations that live in diverse habitats (Hopkins and Tolley, 2011). A key group that could illuminate our understanding of chameleon locomotion is the Dwarf Chameleons from the genus *Bradypodion* (South Africa). The biogeography and phylogenetic relationships among Dwarf Chameleons have been the foci of recent studies (Tolley et al., 2004, 2006; Tolley and Burger, 2007). Thus, there is a wonderful opportunity to link morphology, biogeography, and function in a diverse group of chameleons.

Limb Posture: Are Chameleons Really Upright?

Most lizards exhibit a relatively sprawled posture, which involves limbs whose major movements are closer to a horizontally than vertically oriented plane (Rewcastle, 1981, 1983; Blob and Biewener, 1999; Russell and Bels, 2001). A hallmark of the sprawled posture is the contribution of lateral undulation to forward movement. Because undulation is in the same plane (horizontal) as the proximal segments of the limbs, lateral movement of the body will move the contact point of the limb. Given the relatively low contribution of lateral undulation to step length, as noted above, the general sense is that chameleons are relatively upright. There are a couple of other reasons that lead to the perception that chameleons employ a relatively upright posture. When chameleons are stationary on a branch, for example, they tend to hold their knees and elbows close to the body and therefore appear to be in a parasagittal plane. Second, chameleons are often observed moving on narrow perches that necessarily require their limbs to make contact more medially than those of other terrestrial lizards. In contrast, evidence suggests that chameleons do not exhibit an upright posture relative to other lizards. In a comparison of a terrestrial specialist and a terrestrial generalist, Higham and Jayne (2004b) found, by looking at locomotion on a flat surface, that

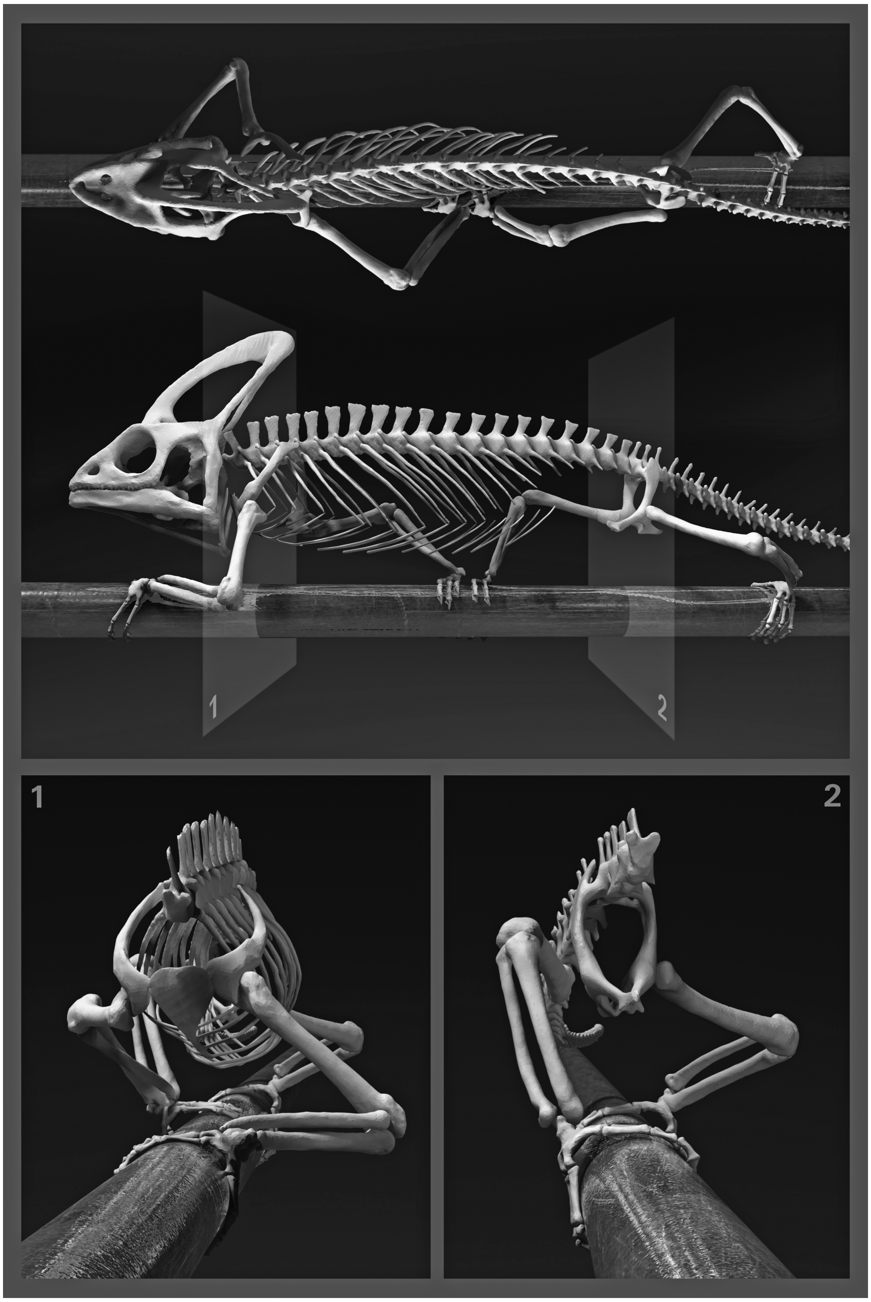

FIGURE 4.3. Dorsal (top) and lateral view (bottom) of an animated chameleon skeleton (X-ray Reconstruction of Moving Morphology, or XROMM) based on a biplanar cineradiographic record. The left forelimb and right hindlimb are in stance phase and the right forelimb and left hindlimb on the verge of lift off. The pictures at the bottom show details in transversal perspective at the height of the shoulder joint (1) and the hip joint (2). Note the high degree of abduction of the forelimb during stance phase and of the hindlimb during liftoff (left extremities). Forelimbs are in a parasagittal position during liftoff and hindlimbs during touchdown (right extremities). Prepared by J. Lauströer und A. Andikfar and reproduced (with permission from Elsevier, license 2892041208388) from Fischer et al. (2010).

maximum femur depression was greater in *Dipsosaurus dorsalis* (terrestrial) than *Chamaeleo calyptratus* (arboreal). Greater femur depression indicates a femur that is more aligned with the vertical plane, indicative of a more upright posture. Fischer et al. (2010) confirmed that maximum limb abduction is as high as in other, more terrestrial, lizards. A basic question that still lingers in comparative biomechanics is how to define posture. Vertebrates commonly move in a dynamic fashion, which means their limbs are moving into different positions throughout a stride. As noted by Fischer et al. (2010), chameleons exhibit parasagittal movements for at least part of the stride. Thus, perhaps the more upright posture that is often noted for chameleons is a result of transient parasagittalization (Fig. 4.3). Future work should aim to solidify a broadly applicable method for defining posture in lizards and use this to more extensively test whether chameleons are indeed more upright.

Limb Mechanics

A single study has examined three-dimensional substrate reaction forces during chameleon (*Chamaeleo calyptratus*) locomotion (Krause and Fischer, 2013). Both the forelimbs and hindlimbs were measured using a force-sensitive element mounted to a force plate. This, coupled, with two high-speed video cameras (500 Hz) facilitated a cohesive assessment of chameleon locomotor mechanics. On a level pole, with a diameter of 2 cm, the forelimbs and hindlimbs exhibit a peak vertical force at 74% and 27% of stance, respectively. Medially directed forces on a level perch are quite small and the magnitudes are comparable between the limbs. When moving uphill at 30 degrees and 60 degrees, the propulsive impulses from both the forelimbs and hindlimbs increase and the braking impulses almost disappear. The vertical impulse increase on the 30- and 60-degree inclines and on the −30-degree decline, but do not continue to decrease as the decline increases to −60 degrees (Krause and Fischer, 2013). Overall, it is clear that future work detailing the mechanical function of the forelimbs and hindlimbs will continue to reveal interesting functional ramifications of morphological and ecological diversity among chameleons.

Muscle Function

Given the strong differences in muscle anatomy and physiology in chameleons relative to other lizards (Abu-Ghalyun et al., 1988; Mutungi, 1992; Russell and Bauer, 2008; Chapter 2), it is commonly assumed that the function of the muscles during locomotion might also differ in relation to other, more generalized, terrestrial lizards. A single study has examined and muscle activation patterns of limb muscles during locomotion in chameleons (Fig. 4.2b) (Higham and Jayne, 2004a). In this study, the timing and magnitudes of electrical activity in nine hindlimb muscles were assessed using electromyographic (EMG) electrodes implanted directly into each muscle. Following surgery, adult veiled chameleons (*Chamaeleo calyptratus*) moved on perches of varying diameter and incline. Overall, changes in the characteristics of the EMG signals with habitat structure are driven primarily by amplitude differences rather than by changes in timing. For example, most propulsive muscles exhibit an increase in amplitude with an increase in incline, indicating an increase in recruitment and possibly force. This is important for moving up an incline given that muscle work (muscle force times muscle strain) must increase in order to increase the height of the animal. In addition, it appears that the function of the proximal muscles, as compared with the distal muscles, is altered to a greater extent when chameleons deal with changes in habitat structure.

As described above, a key aspect of chameleon locomotion that sets it apart from that of other lizards is the ability to pull the body forward with the hindlimbs during the first portion of the stance phase of the stride (Higham and Jayne, 2004a,b). Thus, it is possible that muscles that flex the knee will increase in activity when greater propulsion is required and might be enlarged relative to those of other lizards. Indeed, the amplitude of activity of the M. flexor tibialis externus and the M. puboischiotibialis (see Chapter 2) increases substantially while moving uphill as compared with move on level ground, and the peak amplitude occurs immediately after footfall at the beginning of stance (Fig. 4.2b) (Higham and Jayne, 2004a). Elucidating the underlying physiological mechanisms of chameleon locomotion is critical for understanding the evolution of this unique mode of movement. However, available data are currently limited to the hindlimb in a single species. Future work should examine forelimb muscle activation patterns and mechanics in relation to kinematics. Based on the morphological differences in the forelimb musculature of chameleons as compared with other lizards (Peterson, 1973), it is likely that muscle activity patterns also differ considerably. In addition, muscle activation patterns and mechanics in relation to morphological and ecological diversity within chameleons would reveal how chameleons move in different ways.

Tail Use

Prehensile tails are those that are involved in grasping or clinging, and they can often support the weight of the animal. Prehensile tails are found in a wide variety of vertebrates, including mammals (especially New World monkeys), reptiles (lizards and snakes), amphibians (some salamanders and caecilians) and fishes (syngnathids) (Hurle et al., 1987; Hale, 1996; Bergeson, 1998; Meldrum, 1998; Garber and Rehg, 1999; Zippel et al., 1999; Spickler et al., 2006). Despite the common occurrence of prehensile tails in lizards, there is a paucity of studies examining tail function in relation to locomotion. Tail morphology can be significantly different between chameleons, and even between populations of a single species (Herrel et al., 2011; Hopkins and Tolley, 2011).

A study by Hopkins and Tolley (2011) examined the morphological differences between populations of the Cape Dwarf Chameleon (*Bradypodion pumilum*) that occupy habitats that differ considerably in structure. One morph lives in relatively closed (forested) vegetation, whereas the other morph lives in more open (fynbos) vegetation in South Africa. The former is larger and more colorful than the latter. One of the main differences between the two morphs was tail length, which was longer in the closed-habitat morph. Longer tails could enhance locomotion through the canopy of a closed habitat, whereas longer limbs (not tail) might enhance locomotion in an open habitat.

Tails are often shorter in more terrestrial species of chameleons, including Malagasy Dwarf Chameleons from the genus *Brookesia* (Boistel et al., 2010). Although these species have prehensile feet for grasping, they often ambulate over broad surfaces. Under these circumstances, the distal portion of the tail is used to stabilize the body by making contact with the substrate. Morphologically, *Brookesia* appear to have fewer vertebrae and the mobile regions are restricted to the distal portion (Boistel et al., 2010). Thus, even chameleons that are not arboreal can use their tails for enhancing stability, although stability in a terrestrial habitat is achieved in different ways.

Ecology and Locomotion

Although the impact of morphology on performance is often examined in lizards (Bonine and Garland, 1999), habitat structure can dictate both performance and morphology in diverse groups (Garland and Losos, 1994; Irschick and Losos, 1998; Melville and Swain, 2000; Goodman et al., 2008; Higham and Russell, 2010). However, linking habitat use with a predictable suite of morphological characteristics can sometimes be challenging or may not yield differences (Vanhooydonck and Van Damme, 1999). For groups of lizards that contain both terrestrial and arboreal species, there can be a trade-off between climbing performance (on relatively narrow perches) and sprinting speed (on a level surface) because of the conflicting demands of these behaviors (Losos and Sinervo, 1989; Sinervo and Losos, 1991). However, a key question is whether there is a trade-off between climbing and locomotor speed in chameleons. For two species of chameleons from Kenya (*Chamaeleo dilepis* and *Trioceros jacksonii*), this seems to be the case (Losos et al., 1993). In this study, clinging ability, measured by pulling each chameleon along a dowel attached to a spring scale, decreased for both species as the diameter was increased from 2 mm to 11 mm. Conversely, sprinting performance steadily increased as the diameter was increased from 1.5 mm to a flat surface (Losos et al., 1993). Although clinging ability was used as a proxy for climbing ability, it is still unclear whether there is a direct relationship between these two. However, it is assumed that the ability to grasp a perch will likely be positively correlated with climbing ability given that locomotor stability will increase with increasing grasping ability (Cartmill, 1985).

4.2 FEEDING

Historical Perspectives

As one of the more extraordinary features of chameleon biology, the way chameleons feed has been the subject of scientific attention for centuries. Hypothesized mechanisms of tongue projection have included pneumatic action, tumescence, and muscle action. Despite the long history of scientific attention, however, we are still gaining insight into this highly specialized system today.

Some of the first hypothesized mechanisms of tongue projection in chameleons involve pneumatic extension of the tongue. In 1676, Claude Perrault proposed that an inflow of air from the lungs into the hollows of the tongue caused the extension of the tongue, while its retraction was caused by withdrawal of that air (Houston, 1828; Gnanamuthu, 1930). This view was similarly held by A.M.C. Duméril in 1836 (Gnanamuthu, 1930; Altevogt and Altevogt, 1954; Bell, 1989), while Antonio Vallisneri in 1715 and Mauro Rusconi in 1844 proposed that a cecum, or bladder of the trachea would inflate and thrust the tongue forward (Gnanamuthu, 1930). Subsequent research, however, revealed a lack of connection between the lungs and the tongue (Duvernoy, 1836) and suggests that a tracheal cecum would not be able to project the tongue the observed distances (Gnanamuthu, 1930).

A second proposed mechanism of tongue projection involves tumescence and vascular erection of the tongue. In addition to pneumatic action, Perrault suggested that inflow of blood into the hollows of the tongue, and the resultant tumescence, could serve as an alternative mechanism for tongue projection (Gnanamuthu, 1930). Houston (1828) suggested a similar mechanism, whereby blood flows into a vast vascular network within the tongue, causing tumescence and projection in a manner similar to erectile organs. It has been pointed out, however, that such a mechanism would cause thickening rather than thinning of the tongue as it extends and that it occurs too slowly to explain the rapid projection (Mayer, 1835; Gnanamuthu, 1930).

As early as 1805, however, Cuvier proposed that muscle action was a possible mechanism for tongue projection, but the nature of the suggested muscle action has varied considerably. Among some of these theories, Mayer (1835) proposed a muscular hydrostat model in which contraction of circular fibers in the tongue would cause the tongue to become thinner and longer, thus projecting the tongue out of the mouth. Duvernoy (1836), on the other hand, proposed that rapid protrusion of the hyolingual apparatus from the mouth would cause the tongue to be launched as the tongue skeleton suddenly stopped. A similar theory was also proposed by Dewevre (1895), who indicated that the entoglossal process would act like a billiard cue on the tongue as it was rapidly protruded forward. Finally, work by Brücke (1852a) suggested that the radial fibers of the M. accelerator linguae contracting around the tapered portion of the entoglossal process would push the tongue forward.

With these and subsequent studies, our knowledge of the morphology and mechanism of tongue projection has improved greatly. Despite all this interest in chameleon feeding, however, there are still unanswered questions about the exact mechanism of tongue projection and retraction in chameleons.

Functional Specializations

Given their proclivity to life in an arboreal setting, and on an often precarious substrate, it seems likely that ballistic tongue projection in chameleons may have evolved as a means to minimize lunge and chase during prey capture (Schwenk, 2000). Such a specialized feeding method, however, clearly necessitates a number of functional and anatomical adaptations. While the anatomical conditions of chameleons have been reviewed (see Chapter 2), their functional consequences are important to the mechanics and behavior of chameleons' feeding.

The tongue in nonchameleon iguanians, for instance, is unable to protrude far out of the mouth because the base is tightly adhered to the basihyal (Schwenk, 2000). In chameleons, however, the base of the tongue is free from the basihyal and overall is attached to the hyobranchial apparatus only at the origin of the M. hyoglossus (Schwenk, 2000; Herrel et al., 2001b). This frees the tongue to protrude greater distances.

In order to protrude the tongue greater distances, however, the length of the tongue itself must increase as well. In chameleons, the M. hyoglossus has become greatly elongated to cover the span of observed projection distances (Schwenk, 2000). In order to pack this lengthy muscle within the buccal cavity and onto the base of the hyobranchial apparatus when the tongue is retracted, the M. hyoglossus is pleated at rest and is comprised of supercontracting muscle fibers with perforated Z discs (Rice, 1973; Schwenk, 2000; Herrel et al., 2001a,b, 2002). These supercontracting muscle fibers allow the tongue to lengthen up to 600% of its resting length and exert high force during contraction across a broad range of sarcomere lengths (Herrel et al., 2001a, 2002).

The development of a rapid projectile mechanism itself is also important to reduce the opportunity for prey to evade capture while the tongue is traveling increased distances from the mouth to the prey. This rapid mechanism is accomplished by the combined specialization of aspects of the tongue skeleton, tongue muscles, and collagenous elements. The M. accelerator linguae of chameleons is formed by the M. verticalis linguae, which has hypertrophied and become modified to encircle the lingual process of the tongue skeleton (Schwenk and Bell, 1988; Wainwright and Bennett, 1992b; Meyers and Nishikawa, 2000; Schwenk, 2000). Rather than being tapered along its entire length, the lingual process of the tongue skeleton, called the "entoglossal process" in chameleons, has become more robust and parallel sided along most of its length, except for a tapered tip (Wainwright and Bennett, 1992b; Schwenk, 2000; Herrel et al., 2009). Finally, the space between the entoglossal process, and the M. accelerator linguae and M. hyoglossus contains a layer of dense connective tissue (Gnanamuthu, 1930; Zoond, 1933; Gans, 1967; Bell, 1989; Herrel et al., 2001b; de Groot and van Leeuwen, 2004) and a viscous lubricating fluid similar histochemically to synovial fluid (Bell, 1989; Schwenk, 2000). This connective-tissue layer is comprised of a nested series of collagenous intralingual sheaths with the anterior portion of the sheaths containing helical collagen fibers, which can store and release energy (de Groot and van Leeuwen, 2004). These specializations allow the tongue muscle to load elastic elements of the tongue without projecting out of the mouth before the elastic elements are completely loaded.

Feeding Performance

Chameleons are able to project their tongues relatively long distances at extremely high performance. Published estimates of the maximum length chameleons are able to project their tongues vary but have tended to indicate projection distances from one to two times the snout–vent length of the animal (Zoond, 1933; Gans, 1967; Altevogt, 1977; Schwenk and Bell, 1988; Bell, 1990; So et al., 1992; Wainwright and Bennett, 1992a; Schwenk, 2000;

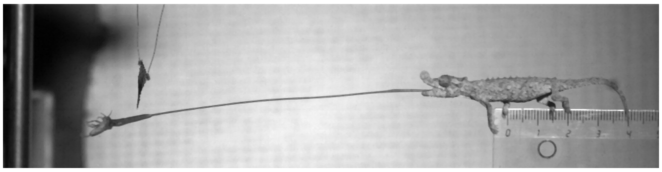

FIGURE 4.4. Lateral image of maximal tongue projection length during a feeding in *Rhampholeon spinosus*. The length of the snout vent in this specimen is 4.7 cm and it projects its tongue 10.4 cm from the mouth, for a projectile distance of 2.21 times the body length. From unpublished data collected by Christopher V. Anderson using a Photron Fastcam 1024 PCI camera operating at 3000 Hz.

Herrel et al., 2001b, 2002, 2009; de Groot and van Leeuwen, 2004; Müller and Kranenbarg, 2004). Recent research, however, has indicated that interspecifically, the length of the M. hyoglossus, and thus projectile distance, may scale with negative allometry relative to snout–vent length (Anderson et al., 2012). This would result in proportionately longer maximum tongue projection distances in smaller chameleon species than in larger species (Anderson et al., 2012). Because many studies have used larger chameleon species (Bell, 1990; Wainwright et al., 1991; So et al., 1992; Wainwright and Bennett, 1992a,b; de Groot and van Leeuwen, 2004; Herrel et al., 2009), the potential projectile distance of some smaller species may not yet have been recognized. For instance, *Rhampholeon spinosus,* a species smaller than those used in most studies, has been observed projecting its tongue 2.21 times its snout–vent length (Fig. 4.4).

The performance of the tongue as it is projected from the mouth is similarly impressive. While muscle alone is known to produce peak mass-specific power outputs of only 1121 W kg^{-1} (Askew and Marsh, 2001), chameleons project their tongues with peak mass-specific power outputs that more than double this value, thus indicating that tongue projection is not powered by muscle activity alone, but also by elastic recoil (de Groot and van Leeuwen, 2004). Incorporation of an elastic recoil mechanism in tongue projection imparts spectacular performance with mass-specific power outputs in chameleons recorded up to 3168 W kg^{-1} (de Groot and van Leeuwen, 2004), peak accelerations of up to 486 m sec^{-2} (Wainwright et al., 1991), or 50 *g* (50 times the acceleration due to gravity), and peak velocities of up to 5.8 m sec^{-1} (Wainwright et al., 1991). These performance parameters tend to be positively correlated with the projection distance within an individual (Bell, 1990; Wainwright et al., 1991; Anderson and Deban, 2010), indicating that as an individual projects its tongue longer distances, the performance tends to increase. Further, while velocity is expected to be size-independent (Hill, 1950), acceleration and power output are negatively correlated with size so smaller individuals would be expected to produce higher accelerations and power outputs than larger individuals (Hill, 1950; Herrel et al., 2009; Anderson et al., 2012). As discussed previously, since most studies use larger species, potential peak acceleration and peak mass-specific power output values attained by chameleons may be underestimated in the literature. Kinematic analysis of *Rieppeleon brevicaudatus,* for instance, has shown peak acceleration values of up to 1642 m sec^{-2}, or 170 *g,* and peak mass-specific power output values up to 11,392 W kg^{-1} (C.V. Anderson, unpublished results).

Prey Capture Kinematics

Previous studies on the kinematics of chameleon feeding have identified five phases of prey capture: (1) fixation, (2) tongue protrusion, (3) tongue projection, (4) tongue retraction, and (5) hyobranchial retraction (Fig. 4.5) (Altevogt and Altevogt, 1954; Schuster, 1984; Bell, 1990; Wainwright et al., 1991; Schwenk, 2000). These phases, however, do not correspond with standard gape-cycle phases (Fig. 4.5) (Bramble and Wake, 1985) and are not all distinct (Wainwright and Bennett, 1992a; Schwenk, 2000). That said, despite having a highly specialized hyolingual apparatus, with the addition of the projectile phase in the feeding sequence, and a prolonged retraction phase, the kinematics of feeding in chameleons is otherwise relatively similar to that of generalized iguanians (Bramble and Wake, 1985; Schwenk and Bell, 1988; Schwenk and Throckmorton, 1989; Bell, 1990; Wainwright et al., 1991; So et al., 1992; Schwenk, 2000).

Prior to the onset of mouth opening or movement of the hyobranchial apparatus, the chameleon must orient and prepare for feeding movements during the fixation phase of prey capture (Fig. 4.5). During this phase, the chameleon turns toward the prey, reduces the distance between them and rotates both eye turrets forward, focusing on the prey (Bell, 1990; Schwenk, 2000). Once oriented toward the prey, the chameleon braces the head and body to be able to withstand the forces imparted during aiming, tongue projection, and tongue retraction (Schwenk, 2000).

Tongue protrusion occurs during the slow open I (SO I) and slow open II (SO II) phases of the gape cycle (Fig. 4.5) (Bramble and Wake, 1985; Bell, 1990; Wainwright et al., 1991; Schwenk, 2000). During the SO I phase, the gape of the jaws slowly increases and the anterior portion of the tongue is slowly protruded through the forward margin of the mouth via hyoid protraction (Bell, 1990; Schwenk, 2000). Hyoid protraction and tongue protrusion continues into SO II and may cease in a plateau of movement where the tongue is held in a protracted position prior to projection (Bell, 1990; Schwenk, 2000). Also during the SO II phase, the folded membrana glandulosa of the tongue pad is evaginated, exposing the glandular inner surface on the tongue (Altevogt and Altevogt, 1954; Altevogt, 1977; Bell, 1990; Herrel et al., 2000; Schwenk, 2000).

Toward the end of SO II, tongue projection and tongue–prey contact occurs (Fig. 4.5). At the onset of tongue projection, the hyoid experiences a short yet rapid forward thrust (Wainwright et al., 1991; Wainwright and Bennett, 1992a; Meyers and Nishikawa, 2000; Herrel et al., 2001b; de Groot and van Leeuwen, 2004). The tongue is then projected rapidly from the mouth, and a slight decrease in gape is observed (Bell, 1990; Wainwright et al., 1991; Wainwright and Bennett, 1992a; Schwenk, 2000). This decrease in gape may be the result of the inertial reaction forces from the tongue projection or of changes in the muscle activity pattern (Schwenk, 2000), but it is unique to chameleons (Wainwright et al., 1991; Schwenk,

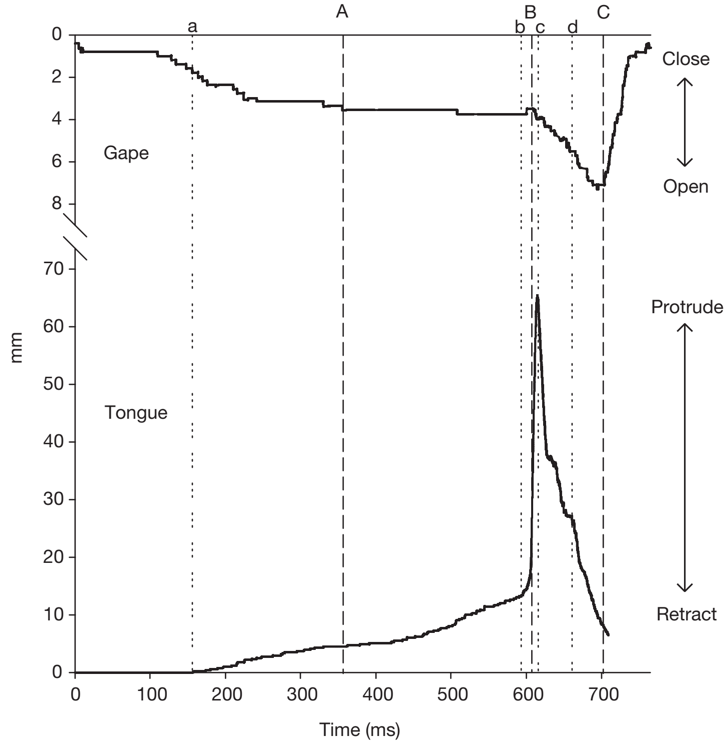

FIGURE 4.5. Kinematic profile of a feeding sequence in *Rieppeleon kerstenii*. Gape width is shown above on inverted y-axis with time correlated tongue protrusion distance below. Gape width and tongue protrusion distance are relative to the tip of the snout. Fine dashed lines and associated lower-case letters correspond with start points of chameleon feeding phases (*sensu* Altevogt and Altevogt, 1954; Schuster, 1984; Bell, 1990; Wainwright et al., 1991; Schwenk, 2000). The fixation phase occurs prior to the onset of the tongue protrusion phase (a), which continues until the onset of the tongue projection phase (b). The tongue retraction phase (c) begins at maximal tongue projection and continues beyond the onset of the hyobranchial retraction phase (d). Broad dashed lines and associated upper-case letters correspond with start points of standard gape cycle phases (*sensu* Bramble and Wake, 1985). The transition between slow open I and slow open II is somewhat ambiguous in some feedings and corresponds approximately with (A). The onset of the fast open phase begins following a sudden decrease in gape after the onset of tongue projection and corresponds with (B). The onset of the fast close phase begins following maximal gape and corresponds with (C). From unpublished data collected by Christopher V. Anderson using a Photron Fastcam 1024 PCI camera operating at 3000 Hz.

2000). The final portion of the SO II phase is the onset of prey prehension (Bell, 1990; Schwenk, 2000) and the beginning of tongue retraction.

After tongue retraction begins, the gape cycle progresses into the fast open (FO) phase with a rapid increase in the gape (Fig. 4.5) (Bell, 1990; Schwenk, 2000). Tongue retraction occurs throughout FO (Bell, 1990; Schwenk, 2000) but likely extends into the beginning of the fast close (FC) phase as well. Maximum gape and the transition between FO and FC coincides with hyobranchial retraction, which thus overlaps with tongue retraction and begins at the end of FO (Wainwright et al., 1991; So et al., 1992; Wainwright and Bennett, 1992a; Schwenk, 2000). Most of the hyobranchial retraction occurs during FC, however, when feeding on large prey, during which initial jaw closure results in a bite and a slow close-power stroke (SC-PS) phase is present, hyobranchial retraction can extend into SC-PS (Schwenk, 2000).

Mechanism of Hyobranchial Protrusion and Retraction

At rest, the tongue skeleton is positioned in the throat with the ceratobranchials and ceratohyals positioned nearly perpendicular to the entoglossal process (Herrel et al., 2001b). The tongue skeleton is protruded from the mouth by muscle action that pulls the hyoid horns backward and downward and brings the entoglossal process upward and forward as the gape of the mouth opens (Gnanamuthu, 1930; Bell, 1990; Herrel et al., 2009). As the lower jaw is depressed, the M. sternohyoideus profundus and M. mandibulohyoideus show a burst of activity corresponding with tongue protrusion (Wainwright and Bennett, 1992a). Activity of the M. sternohyoideus profundus draws the distal end of the ceratobranchials ventrocaudally toward the sternum, causing the ceratobranchials to rotate with respect to the basihyal until positioned nearly parallel with the entoglossal process (Gnanamuthu, 1930; Wainwright and Bennett, 1992a). Meanwhile, the activity of the M. mandibulohyoideus draws the distal end of the tongue apparatus forward through the opening gape of the mouth (Gnanamuthu, 1930; Zoond, 1933; Wainwright et al., 1991; Meyers and Nishikawa, 2000). This burst of activity from these muscles continues through the slow protraction phase and ends prior to tongue projection during the stationary phase of SO II (Wainwright and Bennett, 1992a).

During tongue retraction and at the end of FO, the M. sternohyoideus superficialis shows a burst of activity corresponding with hyobranchial retraction (Wainwright and Bennett, 1992a). Shortly after the onset of M. sternohyoideus superficialis activity, jaw adductor muscles become active as the FC begins (Wainwright and Bennett, 1992a). Activity of the M. sternohyoideus superficialis draws the basihyoid posteriorly toward the sternum, drawing the entoglossal process and tongue into the mouth (Gnanamuthu, 1930; Zoond, 1933; Wainwright and Bennett, 1992a) and presumably in the process, allowing the ceratobranchials to articulate back into their resting position.

Mechanism of Tongue Projection and Retraction

Following tongue protrusion, the posterior, circular portion of the M. accelerator linguae becomes active and remains active until immediately before tongue projection (Wainwright and Bennett, 1992a; Herrel et al., 2000; Anderson and Deban, 2012). This results in the posterior, circular portion of the M. accelerator linguae contracting around the parallel-sided posterior portion of the entoglossal process (Wainwright et al., 1992b; de Groot and van Leeuwen, 2004). During this contraction, the diameter of the M. accelerator linguae is reduced, causing elongation of the muscle along the length of the entoglossal process because that muscle must maintain a constant volume (Herrel et al., 2000; de Groot and van Leeuwen, 2004). Because the tongue is unable to elongate posteriorly because of the presence of the M. hyoglossus, this elongation occurs in the forward direction toward the tapered tip of the entoglossal process (de Groot and van Leeuwen, 2004). In the process of this elongation, it is hypothesized that the intralingual sheaths between the entoglossal process and the M. accelerator linguae are loaded with elastic potential energy by compression and shear stress from the contraction and elongation of the M. accelerator linguae (de Groot and van Leeuwen, 2004). This elongation stretches the intralingual sheaths and causes the angle of their helically wound collagen fibers to change, resulting in energy storage in a longitudinal plane (de Groot and van Leeuwen, 2004). Once tension has been built up in the muscle and intralingual sheaths, activity of the M. accelerator linguae ceases (Wainwright and Bennett, 1992a,b). Tension in the muscle and intralingual sheaths is maintained, however, for a considerable period of time, allowing the onset of projection to occur after the muscle activity has ceased but without a loss of force (Wainwright and Bennett, 1992b; Anderson and Deban, 2012).

The onset of tongue projection is triggered by a second, sudden contraction of the M. mandibulohyoideus, which produces a forward thrust of the entoglossal process (Wainwright et al., 1991; Wainwright and Bennett, 1992a; Meyers and Nishikawa, 2000; de Groot and van Leeuwen, 2004). This thrust is responsible for only a small portion of the total momentum of the tongue (de Groot and van Leeuwen, 2004), but activity of the M. mandibulohyoideus braces the hyobranchial apparatus and resists the posterior reaction force exerted by the tongue as it is projected off the entoglossal process (Meyers and Nishikawa, 2000; de Groot and van Leeuwen, 2004).

The forward thrust of the entoglossal process presumably causes the M. accelerator linguae and intralingual sheaths, still under high tension from the activity of the muscle itself, to slide forward over the tapered tip of the entoglossal process (Wainwright and Bennett, 1992b; de Groot and van Leeuwen, 2004). As the radial forces exerted by the M. accelerator linguae around the parallel sides of the entoglossal process are transferred into longitudinal forces at the tapered tip of the entoglossal process, the M. accelerator linguae rapidly pushes itself off the entoglossal process (Wainwright and Bennett, 1992a; de Groot and van Leeuwen, 2004). In the process, the elastic energy stored in the intralingual sheaths is also released to help power projection as the helically wound fibers are able to recoil to their resting fiber angles (de Groot and van Leeuwen, 2004). The sudden contraction of the M. mandibulohyoideus in conjunction with the largely parallel-sided entoglossal process with a tapered tip thus act as a passive trigger for the onset of tongue projection rather than having an antagonistic muscle that releases the tongue (Wainwright and Bennett, 1992a,b). Once the M. accelerator linguae has lost contact with the entoglossal process, the tongue travels forward toward the prey under its own momentum.

Immediately following the onset of tongue projection, the anterior, noncircular portion of the M. accelerator linguae becomes active and the posterior, circular portion of the M. accelerator linguae shows a second burst of activity (Wainwright and Bennett, 1992a). The activity of the M. accelerator linguae after tongue projection is presumably to provide a rigid structure for the M. "retractor pouch" of the tongue pad to act against during prey prehension (Wainwright and Bennett, 1992a). In addition, the M. hyoglossus becomes active between 10 ms before and 20 ms after the onset of tongue projection (Wainwright and Bennett, 1992a). The two portions of the M. accelerator linguae and the M. hyoglossus remain active throughout tongue and hyobranchial retraction (Wainwright and Bennett, 1992a). The early activity of the M. hyoglossus is presumably to decelerate the tongue as it approaches the prey and prevent overshoot (Bell, 1990; Wainwright and Bennett, 1992a). The M. hyoglossus remains active following prey contact and is responsible for retracting the tongue back onto the entoglossal process (Wainwright and Bennett, 1992a,b; Herrel et al., 2009; Anderson and Deban, 2012).

Mechanism of Prey Prehension

During rest the membrana glandulosa of the tongue pad is folded inward to create a lingual pocket or dimple (Altevogt and Altevogt, 1954; Altevogt, 1977; Schwenk, 1983; Bell, 1989; Bell, 1990; Herrel et al., 2000; Schwenk, 2000). During tongue protrusion, the membrane glandulosa is evaginated so that the center of the tongue pad, which is highly glandular and possesses numerous papillae, is at the apex of the tongue and becomes the contact zone for prey during feeding (Altevogt and Altevogt, 1954; Altevogt, 1977; Schwenk, 1983, 2000; Bell, 1990; Herrel et al., 2000). The tongue pad remains evaginated during tongue projection until just before contact with the prey, at which point the contact zone begins to invaginate, once again forming an upper and a lower lobe (Bell, 1990; Herrel et al., 2000; Schwenk, 2000). As the tongue contacts the prey, the center of the tongue pad is retracted at a higher rate than the upper or lower lobes, thus engulfing the prey item (Herrel et al., 2000). This invagination is caused by activity of the M. retractor pouch, which is active from just prior to prey contact through when the tongue is fully retracted into the mouth (Herrel et al., 2000, 2001b).

A combination of interactions is responsible for grasping the prey during tongue retraction. The first are surface phenomena, such as wet adhesion and interlocking, between the prey and the tongue, which are provided by serous and mucous secretions and a high concentration of filamentous papillae and plumose cells on the tongue pad (Schwenk, 1983, 2000; Bell, 1989; Herrel et al., 2000). The force of these adhesive properties is increased by the shape change of the tongue pad as it engulfs the prey, thus increasing the contact area with the prey and possibly reorienting the tongue's papillae (Herrel et al., 2000). Finally, more than two thirds of the total force grasping the prey is generated by suction resulting from negative pressure produced as the center of the tongue pad is retracted by the M. retractor pouch (Herrel et al., 2000).

Thermal Effects on Feeding Performance

Chameleons inhabit a broad range of environments (see Chapter 5), from deserts, where body temperature can reach over 39°C (Burrage, 1973), to alpine zones, where temperatures can drop below freezing (Reilly, 1982). Within this range of environments, some chameleon species are known to feed at remarkably low body temperatures (Burrage, 1973; Hebrard et al., 1982; Reilly, 1982; Bennett, 2004; Andrews, 2008), including as low as 3.5°C (Burrage, 1973) and at body temperatures below which sympatric lizard species are active (Hebrard et al., 1982).

Temperature, however, exhibits strong effects on a wide range of physiological processes, some of which can have strong impacts on whole-organism performance. Thermal effects on muscle physiology, for instance, can have a profound impact on the contractile rates, and thus locomotor capabilities, of organisms (Huey and Stevenson, 1979; Bennett, 1985; Huey and Bennett, 1987; Rome, 1990; Lutz and Rome, 1996; Herrel et al., 2007a). Because their body temperature is dictated by environmental conditions, ectotherms, like chameleons, are particularly vulnerable to the effect of low environmental temperatures.

While sprint speed in lizards, jump distance in frogs, and swimming speed in fish declines at least 33% with a 10°C decline in body temperature (Huey and Bennett, 1987; Rome, 1990), tongue-projection performance in chameleons declines significantly less (Anderson and Deban, 2010). In fact, as body temperature declines from 25°C to 15°C, peak velocity of tongue projection declines less than 11%, while peak power output declines only 19% (Fig. 4.6) (Anderson and Deban, 2010). Tongue retraction, on the other hand, exhibits a decline in peak velocity of more than 42% across the same temperature range, and a decline in peak power output of more than 64% (Fig. 4.6) (Anderson and Deban, 2010).

While tongue retraction is powered by muscle contraction alone, tongue projection is powered largely by elastic recoil of collagenous tissue that was preloaded by muscle contraction (de Groot and van Leeuwen, 2004). The observed difference in temperature effects is because muscle contractile rate properties are strongly affected by temperature (Bennett, 1985), while static contractile properties, like peak tension, are weakly affected by temperature (Bennett, 1985; Rome, 1990; Lutz and Rome, 1997), and elastic properties exhibit almost no effect of temperature (Rigby et al., 1959). As a result, the M. accelerator linguae is able to exert close to the same level of force during contraction to load the intralingual sheaths prior to the onset of tongue projection (Anderson and Deban, 2010). This loading occurs at a slower rate, but because the mechanism is preloaded, it is able to contract fully prior to the onset of tongue projection and the elastic elements then recoil at close to the same rate as they would at warmer temperatures once projection occurs (Anderson and Deban, 2010). Tongue retraction, on the other hand, is strongly affected by temperature as it relies directly on muscle contractile velocity (Anderson and Deban, 2010).

With an effective prey-prehension mechanism able to capture and hold large prey (Herrel et al., 2000) and a weak effect of temperature on the tension produced by muscle (Bennett, 1985; Rome, 1990; Lutz and Rome, 1997; Anderson and Deban, 2012), chameleons are at a

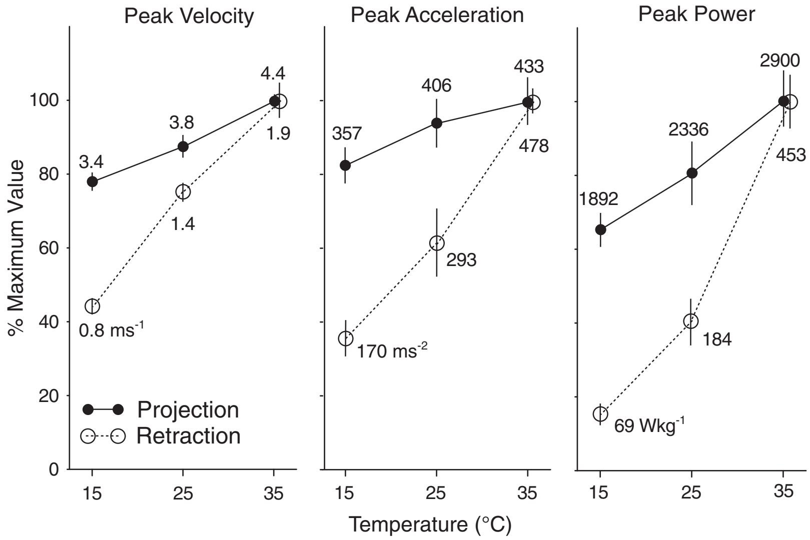

FIGURE 4.6. Performance parameters (mean ±SE) as a percent of maximum for tongue projection (open/dashed) and retraction (solid) in *Chamaeleo calyptratus* showing low thermal dependence of projection as compared with retraction. Absolute values of means are shown in native units. Modified from Anderson and Deban (2010).

limited risk of losing prey once it has been grasped by the tongue. Thus, low thermal dependence of tongue projection serves to increase the thermal breadth of their feeding mechanism (Anderson and Deban, 2010). This increased thermal breadth likely grants chameleons a temporally expanded thermal niche (Anderson and Deban, 2010) and allows them to feed early in the morning before behavioral thermoregulation can elevate their body temperature (Reilly, 1982) and sympatric lizard species are rendered inactive (Hebrard et al., 1982).

Future Directions for Chameleon Feeding Research

While it is now clear how each muscle is involved during the process of tongue projection and retraction, our understanding of the elastic energy storage component is extremely limited. Clearly an elastic power amplifier is involved in powering tongue projection, as is evident by the power output values exceeding that known to be produced by muscle contraction alone (de Groot and van Leeuwen, 2004), but the proposed mechanism has never been shown definitively.

Rectifying how the nested series of collagenous intralingual sheaths interact with each other is one issue that needs continued research. Because of their size, it is difficult to even determine accurately the exact number of sheaths present (de Groot and van Leeuwen, 2004). Further, because the more superficial sheaths, which are attached at their proximal end to the inner fascia of the M. accelerator linguae, are connected to each other by collagenous trabeculae, while the deeper sheaths, which are attached at their proximal end to the fascia of the M. hyoglossus, have no structural connection at their distal end (de Groot and van Leeuwen, 2004), it is unclear how different sheaths interact with each other, particularly those that are not connected by trabeculae.

Of particular interest is how energy stored in the intralingual sheaths is imparted on the tongue to power forward projection. Because the intralingual sheaths do not appear to be connected at their distal end to the entoglossal process, it is unclear how the recoil of these sheaths acts against the tongue skeleton to project the tongue forward. This is particularly confusing because the sheaths must be well enough lubricated so as to slide along each other and the entoglossal process without losing energy to friction, but at the same time, they must exert a force in the posterior direction in order to impart a forward force. Further, direct attachment to the entoglossal process would limit projectile distance because of the short length of each sheath.

Finally, direct measurement of the mechanical properties of the intralingual sheaths still needs to be done. Based on the weight of the sheaths, the energy needed to be stored in them in order to produce the observed energy output during tongue projection is calculated to be significantly lower than the observed capacity of other tendons under maximal stress (de Groot and van Leeuwen, 2004). This indicates that the intralingual sheaths should have the capacity to power tongue projection; however, direct measurement of their mechanical properties is needed to confirm this.

ACKNOWLEDGEMENTS

We thank Anthony Herrel, John Measey, and Lance McBrayer for extremely helpful comments on earlier drafts of this chapter.

List of 196 Described Chameleon Species as of 2012, with the Broad Region in Which They Occur

Species	Region
Archaius tigris (Kuhl, 1820)	Seychelles
Bradypodion atromontanum Branch, Tolley, and Tilbury, 2006	Southern Africa
Bradypodion caeruleogula Raw and Brothers, 2008	Southern Africa
Bradypodion caffer (Boettger, 1889)	Southern Africa
Bradypodion damaranum (Boulenger, 1887)	Southern Africa
Bradypodion dracomontanum Raw, 1976	Southern Africa
Bradypodion gutturale (Smith, 1849)	Southern Africa
Bradypodion kentanicum (Hewitt, 1935)	Southern Africa
Bradypodion melanocephalum (Gray, 1865)	Southern Africa
Bradypodion nemorale Raw, 1978	Southern Africa
Bradypodion ngomeense Tilbury and Tolley, 2009	Southern Africa
Bradypodion occidentale (Hewitt, 1935)	Southern Africa
Bradypodion pumilum (Gmelin, 1789)	Southern Africa
Bradypodion setaroi Raw, 1976	Southern Africa
Bradypodion taeniabronchum (Smith, 1831)	Southern Africa
Bradypodion thamnobates Raw, 1976	Southern Africa
Bradypodion transvaalense (Fitzsimons, 1930)	Southern Africa
Bradypodion ventrale (Gray, 1845)	Southern Africa
Brookesia ambreensis Raxworthy and Nussbaum, 1995	Madagascar
Brookesia antakarana Raxworthy and Nussbaum, 1995	Madagascar
Brookesia bekolosy Raxworthy and Nussbaum, 1995	Madagascar
Brookesia betschi Brygoo, Blanc, and Domergue, 1974	Madagascar
Brookesia bonsi Ramanantsoa, 1980	Madagascar
Brookesia brygooi Raxworthy and Nussbaum, 1995	Madagascar
Brookesia brunoi Crottini, Miralles, Glaw, Harris, Lima, and Vences, 2012	Madagascar
Brookesia confidens Glaw, Köhler, Townsend, and Vences, 2012	Madagascar
Brookesia decaryi Angel, 1939	Madagascar
Brookesia dentata Mocquard, 1900	Madagascar
Brookesia desperata Glaw, Köhler, Townsend, and Vences, 2012	Madagascar

(Continued)

Species	Region
Brookesia ebenaui (Boettger, 1880)	Madagascar
Brookesia exarmata Schimmenti and Jesu, 1996	Madagascar
Brookesia griveaudi Brygoo, Blanc, and Domergue, 1974	Madagascar
Brookesia karchei Brygoo, Blanc, and Domergue, 1970	Madagascar
Brookesia lambertoni Brygoo and Domergue, 1970	Madagascar
Brookesia lineata Raxworthy and Nussbaum, 1995	Madagascar
Brookesia lolontany Raxworthy and Nussbaum, 1995	Madagascar
Brookesia micra , 2012	Madagascar
Brookesia minima Boettger, 1893	Madagascar
Brookesia nasus Boulenger, 1887	Madagascar
Brookesia perarmata (Angel, 1933)	Madagascar
Brookesia peyrierasi Brygoo and Domergue, 1974	Madagascar
Brookesia ramanantsoai Brygoo and Domergue, 1975	Madagascar
Brookesia stumpffi Boettger, 1894	Madagascar
Brookesia superciliaris (Kuhl, 1820)	Madagascar
Brookesia therezieni Brygoo and Domergue, 1970	Madagascar
Brookesia thieli Brygoo and Domergue, 1969	Madagascar
Brookesia tristis Glaw, Köhler, Townsend, and Vences, 2012	Madagascar
Brookesia tuberculata Mocquard, 1894	Madagascar
Brookesia vadoni Brygoo and Domergue, 1968	Madagascar
Brookesia valerieae Raxworthy, 1991	Madagascar
Calumma amber Raxworthy and Nussbaum, 2006	Madagascar
Calumma ambreense (Ramanantsoa, 1974)	Madagascar
Calumma andringitraense (Brygoo, Blanc, and Domergue, 1972)	Madagascar
Calumma boettgeri (Boulenger, 1888)	Madagascar
Calumma brevicorne (Günther, 1879)	Madagascar
Calumma capuroni (Brygoo, Blanc, and Domergue, 1972)	Madagascar
Calumma crypticum Raxworthy and Nussbaum, 2006	Madagascar
Calumma cucullatum (Gray, 1831)	Madagascar
Calumma fallax (Mocquard, 1900)	Madagascar
Calumma furcifer (Vaillant and Grandidier, 1880)	Madagascar
Calumma gallus (Günther, 1877)	Madagascar
Calumma gastrotaenia (Boulenger, 1888)	Madagascar
Calumma glawi Böhme, 1997	Madagascar
Calumma globifer (Günther, 1879)	Madagascar
Calumma guibei (Hillenius, 1959)	Madagascar
Calumma guillaumeti (Brygoo, Blanc, and Domergue, 1974)	Madagascar
Calumma hafahafa Raxworthy and Nussbaum, 2006	Madagascar
Calumma hilleniusi (Brygoo, Blanc, and Domergue, 1973)	Madagascar
Calumma jejy Raxworthy and Nussbaum, 2006	Madagascar
Calumma linota (Müller, 1924)	Madagascar
Calumma malthe (Günther, 1879)	Madagascar
Calumma marojezense (Brygoo, Blanc, and Domergue, 1970)	Madagascar
Calumma nasutum (Duméril and Bibron, 1836)	Madagascar
Calumma oshaughnessyi (Günther, 1881)	Madagascar
Calumma parsonii (Cuvier, 1824)	Madagascar
Calumma peltierorum Raxworthy and Nussbaum, 2006	Madagascar
Calumma peyrierasi (Brygoo, Blanc, and Domergue, 1974)	Madagascar

Species	Region
Calumma tarzan Gehring, Pabijan, Ratsoavina, Köhler, Vences, and Glaw, 2010	Madagascar
Calumma tsaratananense (Brygoo and Domergue, 1967)	Madagascar
Calumma tsycorne Raxworthy and Nussbaum, 2006	Madagascar
Calumma vatosoa Andreone, Mattioli, Jesu, and Randrianirina, 2001	Madagascar
Calumma vencesi Andreone, Mattioli, Jesu, and Randrianirina, 2001	Madagascar
Calumma vohibola Gehring, Ratsoavina, Vences, and Glaw, 2011	Madagascar
Chamaeleo africanus Laurenti, 1768	West-central Africa, North Africa
Chamaeleo anchietae Bocage, 1872	West-central Africa
Chamaeleo arabicus (Matschie, 1893)	Arabia
Chamaeleo calcaricarens Böhme, 1985	North Africa
Chamaeleo calyptratus Duméril & Duméril, 1851	Arabia
Chamaeleo chamaeleon (Linnaeus, 1758)	Europe, North Africa, Arabia
Chamaeleo dilepis Leach, 1819	Pan Africa
Chamaeleo gracilis Hallowell, 1842	East Africa, West-central Africa
Chamaeleo laevigatus (Gray, 1863)	East Africa
Chamaeleo monachus (Gray, 1865)	Socotra Island
Chamaeleo namaquensis Smith, 1831	Southern Africa
Chamaeleo necasi Ullenbruch, Krause, Böhme, 2007	West-central Africa
Chamaeleo senegalensis Daudin, 1802	West-central Africa
Chamaeleo zeylanicus Laurenti, 1768	Asia
Furcifer angeli (Brygoo and Domergue, 1968)	Madagascar
Furcifer antimena (Grandidier, 1872)	Madagascar
Furcifer balteatus (Duméril and Bibron, 1851)	Madagascar
Furcifer belalandaensis (Brygoo and Domergue, 1970)	Madagascar
Furcifer bifidus (Brongniart, 1800)	Madagascar
Furcifer campani (Grandidier, 1872)	Madagascar
Furcifer cephalolepis (Günther, 1880)	Comoros
Furcifer labordi (Grandidier, 1872)	Madagascar
Furcifer lateralis (Gray, 1831)	Madagascar
Furcifer major (Brygoo, 1971)	Madagascar
Furcifer minor (Günther, 1879)	Madagascar
Furcifer nicosiai Jesu, Mattioli, and Schimmenti, 1999	Madagascar
Furcifer oustaleti (Mocquard, 1894)	Madagascar
Furcifer pardalis (Cuvier, 1829)	Madagascar
Furcifer petteri (Brygoo and Domergue, 1966)	Madagascar
Furcifer polleni (Peters, 1874)	Comoros
Furcifer rhinoceratus (Boettger, 1893)	Madagascar
Furcifer timoni Glaw, Köhler, and Vences, 2009	Madagascar
Furcifer tuzetae (Brygoo, Bourgat, and Domergue, 1972)	Madagascar
Furcifer verrucosus (Cuvier, 1829)	Madagascar
Furcifer viridis Florio, Ingram, Rakotondravony, Louis, and Raxworthy, 2012	Madagascar

(Continued)

Species	Region
Furcifer willsii (Günther, 1890)	Madagascar
Kinyongia adolfifriderici (Sternfeld, 1912)	East Africa
Kinyongia asheorum Necas, Sindaco, Korený, Kopecná, Malonza, and Modrý, 2009	East Africa
Kinyongia boehmei (Lutzmann and Necas, 2002)	East Africa
Kinyongia carpenteri (Parker, 1929)	East Africa
Kinyongia excubitor (Barbour, 1911)	East Africa
Kinyongia fischeri (Reichenow, 1887)	East Africa
Kinyongia gyrolepis Greenbaum, Tolley, Joma, and Kusamba, 2012	East Africa
Kinyongia magomberae Menegon, Tolley, Jones, Rovero, Marshall, and Tilbury, 2009	East Africa
Kinyongia matschiei (Werner, 1895)	East Africa
Kinyongia multituberculata (Nieden, 1913)	East Africa
Kinyongia oxyrhina (Klaver and Böhme, 1988)	East Africa
Kinyongia tavetana (Steindachner, 1891)	East Africa
Kinyongia tenuis (Matschie, 1892)	East Africa
Kinyongia uluguruensis (Loveridge, 1957)	East Africa
Kinyongia uthmoelleri (Müller, 1938)	East Africa
Kinyongia vanheygeni Necas, 2009	East Africa
Kinyongia vosseleri (Nieden, 1913)	East Africa
Kinyongia xenorhina (Boulenger, 1901)	East Africa
Nadzikambia baylissi Branch and Tolley, 2010	East Africa
Nadzikambia mlanjensis (Broadley, 1965)	East Africa
Rhampholeon acuminatus Mariaux and Tilbury, 2006	East Africa
Rhampholeon beraduccii Mariaux and Tilbury, 2006	East Africa
Rhampholeon boulengeri Steindachner, 1911	East Africa
Rhampholeon chapmanorum Tilbury, 1992	East Africa
Rhampholeon gorongosae Broadley, 1971	Southern Africa
Rhampholeon marshalli Boulenger, 1906	Southern Africa
Rhampholeon moyeri Menegon, Salvidio, and Tilbury, 2002	East Africa
Rhampholeon nchisiensis (Loveridge, 1953)	East Africa
Rhampholeon platyceps Günther, 1893	East Africa
Rhampholeon spectrum (Buchholz, 1874)	West-central Africa
Rhampholeon spinosus (Matschie, 1892)	East Africa
Rhampholeon temporalis (Matschie, 1892)	East Africa
Rhampholeon uluguruensis Tilbury and Emmrich, 1996	East Africa
Rhampholeon viridis Mariaux and Tilbury, 2006	East Africa
Rieppeleon brachyurus (Günther, 1893)	East Africa
Rieppeleon brevicaudatus (Matschie, 1892)	East Africa
Rieppeleon kerstenii (Peters, 1868)	East Africa, North Africa
Trioceros affinis (Rüppel, 1845)	North Africa
Trioceros balebicornutus (Tilbury, 1998)	North Africa
Trioceros bitaeniatus (Fischer, 1884)	East Africa
Trioceros camerunensis (Müller, 1909)	West-central Africa
Trioceros chapini (De Witte, 1964)	West-central Africa
Trioceros conirostratus (Tilbury, 1998)	East Africa

Species	Region
Trioceros cristatus (Stutchbury, 1837)	West-central Africa
Trioceros deremensis (Matschie, 1892)	East Africa
Trioceros ellioti (Günther, 1895)	East Africa
Trioceros feae (Boulenger, 1906)	West-central Africa
Trioceros fuelleborni (Tornier, 1900)	East Africa
Trioceros goetzei (Tornier, 1899)	East Africa
Trioceros hanangensis Krause & Böhme, 2010	East Africa
Trioceros harennae (Largen, 1995)	North Africa
Trioceros hoehnelii (Steindachner, 1891)	East Africa
Trioceros incornutus (Loveridge, 1932)	East Africa
Trioceros ituriensis (Schmidt, 1919)	East Africa, Central Africa
Trioceros jacksonii (Boulenger, 1896)	East Africa
Trioceros johnstoni (Boulenger, 1901)	East Africa, Central Africa
Trioceros kinangopensis Stipala, Lutzmann, Malonza, Wilkinson, Godley, Nyamache, and Evans, 2012	East Africa
Trioceros kinetensis (Schmidt, 1943)	East Africa
Trioceros laterispinis (Loveridge, 1932)	East Africa
Trioceros marsabitensis (Tilbury, 1991)	East Africa
Trioceros melleri (Gray, 1865)	East Africa
Trioceros montium (Buchholz, 1874)	West-central Africa
Trioceros narraioca (Necas, Modry, and Slapeta, 2003)	East Africa
Trioceros ntunte (Necas, Modry, and Slapeta, 2005)	East Africa
Trioceros nyirit Stipala, Lutzmann, Malonza, Wilkinson, Godley, Nyamache, and Evans, 2011	East Africa
Trioceros oweni (Gray, 1831)	West-central Africa
Trioceros perreti (Klaver and Böhme, 1992)	West-central Africa
Trioceros pfefferi (Tornier, 1900)	West-central Africa
Trioceros quadricornis (Tornier, 1899)	West-central Africa
Trioceros rudis (Boulenger, 1906)	East Africa
Trioceros schoutedeni (Laurent, 1952)	East Africa
Trioceros schubotzi (Sternfeld, 1912)	East Africa
Trioceros serratus (Mertens, 1922)	West-central Africa
Trioceros sternfeldi (Rand, 1963)	East Africa
Trioceros tempeli (Tornier, 1900)	East Africa
Trioceros werneri (tornier, 1899)	East Africa
Trioceros wiedersheimi (Nieden, 1910)	West-central Africa

SOURCE: Glaw and Vences, 2007; Tolley and Burger, 2007; Tilbury, 2010; Uetz, 2012.

ABBREVIATIONS

asl	above sea level
cf.	compare
cm	centimeters
e.g.	for example
i.e.	that is
km	kilometers
m	meters
mm	millimeters
Mya	million years ago
Myr	million years
Ri.	Rieppeleon
Rh.	Rhampholeon
sp.	species (singular)
spp.	species (plural)

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