# 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."

TWO

# Chameleon Anatomy

CHRISTOPHER V. ANDERSON and TIMOTHY E. HIGHAM

The family Chamaeleonidae is a distinctive clade of squamate reptiles with a plethora of unusual structural adaptations. Chameleons exhibit numerous distinctive features, including a laterally compressed body, forcep-like feet with toes grouped in opposing bundles, prehensile tail, enlarged casque, independently rotating eyes, and long tongue capable of being projected from the mouth. While chameleons are unique animals, they are also extremely diverse, with species spanning an approximate 20-fold range in adult total length and a 2000-fold range in body mass. Moreover, chameleons exhibit an extensive range of ornamentation. In addition, chameleons live over incredible ranges of habitats and demonstrate an abundance of variation in their behavior and ecology (Chapters 5 and 6), features of which are often predicated on anatomical specializations.

As a result of their unique nature, people have been interested in the biology of chameleons for centuries. In order to understand many aspects of chameleon biology, however, understanding the associated morphological underpinnings can be of vital importance. Here we summarize what is known about the anatomy of chameleons, emphasizing the differences between chameleons and other reptiles and the differences among chameleons.

## 2.1 MUSCULOSKELETAL MORPHOLOGY

### Axial

### *Cranial*

The lateral compression of the chameleon in conjunction with their enlarged eyes and the formation of an enlarged casque have strong influences on the structure of the chameleon skull and the distribution and orientation of various cranial muscles. The extent to which these characteristics are developed, however, is also variable within the family, and thus examination of the anatomy of the skull and its musculature is not only of interest relative to other lizard groups, but also within the chameleons.

*Skull and Teeth* The extensive studies of the chameleon skull have included discussion and examination of the structure of the skull in *Archaius* (Hillenius, 1988; Rieppel and Crumly, 1997), *Bradypodion* (Fig. 2.1c,d,f) (Parker, 1881; Methuen and Hewitt, 1914; Brock, 1941; Engelbrecht, 1951; Rieppel, 1981; Hillenius, 1988), *Brookesia* (Fig. 2.1a,b) (Siebenrock, 1893; Methuen and Hewitt, 1914; Rieppel 1987; Rieppel and Crumly, 1997), *Calumma* (Methuen and Hewitt, 1914; Hillenius, 1988; Rieppel and Crumly, 1997), *Chamaeleo* (Parker, 1881; Siebenrock, 1893; Methuen and Hewitt, 1914; Prasad, 1954; Rieppel, 1987; Hillenius, 1988), *Furcifer* (Methuen and Hewitt, 1914; Hillenius, 1988; Rieppel and Crumly, 1997), *Kinyongia* (Hillenius, 1988), *Rhampholeon* (Werner, 1902b; Methuen and Hewitt, 1914; Frank, 1951; Rieppel, 1987; Hillenius, 1988), *Rieppeleon* (Rieppel, 1987; Hillenius, 1988), and *Trioceros* (Fig. 2.1e) (Rieppel, 1981, 1987, 1993; Hillenius, 1988). These studies have amassed a list of variations between the skulls of different genera and developmental stages. However, they have also resulted in varying interpretations of the skull bones, particularly of the temporal region. Here we summarize the morphology of the adult skull in chameleons following the terminology and interpretations of Rieppel (1981).

The premaxilla of chameleons is unpaired (fused) and lies medially between the maxillae (Fig. 2.1b,d) (Parker, 1881; Siebenrock, 1893; Werner, 1902b; Brock, 1941; Engelbrecht, 1951; Frank, 1951; Rieppel, 1981, 1987). The premaxilla in *Brookesia* (Siebenrock, 1893), *Chamaeleo* (Siebenrock, 1893), *Rieppeleon* (Rieppel; 1987), and *Rhampholeon* (Werner, 1902b; Frank, 1951) bear two vestigial teeth, whereas the premaxillae in *Trioceros* do not bear teeth (Rieppel, 1981). Engelbrecht (1951) reports that *Bradypodion pumilum* also lack premaxillary teeth. Rieppel (1981), on the other hand, observed indications of two vestigial teeth fused with the premaxilla, noting, however, that histological investigation is required to verify whether these are true teeth or paired bony projections on the transverse process of the premaxilla.

Ventrally, the vomerine (palatal) process of the premaxilla is reduced (Fig. 2.1f) (Romer, 1956), extending only a short distance posteriorly, and in *Bradypodion* (Fig. 2.1f) (Engelbrecht, 1951; Frank, 1951; Rieppel, 1981), it does not contact the vomer, as the palatal process of the maxillae meets behind the premaxilla. The maxillae do not meet behind the premaxilla in *Brookesia* (Siebenrock, 1893; Rieppel and Crumly, 1997), however. Typically, the vomers are fused (unpaired) in chameleons (Frank, 1951; Rieppel, 1981); however, in *Bradypodion pumilum,* the vomers are paired for most of their length and fused only anteriorly where they join with the maxillae (Engelbrecht, 1951; Rieppel, 1981). In *Archaius,* the vomer is paired (Rieppel and Crumly, 1997). At the posterior end, the vomer joins the palatines (Fig. 2.1f) (Engelbrecht, 1951; Rieppel, 1981). The palatines extend posteriorly and flare laterally to join the maxillaries (Fig. 2.1f) (Werner, 1902b; Engelbrecht, 1951; Rieppel, 1981).

Dorsally, the nasal process of the premaxilla extends posteriorly and fully separates the maxillae in most species (Fig. 2.1b,d) (Werner, 1902b; Engelbrecht, 1951; Frank, 1951;

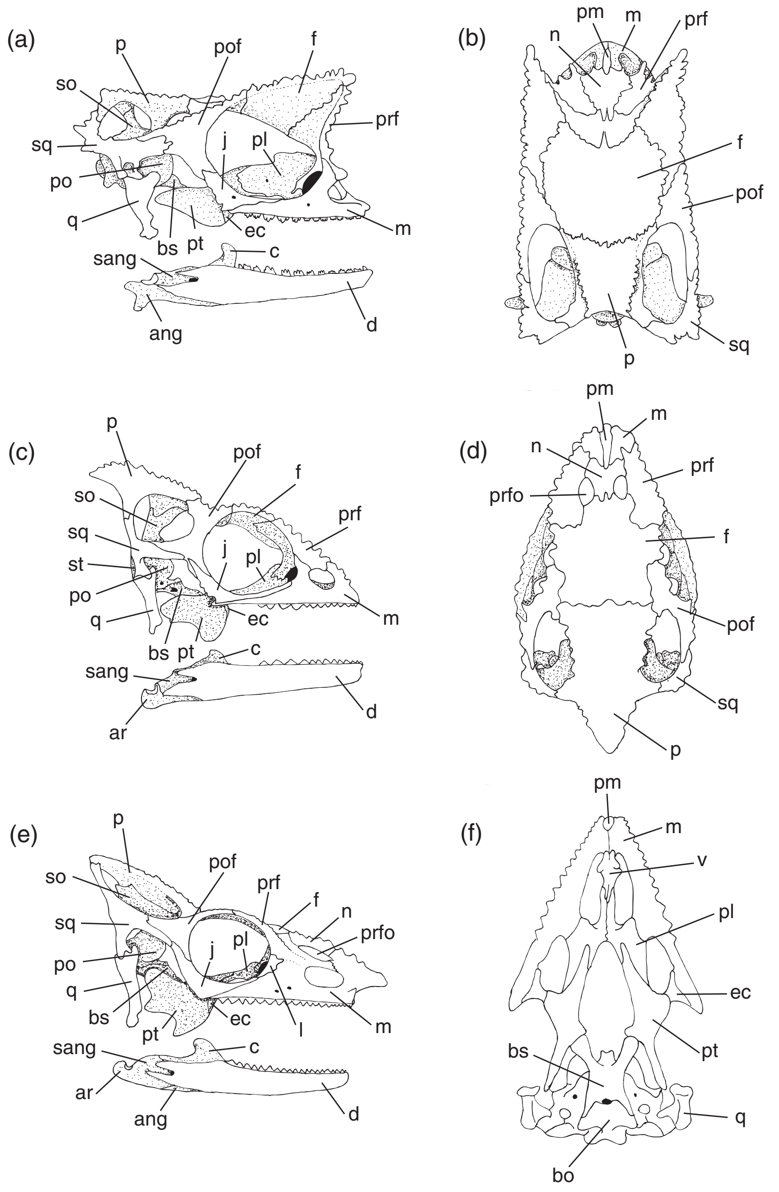

FIGURE 2.1. The skull of *Brookesia superciliaris* (a, b), *Bradypodion pumilum* (c, d, f), and *Trioceros melleri* (e) in lateral (a, c, e), dorsal (b, d), and ventral (f) views. (a, b) redrawn from Rieppel (1987) and (c, d, e, f) from Rieppel (1981).

LABELS: ang = angular; ar = articular; bo = basioccipital; bs = basisphenoid; c = coronoid; d = dentary; ec = ectopterygoid; f = frontal; j = jugal; m = maxilla; n = nasal; p = parietal; pl = palatine; pm = premaxilla; po = prootic; pof = postorbitofrontal; pf = prefrontal; prfo = prefrontal fontanelle; pt = pterygoid; q = quadrate; sang = surangular; so = supraoccipital; sq = squamosal; st = supratemporal; v = vomer.

Rieppel, 1981, 1987; Rieppel and Crumly, 1997). In *Bradypodion, Brookesia,* and *Chamaeleo,* the posterior edge of the nasal process of the premaxilla meets the fused nasals (Fig. 2.1b,d) (Seibenrock, 1893; Camp, 1923; Parker, 1942; Engelbrecht, 1951; Romer, 1956; Rieppel, 1981, 1987). However, the nasal process of the premaxilla separates the nasals and meets an anterior process of the frontal in *Rhampholeon* and *Rieppeleon* (Werner, 1902b; Parker, 1942; Frank, 1951, Rieppel, 1981, 1987). The nasals are paired and variably separated from the frontals by the premaxilla in *Calumma* and *Furcifer* (Rieppel and Crumly, 1997).

*In Brookesia,* the nasals circumscribe the dorsal margin of the nasal aperture (Fig. 2.1a,b) (Siebenrock, 1893; Engelbrecht, 1951; Romer, 1956; Rieppel, 1981). In *Bradypodion* (Fig. 2.1c,d) (Brock, 1941; Engelbrecht, 1951; Rieppel, 1981), *Chamaeleo* (Parker, 1881), and *Trioceros* (Fig. 2.1e) (Rieppel, 1981), the nasals do not participate in circumscribing the nasal aperture. The nasal aperture is bound by the maxillae on the anterior, ventral, and posterior edges (Siebenrock, 1893; Engelbrecht, 1951; Rieppel, 1981) and in *Bradypodion, Chamaeleo, Rieppeleon,* and *Trioceros,* the dorsal margin is bound by an anterior projection of the prefrontal lying lateral to the nasals (Fig. 2.1c–e) (Parker, 1881; Methuen and Hewitt, 1914; Engelbrecht, 1951; Rieppel, 1981, 1987). In *Bradypodion* and *Chamaeleo,* a prefrontal fontanelle is bound by the nasal, prefrontal, and frontal (Fig. 2.1d) (Parker, 1881; Engelbrecht, 1951; Rieppel, 1981). The prefrontal fontanelle is bound by the prefrontal, nasal, and maxilla in *Trioceros* (Fig. 2.1e) (Rieppel, 1981). In *Rhampholeon,* however, the prefrontal fontanelles are continuous with the nasal aperture and combined they are bound by the maxilla, prefrontal, nasal, frontal, and in some cases, the premaxilla (Werner, 1902b; Frank, 1951; Rieppel, 1981, 1987).

The prefrontal circumscribes the anterodorsal margin of the orbit in *Bradypodion* (Fig. 2.1c) (Parker, 1881; Engelbrecht, 1951; Rieppel, 1981), *Brookesia* (Fig. 2.1a) (Siebenrock, 1893; Romer, 1956; Rieppel, 1987), *Chamaeleo* (Parker, 1881), *Rhampholeon* (Werner, 1902b; Frank, 1951), *Rieppeleon* (Rieppel, 1987), and *Trioceros* (Fig. 2.1e) (Rieppel, 1981). The lacrimal is absent in *Bradypodion* (Brock, 1941; Engelbrecht, 1951; Rieppel, 1981), *Brookesia* (Siebenrock, 1893; Rieppel, 1987), *Calumma* (Methuen and Hewitt, 1913), *Rhampholeon* (Frank, 1951), and *Rieppeleon* (Rieppel, 1987), and the prefrontal joins the maxillae at the anterior edge of the orbit, allowing them to circumscribe the anteroventral margin of the orbit in these genera. In *Chamaeleo* (Parker, 1881; Camp, 1923) and *Trioceros* (Fig. 2.1e) (Rieppel, 1981), however, the lacrimal is present and joins the prefrontal at the anterior edge of the orbit, excluding the maxillae from involvement in circumscribing the orbit. Methuen and Hewitt (1914) note that the lacrimal is absent in *Furcifer lateralis,* whereas Rieppel and Crumly (1997) note that the lacrimal is usually observed in most *Furcifer* examined, including *F. lateralis* and with the exception of in *F. oustaleti*. The jugal joins with the lacrimal in *Chamaeleo* (Parker, 1881) and *Trioceros* (Fig. 2.1e) (Rieppel, 1981), and with the maxilla in *Bradypodion* (Fig. 2.1c) (Brock, 1941; Engelbrecht, 1951; Rieppel, 1981), *Brookesia* (Fig. 2.1a) (Siebenrock, 1893; Romer, 1956; Rieppel, 1987), *Calumma* (Methuen and Hewitt, 1914), *Furcifer* (Methuen and Hewitt, 1914), *Rhampholeon* (Werner, 1902b; Frank, 1951), and *Rieppeleon* (Rieppel, 1987); in both cases, they circumscribe the ventral and posteroventral edge of the orbit.

The frontal is fused and, when present, bears the pineal foramen (Romer, 1956; Rieppel, 1981). In *Archaius* (Rieppel and Crumly, 1997), *Bradypodion* (Fig. 2.1c,d) (Parker, 1881; Methuen and Hewitt, 1914; Engelbrecht, 1951; Rieppel, 1981), *Brookesia* (Fig. 2.1a,b) (Siebenrock, 1893; Romer, 1956; Rieppel, 1987), *Calumma* species other than *C. brevicorne* (Methuen and Hewitt, 1914; Rieppel and Crumly, 1997), *Furcifer bifidus* (Rieppel and Crumly, 1997), *Furcifer campani* (Rieppel and Crumly, 1997), and *Rhampholeon* (Werner, 1902b; Frank, 1951), the frontal circumscribes the dorsal margin of the orbit and joins with the prefrontal anteriorly and the postorbitofrontal posteriorly. In *Calumma brevicorne* (Methuen and Hewitt, 1914), *Chamaeleo* (Parker, 1881), *Furcifer* species other than *F. bifidus* and *F. campani* (Methuen and Hewitt, 1914; Rieppel and Crumly, 1997), and *Trioceros* (Fig. 2.1e) (Rieppel, 1981, 1993); however, the frontal is excluded from involvement in circumscribing the orbit by contact of the prefrontal with the postorbitofrontal. The postorbitofrontal joins the jugal at the posterior margin of the orbit (Fig. 2.1a,c,e) (Parker, 1881; Engelbrecht, 1951; Frank, 1951; Rieppel, 1981) and extends deep to meet the ectopterygoid (Rieppel, 1981).

In *Chamaeleo* (Parker, 1881), *Furcifer lateralis* (Methuen and Hewitt, 1914; Rieppel and Crumly, 1997), *F. pardalis* (Rieppel and Crumly, 1997), and *Trioceros* (Fig. 2.1e) (Rieppel, 1981), the dorsal tip of the jugal contacts the squamosal to form the upper temporal arch, with a posterior projection of the postorbitofrontal extending dorsal to the squamosal. In *Calumma* species other than *C. brevicorne* (Methuen and Hewitt, 1914; Rieppel and Crumly, 1997), *Bradypodion* (Fig. 2.1c) (Parker, 1881; Rieppel, 1981), *Brookesia* (Fig. 2.1a) (Siebenrock, 1893; Romer, 1856; Rieppel, 1987), *F. bifidus* (Rieppel and Crumly, 1997), *Rhampholeon* (Werner, 1902b; Frank, 1951), and *Rieppeleon* (Rieppel, 1987), the jugal and squamosal do not connect and the postorbitofrontal bridges the gap between them. Methuen and Hewitt (1914) note that the jugal and squamosal come into contact in *Calumma brevicorne* and *C. nasuta,* whereas Rieppel (1997) notes that the jugal may closely approach the squamosal in *C. nasuta* but does not touch it. A fontanelle in *C. brevicorne* may influence the possibility of contact between the jugal and squamosal. Further, Rieppel and Crumly (1997) note that contact between the jugal and squamosal is variable in *F. oustaleti* and *F. verrucosus*.

In *Archaius* (Hillenius, 1988), *Calumma* (Hillenius, 1988), *Chamaeleo* (Parker, 1881; Methuen and Hewitt, 1914; Hillenius, 1988), *Furcifer* (Hillenius, 1988), *Kinyongia* (Hillenius, 1988), *Rhampholeon* (Werner, 1902b; Frank, 1951; Rieppel, 1987), *Rieppeleon* (Rieppel, 1987), and *Trioceros* (Fig. 2.1e) (Rieppel, 1981; Hillenius, 1988), the parietal narrows posteriorly to form a sagittal crest, the parietal crest, extending posterodorsally to form the casque and meeting the supraoccipital ventrally. This posterior narrowing is slower, forming a more trigonal shape, in *Calumma* and *Rhampholeon* (Hillenius, 1988; Rieppel and Crumly, 1997), with some *Calumma* species having a broadening again posteriorly (Rieppel and Crumly, 1997). In *Archaius* (Rieppel and Crumly, 1997), *Calumma* (Hillenius, 1988), *Chamaeleo* (Parker, 1881; Methuen and Hewitt, 1914), *Furcifer* (Hillenius, 1988), *Rhampholeon* (Werner, 1902b; Frank, 1951; Rieppel, 1987), *Rieppeleon brevicaudatus* (Rieppel, 1987), and *Trioceros* (Fig. 2.1e) (Rieppel, 1981), a dorsal process of the squamosal meets the posterodorsal tip of the parietal crest, whereas in

*Rieppeleon brachyurus* and *Rieppeleon kerstenii,* the dorsal process is reduced and no longer meets the parietal (Rieppel, 1981). In *Bradypodion* (Fig. 2.1d) (Parker, 1881; Methuen and Hewitt, 1914; Engelbrecht, 1951; Rieppel, 1981; Hillenius, 1988) and *Brookesia* (Fig. 2.1b) (Siebenrock, 1893; Rieppel, 1987), the parietal forms a tapered plate extending posterodorsally to form the casque. A sagittal crest is formed on the ventral surface of the parietal, which meets the supraoccipital (Fig. 2.1a,c,e) (Rieppel, 1981) and a lateroventral processes extends off the posterolateral edge of the parietal to meet the dorsal process of the squamosal (Fig. 2.1a,c,e) (Parker, 1881; Methuen and Hewitt, 1914; Brock, 1941; Engelbrecht, 1951; Rieppel, 1981, 1987). A small supratemporal lies medial to the squamosal, wedged between the otic capsule wall and the head of the quadrate and squamosal (Fig. 2.1c) (Brock, 1941; Engelbrecht, 1951; Rieppel, 1981). The supratemporal is absent in *Rieppeleon* (Rieppel, 1987).

The lateral head of the quadrate's cephalic condyle articulates with the anterior surface of the squamosal's posteroventral process (Fig. 2.1a,c,e) (Rieppel, 1981). The pterygoid joins posteriorly with the palatine, laterally with the ectopterygoid, and posteromedially with the basisphenoid (Fig. 2.1f) (Engelbrecht, 1951; Rieppel, 1981). The pterygoid extends posterolaterally from the junction with the basisphenoid toward the quadrate, expanding into a wing-shaped structure in the process, but does not reach the quadrate, forming only a ligamentous connection with it (Fig. 2.1a,c,e,f) (Romer, 1956; Rieppel, 1981). The basisphenoid joins with the basioccipital at its posterior edge, and the occipital condyle is at the posterior edge of the basioccipital (Fig. 2.1f) (Parker, 1881; Werner, 1902b; Rieppel, 1981). In *Calumma,* the occipital condyle can be formed by the exoccipital with only participation of the basioccipital (Rieppel, 1987). The occipital condyle articulates with the proatlas of the vertebral column (Hoffstetter and Gasc, 1969).

The anterodorsal edge of the squamosal, posterodorsal edge of the postorbitofrontal, and the ventrolateral edge of the parietal circumscribes the upper temporal fossa (Fig. 2.1a–e) (Parker, 1881; Werner, 1902b; Engelbrecht, 1951; Frank, 1951; Rieppel, 1981, 1987). The anterior edge of the quadrate, ventral edge of the squamosal, posterior edge of the jugal, and in *Chamaeleo* and *Trioceros,* the posteroventral edge of the postorbitofrontal, circumscribe the posttemporal fossa (Fig. 2.1a–e) (Parker, 1881; Siebenrock, 1893; Werner, 1902b; Engelbrecht, 1951; Frank, 1951; Rieppel, 1981, 1987).

The dentaries are the sole tooth-bearing bones of the lower jaw; they join at a symphysis anteromedially (Fig. 2.1a,c,e) (Parker, 1881; Werner, 1902b; Engelbrecht, 1951; Frank, 1951; Rieppel, 1981, 1987). The coronoid attaches to the dentary medially with a dorsal coronoid process extending beyond the dorsal edge of the dentary (Fig. 2.1a,c,e) (Parker, 1881; Werner, 1902b; Engelbrecht, 1951; Frank, 1951; Rieppel, 1981, 1987). In *Calumma, Chamaeleo,* and *Trioceros,* the tooth row extends posteriorly beyond the anterior edge of the coronoid process (Fig. 2.1a) (Rieppel and Crumly, 1997). The angular attaches to the ventromedial aspect of the dentary (Fig. 2.1a,e) (Parker, 1881; Engelbrecht, 1951; Frank, 1951; Rieppel, 1981, 1987). The surangular joins to the posterior aspect of the coronoid and medial aspect of the dentary (Fig. 2.1a,c,e) (Parker, 1881; Engelbrecht, 1951; Rieppel, 1981, 1987).

The articular joins at the posterior edge of the surangular (Fig. 2.1c,e) (Parker, 1881; Engelbrecht, 1951; Frank, 1951; Rieppel, 1981, 1987). The retroarticular process in chameleons is reduced (Romer, 1956).

Chameleons, as do Agamidae and Leiolepididae, possess an acrodont dentition (Camp, 1923; Romer, 1956; Schwenk, 2000). Acrodont teeth are ankylosed to the apical surface of the upper and lower jaw, are added posteriorly to the tooth row during growth, and are worn throughout life and not replaced (Schwenk, 2000). Because teeth are not replaced, the stability of tooth position allows for strong occlusion patterns (Camp, 1923; Schwenk, 2000).

*Cranial Musculature* The musculature of the skull can be divided into a few broad complexes, the jaw abductor muscles, and the complex jaw adductor musculature, which is very well developed in chameleons, and finally the constrictor dorsalis musculature. Muscles of the throat, buccal cavity and hyobranchial apparatus are presented in the "Hyobranchial" section below and those of the eye in the section titled "Eye," which focuses on the eye as a whole.

JAW ABDUCTOR MUSCULATURE The Musculus (M.) depressor mandibulae complex in chameleons has not been described in detail (Haas, 1973). It is noted, however, to consist of an internus and externus division (Engelbrecht, 1951). Combined, it originates on the ascending process of the squamosal (Meyers and Clarke, 1998), through the posterior surface of the lateral ridge on the quadrate (Frank, 1951; Meyers and Clarke, 1998), and inserts into the posterior end of the mandible (Mivart, 1870; Meyers and Clarke, 1998) on the articular bone (Meyers and Clarke, 1998).

In some species, however, some of the posterior superficial fibers, called the M. depressor mandibulae pars auricularis, insert onto the lateral surface of the occipital lobes (Meyers and Clarke, 1998). The M. depressor mandibulae pars auricularis function to abduct the occipital lobes during display, which are then passively adducted by recoil of the skin and connective tissue on the lobes' medial surface (Meyers and Clarke, 1998). Utilization of a portion of the M. depressor mandibulae for this function, however, also results in movement of the occipital lobes during feeding (C.V. Anderson, personal observation).

JAW ADDUCTOR MUSCULATURE The quadratomaxillary ligament (the zygomatic ligament of Mivart, 1870, and Ogilvie, 1966, and the ligamentum jugomandibulare of Meyers and Clarke, 1998) lies beneath the skin on the side of the head, posterior to the corner of the mouth, and spans between the bones along the posteroventral margin of the orbit and the ventral end of the suspensorium (Mivart, 1870; Poglayen-Neuwall, 1954; Ogilvie, 1966; Rieppel, 1981; Meyers and Clarke, 1998). Deep to this ligament lies the rictal plate (Poglayen-Neuwall, 1954), which serves as a site of muscle attachment for some of the jaw adductor muscles (Schwenk, 2000). Finally, the jaw adductor tendon, called the "bodenaponeurosis" or "basal aponeurosis," which is a large aponeurotic plate attached to the lower jaw, spans between the lower jaw and some of the jaw adductor muscles in multiple sheets or septa (Poglayen-Neuwall, 1954; Rieppel, 1981, 1987). The lateral septum of the bodenaponeurosis is a narrow dorsal projection that extends dorsally from the coronoid process (Rieppel, 1981, 1987). The posterior sheet of the bodenaponeurosis extends dorsally from the posterior to the coronoid process (Rieppel, 1981). The anterior sheet of the bodenaponeurosis is narrow and fan-shaped; it also extends dorsally well into the upper temporal opening from the coronoid process (Rieppel, 1981).

The most superficial of the jaw adductor muscles is the M. levator anguli oris, which consists of an anterior and a posterior division (Rieppel, 1981, 1987). These divisions are weakly separated in some taxa (e.g., *Bradypodion pumilum* [Rieppel, 1981]; *Brookesia superciliaris* [Rieppel, 1987]), whereas in others they are more distinctly separated (e.g., *Trioceros melleri* [Rieppel, 1981]). The M. levator anguli oris anterior originates on the upper temporal arch and the M. levator anguli oris posterior originates on the quadrate (Rieppel, 1981, 1987), with both inserting on the rictal plate at the corner of the mouth (Schwenk, 2000). The M. tensor anguli oris is absent in chameleons (Rieppel, 1981).

Beneath the M. levator anguli oris and rictal plate is the M. adductor mandibulae externus superficialis (Rieppel, 1981). It originates on the medial surface of the upper temporal arch and inserts on the dorsolateral surface of the lower jaw (Rieppel, 1981). Superficially, the fibers of the M. adductor mandibulae externus superficialis extend dorsal to posterodorsally but the deeper fibers transition to more oblique angles approaching the more sharply posterodorsal angle of the fibers of the M. adductor mandibulae externus medialis, which lies beneath it (Rieppel, 1981).

The M. adductor mandibulae externus medialis lies deep to the M. adductor mandibulae externus superficialis and originates and inserts broadly (Rieppel, 1981). The anteriormost fibers originate on the dorsal and dorsoventral edge of the upper temporal fossa on the parietal and squamosal bones, and insert on the dorsal part of the lateral septum of the bodenaponeurosis (Rieppel, 1981, 1987). More medial fibers originate on the medial surface of the posterior side of the upper temporal arch on the squamosal bone and from the cephalic condyle of the quadrate and then insert on the posteroventral portion of the lateral septum of the bodenaponeurosis (Rieppel, 1981, 1987). The posteriormost fibers originate on the lateral surface of the quadrate and insert on the posterior sheet of the bodenaponeurosis (Rieppel, 1981) or on the surangular of the lower jaw (Rieppel, 1987). Some deep fibers of the M. adductor mandibulae externus medialis originate on the parietal and ascending process of the squamosal and insert on the lateral surface of the anterior sheet of the bodenaponeurosis (Rieppel, 1981).

The M. adductor mandibulae externus profundus is divided into three heads, or portions, and overall is enlarged because of the formation of the casque (Rieppel, 1981). The posteroventralmost portion, the so-called 3a-head, corresponds to fibers originating on the anteromedial surface of the quadrate and insert on the dorsomedial surface of the jaw, deep to the posterior sheet of the bodenaponeurosis, but in chameleons cannot be clearly defined (Rieppel, 1981). The pattern of origin and insertion of the anterodorsalmost portion, the so-called 3b-head, varies from one casque structure to another. In *Trioceros,* which have a strong sagittal crest on the parietal bone, the 3b-head originates on the sagittal crest deep to the M. adductor mandibulae externus medialis and inserts on the medial aspect of the anterior sheet of the bodenaponeurosis (Rieppel, 1981). In *Bradypodion,* which have a broad parietal bone with a ventrolateral process, the 3b-head originates on the lower surface of the parietal and on to the ventrolateral process and inserts on the medial surface of the anterior sheet of the bodenaponeurosis (Rieppel, 1981). In both cases, the origin extends anteriorly over the insertion of the M. pseudotemporalis superficialis (Rieppel, 1981) and in some cases onto the posterior edge of the postorbital, where it meets with the parietal (Engelbrecht, 1951). Between the 3a- and 3b-heads lies the so-called 3c-head of the M. adductor mandibulae externus profundus (Rieppel, 1981). The 3c-head originates on the lateral and ventral aspect of the prootic (Rieppel, 1981, 1987), the covering of the surface of the otic capsule wall (Brock, 1941; Engelbrecht, 1951), and the anterior and anterodorsal aspect of the paroccipital process of the back of the skull (Rieppel, 1981). It inserts on the medial surface on the basal portion of the bodenaponeurosis and on the medial surface of the coronoid process itself (Rieppel, 1981).

The M. adductor posterior lies deep to the M. adductor mandibulae externus profundus and is rather large in chameleons (Rieppel, 1981). It originates on the medial edge of the quadrate; on the membrane between the quadrate, prootic, and pterygoid; and on the dorsolateral part of the pterygoid wing (Haas, 1973; Rieppel, 1981). The M. adductor posterior inserts on the medial aspect of the surangular of the lower jaw (Rieppel, 1981).

Although regarded by some as not differentiated (Brock, 1941), the M. pseudotemporalis consists of a superficialis and profundus division and is also deep to the M. adductor mandibulae externus profundus (Haas, 1973; Rieppel, 1981, 1987). The M. pseudotemporalis superficialis originates on the anteromedial aspect of the casque and inserts on the dorsal portion of the tendinous raphe extending dorsally from the coronoid process deep to the bodenaponeurosis (Rieppel, 1981). The M. pseudotemporalis profundus originates on the anterior edge of the prootic and on the membranous sidewall of the braincase anterior to it (Rieppel, 1981). Anterior fibers of the M. pseudotemporalis profundus insert on the posterior base of the tendon, whereas the deeper and more posterior fibers of the M. pseudotemporalis superficialis insert on the medial aspect of the lower jaw direction just posteroventral to the coronoid process (Rieppel, 1981, 1987).

The M. pterygoideus consists of a superficial (ventral) and deep (dorsal) head (Rieppel, 1981). The superficial head originates on the ventral edge and ventromedial aspect of the pterygoid wing and inserts on the lower edge and ventrolateral surface of the lower jaw (Rieppel, 1981). The deep head originates on the lateral aspect of the posteroventral portion of the pterygoid wing and inserts on the medial surface of the lower jaw, just ventral and anteroventral to the jaw joint (Rieppel, 1981).

CONSTRICTOR DORSALIS MUSCULATURE The muscles of the constrictor internus dorsalis complex, which are typically involved in cranial kinesis (Schwenk, 2000), are highly reduced in chameleons (Brock, 1941; Engelbrecht, 1951; Frank, 1951; Haas, 1973; Rieppel, 1981). This is in large part a result of the akinetic structure of the chameleon skull (Haas, 1973).

Whereas the M. levator pterygoidei has been reported in young *Chamaeleo* (Lakjer, 1926; Rieppel, 1981), other research has failed to identify it (Lubosch, 1933; Brock, 1941; Engelbrecht, 1951; Frank, 1951; Poglayen-Neuwall, 1954; Rieppel, 1981, 1987).

The M. protractor pterygoidei is strongly developed in some taxa but only weekly developed in others (Frank, 1951; Haas, 1973; Rieppel, 1981, 1987). It originates on the basipterygoid process (Frank, 1951; Poglayen-Neuwall, 1954; Haas, 1973; Rieppel, 1981, 1987) and inserts on the medial to dorsomedial aspect of the pterygoid wing (Haas, 1973; Rieppel, 1981, 1987). In *Bradypodion,* it is also noted to insert on the ligament connecting the pterygoid wing and the quadrate, thus acting as a quadrate protractor in these taxa (Rieppel, 1981).

The M. levator bulbi ventralis is also lacking in chameleons (Poglayen-Neuwall, 1954; Haas, 1973). The M. levator bulbi dorsalis, however, is present and originates on the prootic wing and inserts on the ventral portion of the eye (Poglayen-Neuwall, 1954; Haas, 1973).

### *Hyobranchial*

One of the more highly specialized features in chameleons is the tongue. In order to achieve ballistic tongue projection, the tongue apparatus has undergone a series of anatomical changes from their agamid-like ancestors. Interest in the tongue of chameleons has resulted in a wide range of studies on its structure and function over the years. These have subsequently resulted in a wide range of varying interpretations and names of the tongue's structures, particularly muscular structures. These name synonyms and the names we've adopted are summarized in Table 2.1 and described in the following sections.

*Tongue Skeleton* The chameleon hyobranchial apparatus is comprised of a reduced basihyoid, an elongate lingual process, and two pairs of cornua (Fig. 2.2a,b) (Bell, 1989; Herrel et al., 2001b; Meyers et al., 2002). The hyobranchial apparatus is suspended in the region of the neck and throat by muscle connection between it and the lower jaw, sternum, and pectoral girdle (Zoond, 1933; Wainwright et al., 1991). The elongate lingual process lies medially and extends anteriorly into the buccal cavity (Houston, 1828).

The elongate lingual process, called the "entoglossal process," is parallel-sided over most of its length, with a tapered anterior tip (Fig. 2.2a,b) (Gnanamuthu, 1930; van Leeuwen, 1997; Wainwright and Bennett, 1992b; Herrel et al., 2001b, 2009; de Groot and van Leeuwen, 2004). The degree of tapering reported in the literature varies from the anterior 10% (Wainwright and Bennett, 1992b) to 1 to 1.5% (Herrel et al., 2001b). Histological sections of the entoglossal process indicate that it is cartilaginous, with hyaline cartilage along its body and a thick layer of dense fibrocartilage near the tip (Herrel et al., 2001b). Some degree of calcification of the entoglossal process is evident, however, as the entoglossal process on cleared and stained specimens stains for bone (Herrel et al., 2001b).

The anterior pair of cornua consists of the ceratohyalia, which are shorter than the posterior pair of cornua (Fig. 2.2a,b) (Gnanamuthu, 1930; Bell, 1989; Wainwright et al., 1991; Herrel et al., 2001b, 2009; Meyers et al., 2002) and are completely cartilaginous (Wainwright et al., 1991; Herrel et al., 2001b; Meyers et al., 2002). Each ceratohyal is divided into two parts, with the proximal part being more robust and the distal part being more flexible (Herrel et al., 2001b). The two parts of the ceratohyals articulate with a synovial joint and the proximal part articulates on the anterior dorsal side of the basihyoid with a U-shaped synovial joint (Herrel et al., 2001b). From the basihyoid, the ceratohyals extend anterodorsally when the tongue apparatus is in its rest position and viewed laterally (Houston, 1828; Bell, 1989;

TABLE 2.1 Muscle Synonomies of Chameleon Hyobranchial Musculature

| This Review | Published Synonyms | Sources |
|---|---|---|
| Musculi (Mm.) mandibulohyoideus medialis[a], lateralis 1[b] et lateralis 2[c] | Mm. geniohyoid "internal"[a] et "external"[b,c] | Houston, 1828; Dewevre, 1895 |
| | M. geniohyoid[a] | Mivart, 1870; Zoond, 1933 |
| | M. ceratomandibular[b,c] | Mivart, 1870 |
| | Mm. geniohyoideus medialis[a] et lateralis[b,c] | Lubosch, 1932; Altevogt and Altevogt, 1954; Altevogt, 1977; Wainwright et al., 1991; So et al., 1992 |
| | M. geniohyoideus | Brücke, 1852a; Wainwright and Bennett, 1992a |
| | M. geniohyoideus[a] | Kathariner, 1894; Germershausen, 1913 |
| | M. genio-ceratoideus[b,c] | Kathariner, 1894; Germershausen, 1913 |
| | M. mandibulohyoideus | Meyers and Nishikawa, 2000; Herrel et al., 2009 |
| | Mm. mandibulohyoideus 1[b], 2[a], et 3[c] | Herrel et al., 2001b |
| | Mm. mandibulohyoideus 1[c], 2[a], et 3[b] | Meyers et al., 2002 |
| M. omohyoideus | M. omohyoid | Houston, 1828; Mivart, 1870 |
| | M. scapula-hyoidien | Dewevre, 1895 |
| | M. omohyoideus | Kathariner, 1894; Germershausen, 1913; Lubosch, 1932; Herrel et al., 2001b; Meyers et al., 2002 |
| Mm. sternohyoideus superficialis[a] et profundus[b] | M. sternohyoideus[a] | Houston, 1828; Mivart, 1870; Kathariner, 1894; Germershausen, 1913; Gnanamuthu, 1930, 1937; Zoond, 1933; Altevogt and Altevogt, 1954; Altevogt, 1977; Wainwright et al., 1991; So et al., 1992; Wainwright and Bennett, 1992a; Meyers et al., 2000; Herrel et al., 2001b, 2009 |
| | M. sternoceratoideus[b] | Houston, 1828; Kathariner, 1894; Germershausen, 1913 |
| | M. sternothyroideus[b] | Mivart, 1870; Gnanamuthu, 1930, 1937; Zoond, 1933; Wainwright et al., 1991; So et al., 1992; Wainwright and Bennett, 1992a; Meyers et al., 2000; Herrel et al., 2001b |

*(Continued)*

TABLE 2.1 *(Continued)*

| This Review | Published Synonyms | Sources |
|---|---|---|
| | Mm. sterno-hyoiden “anterieur”[a] et “postero-lateral”[b] | Dewevre, 1895 |
| | M. sternohyoidei | Lubosch, 1932 |
| | Mm. sternohyoideus superficialis[a] et profundus[b] | Meyers et al., 2002 |
| Mm. genioglossus anterior[a] et posterior[b] | M. genioglossus | Mivart, 1870; Kathariner, 1894; Gnanamuthu, 1930; 1937; Bell, 1989 |
| | M. génio-périglosse | Dewevre, 1895 |
| | Mm. genioglossus anterior[a] et posterior[b] | Herrel et al., 2001b |
| | Mm. genioglossus medialis[b] et lateralis[a] | Meyers et al., 2002 |
| M. constrictor colli | M. constrictor colli | Herrel et al., 2001b |
| Mm. intermandibularis anterior[a] et posterior[b] | M. mylohyoideus | Houston, 1828; Brücke, 1852a; Dewevre, 1895; Gnanamuthu, 1930 |
| | Mm. mylohyoideus anterior[a] and posterior[b] | Mivart, 1870; Kathariner, 1894 |
| | M. intermaxillaris[a] | Germershausen, 1913 |
| | M. mylo-hyoideus posterior[b] | Germershausen, 1913 |
| | Mm. intermandibularis anterior[a] et posterior[b] | Herrel et al., 2001b; Meyers et al., 2002 |
| M. branchiohyoideus | M. ceratohyoideus | Mivart, 1870; Gnanamuthu, 1930 |
| | M. branchiohyoideus | Herrel et al., 2001b |
| M. hyoglossus | M. hyoglossus | Houston, 1828; Brücke, 1852a; Kathariner, 1894; Gnanamuthu, 1930, 1937; Lubosch, 1932; Zoond, 1933; Altevogt and Altevogt, 1954; Altevogt, 1977; Bell, 1989; So et al., 1992; Wainwright and Bennett, 1992a; Herrel et al., 2000, 2001a,b, 2002, 2009; Meyers and Nishikawa, 2000, 2002; de Groot and van Leeuwen, 2004 |
| | M. glosso-hyoidiens | Dewevre, 1895 |
| | “glossohyal muscle” | Gans, 1967 |
| | “retractor muscle” | Wainwright et al., 1991 |
| | “hyoglossal muscle” | Wainwright and Bennett, 1992a |

TABLE 2.1 *(Continued)*

| This Review | Published Synonyms | Sources |
|---|---|---|
| M. accelerator linguae | "Annular muscle" | Houston, 1828 |
| | "ring muscle" | Gnanamuthu, 1930, 1937; Zoond, 1933 |
| | "accelerator muscle" | Gans, 1967; Wainwright et al., 1991; So et al., 1992; Wainwright and Bennett, 1992a,b; van Leeuwen, 1997; Meyers et al., 2002; de Groot and van Leeuwen, 2004 |
| | M. accelerator | Kathariner, 1894; Lubosch, 1932; Altevogt and Altevogt, 1954; Altevogt, 1977; Herrel et al., 2000, 2001a,b, 2009; Meyers and Nishikawa, 2000 |
| | M. accelerator linguae | Brücke, 1852a; Kathariner, 1894; Sewertzoff, 1923; Altevogt and Altevogt, 1954; Altevogt, 1977; Schwenk and Bell, 1988; Bell, 1989 |
| M. "retractor pouch" | M. longitudinales linguae adductoris | Brücke, 1852a; Gnanamuthu, 1930, 1937; Zoond, 1933; Bell, 1989 |
| | M. hyoglossus superficialis | Kathariner, 1894 |
| | M. pouch retractor | Herrel et al., 2000 |
| | M. "retractor pouch" | Herrel et al., 2001b |
| M. longitudinalis linguae ventralis | M. submucosus | Brücke, 1852a |
| | M. hyoglossus profundus | Kathariner, 1894 |
| | M. longitudinalis linguae extensoris | Gnanamuthu, 1930, 1937; Zoond, 1933; Bell, 1989 |
| | M. longitudinalis linguae ventralis | Herrel et al., 2001b |
| M. pulvinaris | M. pulvinar | Brücke, 1852; Lubosch, 1932 |
| | "Ringmuskel für den Fangnapf" | Altevogt, 1977 |
| | M. pulvinaris | Bell, 1989; Herrel et al., 2001b |
| Mm. transversalis linguae anterior[a] et posterior[b] | M. lateralis linguae | Brücke, 1852a |
| | M. transversalis linguae[a] | Gnanamuthu, 1930, 1937 |
| | M. lateralis linguae[b] | Gnanamuthu, 1930 |
| | M. transversalis linguae externi[a] | Bell, 1989 |
| | M. superficialis linguae[b] | Bell, 1989 |
| | Mm. transversalis linguae anterior[a] and posterior[b] | Herrel et al., 2001b |

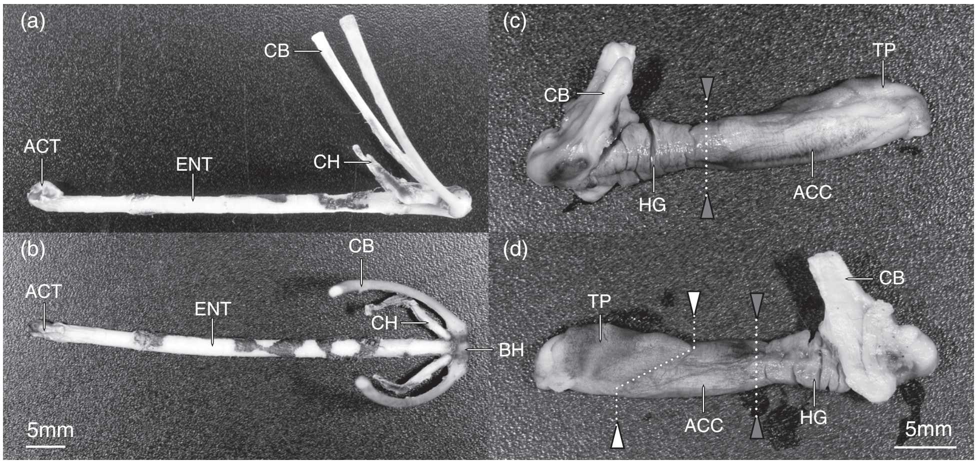

FIGURE 2.2. Skeletal and muscular components of the chameleon tongue apparatus. Lateral (a) and dorsal (b) views of the skeletal elements of the tongue of *C. p. parsonii*. Ventrolateral (c) and dorsolateral (d) views of the muscular elements of the tongue of *T. johnstoni* at rest. Anterior end of elements at left in (a), (b), and (d), and at right in (c). Scale bar at bottom left applies to (a) and (b), and that at bottom right to (c) and (d). Modified from Anderson et al. (2012).

LABELS: ACC = M. accelerator linguae; ACT = articulating cartilaginous tip; BH = basihyoid; CB = ceratobranchial; CH = ceratohyal; ENT = entoglossal process; HG = M. hyoglossus; TP = tongue pad. Dotted lines between gray triangles in (c) and (d) indicate division between HG and ACC. Dotted line between white triangles in (d) indicate posterior limits of the TP.

Herrel et al., 2001b). When viewed in a transverse plane, the ceratohyals form a U-shape. As the entoglossal process is pulled forward during tongue protrusion, the ceratohyals rotate and are pointed upward (Herrel et al., 2001b). In some species, the distal part of the ceratohyal has a flat triangular piece of cartilage attached to it (Gnanamuthu, 1930; Herrel et al., 2001b).

The posterior pair of cornua is the ceratobranchials, which are ossified and longer than the ceratohyals (Fig. 2.2a,b) (Gnanamuthu, 1930; Bell, 1989; Herrel et al., 2001b; Meyers et al., 2002). The ceratobranchials articulate with the posterior side of the basihyoid with a saddle-shaped synovial joint (Herrel et al., 2001b; Meyers et al., 2002). At rest, the ceratobranchials extend anterodorsally (Gnanamuthu, 1930; Bell, 1989) to dorsally in a nearly perpendicular direction to the long axis of the hyobranchial apparatus when viewed laterally (Herrel et al., 2001b; Meyers et al., 2002). When viewed in a transverse plane, the ceratobranchials form a U-shape. During protrusion of the tongue, the ceratobranchials rotate and are folded backward (Wainwright et al., 1991; Herrel et al., 2009).

*Hyobranchial Musculature* The hyobranchial apparatus is suspended in the throat by muscles that originate outside the hyobranchial apparatus and insert on the hyobranchial skeleton (Bell, 1989; Wainwright et al., 1991). These muscles serve to draw the hyobranchial apparatus forward and back during tongue protrusion and hyobranchial retraction (Gnanamuthu, 1930; Bell, 1990; Herrel et al., 2009).

The paired M. mandibulohyoideus consists of three distinct divisions (Gnanamuthu, 1930; Herrel et al., 2001b). The M. mandibulohyoideus medialis originates near the symphysis of the lower jaw via a short aponeurosis and inserts on the ventral surface of the basihyoid (Wainwright and Bennett, 1992a; Herrel et al., 2001b). The M. mandibulohyoideus lateralis 1 originates lateral to the symphysis of the lower jaw and inserts on the tip of the ceratohyal (Herrel et al., 2001b). The M. mandibulohyoideus lateralis 2 originates on the jaw between the M. mandibulohyoideus medialis and M. mandibulohyoideus lateralis 1, is attached to the M. mandibulohyoideus lateralis 1 for most of the latter's length, and inserts on the distal third of the ceratobranchial (Herrel et al., 2001b). Together, the M. mandibulohyoideus serves to draw the hyobranchial apparatus anteriorly during tongue protrusion and protraction and is active during prey transport (Brücke, 1852a; Dewevre, 1895; Gnanamuthu, 1930; Zoond, 1933; Wainwright et al., 1991; Wainwright and Bennett, 1992a; Meyers and Nishikawa, 2000). The two divisions of the M. mandibulohyoideus lateralis may also serve to facilitate articulation of the cornua with the basihyoid by drawing the tips of the cornua forward as the M. sternohyoideus draws the basihyoid back during hyobranchial retraction (Dewevre, 1895; Gnanamuthu, 1930).

The paired M. omohyoideus originates on the anterior, ventral side of the scapula and inserts on the posterior side of the lateral aspect of the basihyoid (Mivart, 1870; Gnanamuthu, 1930, 1937; Meyers et al., 2002). From the basihyoid, however, it extends dorsally to wrap around the M. sternothyroideus before returning ventrally and curving under the M. episternocleidomastoideus toward the scapula (Herrel et al., 2001b; Meyers et al., 2002). It serves to draw the basihyoid upward (Mivart, 1870; Gnanamuthu, 1930).

The paired M. sternohyoideus consists of a superficialis and a profundus division (Meyers et al., 2002). The M. sternohyoideus superficialis originates on the posteroventral surface of the xiphisternum (xiphoid process) and inserts on the ventral side of the basihyoid (Gnanamuthu, 1930; Herrel et al., 2001b; Meyers et al., 2002). It serves to draw the basihyoid posteriorly during hyobranchial retraction (Gnanamuthu, 1930, 1937; Zoond, 1933; Wainwright and Bennett, 1992a). The M. sternohyoideus profundus consists of two divisions (Herrel et al., 2001b). The anterior division originates on the midbody connective-tissue band anterior to the xiphisternum and inserts on the posterior tip of the ceratobranchial (Herrel et al., 2001b). The posterior division also originates on the midbody connective-tissue band but immediately anterior to the xiphisternum and inserts onto the posterior side of the dorsal half of the ceratobranchial (Herrel et al., 2001b). Together, they serve to draw the distal end of the ceratobranchials in a posteroventral direction during tongue protrusion (Gnanamuthu, 1930, 1937; Wainwright and Bennett, 1992a).

Within the throat and buccal cavity, support and movement of the hyobranchial apparatus is facilitated by intermandibular musculature (Gnanamuthu, 1930; Herrel et al., 2001b). These muscles originate on the skull and mandible and generally serve to elevate the throat and gular regions, and in doing so elevate the hyobranchial apparatus within the throat and buccal cavity (Gnanamuthu, 1930).

The paired M. genioglossus consists of an anterior and a posterior division (Herrel et al., 2001b). They originate on the inner surface of the mandible and insert on the buccal-floor epithelium (Gnanamuthu, 1930; Bell, 1989; Herrel et al., 2001b), with the anterior portion inserting via a tendon (Herrel et al., 2001b). The anterior division inserts at the level of the basihyoid, whereas the posterior division inserts on an aponeurosis at the floor of the throat (Herrel et al., 2001b). The M. genioglossus forms a pouch around the tongue inside the mouth and when contracted form paddle-like lips on either side of the tongue (Gnanamuthu, 1930, 1937; Bell, 1989).

The paired M. constrictor colli originates on the dorsal nuchal/cervical fascia and inserts on the midventral fascia (Herrel et al., 2001b; Meyers et al., 2002). From its origin, it extends ventrally and then posterior to the lower jaw and curves medially toward the midventral fascia (Herrel et al., 2001b). It serves to elevate the throat (Gnanamuthu, 1930).

The paired M. intermandibularis consists of two divisions, an anterior and a posterior one (Gnanamuthu, 1930; Herrel et al., 2001b), with the anterior division being further divided into a principalis and profundus sheet by some researchers (Gnanamuthu, 1930, 1937). They originate broadly along the inner surface of the mandible and lower jaw, with the posterior division originating via a short aponeurosis (Herrel et al., 2001b). The anterior division inserts on the midventral fascia, which is attached to the jaw symphysis, and the posterior division inserts on the midventral fascia via an aponeurosis (Herrel et al., 2001b; Meyers et al., 2002). The M. intermandibularis anterior principalis runs anteromedially toward its insertion, whereas the M. intermandibularis anterior profundus runs posteromedially toward its insertion (Gnanamuthu, 1930). Together they serve to elevate the floor of the mouth.

Within the hyobranchial apparatus itself, the paired M. branchiohyoideus spans between the posterior edge of the distal third of the ceratohyal and the anterior side of the distal quarter of the ceratobranchial (Gnanamuthu, 1930; Herrel et al., 2001b). It enables movement of the cornua with respect to each other, as the aforementioned muscles that insert on them modulated their position.

The paired M. hyoglossus originates on the medial surface of the ceratobranchial along its entire length and inserts under the strong outer layer of connective tissue on the lateral aspect of the M. accelerator linguae at approximately a quarter of its length (Fig. 2.2c,d) (Herrel et al., 2001b; Meyers et al., 2002). The muscle is bulky near its origin and quickly narrows as it runs ventrally to the proximal end of the ceratobranchial (Gnanamuthu, 1930; Bell, 1989; Herrel et al., 2001b). It then passes under the ceratohyal by its articulation with the basihyoid (Gnanamuthu, 1930; Bell, 1989; Herrel et al., 2001b). At rest, the M. hyoglossus is heavily pleated around the posterior end of the entoglossal process until it reaches the posterior edge of the M. accelerator linguae (Fig. 2.2c,d) (Herrel et al., 2001b; Meyers et al., 2002). The M. hyoglossus is surrounded by a sheath of epimysium between the M. accelerator linguae and the base of the entoglossal process (Meyers et al., 2002). Fully elongated, the M. hyoglossus extends up to 600% of its resting length (Herrel et al., 2001a, 2002). This extreme shortening capability is the result of supercontracting muscle fibers with perforated Z discs, which allow filaments within each muscle sarcomere to extend through the Z discs and into adjacent sarcomeres (Rice, 1973; Bell, 1989; Schwenk, 2000; Herrel et al., 2001a, 2002). The M. hyoglossus serves to retract the M. accelerator linguae back onto the entoglossal process following tongue projection (Altevogt and Altevogt, 1954; Gans, 1967; Bell, 1989; Wainwright and Bennett, 1992a).

The M. accelerator linguae surrounds the entoglossal process at rest and is surrounded by an inner and outer tendinous connective-tissue sheath (Fig. 2.2c,d) (Gnanamuthu, 1930; Bell, 1989; Herrel et al., 2001b). The posterior three quarters form a muscular tube around the entoglossal process (Gnanamuthu, 1930; Bell, 1989; Herrel et al., 2001b), with muscle fibers extending radially between the inner and outer tendinous sheaths in a cross-helical fashion (Gnanamuthu, 1930; Gans, 1967; Bell, 1989; van Leeuwen, 1997; Herrel et al., 2001b; de Groot and van Leeuwen, 2004). The anterior quarter of the M. accelerator linguae divides into a dorsal and a ventral projection (Gnanamuthu, 1930; Bell, 1989; Herrel et al., 2001b). The dorsal bundle extends to the posterior edge of the tongue pouch, whereas the ventral bundle extends all the way to the tip of the tongue (Herrel et al., 2001b). The dorsal bundle is continuous with the posterior three quarters of the M. accelerator linguae, with muscle fibers oriented perpendicularly to the long axis of the hyobranchial apparatus (Herrel et al., 2001b). The ventral bundle has similarly oriented muscle fibers and is continuous with the posterior three quarters up to the approximate location where the dorsal bundle ends, at which point a vertical connective-tissue septum separates the remaining length of the ventral projection of the M. accelerator linguae (Herrel et al., 2001b). The M. accelerator linguae serves to push the tongue off the entoglossal process (Gans, 1967; Altevogt, 1977; Bell, 1989; Wainwright and Bennett, 1992a,b) and load elastic elements involved in tongue projection (de Groot and van Leeuwen, 2004).

The paired M. "retractor pouch" originates on the dorsolateral side of the M. accelerator linguae on the posterior third of its length and inserts medially on the inner side of the membrana grandulosa of the tongue pad, which is invaginated at rest (Herrel et al., 2001b). It serves to draw the center of the tongue pad posteriorly during prey prehension (Herrel et al., 2000), thus invaginating the membrane grandulosa of the tongue pad.

The paired M. longitudinalis linguae ventralis originates immediately posterior to the bifurcated tongue tip on the internal surface of the tongue pad and inserts on the lateral side of the anteroventral, noncircular portion of the M. accelerator linguae (Bell, 1989; Herrel et al., 2001b). Whereas some studies suggest that this muscle's action involves extension of the tongue (Gnanamuthu, 1930), it appears clear that it is not an extensor (Herrel et al., 2001b) but likely serves to draw the ventral aspect of the tongue pad back, possibly drawing the bifurcated tongue tip ventrally in the process.

The paired M. pulvinaris is restricted to the tongue pad, where it develops at its posterior end, extends anteriorly, and ends immediately anterior to the tongue pouch (Brücke, 1852a; Bell, 1989; Herrel et al., 2001b).

The M. transversalis linguae consists of an anterior and a posterior division. The paired M. transversalis linguae anterior originates on the dorsal aspect of the anterior, noncircular portion of the M. accelerator linguae and inserts immediately anterior to the pouch on the inner surface of the tongue pad (Herrel et al., 2001b). The paired M. transversalis linguae posterior originates on the dorsolateral surface of the M. accelerator linguae on its posterior end and inserts posterior to the pouch on the medial inner surface of the tongue pad (Herrel et al., 2001b).

Located between the entoglossal process and the tongue muscles that surround it is an assortment of connective tissue (Gnanamuthu, 1930; Zoond, 1933; Gans, 1967; Bell, 1989; Herrel et al., 2001b; de Groot and van Leeuwen, 2004) that is comprised of a series of nested intralingual sheaths (Gnanamuthu, 1930; Bell, 1989; de Groot and van Leeuwen, 2004). At the anterior tip of the entoglossal process, a short articulating cartilaginous projection, which is folded back on the entoglossal process at rest, is found (Herrel et al., 2001b). This articulating cartilaginous tip connects the layer of longitudinal collagen fibers surrounding the entoglossal process, the perichondrium, to the innermost intralingual collagen sheath between the entoglossal process and the M. accelerator linguae (de Groot and van Leeuwen, 2004). The innermost intralingual sheaths are longer than more peripheral sheaths, as the inner sheaths attach more proximally on the hyobranchial apparatus than the outer sheaths (de Groot and van Leeuwen, 2004). The innermost sheath is attached at its posterior end to the fascia of the M. hyoglossus, near the articulation of the entoglossal process and the certobranchials, and each subsequent sheath attaches slightly anterior to the previous sheath (de Groot and van Leeuwen, 2004). More peripheral sheaths eventually are connected to the inner fascia of the M. accelerator linguae (de Groot and van Leeuwen, 2004). The inner sheaths are connected to each other only via their attachment to the M. hyoglossus and are able to slide past each other in a telescoping fashion as the tongue extends (de Groot and van Leeuwen, 2004). In addition to their structural connection at their attachment, the more peripheral sheaths are also interconnected by collagenous trabeculae (de Groot and van Leeuwen, 2004). The collagen fibers of the peripheral sheaths, which lie medial to the M. accelerator linguae, are arranged in a cross-helical pattern (de Groot and van Leeuwen, 2004). The fibers of the inner sheaths are also arranged in a cross-helical pattern in the portions of these sheaths that lie medial to the M. accelerator linguae; however, the fibers in the portions that are posterior to the M. accelerator linguae run parallel to the long axis of the entoglossal process (de Groot and van Leeuwen, 2004).

### *Trunk and Tail*

Chameleons are adapted to be able to produce a large amount of dorsoventral flexion. This is particularly true in their highly prehensile tail, which they are able to curl tightly under their body. Various works have been done on the vertebral column and tail of the chameleon (e.g. Siebenrock, 1893; Camp, 1923; Ali, 1948; Romer, 1956; Etheridge, 1967; Hoffstetter and Gasc, 1969; Zippel et al., 1999) but surprisingly little has been done on the trunk musculature (e.g., Mivart, 1870; Sathe, 1959).

*Vertebral Column and Ribs* The vertebral column of chameleons has been examined in only a handful of taxa. These studies have found the vertebral column within the family to be variable in a number of regards and to possess a number of functional specializations as compared with other Saurians.

One of the most variable features of the chameleon vertebral column is the number of vertebrae. The number of presacral (cervical, thoracic, and lumbar) vertebrae is known to range from 14 (Bergmann and Irschick, 2011) to 23 (Hoffstetter and Gasc, 1969). Whereas having fewer

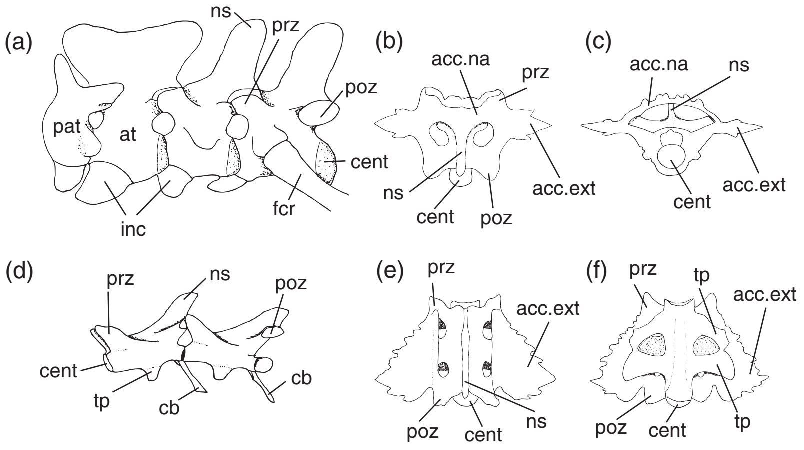

FIGURE 2.3. Vertebral elements of a generalized *Bradypodion* (a), *Brookesia superciliaris* (b, c, e, f) and *Chamaeleo zeylanicus* (d). Depicted are a lateral view of the first four cervical vertebrae (a), a dorsal (b) and transverse (c) view of a trunk (thoracic/lumbar) vertebrae, a lateral view of two proximal caudal vertebrae (d), and a dorsal (e) and ventral (f) view of the sacral vertebrae (fused into a synsacrum in *Brookesia*). (a) redrawn from Raw (1976; originally based on Hoffstetter and Gasc, 1969), (b, c, e, f) from Siebenrock (1893), and (d) from Ali (1948).

LABELS: acc.ext = accessory extension; acc.na = accessory neural arch; at = atlas; cb = chevron bone (hemal arch); cent = centrum; fcr = first cervical rib; inc = intercentra; ns = neural spine; pat = proatlas; poz = postzygapophysis; prz = prezygapophysis; tp = transverse process.

than 23 presacral vertebrae is known only within Saurians that occur in the suborder Iguania, this range represents a reduction in the typical number of presacral vertebrae seen in the Iguanidae and Agamidae (Hoffstetter and Gasc, 1969). Further, with 14 presacral vertebrae, *Brookesia superciliaris* has among the lowest number of trunk vertebrae of all squamate reptiles (Bergmann and Irschick, 2011). Posteriorly, there are two sacral vertebrae in all taxa (Hoffstetter and Gasc, 1969) and caudal vertebrae are known to range from 17 (Nečas, 2004) to 62 (Etheridge, 1967) with smaller, more terrestrial genera typically having fewer caudal vertebrae then larger, more arboreal genera (Etheridge, 1967; Nečas, 2004; Boistel et al., 2010).

All vertebrae have large procoelous centrums (Camp, 1923; Hoffstetter and Gasc, 1969; Raw, 1976) with elongated, cylindrical centra (Camp, 1923; Romer, 1956) and intercentra confined only to the cervical region (Fig. 2.3a) (Hoffstetter and Gasc, 1969). The neural spine is generally quite tall and typically extends posterodorsally with a posterior incline and terminates with a straight, axe-shaped dorsal edge (Fig. 2.3a,d) (Hoffstetter and Gasc, 1969). The neural spine can be elongated considerably in certain regions of the spine in some species, such at *Trioceros cristatus* or *T. montium* (Case, 1909). In these cases, the distal ends of the neural spines are connected by strong connective tissue threads and covered with a skin membrane forming a strongly elevated crest (Case, 1909). Zygosphenes and zygantra are absent from the vertebra (Raw, 1976). The articular facets of the prezygapophyses and postzygapophyses are steep, resulting in near-vertical articulation, thus allowing for increased dorsoventral flexion (Hoffstetter and Gasc, 1969). Precaudal vertebrae lack ventral hypapophyses in some species (Raw, 1976); however, three or four cervical intercentra are typical (Fig. 2.3a) (Hoffstetter and Gasc, 1969).

All chameleons have five cervical vertebrae (Siebenrock, 1893; Werner, 1902b; Hoffstetter and Gasc, 1969; Raw, 1976; Nečas, 2004). However, some researchers (Camp, 1923; Romer, 1956) have indicated the presence of only three, because the last two cervical vertebrae bear long cervical ribs (Fig. 2.3a) (Siebenrock, 1893; Werner, 1902b; Hoffstetter and Gasc, 1969; Raw, 1976; Nečas, 2004). These cervical ribs do not fuse to the sternum, however (Siebenrock, 1893; Hoffstetter and Gasc, 1969). The first two cervical vertebrae are the proatlas and atlas, respectively (Fig. 2.3a) (Hoffstetter and Gasc, 1969; Raw, 1976), with the proatlas appearing among Saurians only in the chameleons (Hoffstetter and Gasc, 1969). The three or four intercentra are always separated and maintain an intervertebral position on the ventral aspect of the cervical region of the vertebral column (Fig. 2.3a) (Hoffstetter and Gasc, 1969).

Given a constant number of cervical vertebrae (Hoffstetter and Gasc, 1969; Raw, 1976; Nečas, 2004), the combined number of thoracic and lumbar vertebrae varies from 9 (Bergmann and Irschick, 2011) to 18 (Hoffstetter and Gasc, 1969). Thoracic vertebrae have both sternal and parasternal ribs (Hoffstetter and Gasc, 1969), and the first two lumbar vertebrae typically have reduced lumbar ribs (Hoffstetter and Gasc, 1969; Raw, 1976).

The ribs in chameleons are unicipital, with a single articulation between the rib and the vertebra (Hoffstetter and Gasc, 1969) on the lateral margin of the vertebra (Rieppel, 1993). The ribs generally have two proximodistal segments, a bony vertebrocostal and a cartilaginous sternocostal segment, although a third cartilaginous intercostal segment between the two aforementioned segments is sporadically seen within the Chamaeleonidae (Hoffstetter and Gasc, 1969). Three to four sternal ribs, which are joined to the sternum or mesosternum, are seen (Methuen and Hewitt, 1914; Hoffstetter and Gasc, 1969). Parasternal ribs have their distal cartilaginous segments fuse on the midventral line, forming a parasternum posterior to the sternum (Camp, 1923; Hoffstetter and Gasc, 1969) and range in number from 5 to 11 (Sathe, 1959; Hoffstetter and Gasc, 1969). Two reduced lumbar ribs are observed on the anteriormost lumbar vertebrae (Hoffstetter and Gasc, 1969; Raw, 1967).

The thoracic and lumbar vertebrae in *Brookesia* are somewhat different from those of other chameleons. Their thoracic and lumbar vertebrae have a bony arch between the prezygapophyses and postzygapophyses on one side of a single vertebrae and an accessory neural arch extending from this arch to the ridge of the neural spine (Fig. 2.3b,c) (Siebenrock, 1893; Parker, 1942; Rieppel, 1987). These bony shields (Romer, 1956) result in channels on either side of the neural spine, which have muscles running within them (Fig. 2.3c) (Siebenrock, 1893; Parker, 1942), and a more rounded dorsal crest with a less distinct ridge. In addition, some *Brookesia* have accessory extensions projecting laterally off the arch between the prezygapophyses and postzygapophyses, corresponding to their laterovertebral spines (Fig. 2.3b,c,e,f) (Siebenrock, 1893; Parker, 1942).

The sacrum is typical in possessing two vertebrae (Werner, 1902b; Hoffstetter and Gasc, 1969; Raw, 1976). These vertebrae bear wing-like transverse processes or sacral pleurapophyses (Hoffstetter and Gasc, 1969; Raw, 1976), which are made up of fused sacral ribs (Hoffstetter and Gasc, 1969). The sacral vertebrae in *Brookesia* are fused to form a synsacrum (Fig. 2.3e,f) (Siebenrock, 1893; Klaver, 1979; Nečas, 2004).

The number of caudal vertebrae varies considerably between species (Etheridge, 1967; Nečas, 2004; Boistel et al., 2010). The transverse processes are dorsoventrally compressed and project ventrally rather than laterally in *Chamaeleo* (Fig. 2.3d) (Ali, 1948); however, in *Furcifer*, there is a transition from the transverse processes projecting ventrolaterally on the proximal portion of the tail to more laterally on the more distal portions of the tail (Zippel et al., 1999). Intervertebral chevron bones form the hemal arch (Fig. 2.3d) (Ali, 1948; Romer, 1956; Etheridge, 1967; Hoffstetter and Gasc, 1969) and become smaller in size distally, disappearing toward the end (Etheridge, 1967; Hoffstetter and Gasc, 1969). These chevron bones start on the first caudal vertebra in *Brookesia*; however, in other chameleons they do not begin immediately and result in up to four proximal caudal vertebrae lacking a chevron bone (called "pygal vertebrae") (Hoffstetter and Gasc, 1969). No caudal autotomy and no autotomy planes exist in chameleons (Romer, 1956; Etheridge, 1967; Hoffstetter and Gasc, 1969).

A number of adaptations for increased dorsoventral flexion of the tail are seen in the morphology of the caudal vertebrae. The surface of the anterior and posterior vertebral centrum are not evenly rounded, with a reduced ventral lip on the concave surface of the anterior centrum and a stronger sloped dorsal half of the convex surface of the posterior centrum (Ali, 1948). This pattern becomes more prominent distally and allows for increased dorsoventral articulation between adjacent caudal vertebrae (Ali, 1948). In addition, the prezygapophysis and postzygapophysis of the caudal vertebrae are elongated (Fig. 2.3d) (Ali, 1948; Zippel et al., 1999). The steep slope of the facets on the prezygapophysis and postzygapophysis (Ali, 1948; Hoffstetter and Gasc, 1969), allow for dorsoventral movement, while restricting lateral movements, and their length allows the interlocking prezygapophysis and postzygapophyses to remain in close contact even when the tail is fully coiled (Ali, 1948).

The form of the caudal vertebrae differs once again in *Brookesia*. Like the thoracic and lumbar vertebrae, the more proximal caudal vertebrae of *Brookesia* have a bony arch extending from the ridge of the neural spine to an arch between the prezygapophysis and postzygapophyses (Boistel et al., 2010). They also have an additional arch extending from the arch between the zygapophyses and the ridge of the transverse processes, which extends ventrolaterally in *Brookesia* (Boistel et al., 2010). More terminal caudal vertebrae, however, lack this bony shield, likely resulting in increased vertebral mobility of the distal portion of the tail (Boistel et al., 2010).

*Trunk Musculature* The trunk musculature in reptiles is broadly arranged into epaxial and hypaxial musculature based on innervation from either the dorsal or the ventral branch of the spinal nerves, respectively, rather than on topographic criteria, as in fishes (Gasc, 1981). In general, however, the trunk musculature in chameleons has not been thoroughly examined (see Mivart, 1870, and Sathe, 1959) and is only superficially discussed here as a result.

In general, epaxial muscles of reptiles are divided into medial, central, and lateral columns, consisting of the M. transversospinalis group, M. longissimus group, and M. iliocostalis group, respectively (Gasc, 1981). The epaxial musculature in chameleons is highly reduced (Gasc, 1981), largely because movements of the girdles substitute for bending of the body column (Peterson, 1973; Gasc, 1981). Mivart (1870) refers to upper and inferior portions of the longissimus dorsi, presumably referring to the M. transversospinalis and M. longissimus, respectively, which extend onto the tail (see "Tail Musculature," below). Muscles that could be associated with the M. iliocostalis group are not clearly described by Mivart (1870) and the arrangement in other Saurians is diverse (Gasc, 1981).

Hypaxial musculature in reptiles is typically divided into medial, lateral, and subvertebral layers (Gasc, 1981). The medial layer includes the M. transversus, M. obliquus internus, M. intercostalis internus, and M. rectus (Mivart, 1870; Gasc, 1981). The lateral layer consists of the M. intercostalis externus and M. obliquus externus (Mivart, 1870; Gasc, 1981). Finally, the subvertebral layer is generally restricted to the neck in Saurians (Gasc, 1981), and muscles that could be associated with this layer are not clearly described by Mivart (1870).

*Tail Musculature* The caudal muscles are primarily organized into four longitudinal muscle bundle pairs (Ali, 1948; Zippel et al., 1999). Two of these pairs lie dorsal to the axis of rotation of the vertebrae and represent the epaxial musculature of the tail (M. transversospinalis and M. longissimus), whereas the other two pairs lie ventral to the axis of rotation and represent the hypaxial musculature (M. iliocaudalis and M. inferocaudalis) (Ali, 1948; Zippel et al., 1999). One to two tendinous bands originate from each of these muscles every vertebral length, creating a segmented pattern to the tail musculature (Zippel et al., 1999). These tendinous bands insert onto one or more distal or proximal vertebral processes (Ali, 1948; Zippel et al., 1999). Activity of the epaxial musculature is responsible for extending the tail, whereas activity of the hypaxial musculature is responsible for curling it (Ali, 1948; Zippel et al., 1999).

The M. transversospinalis occupies the space between the neural spine and the zygapophyses on each side of the caudal vertebrae (Ali, 1948; Zippel et al., 1999). Each segment of this muscle gives rise to a single tendinous band, about halfway between two successive neural spines, which extend posteroventrally (Zippel et al., 1999). Approximately halfway between the posterior of the two aforementioned neural spines and the next most distal neural spine, these tendons bifurcate, with one branch continuing to run posteroventrally to insert on the next postzygapophysis and the second branch running posterodorsally to insert on the next neural spine before continuing posteroventrally (Zippel et al., 1999). A division of the M. transversospinalis, called the "M. interspinalis," originates on a neural spine and inserts on the next most distal neural spine via a tendon, which continues posteroventrally (Zippel et al., 1999).

The M. longissimus occupies the space between the zygapophyses and the transverse process on each side of the caudal vertebrae (Ali, 1948; Zippel et al., 1999). Each segment gives rise to a single, broad tendon posteroventrally to a zygapophysis (Zippel et al., 1999). This tendinous band runs anteriorly past the next most proximal zygapophysis, where it extends superficially from beneath the previous muscle segment's tendon (Zippel et al., 1999). The tendon continues anteriorly, where it is supplanted by the next tendon, to which it continues to run dorsal, eventually inserting on a prezygapophysis a few vertebrae anterior to where its associated muscle gave rise to it (Zippel et al., 1999). While the tendon is running superficially to the previous muscle segment's tendon and before it is supplanted by the next muscle segment's tendon, a branch splits off the tendon and runs anteroventrally and inserts onto circumferential connective tissue dorsal to the transverse processes (Zippel et al., 1999).

The M. iliocaudalis occupies the space below the transverse processes on each side of the caudal vertebrae but also extends between and slightly above them as well (Ali, 1948; Zippel et al., 1999). This muscle is composed of distinct dorsalis and ventralis divisions (Ali, 1948; Zippel et al., 1999), but because of the transition of the transverse process from a ventrolateral projection proximally to a primarily lateral projection more distally in some species, their positions relative to this process may vary along the length of the tail (Zippel et al., 1999). On the proximal portion of the tail, the tendinous band of the M. iliocaudalis dorsalis originates above the transverse process but transitions to originating below the transverse process more distally (Zippel et al., 1999). This tendon runs posteriorly and spans at least one vertebra before inserting on the tip of the transverse process on a more posterior vertebrae on the proximal end of the tail or on the circumferential connective tissue more distally (Zippel et al., 1999). As it runs across the transverse process of the vertebrae proximal to its insertion, a branch breaks off of this tendon and extends posterodorsally (Zippel et al., 1999). The insertion of this branch, however, varies along the length of the tail (Zippel et al., 1999). On the proximal portion of the tail, the tendinous band of the M. iliocaudalis ventralis originates anteroventral to the transverse process but transitions to originating in the cleft separating the M. iliocaudalis and M. inferocaudalis more distally (Zippel et al., 1999). Although Ali (1948) finds that these tendons run anteriorly, Zippel et al. (1999) find that they run posteriorly and emerge from within the muscle at the next transverse process. Zippel et al. (1999) go on to describe that approximately halfway to the next transverse process, the tendon bifurcates, with the dorsal branch extending beyond that of the next transverse process and inserting on the next more distal one; the ventral branch joins with the superficial circumferential connective tissue as it goes deep between the M. iliocaudalis ventralis and M. inferocaudalis, presumably then inserting on the hemal arch (Zippel et al., 1999).

The M. inferocaudalis occupies the space along the ventral side of the caudal vertebrae and is separated at the midline by a vertical septum (Ali, 1948). The tendinous bands from this muscle originate along this septum and run posteriorly into the cleft between the two sides of this muscle, where they presumably insert on the hemal arches (Zippel et al., 1999). The number of vertebrae these bands span appears to increase distally (Zippel et al., 1999). A branch off the more proximal tendons extends dorsally along the surface of the muscle and joins with the superficial circumferential connective tissue as it runs deep between the M. iliocaudalis ventralis and M. inferocaudalis (Zippel et al., 1999). In *Brookesia*, in which the proximal portion of the tail is largely immobile in many species, these ventromedial tendons are more strongly developed distally where tail mobility is increased (Boistel et al., 2010).

### Appendicular

As with other aspects of chameleon biology, the appendicular musculoskeletal system is highly specialized. This is likely influenced by the arboreal habitat in which most (but not all) chameleons live. In particular, chameleons tend to use perches of relatively small diameter, and there is often considerable perch discontinuity (Peterson, 1984). In addition to the constraints imposed by an arboreal habitat (see Chapter 4), chameleons are cryptic and move very slowly in their natural habitat (Hopkins and Tolley, 2011). Despite the unique morphological and behavioral attributes, a paucity of information exists on the locomotor system of chameleons. This is in contrast to our understanding of general appendicular morphology in other lizards (Jackson, 1973; Losos, 1990; Garland and Losos, 1994; Aerts et al., 2000; Melville and Swain, 2000; Johnson and Russell, 2009; Higham and Russell, 2010). The terminology used in this section follows that of Russell and Bauer (2008) and is somewhat different from the older terminology used by Mivart (1870). This section is not meant to be exhaustive. Rather, we will focus on the skeletal elements and muscles that differ in anatomy from other lizards, such as *Iguana iguana* and *Agama agama*.

#### *Pectoral Girdle and Forelimb*

*Skeletal Elements* The shoulder region is probably one of the most noted features of the chameleon locomotor apparatus (Peterson, 1984). When considering the anatomy of the pectoral girdle, a common theme is the increased girdle mobility (Peterson, 1984). In addition, the girdle of chameleons is more laterally compressed, which has traditionally been linked to a relatively upright posture as compared with other lizards. However, see Chapter 4 for a detailed discussion regarding posture in chameleons.

The breast–shoulder apparatus in chameleons differs in key respects from that of other lizards. For example, the two halves of the sternum form an acute angle opposite the posterior end of the coracosternal joint, and the sternum is compressed into a V-shape (Russell and Bauer, 2008). The midventral edge of the sternum is sharp and keeled, and the M. sternohyoideus and the M. pectoralis attach here. Although the presternum is often perforated with fontanelles in lizards, this is the derived state (Lecuru, 1968a). Interestingly, chameleons were noted by Lecuru (1968a) as having an imperforate presternum, whereas others have noted the presence of a sternal fontanelle, such as in the genus *Bradypodion* (Skinner, 1959). The presence of a sternal fontanelle in other chameleons was also noted by (Peterson, 1973).

Another key difference between chameleons and other lizards is the way in which the sternum articulates with the coracoid (coracosternal articulation). In most lizards, this articulation lies in the horizontal plane (Russell and Bauer, 2008). In chameleons, however, this articulation is turned dorsally (Werner, 1902b). In this case the glenoid is located considerably dorsal to the coracosternal articulations. This ultimately leads to a more depressed posture of the limb and passive closing (at least partially) of the coracosternal articulation (Russell and Bauer, 2008).

The predominant feature of the scapulacoracoid that has distinguished different groups of lizards is the fenestration pattern (Russell and Bauer, 2008). It was proposed by Lecuru (1968b) that there are six types of lacertilian scapulacoracoid, based primarily on the pattern of fenestrae. In this scheme, chameleons share a similar type with some geckos, characterized by an emarginated scapula and an unfenestrated coracoid separated by a scapulocoracoid emargination (Lecuru, 1968b).

The clavicle apparently appears early during development in *Bradypodion* and is then reabsorbed and replaced (in terms of location) by the sternocoracoid ligament (Skinner, 1959). It has consequently been suggested that this ligament is homologous with the clavicle. Interestingly, in a developmental study of *Trioceros hoehnelii*, there was no indication of a clavicle at any stage (Rieppel, 1993). The interclavicle is also lacking in chameleons (Peterson, 1973; Russell and Bauer, 2008). However, the longitudinal arm of the sternocoracoid ligament is homologous with the bony interclavicle (Peterson, 1973).

Another ligament, the scapulosternal, is important for preventing anterior and lateral displacement of the girdle (Peterson, 1973). Although terrestrial lizards have a coracoidal arm of this ligament, which limits displacement in the coracosternal joint, chameleons lack this arm. This permits increased movement of the coracosternal joint during locomotion.

The humerus lies distal to the pectoral girdle and articulates with the glenoid (glenohumeral joint). In lacertilians, the glenohumeral joint is relatively flexible, approximating a ball-and-socket joint (Haines, 1952; Russell and Bauer, 2008). In chameleons, the main articulation (there is a small second articulation on the lateral surface of the scapulocoracoid) faces posteriorly on the girdle (Peterson, 1973). In general, the ligaments of the articulation tend to be looser and are fewer in number relative to other lizards. This likely contributes to the increased range of movement of the humerus. The articular surface itself is relatively larger in chameleons, as compared with generalized nonarboreal lizards.

The humerus of chameleons has a number of attributes that differ from other terrestrial lizards. First, the humerus tends to be longer, there is reduced torsion, and the bone is straighter (Peterson, 1973). In a study of eight species of lizard comprising both arboreal and terrestrial forms, including *Anolis* (5 species), *Dipsosaurus, Chamaeleo,* and *Agama*, chameleons exhibited the longest standardized humerus length. In addition, *Chamaeleo* exhibited 22 degrees of long-axis torsion, which was considerably lower than that of other terrestrial genera such as *Dipsosaurus* (44 degrees) and *Agama* (28 degrees) (Peterson, 1973). Other differences between *Chamaeleo* and terrestrial lizards include a narrower humerus, and muscle attachments that are located more proximally. Finally, the humerus is longer in terrestrial chameleons than in arboreal ones (Bickel and Losos, 2002).

Chameleons have extremely mobile forelimbs that emphasize an increased range of motion associated with moving in an arboreal habitat. Their limb motion tends to be more in a parasagittal plane than that of other lizards given the relatively upright posture. This also results in a reduced amount of long-axis humeral rotation. The glenohumeral articulation is thus modified to enhance motion via expansion of the articular surfaces. This allows the humerus to slide laterally during protraction. The lateral orientation of the articular surface also enhances excursion into the anterior quadrants of the glenoid (Russell and Bauer, 2008). Together, these morphological specializations allow up to 150 degrees of movement in the horizontal plane (Peterson, 1973, 1984).

The wrist in chameleons is highly modified over that of other lizards, and this is associated with their specialized pattern of locomotion. In both anatomical and developmental studies, it is clear that fusion of elements in the carpus is prevalent among chameleons (Gasc, 1963; Rieppel, 1993). However, several aspects of this fusion have been the source of debate, with studies presenting varying conclusions (for a discussion, see Russell and Bauer, 2008).

In terms of function, the proximal carpal row is aligned functionally with the antebrachium. In this case, the wrist joint is a pivot between the proximal and distal rows of carpals. This joint, which involves articulation between the ulnare and the large element of the distal carpal row, has been interpreted as being mechanically equivalent to a ball and socket joint (Gasc, 1963).

The metacarpals of chameleons are extremely different from those of other lizards. The metacarpals are divided into two bundles that articulate with the largest element of the distal carpal row (Gasc, 1963), where the first three digits form one bundle (mesial) and the fourth and fifth form another (lateral). These two groups of digits form the grasping mechanism of the forelimb.

### *Muscular Elements*

AXIAL MUSCULATURE ACTING ON THE PECTORAL GIRDLE The M. episternocleidomastoideus has been a challenging muscle for anatomists studying lizards, given that not all of the skeletal elements are actually associated with this muscle in all species. The association of the M. episternocleidomastoideus with the M. trapezius has been discussed previously, and it has been suggested that this muscle is actually part of the M. trapezius (Jollie, 1962). This muscle originates at the posterior aspect of the ascending process of the parietal and the posterolateral margin of the paroccipital process of the exoccipital and inserts onto the anterolateral borders of the sternum (Mivart, 1870; Skinner, 1959).

The M. trapezius is small and thin in chameleons, relative to other lizards. The fibers insert along the anterior margin of the dorsal part of the scapula (Peterson, 1973). As for the origin, cervical fibers are absent, which differs from other lizards. Instead, the origin is from the first three thoracic vertebrae. The clavotrapezius is absent in chameleons.

The M. levator scapulae originates from the transverse processes of the first cervical vertebra (atlas). The insertion is entirely marginal and lies dorsal to the acromial region (Skinner, 1959). There is an additional origin of this muscle in chameleons. It is from the basioccipital condyle of the skull, which is tendinous and shared with the cervical axial muscles (Mivart, 1870). This muscle is typically associated with lateral undulation in terrestrial lizards (Peterson, 1973). Given the reduced lateral undulation in chameleons (Peterson, 1984), and the lack of clavicular attachment, this muscle brings about scapular rotation in the parasagittal plane.

The M. serratus anterior is primarily involved in suspending the body from the pectoral girdle. Lizards typically have both dorsal and ventral portions, including multiple bellies within each portion (Russell and Bauer, 2008). This muscle is reduced in chameleons, which have only two dorsal bellies and a single ventral belly (Mivart, 1870; Furbringer, 1900; Skinner, 1959). In addition to this reduction, the fibers of this muscle are all in line with the M. levator scapulae (Peterson, 1973). Finally, the bellies of this muscle in chameleons are longer than in other lizards, and this is thought to assist in the displacement of the girdle on the body wall (Peterson, 1973).

SHOULDER MUSCULATURE The shoulder musculature is typically important for protraction and retraction of the humerus in lizards and also plays an important role in stabilizing the shoulder joint. As described below, the shoulder musculature of chameleons is drastically different from that of other lizards because of, or associated with, increased mobility of the forearm. The M. sternocoracohumeralis is comparable to the M. clavodeltoideus in lizards other than chameleons. However, it maintains a different name because of the altered origin and the lack of a clavicle in chameleons (Peterson, 1973). There is also considerable variation in the morphology of this muscle among lizards. In chameleons, a small M. sternohumeralis belly originates from the superficial surface of the L. scapulosternale anterior. This is near the junction of the transverse with the longitudinal arm of the ligament. This region is analogous with the interclavicle–clavicle joint region (Peterson, 1973). The M. coracohumeralis portion exhibits a dorsolateral origin, at the level of the glenoid. In chameleons, as compared with other lizards, the M. sternocoracohumeralis is relatively small. The M. sternohumeralis fibers and the ventral M. coracohumeralis fibers form a bipinnate tendon that inserts along the proximal part of the dorsolateral aspect of the deltopectoral crest of the humerus (Peterson, 1973).

The M. supracoracoideus has been noted to be very different in chameleons as compared with other lizards (Mivart, 1870; Furbringer, 1900; Ribbing, 1938; Skinner, 1959; Gasc, 1963; Peterson, 1973). This muscle is divided into two discrete portions, originating from the lateral surface of the coracoid and the ventral scapula. The dorsal limit of the origin is the acromion. In chameleons, this muscle inserts along the anterior face of the lateral tuberosity between the glenohumeral joint capsule medially and the insertion of the M. pectoralis laterally. This muscle pulls the head of the humerus forward, protracts the humerus, and stabilizes the glenohumeral joint (Peterson, 1973).

The M. medial suprascapularis was first named by Peterson (1973) and is present only in chameleons. This muscle is found on the anteromedial surface of the scapular blade and is deep to the M. levator scapulae insertion. This muscle lies anterior to the origin of the M. subscapularis (Peterson, 1973). The M. suprascapularis medialis inserts on the proximal humerus. The origin includes the anteromedial margin of the scapula and suprascapular cartilage and a sheet of dense fascia, which separates the muscle belly from the M. subscapularis. Peterson (1973) noted the unique arrangement of fibers in this muscle. For example, the dorsalmost origin is fleshy or has short, fine tendons arising from the fascial sheath. Within a few millimeters of the dorsal limit of the origin, there exists a central tendon within the muscle belly. Interestingly, as muscle fibers stem from the scapular margin, they coil anteriorly, then medially, and ultimately posteriorly and deep into the belly, where they meet the tendon (Peterson, 1973). It is thought that the M. medial suprascapularis is derived from the M. supracoracoideus complex, and that it shares the actions of this complex. In addition, the evolutionary origin of this muscle suggests that it is related to the adaptation for protraction and a greater range of forelimb movement in chameleons (Peterson, 1973).

The M. biceps originates between the origins of the M. supracoracoideus and the M. coracobrachialis brevis, and near the ventral border of the coracoid (Peterson, 1973). The tendon of chameleons, which is small and round, originates more dorsally and occurs at the level of the inferior glenoid buttress. The M. biceps fuses with the M. brachialis over the distal third of the arm and then inserts on the proximal portion of the radius and ulna (Peterson, 1973).

The M. pectoralis is the largest muscle in the shoulder area; it covers the entire ventral aspect. In chameleons, this muscle originates from a sternal keel in the midline and the lateral surface of the sternum posterior to the first sternocostal articulation (Peterson, 1973). The insertion of the M. pectoralis is the deltopectoral crest, but is less tendinous and involves a smaller humeral area in chameleons. Relative to other lizards, the insertion onto the humerus is more proximal, which permits a greater range of motion (greater arc) of the humerus. This muscle will retract the humerus.

The M. latissimus dorsi is biarticular, spanning both the coracosternal and glenohumeral articulations. It is essentially a flat sheet that originates from an aponeurosis near the dorsal midline over the level of cervical vertebra 5 to thoracic vertebra 5 (Peterson, 1973). The origin in chameleons also incorporates the third, fourth, and fifth thoracic ribs. The M. latissimus dorsi inserts onto the proximal portion of the humerus. Like the M. pectoralis, this muscle is also a humeral retractor (within the parasagittal plane) with little ability to rotate the humerus.

In lizards, the M. triceps complex is typically comprised of four bellies, two of which originate from the shaft of the humerus and two of which originate from the primary girdle (Russell and Bauer, 2008). They all have a common tendinous insertion on the ulna. However, chameleons exhibit a three-headed condition, missing the coracoid arm of the sternoscapular ligament and the M. coracotriceps. It is thought that the absence of this ligament and the M. coracotriceps permits an increased range of motion and forward reach in chameleons. In other species of lizard, this ligament and muscle impose limitations.

LOWER FORELIMB MUSCULATURE Much of what is known about forelimb musculature in chameleons is related to the muscles acting at the girdle. This is likely due to the extreme motion at the level of the girdle during locomotion. The function of the lower forelimb (antebrachium) has not received as much attention, and future work will help illuminate the functional consequences of the specialized morphology of chameleons.

The M. extensor digitorum longus typically occupies the anterior area of the forearm. The origin, via a short tendon, is just dorsal to the radial condyle of the humerus (Russell and Bauer, 2008). In chameleons, there are two bellies. The first runs along the ulna and inserts close to the proximal ends of the fourth and fifth metacarpals. The second belly exhibits a tendinous insertion onto the third metacarpal. Although the exact function of this muscle could be related to flexing the carpus dorsally during the swing phase or pulling the antebrachium forward over the manus, more work is needed. The fact that the number of insertion points in chameleons is reduced from three (typical lizard) to two suggests a relation to the pincer-like nature of the manus and the specialized locomotor behavior.

The M. flexor digitorum longus of chameleons exhibits substantial differences from that of other lizards, but appears to share some similarities with *Gekko* (Russell and Bauer, 2008). This muscle is divided into four heads. Two of them originate from the humerus and the other two originate from the ulna. The posterior head that originates from the humerus inserts on digit five only. The other head, originating from the humerus, serves the other digits. The ulnar heads follow an insertion pattern similar to that of the humeral heads, with the anterior deep head inserting on digits one to four. The posterior deep head inserts onto digit five.

### *Pelvic Girdle and Hindlimb*

*Skeletal Elements* The pelvic girdle is comprised of the dorsal ilia, anteroventral pubes, and the posteroventral ischia (Russell and Bauer, 2008). On each side, the three components share a common suture, which is centered on the acetabulum. In the midventral line, the pubes and ischia also share a suture. The epipubis is an ossified structure that is between and anterior to the pubes in chameleons.

The femur articulates with the acetabulum via an oval and gently curving condyle. For most lizards, an internal trochanter lies anterior and somewhat ventral to the condyle. However, the internal trochanter has been reduced to a ridge in chameleons (Cope, 1892). The distal portion of the femur has rarely been examined in lizards, but it is clear that chameleons exhibit differences that are related to their locomotor mode. The lateral distal condyle in lizards is typically larger than the mesial condyle, but chameleons do not follow this pattern (Russell and Bauer, 2008). Instead the lateral and mesial condyles are comparable in size. In addition, the demarcation of the patellar surface is absent in chameleons.

The tarsus is made up of a proximal row, including the astragalocalcaneum, and a distal row, which is functionally a part of the pes (Russell and Bauer, 2008). The mesotarsal joint (ankle joint) is located between the crus (lower limb) and the proximal tarsal row. The astragalus and calcaneum of lizards typically develop as independent condensations, with the astragalus ossifying first. The tarsus of chameleons, however, is unique in that it originates from a single large cartilage distal to the tibia and fibula (Russell and Bauer, 2008).

With the exception of chameleons, all lizards that have been examined exhibit a flattened astragalocalcaneum. (For a more detailed description for lizards other than chameleons, see Russell and Bauer [2008].) In chameleons, it is curved and depressed to form a ventrally directed concavity. Tendons run within this concavity, and the astragalocalcaneum takes on the role of a pulley. However, chameleons do not exhibit this modification.

In chameleons, a globular fourth tarsal alone articulates with all of the metatarsals. As with the metacarpals, the metatarsals are grouped into two bundles. However, unlike the forelimb, the first and second are grouped together while the third, fourth, and fifth are grouped together (Rieppel, 1993).

*Muscular Elements* The musculature of the hindlimb of the chameleon was first determined by Mivart (1870), using the Parson's chameleon (*Calumma parsonii*). A more recent study of hindlimb muscle anatomy examined the veiled chameleon, *Chamaeleo calyptratus* (Higham and Jayne, 2004a).

The M. caudofemoralis is a robust muscle originating from the transverse processes of the four most proximal caudal vertebrae and inserting to both the greater trochanter of the femur and the proximal portion of the fibula via an auxiliary tendon (Fig. 2.4 in the color insert). This muscle typically slows femur protraction during late swing in lizards. However, this does not seem to be the case in chameleons, which is likely due to their slow locomotor speeds (Higham and Jayne, 2004a). Instead, the M. caudofemoralis likely flexes the knee during early stance.

The M. iliofibularis originates via a tendon from the posterior and lateral margin of the ilium and inserts on the fibula distal to the insertion of the M. caudofemoralis auxiliary tendon (Fig. 2.4). Like other lizards, activity in the M. iliofibularis is predominantly during swing (Higham and Jayne, 2004a).

In chameleons, the M. iliotibialis originates via a tendon from the posterior portion of the ilium just dorsal to the origin of the M. iliofibularis and inserts to the proximal tibia via the connective tissue on the anterior face of the knee.

The M. flexor tibialis externus originates from the ilioischiadic tendinous arch, runs along the posterior and ventral portion of the thigh and sends a long tendon, running along the posterior edge of the lower leg, to the plantar ossicle (Fig. 2.4). In addition, the M. flexor tibialis externus sends a shorter tendon that crosses the M. iliofibularis and inserts on the fibula just proximal to the insertion of the M. iliofibularis (Fig. 2.4).

The M. puboischiotibialis is on the ventral surface of the thigh and originates from the puboischiatic symphysis (midventral line) and inserts on the proximal portion of the tibia (Fig. 2.4). This muscle likely contributes to knee flexion and perhaps maintains the horizontal orientation of the femur (Higham and Jayne, 2004a).

The M. gastrocnemius originates from both the distal part of the femur and the posterior aspect of the tibia and runs along the posterior edge of the lower leg where it inserts on the plantar ossicle (Fig. 2.4). This is a stance phase muscle and is primarily involved in ankle extension.

The M. extensor digitorum longus originates from the distal portion of the femur and from the posterior portion of the fibula and inserts onto both the fourth and fifth digit (Fig. 2.4). However, others have suggested that this muscle inserts only onto the third metatarsal (Mivart, 1870). This muscle, according to the muscle-activation patterns, is predominantly a stance-phase muscle, with a smaller burst occurring during the swing phase (Higham and Jayne, 2004a).

The M. peroneus originates from the proximal portion of the anterior face of the fibula and from the proximal portion of the posterior tibia and inserts on the proximal and dorsal portion of the fifth metatarsal (Fig. 2.4 in the color insert). This muscle is typically active during the first half of stance and is likely responsible for knee flexion (Higham and Jayne, 2004a).

The M. tibialis anterior originates from the proximal portion of the tibia and inserts onto the proximal portion of the first metatarsal (Fig. 2.4). When measured under *in vivo* conditions, this muscle exhibits variable activity and is often active for a large portion of the stride (Higham and Jayne, 2004a).

## 2.2 EXTERNAL MORPHOLOGY AND INTEGUMENT

In addition to functions of protection, water balance, grasping and substrate interaction, etc., the external integument in chameleons also contains an assortment of signaling capabilities. These signals range from color and pattern changes, the mechanistic basis of which range from sexual selection to species-recognition characteristics (Chapter 6). The structure of many of these external morphological characteristics is therefore important to much of the broader biology of chameleons.

### Scalation

Whereas superficial ossifications in the form of bony shield arches and accessory extensions are found in *Brookesia* above portions of the vertebral column (Siebenrock, 1893; Romer, 1956; Boistel et al., 2010), body osteoderms, as in other iguanian lizards, are absent in chameleons (Romer, 1956). Further, whereas some species exhibit small patches of bare skin (e.g., *Bradypodion damaranum*), the majority of the skin and external surface in chameleons is covered with keratinous and generally nonoverlapping scales (Nečas, 2004; Tilbury, 2010). These scales come in various sizes, shapes, and arrangements and are often the basis of some of the larger ornamentations.

#### *Scale Types and Scalation Patterns*

Broadly, the scalation of chameleons is characterized by the consistency of the size and shape of the scales. When the scales appear to be of much the same size and shape, the animal is said to exhibit homogeneous scalation. When the scales appear to be of highly variable size and shape, the animal is said to exhibit strongly heterogeneous scalation. In species with heterogeneous scalation, these scales can be distributed seemingly randomly or can be organized into distinct patterns, such as rows of enlarged scales or circular rosettes of scales on the flanks. Largely homogeneous or heterogeneous scalation patterns, however, can involve a variety of scale types.

While all scale-type designations are intended to be descriptive of the shape of the different scales, scale shapes are often grouped differently (e.g., Nečas, 2004; Tilbury, 2010). Because there is no single accepted set of scale types for chameleons, our chosen set of scale types may vary from other sources; however, examination of their respective descriptions should help rectify inconsistencies. Here we divide the scale types in chameleons into conical, granular, labial, keeled, tubercular, lenticular, plate-like, and stellate and polygonal scales.

Conical scales are elongate, lanceolate, or cone-shaped (Nečas, 2004; Tilbury, 2010). They are typically found the dorsal and gular crests but can also be found on the flanks, throat, tail, and head and rostral processes in some species (Nečas, 2004).

Granular scales are small, bumpy, and granular-shaped. A more or less homogeneous arrangement of granular scales, such as in *Chamaeleo senegalensis* or *C. laevigatus,* is seen when these scales are spread across almost the entire body or in large patches with occasional interspersed larger scales. Arrangements of these scales can also span the spectrum to arrangements in which these granular scales are seemingly found only interstitially between larger scale types (Tilbury, 2010).

Labial scales are semicircular scales found around the mouth. They are found in a single row around the mouth in all chameleons and form what appear to be lips.

Keeled scales exhibit a ridge down the middle of the scale coming to a point. They are uncommon in chameleons but are observed in the caudal scales of some *Brookesia* (Müller and Hildenhagen, 2009).

Tubercular scales are scales that form a rounded eminence or projection from the surface. These scales are typically found on the cranial crests (Nečas, 2004); however, some authors group lenticular, plate-like, and stellate scales as forms of tubercular scales (Tilbury, 2010).

Lenticular scales are rounded, circular scales that are taller in their center than on their periphery and are often lumped together with tubercular scales. They are often found on the flanks but can also be found on the limbs, tail, throat, and head (Nečas, 2004). They are often interspersed among smaller granular scales and can be enlarged to varying degrees, even within a single individual.

Plate-like scales are rounded, flat scales and are often considered a type of tubercular scale. They are frequently found on the flanks but are also seen on the casque, rostral protuberances, occipital lobes, and extremities of some species (Nečas, 2004). They are often interspersed among smaller grandular and lenticular scales and can be of varying size, even within a single individual.

Stellate and polygonal scales are scales typically found on the flanks that have irregular-shaped sides. In some *Brookesia, Rhampholeon,* and *Rieppeleon* species, the scalation of the body consists of heterogeneous, interlocking, star-shaped, or stellate, scales (Nečas, 2004; Tilbury, 2010). Some other chameleon species have body scalation consisting of heterogeneous polygon-shaped scales (Tilbury, 2010).

### *Feet*

The scales on the palms and soles of the feet in chameleons are generally rounded to give a cobblestoned or smooth appearance (Mariaux and Tilbury, 2006; Tilbury, 2010). In *Brookesia* and *Rieppeleon,* however, the scales on the feet are sharply pointed or spinous with acuminate spines (Mariaux and Tilbury, 2006; Tilbury, 2010). In *Rhampholeon,* one to three spinous projections, called “accessory plantar spines,” are found at the base of each claw (Mariaux and Tilbury, 2006; Tilbury, 2010).

### *Dermal Pits*

In many chameleon species dermal invaginations are found at the base of the limbs (Mariaux and Tilbury, 2006; Tilbury, 2010), which frequently contain mites (Tilbury, 2010). They take the form of axillary pits on the posteroventral base of the forelimbs and the inguinal pits on the anteroventral base of the hindlimbs. At least one of these sets of pits are found in most *Calumma, Furcifer, Rhampholeon,* and *Rieppeleon* species, but in some species their presence is inconsistent between individuals (Tilbury, 2010).

### *Microstructure*

Scanning electron microscope examination of the scales on the subdigital and subcaudal surfaces in chameleons shows a complex microstructure in many species. This can include complex arrangements of adhesive bristles or setae (Schleich and Kästle, 1979, 1985; Canham, 1999; Müller and Hildenhagen, 2009), rectangular to hexagonal honeycomb shapes, or thorny points (Müller and Hildenhagen, 2009). The length, shape, and combination of different microstructures in these regions varies between genera and species (Schleich and Kästle, 1979; Canham, 1999; Müller and Hildenhagen, 2009). For instance, the setae in some species appear rounded, whereas in other species they appear to come to a point or even appear heterogeneous in length and shape (Schleich and Kästle, 1979; Canham, 1999; Müller and Hildenhagen, 2009). There can also be variation in the length and shape of setae within individual pads (Müller and Hildenhagen, 2009). Finally, within the subcaudal region, there also appears to be differentiation between different areas, with a scansorial pad displaying distinct features relative to adjacent portions in some taxa (Schleich and Kästle, 1979).

Although most genera exhibit some form of setae and honeycomb-shaped surfaces on their subdigital and subcaudal scales, there are also some distinct differences. The more agama-like thorny points, for instance, are only found in *Brookesia* and *Rieppeleon* (Müller and Hildenhagen, 2009). Further, *Brookesia* lack adhesive bristles altogether, having only a thorny point and/or rounded honeycomb structure (Müller and Hildenhagen, 2009).

### Claws

Chameleons have a claw projecting from each toe or two to three claws on each set of fused digits for a total of five claws per foot. All species of *Archaius, Bradypodion, Brookesia, Calumma, Chamaeleo, Furcifer, Kinyongia, Nadzikambia,* and *Trioceros* have a simple claw, whereas all species of *Rhampholeon (Rhinodigitum), Rhampholeon (Bicuspis),* and *Rieppeleon* have bicuspid claws with the formation of a secondary point approximately midway along the main claw Klaver, 1979; Nečas and Schmidt, 2004; Mariaux and Tilbury, 2006; Tilbury, 2010). These claws are strongly bicuspid in *Rhampholeon (Rhinodigitum)* and *Rhampholeon (Bicuspis)* but only weakly bicuspid in *Rieppeleon,* although *Rieppeleon kerstenii* may have strongly bicuspid rear feet (Tilbury, 2010). Within *Rhampholeon* (*Rhampholeon*), on the other hand, only *Rhampholeon (Rhampholeon) spectrum* has bicuspid claws (Müller and Hildenhagen, 2009), whereas all others have simple claws (Tilbury, 2010).

## Ornamentation

Chameleons exhibit a vast assortment of ornamentation based on their skeletal, dermal, and other structures. This ornamentation takes the form of various crests, cranial protuberances, fan-like elongations on the vertebral column, occipital lobes, and intricate arrangements of their scalation.

### *Crests*

The bones of the skull form a number of sharp angles and ridges on the head, which are often subsequently adorned with tubercular scales of varying sizes. The degree to which these crests are developed and their shape are often associated with species recognition and sexual-selection characteristics.

The paired lateral crest extends anteriorly from the apex of the casque, over the orbits, and to above the mouth tip, where they fuse (Nečas, 2004). Each lateral crest is divided into three parts: the rostral crest, orbital crest, and lateral crest proper (Nečas, 2004). The rostral crests extend from the anterodorsal margin of the orbit forward to just above the mouth tip, where they join. They are formed by the prefrontals, maxillae, and premaxilla. The ocular crests are constrained to the upper margin of the orbits and are formed by either the prefrontals and postorbitofrontals, or the prefrontals, frontals, and postorbitofrontals, depending on whether or not the prefrontals and postorbitofrontals join. The lateral crest proper extends from the posterior margin of the orbit to the apex of the casque and is formed by the postorbitofrontal and squamosal portion of the upper temporal arch and ascending process of the squamosal.

In species with a narrow parietal bone, the parietal crest lies medially and extends posterodorsally from immediately posterior to the eyes to the apex of the casque (Nečas, 2004) and is formed by the elevated ridge of the parietal bone. The parietal crest can be flat or highly concave and can be quite tall in some species. In species with a broad parietal bone, such as *Bradypodion* and *Brookesia,* the lateral aspects of the parietal bone form a pair of ridges lateral to the midline and medial to the lateral crests on each side called the "parasagittal crests" (Raxworthy, 1991).

In some species, an additional crest, called the "temporal crest," extends anteroventrally from the lateral crest posterior to the eye (Nečas, 2004). This crest is formed by the postorbitofrontal and in some cases the dorsal projection of the jugal.

Along the spine from behind the skull backward, a medial ridge is present in most chameleons. A dorsal crest is said to be present when a series of enlarged, often conical, scales are present along this ridge. The dorsal crest, however, can be limited to only a few conical scales immediately behind the head or consist of a large number of conical scales extending down the back and even onto the tail. In *Brookesia* species, a dorsal crest is not seen; however, many species have accessory extensions projecting laterally off the vertebrae to form laterovertebral spines (Siebenrock, 1893).

A ridge of enlarged scales is also frequently found along the midline on the ventral side of the body, running from the symphysis of the lower jaw posterior to the cloaca. From the jaw symphysis to the anterior edge of the sternum, this ridge is called the "gular crest," whereas from the sternum back to the cloaca it is called the "ventral crest." In most species, the gular crest is formed by a single medial row of enlarged scales, whereas in *Trioceros tempeli* it is formed by two rows of enlarged scales and in *Trioceros affinis* it is formed by paired dermal ridges.

### *Cranial Protuberances*

Perhaps the most notable ornamentations in chameleons are the variety of cranial protuberances adorned by many members of the family. These protuberances are highly variable in their form and function but include keratin-covered annulated horns, bony projections, and soft dermal lobes.

Among the most recognized of these cranial protuberances are the true or annulated horns. These horns have a bony base, are elongated and narrow, and are covered by an annulated keratin sheath formed by a single hypertrophied scale (Nečas, 2004). These horns are typically located preorbitally or rostrally along the lateral crests; however, *Trioceros melleri* has an unusual structure, in which a single annulated horn is located on the end of a medial bony rostral projection separate from the rostral crest portion of the lateral crest (Rieppel, 1981). When present, preorbital annular horns are paired with a single horn projecting from the anterodorsal aspect of each ocular crest. Rostral horns, on the other hand, can be either one, two, four, or six in number, and project side by side from one another on the anterior portion of the rostral crest.

Additional types of cranial protuberances are false or bony horns (Fig. 2.5). These horns are formed by projections of the cranial bones with a layer of scale-covered skin over them (Nečas, 2004). These scales are typically enlarged tubercular or plate-like scales. Often the false horns are paired and laterally compressed extensions of the rostral crest projecting forward beyond the tip of the jaw and formed by modified prefrontal and maxillary bones (Fig. 2.5) (Rieppel and Crumly, 1997). In some species, these paired false horns have become medially fused to each other, giving the appearance of a single laterally compressed paddle. False horns can also take the form of smaller elevated points along the lateral crests, such as the superior nasal cones and superior ocular cones in *Brookesia* (Raxworthy, 1991), or the single elevated rostral cones of species like *Trioceros hoehnelii*.

The cranial protuberances of some species, however, are entirely flexible. These soft or dermal horns lack a bony base and are made of soft, scale-covered skin (Nečas, 2004). These dermal horns are typically covered by granular scales or other slightly enlarged scales that remain soft and pliant. They can be found preocularly or rostrally. Preocular dermal horns are typically paired, and rostral dermal horns can be either bulbous or laterally compressed.

Finally, semipliant horns are seen in a couple species and appear as intermediaries between false and dermal horns (Nečas, 2004). These horns have a bony base and a flexible tip (Nečas, 2004). The rigidity of this tip varies, possibly because of a fibrous or cartilaginous tissue structure in the distal portions.

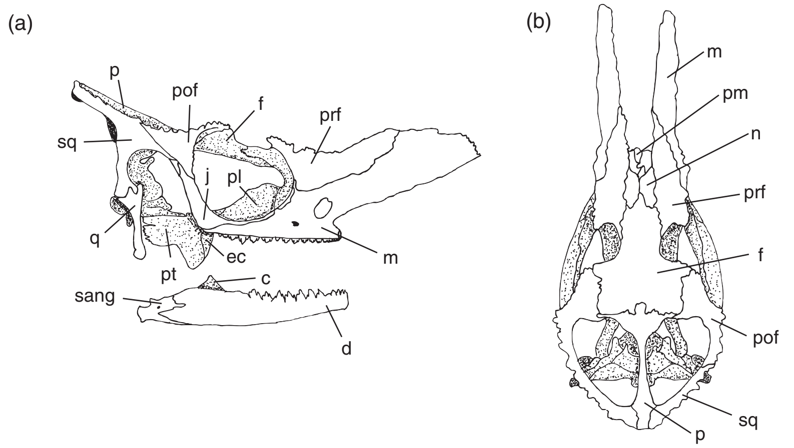

FIGURE 2.5. The skull of a male *Furcifer bifidus* in lateral (a), and dorsal (b) views showing formation of false horn. Redrawn from Rieppel and Crumly (1997).

LABELS: ang = angular; ar = articular; bo = basioccipital; bs = basisphenoid; c = coronoid; d = dentary; ec = ectopterygoid; f = frontal; j = jugal; m = maxilla; n = nasal; p = parietal; pl = palatine; pm = premaxilla; po = prootic; pof = postorbitofrontal; pf = prefrontal; prfo = prefrontal fontanelle; pt = pterygoid; q = quadrate; sang = surangular; so = supraoccipital; sq = squamosal; st = supratemporal; v = vomer.

### *Sails*

In some species, a tall sail along the vertebral column of the back or proximal portion of the tail is seen. This sail is formed by elongated neural spines of the vertebrae with strong connective-tissue threads between their distal ends and a skin covering (Case, 1909). These elongations form a fan-like sailfin on the proximal portion of the tail in some male West African *Trioceros* species, an elevated sail-like dorsal ridge in *Trioceros cristatus* and to a lesser extent *T. deremensis*, and a crenulated dorsal crest in *T. melleri*.

### *Occipital Lobes*

At the posterior margin of the head, many chameleon species have posteriorly oriented skin flaps called “occipital lobes.” These lobes can vary from quite narrow strips to large ear-like lobes. In some species, these occipital lobes have a connective-tissue structure and attachment to the squamosal bone, giving the lobes a semirigid structure (Meyers and Clarke, 1998). This connective-tissue “skeleton” is covered with mostly plate-like scales and in some species has an insertion by the M. depressor mandibulae pars auricularis, enabling the lobes to be erected during display (Meyers and Clarke, 1998).

### *Tarsal Spurs*

Whereas most species lack them, some species and some sexes of certain species exhibit a short posterior projection from their hindfoot called the “tarsal spur,” which is a bony extension of the tarsal bone covered in skin and scales (Tilbury, 2010). Of the species that do exhibit them, in most it is more strongly developed in males; however, in some species they are present in both males and females.

## 2.3 SENSORY STRUCTURES

Chameleons are known to have an increased dependence on visual cues relative to their other senses. As a result, chameleons' eyes have become highly developed. The remaining sensory structures, on the other hand, have become reduced or even vestigial in some cases.

### Eye

The eye of chameleons is their most developed sensory organ, with higher image magnification than any other vertebrate eye when scaled to the same size (Ott and Schaeffel, 1995). The eyes are notably enlarged, are placed laterally on the head, bulge almost entirely out of the orbit, and move independently of each other. They are surrounded exteriorly by scale-covered eyelids, which are fused to the sclera of the eye and have only a small center opening for the pupil. This arrangement allows for an impressive oculomotor range, which exceeds both 180 degrees horizontally and 90 degrees vertically (Sándor et al., 2001). Moreover, they are likely the only reptiles to achieve binocular fixation with a central fovea (Underwood, 1970).

Their oculomotor range is enabled by four rectus muscles and two oblique muscles (Leblanc, 1924, 1925). The four rectus muscles have a fascicular origin posteroventrally on the medial side of the orbit on the interorbital membrane (Leblanc, 1925). The two oblique muscles, on the other hand, originate on the anteromedial aspect of the orbit at the junction of the palatine and prefrontal (Leblanc, 1925).

The M. rectus superior is very broad and extends anterolaterally to inserts on the sclera on the dorsal surface of the eye just behind the cornea (Leblanc, 1925). It serves to elevate the cornea and rotate the dorsal surface of the eye posteroventrally (Leblanc, 1924, 1925). The M. rectus medialis extends horizontally behind the eye and then turns laterally to insert on the sclera on the anterior surface of the eye behind the cornea (Leblanc, 1925). It serves to draw the cornea anteromedially (Leblanc, 1924, 1925). The M. rectus inferior has two bundles (Leblanc, 1924, 1925) that extend ventrolaterally and insert on the sclera behind the cornea on the ventral side of the eye and just ventromedially to the insertion of the M. rectus medialis (Leblanc, 1925). They serve to draw the cornea ventromedially (Leblanc, 1924, 1925). Finally, the M. rectus lateralis has two bundles that extend laterally to slightly dorsolaterally (Leblanc, 1924, 1925). The upper bundle inserts on the sclera behind the cornea on the posterior side of the eye, whereas the lower bundle inserts on the anteroventral side of the conjunctival sac (Leblanc, 1925). They serve to draw the cornea posteromedially and draw the conjunctival sac over the Harderian gland (Leblanc, 1924, 1925).

The M. obliquus superior extends posteriorly in a dorsolateral direction and inserts broadly onto the sclera of the dorsal portion of the eye immediately behind and below the M. rectus superior (Leblanc, 1925). It serves to rotate the dorsal surface of the eye anteroventrally and thus is an antagonist to the M. rectus superior (Leblanc, 1925). The M. obliquus inferior extends horizontally and slightly laterally to insert on the sclera on the ventral side of the eye, perpendicular to the insertion of the M. rectus inferior, which inserts along the edge of the cornea (Leblanc, 1925). It serves to rotate the ventral surface of the eye anterodorsally and thus acts with the M. rectus superior as an antagonist to the M. obliquus superior (Leblanc, 1925).

The scleral cartilage (ring) is present and in *Chamaeleo* is formed by 11 scleral ossicles, creating a conical form (Gugg, 1939; Underwood, 1970). It is confined to the orbital hemisphere in the scleral layer of eye, with the cornea extending out of center (Leblanc, 1925; Underwood, 1970; Pettigrew et al., 1999). This scleral ossicle is coated with fine muscle fibers from the M. depressor palpebralis inferior of the eyelid just below the surface of the skin (Leblanc, 1924, 1925). This eyelid depressor muscle extends from the rim of the eyelid ventromedially around the eye in a thin sheet to the ventral and medial aspect of the orbit, where it originates on the palatine and interorbital membrane (Leblanc, 1925). This muscle serves to draw the rim of the eyelid and scleral ossicle ventrally to cover and protect the eye (Leblanc, 1924, 1925), as seen when chameleons rub their eyes during cleaning. The M. levator bulbi is absent in chameleons (Underwood, 1970).

Chameleons are unique among vertebrates in having a negatively powered lens (Ott and Schaeffel, 1995), thus reducing the contribution of the lens and increasing the contribution of the cornea to the total optical power of the eye (Ott and Schaeffel, 1995; Pettigrew et al., 1999). This serves to elongate the focal length of the eye and create a large retinal image (Ott and Schaeffel, 1995; Ott, 2001). Because the crystalline lens is relatively thick, with its lateral and medial surfaces being relatively flat, the internal isoindical shells of the lens are concave in shape in order to establish this negative refractive power (Ott and Schaeffel, 1995). The cornea is small (Underwood, 1970) and has a very small radius of curvature (Ott and Schaeffel, 1995), indicating that the cornea extends abruptly outward. Corneal curvature, however, is modulated for corneal accommodation by the M. cornealis, which inserts directly onto the corneal stroma (Pettigrew et al., 1999).

Finally, chameleons have extremely high visual resolution. They have a deep-pit fovea, with the retina being thick at its center and declining in thickness at its periphery (Ott and Schaeffel, 1995; Pettigrew et al., 1999). This retina has a dense photoreceptor package, with an estimated 756,000 cones/mm$^2$ (Harkness, 1977; Ott, 2001). This estimate is the higher than in all other lizards, and whereas some researchers have indicated that this estimate is likely high, it is within the range found in humans and birds of prey (Harkness, 1977).

### Parietal Organ and Pineal Gland

The function of the parietal organ and pineal gland in chameleons is not clear, and it is thought to be rudimentary in mature chameleons (Nečas, 2004). The pineal gland in chameleons is located dorsal to the midbrain and cerebellum (Schmidt, 1909; Quay, 1979). Overall, it is tubular in shape, first extending posterodorsally and then bending at nearly a right angle into a strongly inclined anterodorsal extension toward the roof of the skull, terminating in a long, thin tip (Schmidt, 1909).

When present, the parietal organ, or pineal eye, is dorsoventrally compressed and has either a round or slight sagittally elongated shape (Schmidt, 1909). It lies just under the skin and considerably anterior to the pineal gland, or pineal organ (Schmidt, 1909; Quay, 1979), in or above the pineal (parietal) foramen of the frontal bone (Romer, 1956; Rieppel, 1981). The location of this foramen in the frontal bone represents a forward shift from ancestral forms (Trost, 1956).

The parietal organ is connected to the pineal organ by the parietal eye nerve (Quay, 1979). A spot associated with the presence of the parietal organ, called the “parietal spot,” is visible in *Bradypodion, Brookesia, Chamaeleo,* and *Furcifer*, but absent in *Rhampholeon, Rieppeleon*, and *Trioceros* (Schmidt, 1909; Gundy and Wurst, 1976). The diameter of the parietal organ relative to the diameter of the pineal foramen in chameleons is known to vary from half its size to nearly twice its size (Edinger, 1955), so estimating development of the parietal organ based on the size of the pineal foramen is difficult.

### Ear

The ear in chameleons is greatly reduced. There is no external ear opening or tympanic membrane (Brock, 1941; Engelbrecht, 1951; Frank, 1951; Wever, 1968, 1973; Wever and Werner, 1970), and the traditional round window is absent or extreme reduced (Wever, 1968, 1969a, 1973). Some species further lack a tympanic cavity (Engelbrecht, 1951; Frank, 1951; Simonetta, 1957; Toerien, 1963; Wever, 1968), and the columella is often reduced or modified to a level that it is regarded as nonfunctional (Toerien, 1963; Wever, 1968, 1969b). Further, the extracolumella exhibits various modifications and is noted to terminate on various tissues, affecting potential conductance (Wever, 1968, 1969b; Wever and Werner, 1970). Whereas these reductions have not resulted in the loss of ability to detect airborne sound, their hearing is greatly reduced (Wever, 1968, 1969a,b, 1973; Wever and Werner, 1970).

Whereas *Rhampholeon* lack a tympanic cavity (Frank, 1951) and *Bradypodion* is said to either lack (Engelbrecht, 1951; Simonetta, 1957) or possess a vestigial tympanic membrane (Brock, 1941), in *Chamaeleo* and *Trioceros* the tympanic cavity is well defined and encloses the middle ear (Wever, 1968, 1969b). In these taxa, the tympanic cavity is separated from the pharyngeal region by a membrane, although a small oval-shaped opening corresponding to the Eustachian tube is found (Wever, 1968).

The stapedial footplate of the osseous columella rests in the oval window at the floor of the otic capsule (Fig. 2.6) (Toerien, 1963; Wever, 1968, 1969a,b). In *Chamaeleo* and *Trioceros* the footplate is large and nearly fills the oval window (Fig. 2.6) (Wever, 1968, 1969b), whereas in *Bradypodion* the footplate is small and does not fit closely within the oval window (Toerien, 1963) and in *Rhampholeon* the footplate is extremely small or vestigial (Frank, 1951; Toerien, 1963).

In *Bradypodion* (Engelbrecht, 1951; Toerien, 1963) and *Rhampholeon* (Frank, 1951) the columella is poorly developed and may not form a connection with the quadrate (Toerien, 1963). When it does, a cartilaginous extracolumella lies at the distal end of the columella (Brock, 1941; Wever, 1968, 1969b). In *Chamaeleo*, the extracolumella has anterior and posterior processes (Fig. 2.6a) (Wever, 1968), whereas the anterior process is lacking in *Trioceros* (Fig. 2.6b) (Wever, 1969b). The anterior process of *Chamaeleo* extends along a membrane between the

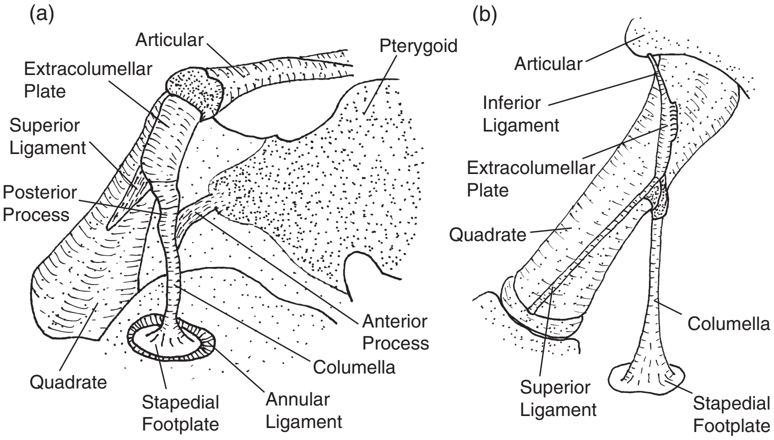

FIGURE 2.6. Drawings of the inner aspects of the right ears of *C. senegalensis* (a) and *T. hoehnelii* (b) from a ventral, medial, and slightly anterior direction. (a) redrawn from Wever (1968) and (b) from Wever (1969b).

quadrate and pterygoid to the thin edge of the pterygoid wing, where it forms a ligamentous attachment (Fig. 2.6a) (Wever, 1968). The posterior process of the extracolumella extends to the ventral part of the quadrate, forming a flat plate in the process (Fig. 2.6) (Wever, 1968, 1969b), which is smaller in *Trioceros* (Wever, 1969b). Dorsal (superior) and ventral (inferior) ligaments extend from the extracolumellar plate, with the dorsal ligament extending from the proximal end of the plate along the quadrate toward the squamosal (Fig. 2.6) (Wever, 1968, 1969b), and the ventral ligament extending from the distal end of the plate to the articulation between the quadrate and articular in *Chamaeleo* (Fig. 2.6a) (Wever, 1968), and to the posterior end of the articular in *Trioceros* (Fig. 2.6b) (Wever, 1969b).

In *Chamaeleo*, it is hypothesized that the pterygoid wing and the membrane extending to the quadrate, combined with the columellar system acts as a substitute tympanic membrane by serving as a conductive mechanism for airborne sound (Fig. 2.6a) (Wever, 1968). The lack of ligamentous connection between the columellar system and the pterygoid in *Trioceros*, however, results in a lack of a tympanic membrane substitute (Wever, 1969b).

Whereas a traditional round window is lacking in chameleons (Wever, 1968, 1969a, 1973), a substitute for it and its pressure discharge mechanism during oscillation of the oval window is known in *Chamaeleo* and *Trioceros* (Wever, 1968, 1969a, 1973). This substitute is present in the form of a fluid-filled path extending from the posterior wall of the scala tympani of the ear, posteriorly into the exoccipital bone and then laterally through the foramen of the glossopharyngeal nerve and into the tympanic cavity (Wever, 1968, 1969a).

The vestibular system of the inner ear has been examined in only a limited number of taxa. It is characterized by three well-developed semicircular canals with the curves of the posterior and anterior canals extending ventrally and the curve of the horizontal canal extending medially (Boistel et al., 2010). These semicircular canals are relatively flattened and oblong in shape in *Brookesia*, whereas in *Archaius*, they are more rounded (Boistel et al., 2010). Curiously, the horizontal canal in chameleons is only oriented horizontally when the head it elevated (Boistel et al., 2010).

### Tongue Pad and Taste Buds

The bulbous portion of the tongue in chameleons that is projected from the mouth can be divided into the tongue tip, the foretongue, and the hindtongue (Herrel et al, 2001b). The tongue tip is composed of the bifurcated anteroventral end of the tongue and the area adjacent and posterior to it (Herrel et al., 2001b). The foretongue consists of the portion of the tongue pad that is invaginated to create a lingual pocket, or dimple, with an upper and lower lobe (Herrel et al., 2000, 2001b) and is often called the "membrana glandulosa" (Bell, 1989). The hindtongue consists of the epithelium surrounding the M. accelerator linguae posterior to the tongue pad (Herrel et al., 2001b).

The tongue tip is bifurcated, with paired ventral plicae. This region is comprised of dense, closely packed papillae that show little to no visible microstructure (Herrel et al., 2001b). At the bifurcated tip, these papillae appear to be randomly oriented; however, posteriorly toward the foretongue, they are arranged in transverse rows (Herrel et al., 2001b). Taste buds are present on the tongue tip, but they are not abundant (Schwenk, 1985; Herrel et al., 2001b).

The foretongue or membrana glandulosa consists of densely packed reticular papillae oriented in transverse rows and exhibiting a prominent microstructure (Herrel et al., 2001b). Extending posteriorly, the density of these papillae decreases (Herrel et al., 2001b). This region is rich in epithelial-gland cells producing serous and mucous secretions (Bell, 1989; Herrel et al., 2000; Schwenk, 2000). Free plumose cells are known to be scattered occasionally on the edges of the foretongue in some species (*Trioceros melleri*; Herrel et al., 2001b); however, they are reported to be numerous in the lingual pouch of chameleons (Schwenk, 1983, 2000). Further, studies have found this region to lack taste buds in some species (*Trioceros melleri*; Herrel et al., 2001b), whereas others have indicated that they are present, although not abundant, in other species (*Trioceros jacksonii*; Schwenk, 1985).

The hindtongue lacks papillary structures and consists instead of a smooth epithelium around the M. accelerator linguae (Herrel et al., 2001b). Still, a prominent microstructure can be observed (Herrel et al., 2001b). Some studies have located taste buds in this region at higher concentrations than in the anterior regions (Herrel et al., 2001b), whereas other studies have found this region to be devoid of taste buds (Schwenk, 1985).

Overall, chameleons possess fewer gustatory receptors than other Iguanian lizards (Schwenk, 1985; Herrel et al., 2001b). More broadly, however, taste buds are said to always be numerous in the oral epithelium of lizards, with the exception of varanids, which lack taste buds altogether, and chameleons, which lack them on the oral epithelium (Schwenk, 1985).

### Nasal Capsule and Nasal Cavity

Overall, the nasal capsule and nasal cavity is of reduced size, having been shortened and compressed in the process of being pushed anterodorsally because of the enlarged eye and tongue (Brock, 1941; Malan, 1945; Engelbrecht, 1951; Frank, 1951; Visser, 1972; Slaby, 1984). The reduction and poor development of a number of features of the nasal capsule and nasal cavities, in addition to the olfactory nerves and olfactory nerve branches, has generally resulted in chameleons being considered microsmatic at best (Haas, 1937).

The cartilaginous nasal capsule is highly complex and differs considerably from that in ancestral lineages (Haas, 1937; Malan, 1945; Engelbrecht, 1951; Slaby, 1984; Hallermann, 1994). Its roof and sidewalls are quite complete, whereas the floor is relatively incomplete (Haas, 1937; Engelbrecht, 1951). The interpretation of the formation or the floor, however, is the subject of a variety of interpretations, particularly with regard to the presence or absence of paraseptal cartilages (Haas, 1937; Brock, 1941; Malan, 1945; Engelbrecht, 1951; Slaby, 1984). Discussion of the specific fine structure of the nasal capsule is not discussed here but can be reviewed elsewhere (Haas, 1937; Brock, 1941; Malan, 1945; Engelbrecht, 1951; Frank, 1951; Visser, 1972; Slaby, 1984; Hallermann, 1994).

The nostrils in chameleons are positioned laterally and enter the elongate and large diameter nasal vestibules at an oblique anterior direction (Engelbrecht, 1951; Parsons, 1970; Visser, 1972). The vestibular wall is composed of erectile muscular tissue with a layer of keratinized epithelium covering it (Malan, 1945; Engelbrecht, 1951; Frank, 1951), whereas the rest of the nasal cavities are lined with ciliated epithelium (Engelbrecht, 1951). The vestibules open laterally at their posterior end into the olfactory chamber located beneath it via a wide slit (Malan, 1945; Engelbrecht, 1951; Parsons, 1970). This slit is elongated in *Bradypodion* but shorter in *Chamaeleo*, forming a blind cavity posterior to the opening to the olfactory chamber (Malan, 1945; Haas, 1937; Parsons, 1970). The olfactory chamber is small, the most reduced of any reptile, and the olfactory epithelium is highly reduced (Haas, 1937; Malan, 1945; Frank, 1951; Parsons, 1970). The nasal conchae, or turbinates, are reduced to a rudimentary flat ledge (Haas, 1937) or absent altogether (Hallermann, 1994). The choanae lie directly beneath the opening between the vestibules and olfactory chamber in *Bradypodion* (Malan 1945; Engelbrecht, 1951). Inspired air is thus able to travel from the vestibules directly into and through the choanae in *Bradypodion* (Malan, 1945; Engelbrecht, 1951), whereas air must travel a more elaborate route in *Chamaeleo* through the olfactory chamber and into the choanae (Haas, 1937; Malan, 1945). Inspired air then travels from the choanae into the oral cavity (Engelbrecht, 1951). The paired choanal grooves in the palate of the oral cavity are deep and bordered by choanal folds, which are supported by the ectochoanal cartilages, which are in turn supported by the medial process of the maxillae (Engelbrecht, 1951; Frank, 1951).

### Vomeronasal Organ

The predominating theory on the presence and development of a vomeronasal, or Jacobson's, organ in chameleons is based on that of Haas (1947), who described the presence of a "reduced" and "functionless" vomeronasal organ in *Chamaeleo chamaeleon*. Based on this study, many report chameleons in general to possess a rudimentary or vestigial vomeronasal organ (Nečas, 2004; Gehring and Lutzmann, 2011); however, some others simply state that the vomeronasal organ is absent in chameleons (Døving and Trotier, 1998). In reality, there is no standard condition within the family (Parsons, 1970). For instance, the vomeronasal organ has been reported to be completely absent in some taxa (Slaby, 1984), including in *Trioceros hoehnelii* (Malan, 1945) and *Rhampholeon platyceps* (Frank, 1951), whereas it is regarded as rather rudimentary in *C. dilepis* (Born, 1879) and *C. chamaeleon* (Born, 1887; Haas, 1947) and well developed in *Bradypodion pumilum* (Malan, 1945; Engelbrecht, 1951; Visser, 1972) and *B. ventrale* (Brock, 1941). This lack of ubiquity within the family is not typically discussed, because while we know very little about the structure of the vomeronasal organ in different chameleons, we know even less about its functionality.

When present, the paired vomeronasal organs are located in the roof of the mouth anterior to the nostrils (Brock, 1941; Malan, 1945; Haas, 1947; Engelbrecht, 1951; Visser, 1972). Their openings into the oral cavity lie between the anterior tip of the vomer and maxillae (Brock, 1941; Haas, 1947; Engelbrecht, 1951), and the vomeronasals are separated from the choanae by Fuchs secondary palate rather than opening into them (Malan, 1945; ngelbrecht, 1951). Their height is reduced, and whereas the vomeronasal organ in most lizards lies beneath the nasal vestibules, they lie medial to them in chameleons (Brock, 1941; Malan, 1945; Engelbrecht, 1951; Visser, 1972). This more anterior and dorsal positioning is thought to be due to the need to accommodate the large eyes and tongue (Malan, 1945; Engelbrecht, 1951; Visser, 1972; Slaby, 1984).

The vomeronasal organs are covered dorsally and laterally by two cartilaginous plates (Brock, 1941; Malan, 1945; Engelbrecht, 1951), likely derived from the roofing cartilage, forming their own cartilaginous roof (Malan, 1945; Engelbrecht, 1951). Coverage by these cartilaginous plates is interrupted dorsolaterally by a fontanelle (Brock, 1941; Malan, 1945; Engelbrecht, 1951), which is not covered by the septomaxillary as in other lizards, as it is absent in chameleons (Malan, 1945; Engelbrecht, 1951; Frank, 1951; Visser, 1972; Hallermann, 1994). The ventral edges of the lateral cartilaginous plates are bent medially, forming a floor for the lateral portions of each vomeronasal organ (Brock, 1941; Malan, 1945; Engelbrecht, 1951). The vomeronasal organs are lined with ciliated epithelium (Engelbrecht, 1951). There is no connection between the ductus nasolacrimalis and the vomeronasal organs in chameleons (Malan, 1945; Engelbrecht, 1951).

### Brain and Nervous System

The neurology of the chameleon has been studied by a number of researchers over the years. Here we very briefly comment on a couple of general trends as compared with other reptilian brains that apply more broadly to trends seen in other aspects of chameleon anatomy and ecology.

The cerebellum in chameleons is highly developed; it is long, narrow, and curved forward in shape, possibly because of its function in maintaining equilibrium, which is important in arboreal animals (Shanklin, 1930). Further, whereas the olfactory bulbs are typically large in reptiles, in chameleons they are minute, and the peduncles are very slender, adding further support to the notion that chameleons are microsmatic (Shanklin, 1930; Goldby and Gamble, 1957). Similarly, the main vomeronasal-recipient structure, the nucleus sphaericus, is reduced in size and devoid of a cortical-like arrangement (Senn and

Northcutt, 1973; Northcutt, 1978). The basal optic-root ganglion is well developed and likely correlated with the wide range of eye movements in chameleons (Shanklin, 1930). Finally, the hypoglossal nucleus is highly differentiated, likely in association with the complex and highly evolved tongue and its complex projection mechanism (Shanklin, 1930).

Further information on the neurology of the chameleon brain can be found in Shanklin (1930). Other studies of the chameleon brain and nervous system have focused on the cerebral tube (Bergquist, 1952), neopallium (Dart, 1934), wall of the forebrain (Källén, 1951a,b), motor pathways of the eye (Stefanelli, 1941), and the nucleus opticus tegmenti (Shanklin, 1933).

## 2.4 VISCERAL SYSTEMS

In general, relatively little is known about the visceral systems in chameleons. Of note, however, are the lung and hemipenal morphology, which has been extensively examined for taxonomic purposes. Here we briefly describe the anatomy of these and other visceral systems.

### Circulatory

Overall, the circulatory system of chameleons has not been well studied. The pathways and branching patterns of aspects of the arterial (Rathke, 1857; Mackay, 1886; Beddard, 1904; Adams, 1953, 1957) and venous (Beddard, 1904; Bruner, 1907) systems have been described in detail elsewhere and are not discussed here. Instead, a brief summary is provided on the aspects of the anatomy of the three-chambered heart of chameleons, which has received only minimal attention from researchers.

Internally, the ventricle of the heart is known to have seven apical chambers, as is typical of most reptilian hearts, but little else is known of the internal structure (Farrell et al., 1998). Externally, the sinus venosus is well developed, with visible swelling at the confluence of the postcaval and right precaval veins (Kashyap, 1960; Farrell et al., 1998). The terminal portion of the left precaval vein is also swollen but has a considerable constriction at its junction with the aforementioned confluence (Kashyap, 1960; Farrell et al., 1998). The right and left atria are of approximately equal size and an atrial diverticulum is present between the paired carotid arteries (Kashyap, 1960; Farrell et al., 1998). Whereas in most reptiles the conus arteriosus has been absorbed into the ventricle, traces of a vestigial conus arteriosus are visible at the base of the arterial trunk in chameleons (Kashyap, 1960; Farrell et al., 1998). The apex of the heart is attached to the pericardium by a gubernaculum cordis and the apical two thirds of the ventricle is attached to the pericardium by a mesocardial membrane (Kashyap, 1960; Farrell et al., 1998).

### Respiratory

The lungs in chameleons are highly variable and can be extremely elaborate. Their structure has been extensively studied for use as a taxonomic marker (e.g., Klaver, 1973, 1977, 1979, 1981) as the configuration of the pulmonary septa are conserved within groups of related species (Klaver and Böhme, 1986).

The larynx is formed, as in other reptiles, by the cricoid cartilage and arytenoid cartilages (Germershausen, 1913). In some species, an inflatable sac, called the “gular pouch,” is connected with the ventral wall of the trachea just behind the larynx (Germershausen, 1913; Klaver, 1981; Klaver and Böhme, 1986).

The lungs in chameleons occupy a large portion of the body cavity, with lung volumes that are among the largest for their size of any reptile (Perry, 1998). The luminal walls of the lungs have numerous terminal air sacs for gas exchange, called “edicula,” which are at least as wide as they are deep (Perry, 1998) and supported by a trabeculated smooth-muscle network (Klaver, 1981; Perry, 1998; Tilbury, 2010). The lungs can be simple and sac-like or can have internal septa that project into the lumen of the lung in one of five patterns (Klaver, 1981; Klaver and Böhme, 1986; Tilbury, 2010). Further, diverticula of differing shape, size, position, and number can project off the ventral and terminal aspects of the lungs in some species (Beddard, 1907; Methuen and Hewitt, 1914; Klaver, 1973, 1977, 1979, 1981; Klaver and Böhme, 1986; Tilbury, 2010).

A nonseptate condition is seen in all *Brookesia, Rhampholeon*, and *Rieppeleon* species (Klaver, 1979; Klaver and Böhme, 1986; Tilbury, 2010), except *Rhampholeon spinosus* (Klaver, 1981). In this condition, the lung lumen forms a simple sac devoid of any septae (Klaver, 1979; Klaver and Böhme, 1986; Tilbury, 2010).

The first septation condition lacks long longitudinal septa, but the lungs are clearly divided, with the dorsal, cranial and ventral walls having varying numbers of small to moderately sized septa (Klaver, 1973, 1977, 1981; Klaver and Böhme, 1986; Tilbury, 2010). This pattern is seen in *Rhampholeon spinosus* (Klaver, 1981) and members of the *Bradypodion, Calumma, Furcifer, Kinyongia,* and *Nadzikambia* genera (Klaver, 1973, 1977, 1981; Klaver and Böhme, 1986; Tilbury, 2010).

The remaining four types of divisions are characterized by large longitudinal septa running posteriorly through the lumen from the orifice of the bronchus (Klaver and Böhme, 1986). One of these types, as seen in *Chamaeleo* species, has two septa that end freely in the lumen (Klaver, 1973, 1977; Klaver and Böhme, 1986; Tilbury, 2010). The other three types are seen in the genus *Trioceros* and have one, two, and three septa that connect to the ventral wall at their distal end, completely subdividing the lumen into chambers (Klaver, 19,73 1977, 1981; Klaver and Böhme, 1986; Tilbury, 2010).

### Digestive

A limited number of studies have discussed the anatomy of the digestive system in chameleons, and most of this is related to the folding relief of the gastrointestinal tract. Therefore, here we only briefly describe some of the structure of the digestive system in chameleons.

Whereas in most lizards the esophagus has smooth-surfaced longitudinal folds of relatively consistent diameter, the esophageal folds in chameleons are rough-surfaced and of varying diameter (Parsons and Cameron, 1977). The liver in chameleons is typically brownish gray in color and has two lobes, with the left lobe being larger and having the greenish-colored gallbladder positioned on its dorsolateral edge (Beddard, 1907; Nečas, 2004).

The pancreas is yellowish in color (Nečas, 2004) and bilobed, although these lobes are not always distinct, forming instead a single curved, elongated mass (Beddard, 1907). Part of the pancreas lies on the ventral side of the stomach, between the stomach and duodenum, with an additional portion extending toward the dorsal side of the stomach and back toward its posterior end (Beddard, 1907). The spleen is purplish red in color and located just ventral to the stomach (Nečas, 2004).

Longitudinal folds in the stomach are of varying diameter and are not parallel, with both wavy and straight portions (Parsons and Cameron, 1977). The wall of the stomach between the longitudinal folds has a fine pebble-like surface (Parsons and Cameron, 1977). The tunica muscularis of the stomach is smooth muscle with an inner circular and outer longitudinal layer (Luppa, 1977). The muscular layer is of reduced thickness toward the pylorus of chameleons (Luppa, 1977).

The intestinal tract is short and poorly differentiated (Nečas, 2004). Longitudinal folds of the duodenum have an irregular pattern with tall, thin folds that can appear membranous (Parsons and Cameron, 1977). Their borders are crenulated and the edges bear projections (Parsons and Cameron, 1977). The wall of the duodenum between the folds is very rough and has occasional fine longitudinal ridges (Parsons and Cameron, 1977). The rest of the small intestine has thicker folds with borders that are even more irregular (Parsons and Cameron, 1977).

The colon has very large, thick, transverse folds that are separated by deep clefts (Parsons and Cameron, 1977). These folds have smaller, randomly arranged, longitudinal folds running along their surface (Parsons and Cameron, 1977). The large folds are very rough, with grooves and small projections similar to villi (Parsons and Cameron, 1977). Intestinal glands (glands of Lieberkühn) are reported in the colon of chameleons (Luppa, 1977). The cloaca also is reported to have simple tubular (unbranched) glands, which are independent of one another (Luppa, 1977).

### Urogenital

Most of our knowledge of the chameleon urogenital system stems from the use of the male reproductive parts as taxonomic markers (e.g., Klaver and Böhme, 1986). Here we only briefly discuss the structure of other urogenital structures and focus on the hemipenes, because of their importance in species differentiation and taxonomy.

The kidneys are located in the posterodorsal portion of the body cavity along the spine (Nečas, 2004) and are elongate pear-shaped to uniformly elongate (Fox, 1977). A urinary bladder is present in chameleons and opens ventrally into the cloaca (Fox, 1977). The urinary bladder may be used for water storage (Burrage, 1973).

In females, the oviducts and eggs occupy a large portion of the body cavity when a clutch is being developed (Nečas, 2004). In males, the testes are black and the seminal vesicles have a tubular arrangement (Fox, 1977).

Male chameleons, like other squamates, have a paired intromittent organ called the "hemipenes." The hemipenes are held inside the body in an inverted position while at rest.

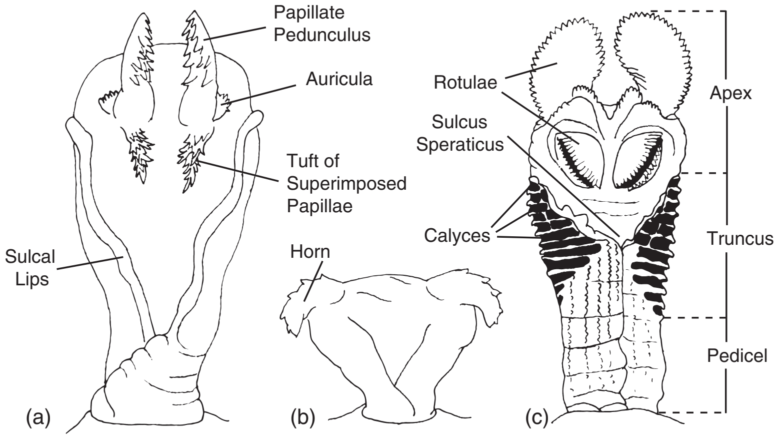

FIGURE 2.7. Schematic sulcal views of hemipenis morphology for *F. lateralis* (a), *R. platyceps* (b), and *C. calyptratus* (c). Redrawn from Klaver and Böhme (1986).

It is held in a pocket posterior to the vent in the base of the tail, often forming a hemipenal bulge, which can be useful in determining the sex of individuals.

Each hemipenis in chameleons has either a strong clavate shape, in the case of *Brookesia, Rhampholeon,* and *Rieppeleon* species (Fig. 2.7b), or weakly clavate to subcylindrical shape, as in other genera (Fig. 2.7a,c), when everted (Klaver and Böhme, 1986). Overall the hemipenis can be divided into three regions: the pedicle, the truncus, and the apex (Fig. 2.7c) (Klaver and Böhme, 1986). The pedicle is the proximal base of the hemipenis, the truncus is the medial portion, and the apex is the distal tip (Fig. 2.7c) (Klaver and Böhme, 1986).

The pedicle of the hemipenis has a relatively smooth surface (Klaver and Böhme, 1986). The truncus can either be calyculate, with reticulated honeycomb-like pits, called "calyces," ornamenting its surface (Fig. 2.7c), or acalyculate, with a smooth surface, making differentiation between the pedicle and truncus difficult (Fig. 2.7b) (Klaver and Böhme, 1986).

A channel-shaped groove, called the "sulcus spermaticus," bordered by sulcal lips, runs along the hemipenal surface of the pedicle and truncus for sperm transport during copulation (Fig. 2.7) (Klaver and Böhme, 1986; Nečas, 2004). The sulcus spermaticus is smooth, whereas the sulcal lips can be smooth or have ridge traces from the surrounding calyces (Klaver and Böhme, 1986). The sulcal lips may exhibit a capitate state, where they diverge distally to form a clear ridge boundary between the truncus and apex, or be noncapitate (Klaver and Böhme, 1986).

The apex is simple to slightly bilobed at its distal end and is often elaborately ornamented, with ornamentation being arranged bilaterally (Klaver and Böhme, 1986). Ornamentation may include papillae, pedunculi, auriculae, rotulae, horns, and crests (Klaver and Böhme, 1986). Papillae are fleshy and flexible projections that vary in size and shape and can be single, paired, scattered, arranged in rows, or concentrated in papillary fields (Fig. 2.7a) (Klaver and Böhme, 1986; Nečas, 2004). Pedunculi are thick stalks protruding over the distal end of the sulcus spermaticus and can be papillate themselves (Fig. 2.7a) (Klaver and Böhme, 1986). Auriculae, on the other hand, are curved dentriculate ridges that occur on the asulcal side of the apex— that is, the opposite side of the hemipenis from where the sulcus spermaticus occurs (Fig. 2.7a) (Klaver and Böhme, 1986; Nečas, 2004). Rotulae are similar to auriculae but are more developed and semicircular discs with a denticulate or serrated outer margin (Fig. 2.7c) (Klaver and Böhme, 1986). Horns, as seen in many *Rhampholeon* species, are broad, rotund projections that taper toward their distal ends and curve toward the sulcal side of the apex (Fig. 2.7b) (Klaver and Böhme, 1986). Finally, crests, as seen in some *Brookesia* species, are papillate or dentriculate crests or crested lobes on the apex of the hemipenis (Klaver and Böhme, 1986). Interestingly, the development of these apical structures appears to be related to seasonal and hormonal factors, and specimens may exhibit intraspecific variation depending on reproductive state or the time of year (Klaver and Böhme, 1986; Tilbury, 2010).

### Endocrine and Exocrine

Our knowledge of the anatomy of endocrine and exocrine structures in chameleons is extremely limited. Endocrine glands in chameleons have been examined only to a limited extent, and the description of their morphology is extremely superficial or limited to the broader context of larger groups of lizards (e.g., Lynn and Walsh, 1957; Gabe and Martoja, 1961; Bockman, 1970; Gabe, 1970; Girons, 1970; Lynn, 1970), and is therefore not discussed here. Examinations of exocrine structures in chameleons are similarly limited; however, a unique, suspected holocrine gland is known in some chameleons.

Whereas chameleons lack the femoral glands common to many other lizards (Camp, 1923), some do have a structure that is thought to be similar to the femoral gland in lizards and analogous to the sebaceous gland of mammals (Ogilvie, 1966). This structure, called the “temporal gland,” is a dermal pouch in the temporal region of the head that excretes decaying cornified skin cells (Ogilvie, 1966). When present, it is located between the superficial muscles of the temporal region of the skull and the external layer of skin, anterior to the M. depressor mandibulae (Ogilvie, 1966). Its base lies beneath the quadratomaxillary ligament, and the pouch opens into the commissure of the jaws when the lower jaw is depressed (Ogilvie, 1966). It is believed that this pouch may have arisen as a result of an increased area of skin present at the angle of the jaw (Ogilvie, 1966).

The development of the temporal gland is highly variable between chameleon species and genera, with some of the most developed examples occurring in *Trioceros*, whereas *Rieppeleon* have only a small temporal pouch that is difficult to detect under a microscope, and *Rhampholeon* are believed to lack the pouch altogether (Ogilvie, 1966). Overall, the pouch has been observed to varying degrees of development in *Bradypodion, Chamaeleo, Kinyongia, Rieppeleon*, and *Trioceros*, but it is absent in *Calumma, Furcifer*, and *Rhampholeon* (Ogilvie, 1966).

In addition, some chameleons are known to excrete salt from nasal salt glands (Burrage, 1973). The structure of the nasal salt glands has not been examined in chameleons specifically; however, in lizards the salt gland is formed by the modified lateral nasal gland (Dunson, 1976; Hazard, 2004) and consists of branching secretory tubules projecting radially around a central duct (Burrage, 1973; Dunson, 1976) that opens into the nasal vestibule (Peaker and Linzell, 1975). These glands produce a brine of potassium, sodium, and chloride that is exuded from the nostrils and dries, forming deposits around the nares (Burrage, 1973).

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While the multitude of unique features of chameleons has resulted in many researchers examining various aspects of chameleon anatomy over the years, a considerable gap in our knowledge remains. Future work will likely reveal morphological differences between species and genera of chameleons, especially those that live in different types of habitats.

Not all chameleons, for example, are arboreal, although terrestrial chameleons still appear to maintain many of the same morphologies as their arboreal relatives. Key questions regarding commonalities and divergence between disparate groups of chameleons remain, however. As noted by Tolley and Burger (2007), terrestrial chameleons tend to be small, and they typically exhibit relatively short tails. How internal morphology relates to a terrestrial lifestyle in chameleons remains relatively unknown.

Further, a great deal of behavioral variation exists between different lineages within the family. Many of these behavioral differences may have underlying morphological variations associated with them. Behavioral observations of tongue-touch behavior in various species (Ogilvie, 1966; Gehring and Lutzmann, 2011; C.V. Anderson, personal observation) suggest a need for more in-depth examination of the morphological variation and functionality of the vomeronasal organ, for example.

### ACKNOWLEDGMENTS

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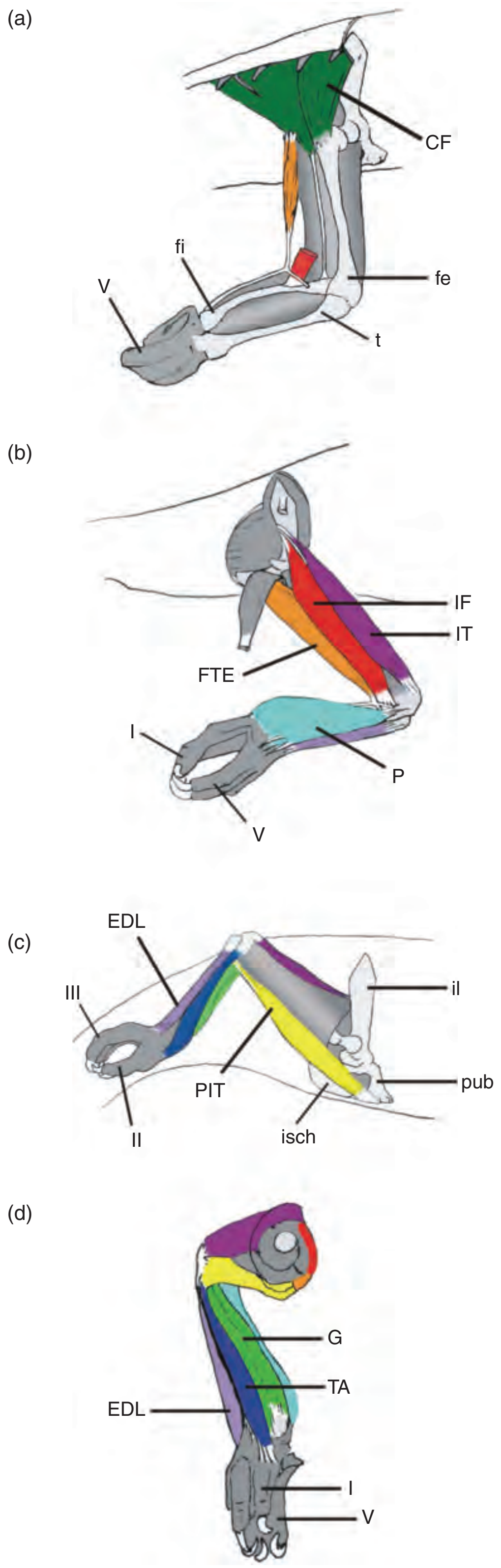

FIGURE 2.4. Right hindlimb muscles of *C. calyptratus* represented by a lateral view of the deeper musculature (a), a lateral view of a protracted and depressed limb (b), a fully retracted and abducted limb (c), and an anterior view of a fully retracted and disarticulated limb (d). Bones are in light gray and connective tissue is in white. Originally published in Higham and Jayne (2004a).

LABELS: I, II, III, V = digit numbers; CF = caudofemoralis; EDL = extensor digitorum longus; fe = femur; fi = fibula; FTE = flexor tibialis externus; G = gastrocnemius; IF = iliofibularis; il = ilium; IT = iliotibialis; isch = ischium; P = peroneus; PIT = puboischiotibialis; pub = pubis; t = tibia; TA = tibialis anterior.

APPENDIX

# 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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