How Do Flap-Necked Chameleons Move Their Flaps?

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Many lizards possess a variety of dewlaps, frills, horns, and casques on their heads. Dewlaps and frills move via muscles attached to the hyoid (Throckmorton et al., 1985; Bels, 1990), but most cranial appendages (horns and casques) are not moveable. The family Chamaeleonidae is, in part, characterized by head casques (Zug, 1993). The flap-necked chameleon, *Chamaeleo dilepis*, of southern Africa, possesses flaplike structures extending caudally from the head casque. They can be spread forward or abducted up to a maximum angle of 90° (Carpenter and Ferguson, 1977; Schmidt et al., 1994). Brain (1961) indicated that forward movement of one or both of the "occipital flaps" was part of the threat posture of *C. dilepis*, in addition to flattening the body laterally and expanding the gular skin. Similar flaps have also been described in at least 25 species (C. Klaver, pers. comm.) including *C. cucullatus* (Mertens, 1946) and *C. brevicornis* (Grzimek, 1975). In this study, we describe the anatomy and propose a mechanism for movement of the neck flaps in *C. dilepis*.

MATERIALS AND METHODS

Four preserved specimens of *C. dilepis* were obtained from a local animal supplier and from the California Academy of Sciences. Dissections were performed with an Olympus SZH dissecting microscope, and an iodine stain (Bock and Shear, 1964) was used to contrast muscle against connective tissue. Anatomical nomenclature is from Haas (1973). Flap surface area was measured using Simpson's Rule (Thomas and Finney, 1996).

RESULTS

The paired neck flaps of *C. dilepis* extend caudally from the caudal edge of the skull (Fig. 1). Surface area of the flaps range from 25 mm² to 213 mm². This variation in flap size seems to result from a variation between subspecies (Martin, 1992) and/or geographic range (Branch, 1997). The lateral surface of each flap is covered by relatively large scaled skin and is tightly attached to the underlying flap skeleton. The medial surface is covered by small, finely scaled skin that is loosely attached to the flap "skeleton." The medial flap skin is connected to the head by loose connective tissue and has sufficient folds to expand during flap abduction.

The flap skeleton is a connective tissue structure that is continuous with all borders of the flap and forms its semirigid framework. On its dorsocranial border, the skeleton attaches via connective tissue to the squamosal bone of the skull (Fig. 1).

The M. depressor mandibulae, the primary jaw-opening muscle of reptiles, is positioned deep to the cranial half of each flap. In *C. dilepis*, this muscle originates from the ascending process of the squamosal and also from the caudal surface of the quadrate and adjacent fascia (see Haas, 1973) and inserts on the articular bone of the lower jaw, caudal to the jaw articulation. A number of caudal superficial fascicles separate from the main portion of the muscle and insert onto the flap skeleton (Fig. 1). These fascicles are here defined as M. depressor mandibulae pars auricularis. Whereas all of M. depressor mandibulae lies medial to the flap skeleton, pars auricularis wraps over the cranial edge of the flap and attaches onto this edge in addition to the adjacent lateral surface of the flap (Fig. 1).

DISCUSSION

In *C. dilepis*, flap abduction is produced by the nature of the attachment of pars auricularis to the flap skeleton. The M. depressor mandibulae pars auricularis attaches onto the cranial edge of the flap skeleton in addition to fanning out onto the adjacent lateral surface of the flap (Fig. 1). When pars auricularis contracts, its caudoventral direction of pull causes a small amount of twist (torque) that helps to lift the flap away from the body. Instead of being pulled toward the neck (adduction), the flap is rotated outward (abduction). Since there is no muscle present to adduct the flap, we believe that the flap returns passively to the side of the neck. Passive return of the flap could result from muscle relaxation and the elastic recoil of the stretched skin and connective tissue on the medial side of the flap, and from compression laterally along the crease where the flap attaches to the casque. Gravity may also play a role in the adduction of the flaps.

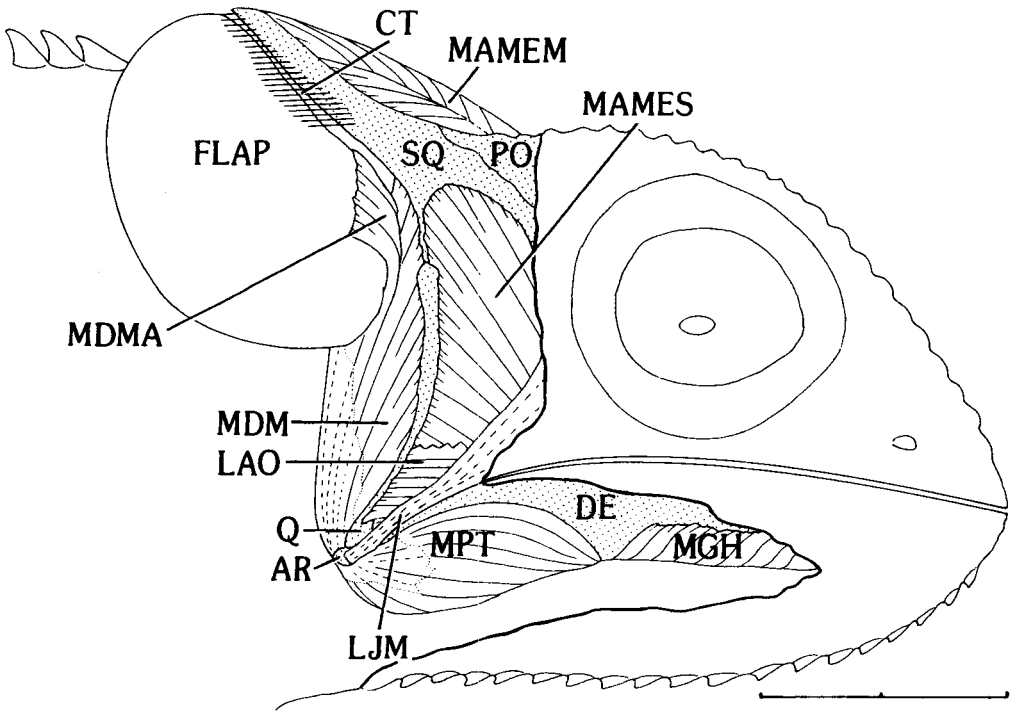We believe this to be the first description of

Fig. 1. Right lateral view of the head and flap of a flap-necked chameleon, *Chamaeleo dilepis*, illustrating the derivation of M. depressor mandibulae pars auricularis and its attachment to the flap "skeleton." AR = articular bone. CT = connective tissue attaching flap to head casque. DE = dentary bone. LAO = M. levator anguli oris (cut). LJM = Ligamentum jugomandibulare. MAMEM = M. adductor mandibular externus medialis. MAMES = M. adductor mandibular externus superficialis. MDM = M. depressor mandibulae. MDMA = M. depressor mandibulae pars auricularis. MGH = M. geniohyoideus. MPT = M. pterygoideus. PO = postorbital bone. Q = quadrate bone. SQ = squamosal bone. Scale bar = 1 cm.

the flap anatomy and movement mechanism in *C. dilepis*. Previous work has documented flap abduction as a component of defensive behavior (Mertens, 1946; Grzimek, 1975; Carpenter and Ferguson, 1977). Tornier (1904) described a system of air sacs in the neck and throat of *C. gracilis*, and presumed that *C. dilepis* used a similar inflation mechanism to erect or abduct the flaps. Muscle activity (particularly M. depressor mandibulae) was viewed as responsible for flap adduction, not abduction. According to Werner (1912), the inflation mechanism described by Tornier has never been observed in live animals and is incorrect. We too saw no system of air sacs extending into the neck flaps in any of the chameleons we examined.

To address whether the morphological arrangement of pars auricularis is unique to *C. dilepis*, we examined the flap morphology of four other species of flapped chameleons: the veiled chameleon, *C. calyptratus*; the short-horned chameleon, *C. brevicornis*; the hooded chameleon, *C. cucullata*; and Meller's chameleon, *C. melleri*. All of these species possess a pars

auricularis and an attachment to the flap identical to *C. dilepis*. The chameleon phylogeny of Klaver and Böhme (1986), places these five species into three separate genera or subgenera: *Chamaeleo* (*dilepis, calyptratus*), *Calumma* (*brevicornis, cucullata*), and *Trioceros* (*melleri*). However, Rieppel and Crumly (1997) support the traditional view of placing them all into *Chamaeleo*. No mention of neck flaps was made in either study. If the first phylogeny is correct, it means that neck flaps and their musculature have evolved more than one time (at least) since each group contains both flapped and nonflapped species. If the second phylogeny is correct, it means that neck flaps may have evolved only once.

Separation of the depressor mandibulae muscle into two portions, although uncommon in members of the family Chamaeleonidae (see Mivart, 1870; Haas, 1973), is fairly common in other lizard families (Haas, 1973). The attachment of a separate slip of muscle fascicles to the flap represents a relatively simple modification of the existing muscle for a new function. Al-

though pars auricularis is derived from a jaw opener, we have observed *C. dilepis* and *C. calyptratus* abducting the flaps without opening the jaw. Two hypotheses can be suggested to explain this action. First, recruitment of pars auricularis independent of the depressor mandibulae muscle can move the flaps without opening the jaw. Alternatively, simultaneous activation of depressor mandibulae and adductor mandibulae could produce flap abduction while keeping the jaw closed. In vivo electromyography can be used to determine which of these hypotheses is correct.

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