OGILVIE, Philip Woodworth, 1931–
AN ANATOMICAL AND BEHAVIORAL INVESTIGATION OF A PREVIOUSLY UNDESCRIBED POUCH FOUND IN CERTAIN SPECIES OF THE GENUS CHAMAELEO.

The University of Oklahoma, Ph.D., 1966
Zoology

University Microfilms, Inc., Ann Arbor, Michigan

THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

AN ANATOMICAL AND BEHAVIORAL INVESTIGATION OF A PREVIOUSLY UNDESCRIBED POUCH FOUND IN CERTAIN SPECIES OF THE GENUS *CHAMAELEO*

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

DOCTOR OF PHILOSOPHY

BY

PHILIP WOODWORTH OGILVIE

Norman, Oklahoma

1966

AN ANATOMICAL AND BEHAVIORAL INVESTIGATION OF A PREVIOUSLY UNDESCRIBED POUCH FOUND IN CERTAIN SPECIES OF THE GENUS *CHAMAELEO*

APPROVED BY

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DISSERTATION COMMITTEE

ACKNOWLEDGMENTS

I wish to take this opportunity to thank the following people for the help that they have extended during the preparation of this dissertation: Dr. Charles C. Carpenter, my major professor, and the other members of my committee, for the counsel that they have offered; Dr. W. E. Duellman, Dr. D. Broadley, Dr. I. W. Whimster, Dr. D. Muller, and Mr. Semakula for supplying vital specimens; Miss Nadine Chowning for the preparation of microscopic sections; Miss Robin Young for the preparation of the drawings; Mr. Barney Hillerman for the photographic reproductions; Mrs. Caroline Stone for typing the dissertation; and finally, my wife, Marilyn, for her help and encouragement.

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CHAPTER I

INTRODUCTION

This problem became apparent during a field investigation of the genus Chamaeleo[1] conducted in east and central Africa. Many of the animals that I collected exhibited a white, foul smelling, viscous substance at the angle of the jaw. The odor of this substance was similar to that of decaying meat. When the jaws were opened, the quantity of the substance increased. After examination, it was found to come from a pouch or fold of skin located dorsal and median to the upper lip at the posterior junction of the lips.

At first, I thought this was the secretion of a gland and I kept records in order to determine if the "gland" was active only during certain periods of the year. I soon found that it was "secreting" at all times. This led me to believe that perhaps this was something

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[1] In this dissertation, I have used the nomenclature of Hillenius, 1959, the most recent revision of the genus Chamaeleo except where otherwise indicated.

other than a gland; therefore, I undertook dissections. I found that there was neither obvious glandular material lying adjacent to nor ducts leading into this pouch and that the only glands near this region were salivary glands. Upon microscopic examination, I found no tissues that were glandular in nature associated with this pouch. Observations on the behavior of these animals in the field led me to believe that certain of their behavioral patterns were related to this same pouch.

A detailed search of the literature led me to conclude that no one has previously described these pouches nor discussed the function of their product. I found many papers that were concerned with the anatomy of *Chamaeleo*--particularly with reference to specific systems. However, in none of these papers is there any discussion or description of such a pouch. This led me to the conclusion that this is a previously undescribed structure deserving of a certain degree of investigation.

It is the purpose of this dissertation not only to describe this structure in several of the representatives of the genus *Chamaeleo*, but also to indicate several possible functions for this previously undescribed anatomical structure. This will be undertaken in the following way: a detailed description of the morphology of this pouch, as found in several species of the genus *Chamaeleo*, a description of the histology of the pouch and finally a section detailing the related behavior of chameleons.

The lack of a single source of information on the anatomy of Chamaeleontidae justifies a fairly extensive treatment of the papers concerned with the anatomy of members of this very distinctive and relatively poorly known family. I will; therefore, designate the specific papers dealing with this anatomy in some detail.

The skeletal system has been described in a general way by Siebenrock (1893) and more recently by Romer (1956). That portion of the skeletal system that has received the greatest amount of attention is the skull. The best coverage of the skull of the chameleon is also the oldest, that of Parker (1881). Others who have discussed either the entire skull or specific regions of it are Germershausen (1913), Frank (1951), Engelbrecht (1951), Prasad (1954), Edinger (1955), Trost (1956), and Jollie (1960). The only other parts of the skeletal system which have been studied in detail are the pectoral girdle and the carpals and tarsals. The pectoral girdle has been studied in some detail by Skinner (1959). The very distinctive and specialized carpals and tarsals were first discussed by Stecker (1877) and later by Born (1880).

Mivart (1870) wrote a general description of the muscles of a chameleon, *Chamaeleo parsonii*, that is accompanied by a fine series of engravings of the musculature that are easily interpreted, thus making this an excellent source for muscular terminology. Several studies of specific groups of muscles or muscles associated with specific organs have been undertaken. These studies vary greatly both with respect to depth and approach. The trunk muscles were discussed by Lubosch (1933) and Sathe (1959). Ribbing (1913) discusses the musculature of the limbs, while Ali (1948) discusses the highly specialized musculature of the tail. Poglayen-Neuwall (1954) discusses the jaw muscles. The extremely specialized nature of the tongue has led to a series of most interesting papers on its musculature and its function. The study by Gnanamuthu (1930) includes an extensive bibliography of the earlier work on the tongue. This organ has recently been studied by Gans (Carl Gans, *personal communication*).

Leblanc (1924, 1925) discusses the muscles of the eye.

The circulatory system was discussed in general terms by Beddard (1904). But while this work is general, it is by no means comprehensive. The blood was studied in greater detail by Sabrazes and Maratet (1924). A detailed study of the heart was presented by Kashyap (1960). The cervical blood vessels with particular reference to the carotid bifurcation were described by Adams in a series of papers (1939, 1953, 1957). The cephalic veins and sinuses were discussed by Bruner (1907) in his general coverage of the cephalic veins of the lizards. The arterial system was discussed by Rathke (1857) and Mackay (1886).

The characteristics of the respiratory system have been used by several authors as taxonomic criteria for the fragmentation of the Chamaeleontidae. The only purely anatomical discussion of the unusual lungs found in chameleons is that of Beddard (1907). The nasal cavity was discussed in great detail by Haas (1937).

There is no general treatment of the nervous system and Adams (1942) in his general paper on the sympathetic system of lizards fails to mention the family

Chamaeleontidae. There have been several discussions of the parts of the brain and Shanklin (1930) correlates many of these in an excellent coverage of the central nervous system in *Chamaeleo vulgaris*. The development of the cerebral tube was presented by Bergquist (1952). Golby and Gamble (1957) described the cerebral hemispheres. The neopallium of the chameleon was discussed by Dart (1934). A developmental study of the wall of the forebrain was presented by Källén (1951 a, b) in two papers. The motor pathways of the eye have been defined by Stefanelli (1941) and Shanklin (1933) produced a definitive work on the *nucleus opticus tegmenti*. Krabbe (1934) presented a general discussion of the parietal organ. The middle ear has been discussed by Simonetta (1957) and compared to the same structure in many other vertebrates. A very detailed histological study of Jacobson's organ in the developing chameleon was presented by Haas (1946). The specialized nature of the eye of the chameleon has led to a great deal of interest in this organ. Walls' (1942) presentation is the most general and includes what little information he has on chameleons within a general treatise on the vertebrate eye. Loewenthal (1935) discusses the glands of the eye and also (1936) presents a discussion of the nictitating membrane.

The only two papers concerned with the endocrine system have been that of Lynn and Walsh (1957) which discusses the thyroid gland and that of Gabe and Martoja (1961) which discusses the adrenals.

While none of the above papers is specifically concerned with the problem at hand, they are all intimately related in that they represent the sum total of anatomical knowledge recorded about the family Chamaeleontidae. It should be apparent from an examination of the topics covered by these papers that none of them discusses specifically the area under study in this dissertation. The only explanation that I can offer for the apparent lack of previous recognition of this structure is the fact that most authors working with chameleons have used dead animals, preserved prior to examination by the author investigating the anatomy. One detailed study that probably should have led to a discovery of the presence of this pouch was Mivart's study of the muscles, but in this instance Mivart studied *Chamaeleo parsonii*, a Madagascan chameleon, in which the pouch is not developed. Those authors who have studied chameleons in which the pouch is not only present but may be both large and obvious have concerned themselves in each instance with regions anatomically distant from the pouch, while those authors who have studied the living animals have not followed up their investigations with anatomical studies.

CHAPTER II

GROSS MORPHOLOGY

This chapter presents a description of the gross morphology of the dermal pouch found in the temporal region of the chameleon. Considering the location of this pouch, the term "temporal pouch" is proposed as a descriptive name for this structure.

This pouch is located in the temporal region of the head and is framed by a series of bones as described below. I have followed the nomenclature of Romer (1956), Prasad (1954), and Parker (1881) with respect to the bones of the skull. Starting at the anterior margin and progressing in a clockwise manner, when examining the left side of the skull, the bones that compose the perimeter of this space are as follows: The jugal forms both the posterior boundary of the orbit and also the anterior margin of this temporal vacuity. The post-frontal (post-orbital of Parker, 1881 and Prasad, 1954), may or may not take part in the framing of this vacuity but when it does so it fills the anterior dorsal corner

(Romer, 1956). The temporal crest of the squamosal forms the dorsal margin. The dorsal portion of the bone suspending the lower jaw has been demonstrated by Prasad (1954) to be the supra-temporal; the remainder of this posterior margin is formed by the quadrate. The ventral edge is formed by three bones of the lower jaw--the articular, the surangular (which is not uniformly present, Romer, 1956), and the coronoid. Finally the maxilla completes the ventral anterior corner. The relationships of all these bones are shown in Fig. 1.

The pouch lies over the superficial temporal muscles and anterior to the depressor mandibulae (_sensu_ Mivart, 1870), see Fig. 2. In each instance, the base of the temporal pouch was found to lie beneath the zygomatic ligament (_sensu_ Mivart, 1870) which connects the posterior margin of the jugal with the lateral border of the articular. In some instances this ligament was linear and thick attaching only to the ventral posterior portion of the jugal, whereas in others the attachment to the jugal was much broader, making a triangularly shaped, thin, ligamentous structure completely covering the pouch. All of the above structures are labeled in Figs. 1 and 2.

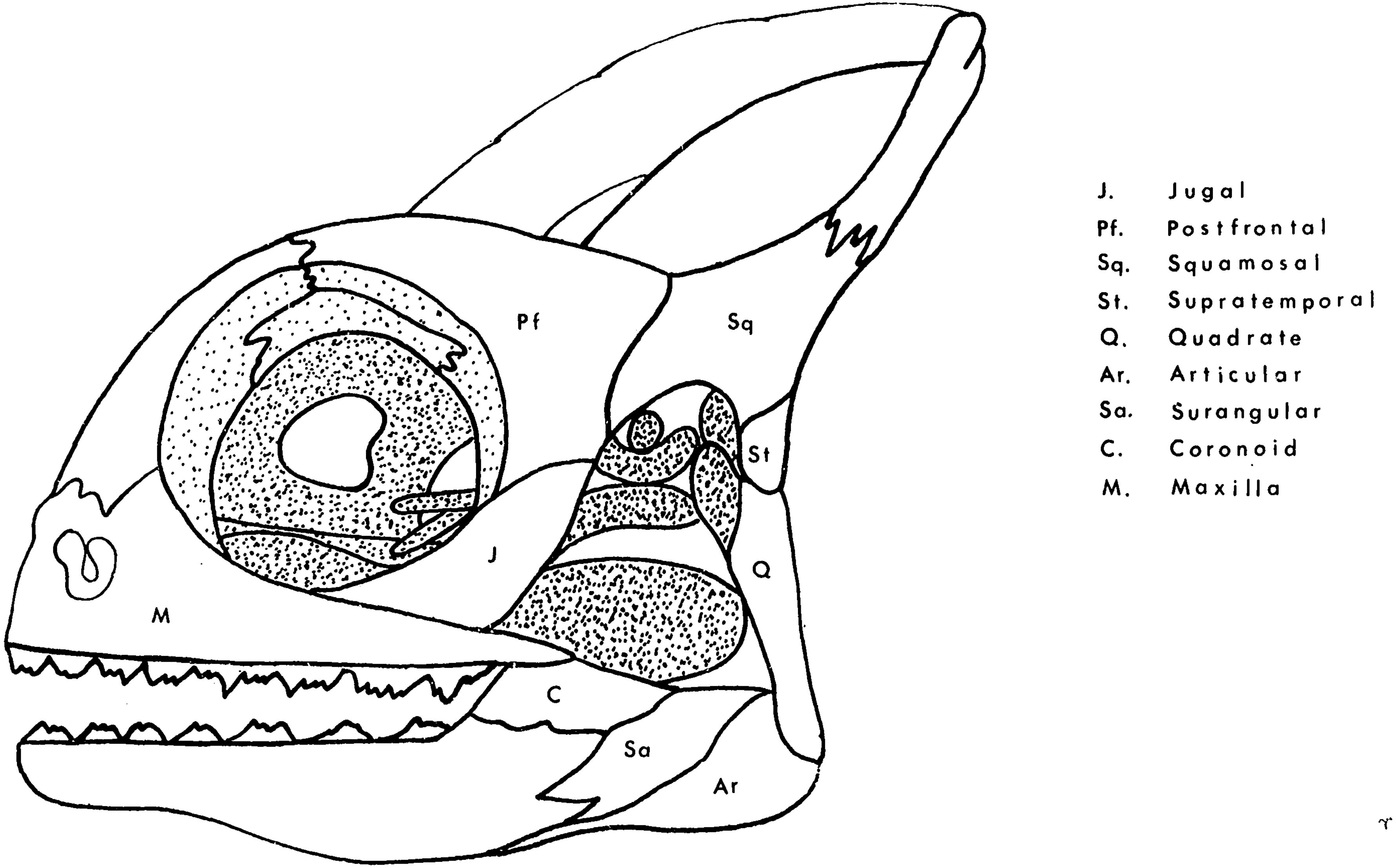

FIG. 1. Idealized skull of hypothetical chameleon showing the relationships of all of the bones that may take part in the temporal vacuity.

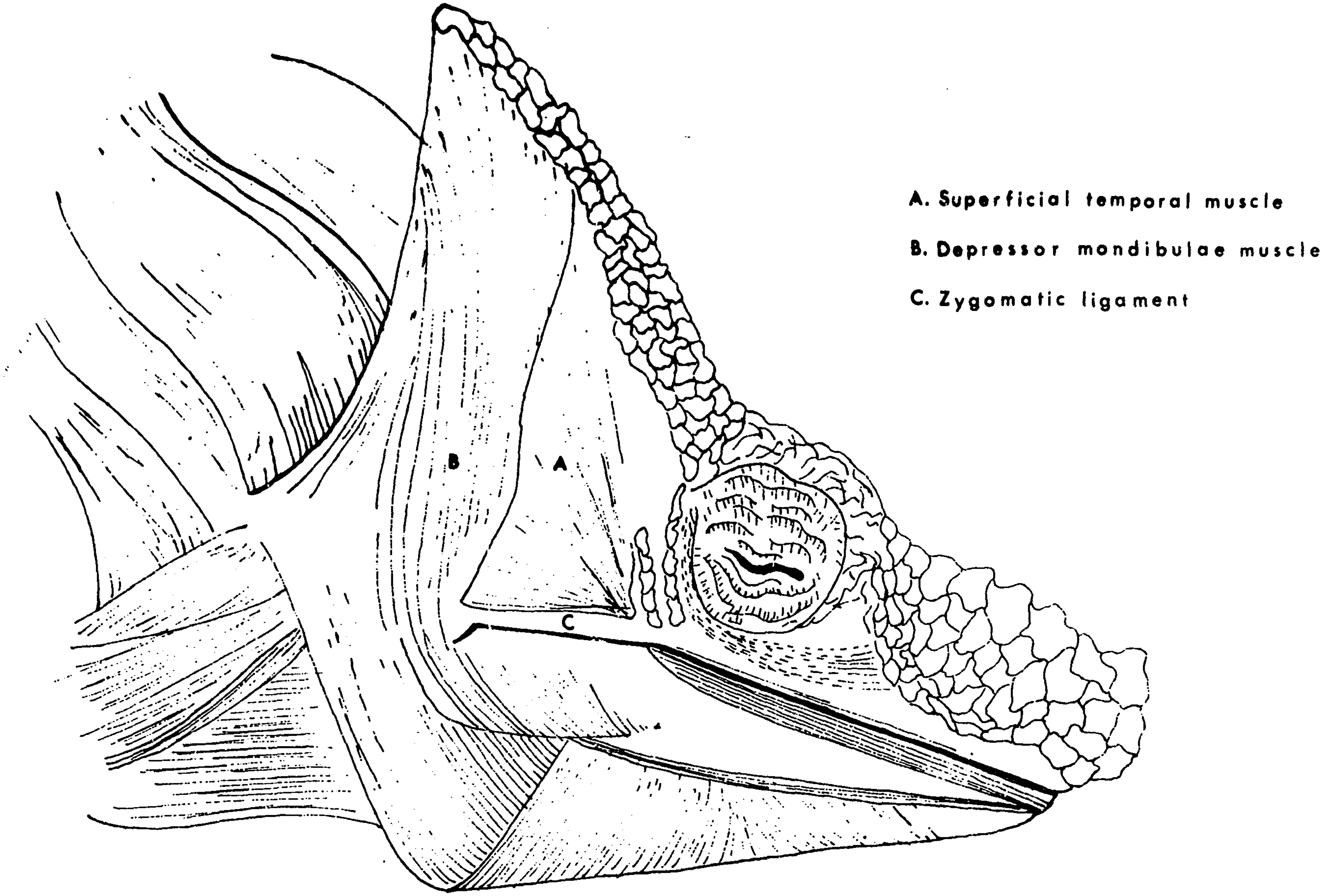

FIG. 2. Right view of the temporal region of *Chamaeleo parsonii* with the skin removed in order to show the superficial musculature and ligaments (after Mivart: 1870).

As the chameleon depresses its mandible by the action of the digastric muscle and thus opens its mouth, the skin in the region of the commissure of the lips is stretched. This action pulls the pouch beneath the taut zygomatic ligament and expresses some of the contents of the pouch.

Dissection in order to demonstrate this structure is a relatively simple matter and involves the removal of a flap of skin. This flap is formed by making a dorsad directed cut starting at a point immediately posterior to the posterior border of the orbit and cutting to the temporal crest, then following posteriorly along the temporal crest to the posterior margin of the head, then ventrally to a point level with the commissure of the lips. This superficial flap of skin may then be retracted ventrally to disclose the pouch lying immediately beneath the skin and beneath the zygomatic ligament. Photographs of such dissections with the flap removed are shown in Fig. 3. The above described dissection was carried out on the representatives of eleven species of the family Chamaeleontidae. Ten of these are normally listed in the genus Chamaeleo, whereas one is listed in the genus

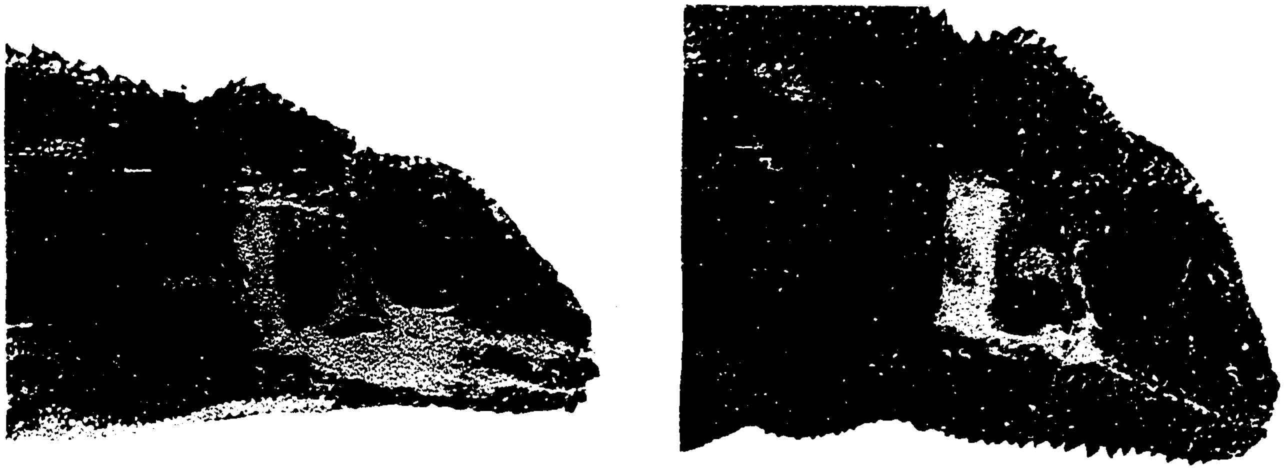

FIG. 3. Photographs of the dissections in two individuals of <u>Chamaeleo bitaeniatus</u> exposing the temporal pouches.

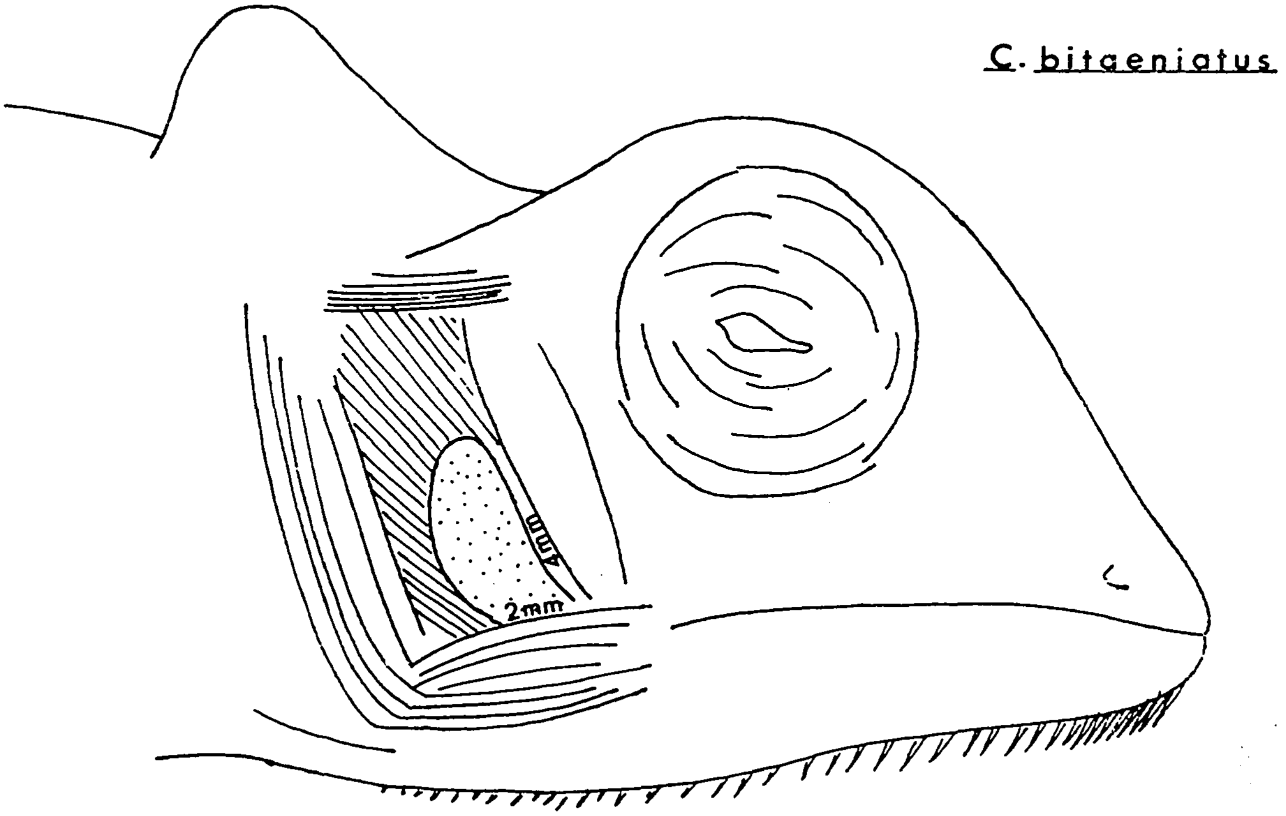

FIG. 4. Drawing of a dissection of <u>Chamaeleo bitaeniatus</u> showing the size of the temporal pouch.

Brookesia. Nine of the eleven species were from mainland Africa, and two were from the island of Madagascar. Appendix A gives a list of all the species examined together with the collecting localities and a map with the localities labeled. In all species examined except for the two Madagascan species and two of the mainland species, the pouches proved to be quite evident and easily measured. Those species examined but showing no gross evidence of the pouch were, from the mainland, Brookesia brachyura and Chamaeleo marshalli; those from Madagascar were C. brevicornis and C. lateralis. The measurements for the pouches found in the remaining species are given in Table 1. I selected the particular measurements given in this table as indices of head size as compared with pouch size. The length of the lips was measured on a straight line from the commissure of the lips to their most anterior point. The diameter of the orbit was measured in a dorso-ventral axis. The width of the base of the pouch and its greatest height from the base were also measured. All measurements in this and the following tables are in millimeters.

In Chamaeleo bitaeniatus (Figs. 3 and 4), the pouch was higher than broad. It was quite obvious and in many

TABLE 1. SELECTED HEAD MEASUREMENTS OF THOSE SPECIES OF CHAMELEONS EXAMINED AND FOUND TO POSSESS TEMPORAL POUCHES. (ALL MEASUREMENTS IN MILLIMETERS.)

Species	Sex	Location of Capture	Length of Lips	Diameter of Orbit	Base Breadth of Pouch	Height of Pouch
Chamaeleo bitaeniatus	M	Kampala, Uganda	14.1	6.8	2.6	4.6
C. bitaeniatus	F	Kampala, Uganda	14.6	6.9	2.6	4.6
C. dilepis	M	Minaki, Tanzania	17.7	8.2	3.4	2.6
C. dilepis	F	Minaki, Tanzania	24.2	12.1	3.9	3.2
C. dilepis	F	Johannesburg, R.S.A.	23.7	10.5	5.4	3.7
C. dilepis	F	Johannesburg, R.S.A.	25.2	10.6	5.3	4.0
C. fischeri	M	Lushoto, Tanzania	26.8	11.6	5.2	3.2
C. fischeri	F	Lushoto, Tanzania	21.2	9.4	3.9	2.3
C. höhnelii	M	Limuru, Kenya	20.3	7.5	4.5	7.1
C. höhnelii	F	Limuru, Kenya	17.5	7.2	4.6	6.9
C. jacksoni	M	Nairobi, Kenya	17.3	7.9	4.6	4.2
C. jacksoni	F	Nairobi, Kenya	19.5	8.2	4.5	4.2
C. jacksoni	M	Meru, Kenya	23.0	11.5	7.4	7.1
C. jacksoni	F	Meru, Kenya	21.6	8.4	5.3	4.8
C. melleri	M	Minaki, Tanzania	39.3	12.9	12.3	6.6
C. melleri	F	Minaki, Tanzania	40.2	13.6	10.2	6.4
C. pumilus	M	Johannesburg, R.S.A.	15.6	6.7	4.8	3.0
C. pumilus	F	Johannesburg, R.S.A.	15.7	5.8	4.9	3.7

instances could be discerned before the skin was removed as a swelling beneath the skin. The zygomatic ligament in this species tended to be linear and heavy. The surface of the pouch was pigmented with differing degrees of pigmentation in different individuals varying from almost white to completely black. Variation in a sample of thirty-five individuals of this species is indicated in Table 2. Six of the individuals showed aberrant, bilobed pouches.

In *Chamaeleo dilepis* (Fig. 5), the pouch was much broader than tall and was completely covered by the broad triangularly shaped zygomatic ligament. The pouch in this species was unpigmented. Individuals from two widely separated localities within the range of this species were examined and while there were differences in the measurements, these differences seemed to be accounted for by variation in the size of the animals rather than from characteristics that might be attributed to subspecific differences in the animals. No attempt has been made in this paper to assign subspecific names to the animals examined.

In *Chamaeleo fischeri* (Fig. 6), the pouch was so short that it was difficult to differentiate and was the

TABLE 2. VARIATIONS IN THE SELECTED HEAD MEASUREMENTS IN A SAMPLE OF _C. BITAENIATUS_ FROM KAMPALA, UGANDA. (ALL MEASUREMENTS IN MILLIMETERS.)

MALES				FEMALES			
Length of Lips	Diameter of Orbit	Base Breadth of Pouch	Height of Pouch	Length of Lips	Diameter of Orbit	Base Breadth of Pouch	Height of Pouch
14.1	6.8	2.6	4.6	14.6	6.9	2.6	4.6
14.2	6.4	2.4	4.2	15.7	6.4	2.5	5.3
13.4	6.9	3.2	5.8	14.6	6.3	2.9	5.3
12.3	5.9	2.3	5.3	13.2	6.1	2.7	4.3
12.8	5.5	2.3	4.5	13.2	5.7	1.6	3.9
12.4	6.0	2.7	3.4	15.3	6.4	2.3	4.2
13.2	6.4	2.4	6.6	12.8	6.4	3.2	5.0
13.1	6.4	3.0	6.5	13.9	6.3	2.2	4.4
13.6	6.0	2.8	5.8	12.0	5.8	2.3	4.2
12.4	6.1	2.3	6.0	14.6	6.2	3.6	4.0*
11.0	5.9	2.6	5.6	12.6	5.8	1.9	3.5
11.5	5.5	2.2	4.4	12.4	5.5	3.2	4.0*
14.2	6.3	4.1	5.6*	13.1	6.2	2.3	6.3
14.8	6.6	4.0	7.9	14.3	6.7	3.7	7.7
15.2	6.7	4.0	7.5*	15.0	6.2	3.1	6.9
10.9	5.6	3.2	5.0*	13.7	6.2	2.7	6.7
				14.5	6.9	3.8	7.0
				12.3	5.6	2.8	5.9
				13.7	5.6	2.9	5.0*

*Pouches aberrant, bilobed.

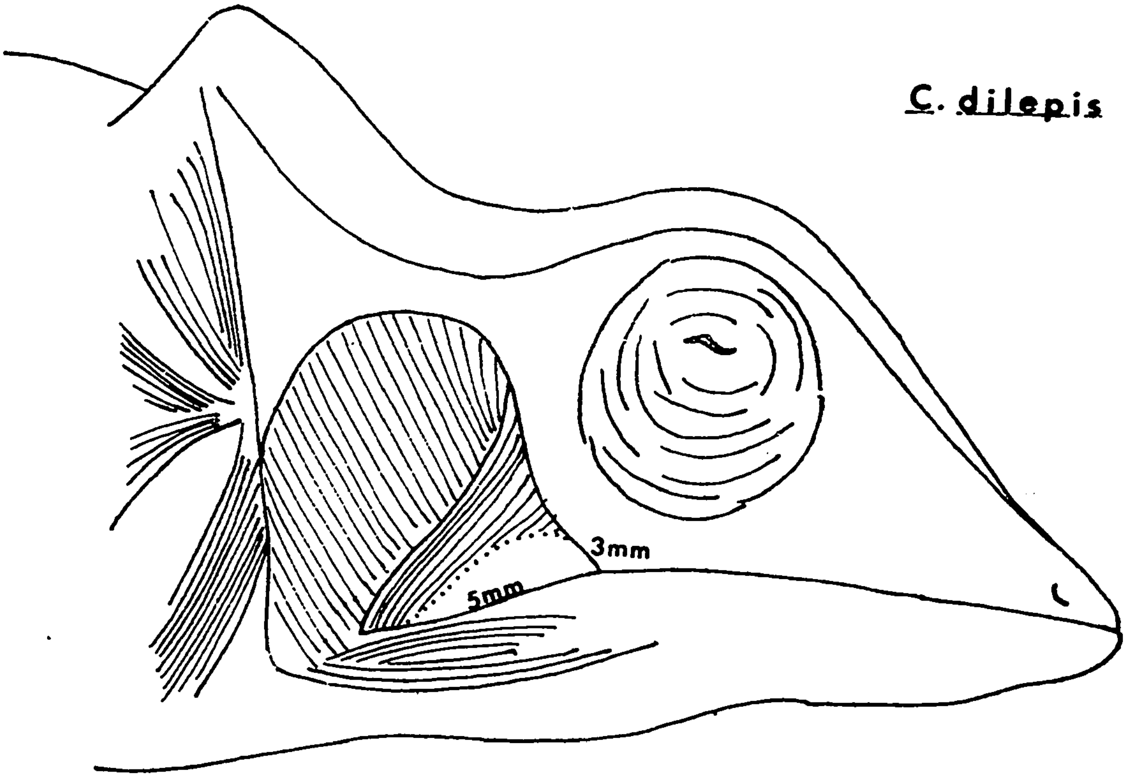

FIG. 5. Drawing of a dissection of *Chamaeleo dilepis* showing the size of the temporal pouch.

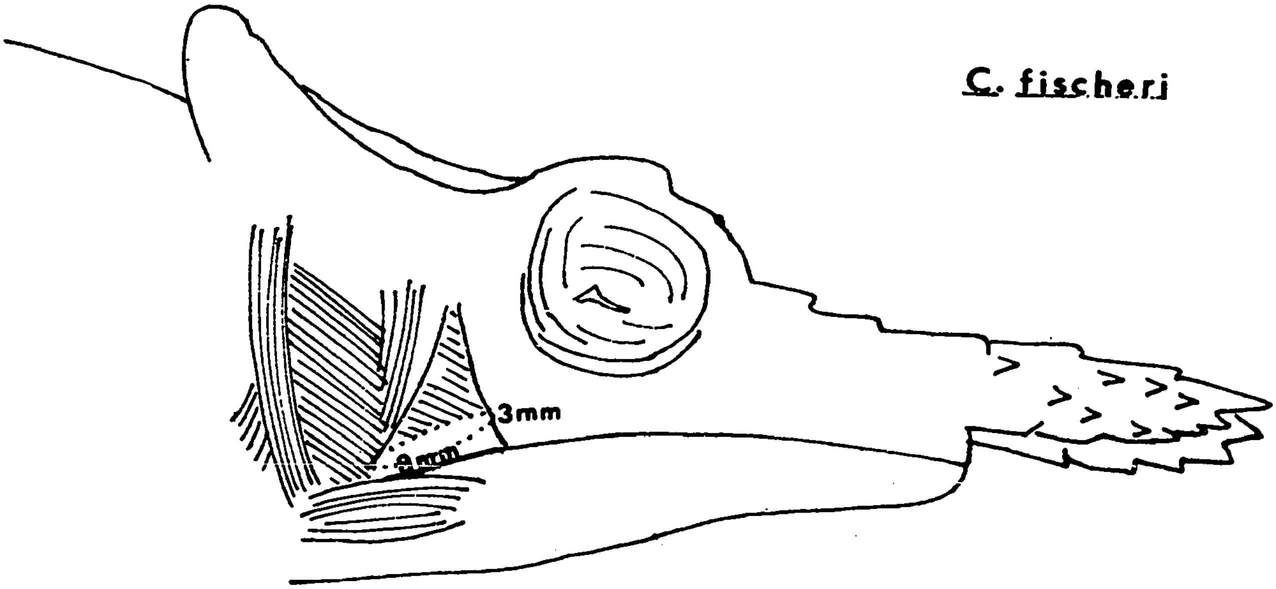

FIG. 6. Drawing of a dissection of *Chamaeleo fischeri* showing the size of the temporal pouch.

least obvious than in others of the mainland species examined in which a pouch was grossly discerned. It was completely obscured by the broad zygomatic ligament and there were no melanophores present.

In Chamaeleo höhnelii (Fig. 7), the pouch is again higher than broad and heavily pigmented. The zygomatic ligament is linear and extremely heavy, lying across the base of the pouch. Table 3 shows the range of individual variation in a sample of twenty-nine specimens captured at Limuru, Kenya. Eight individuals showed bilobed pouches similar to the aberrant pouches found in C. bitaeniatus.

In Chamaeleo jacksoni (Fig. 8), the pouch was nearly the same dimension in both directions, and whereas it was normally broader than high it was occasionally higher than broad. It was lightly pigmented and the zygomatic ligament was moderately broad. The condition in this species would seem to be intermediate between that found in the extremes of C. bitaeniatus or C. höhnelii and C. fischeri. The animals measured for Table 1 and listed as C. jacksoni represent two populations that while close together geographically are as distinct morphologically as any two populations of chameleons with which I am

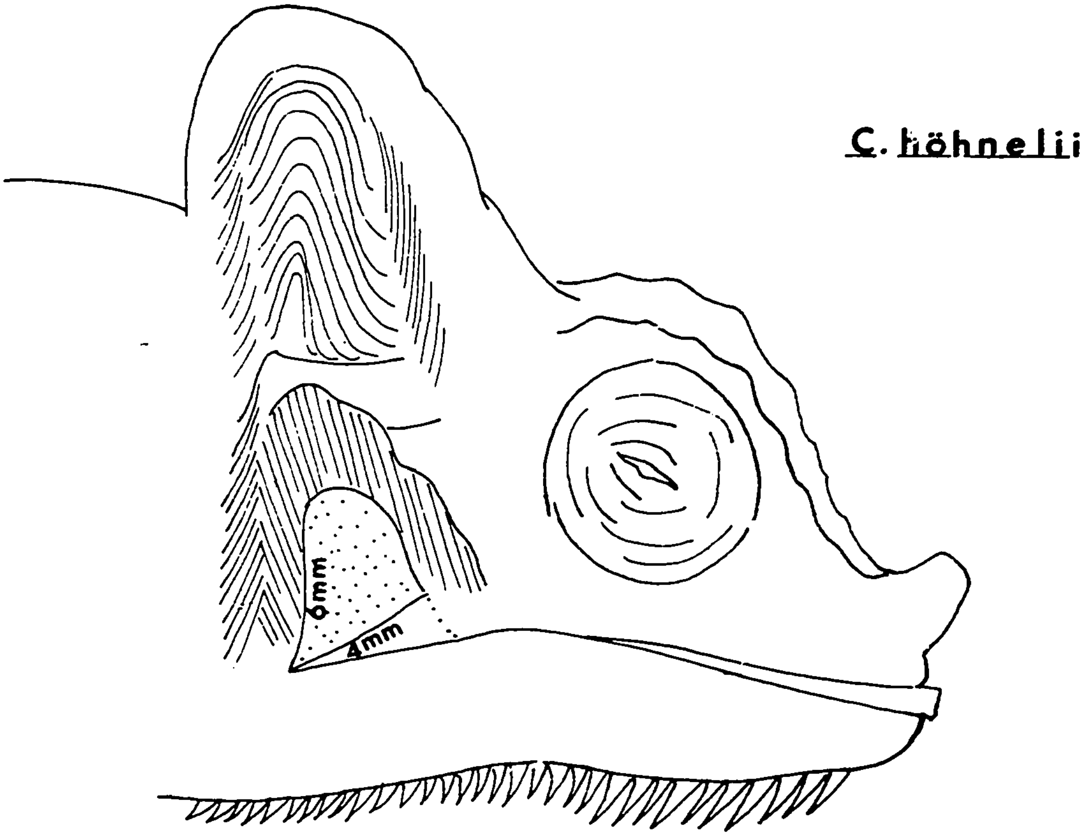

FIG. 7. Drawing of a dissection of *Chamaeleo höhnelii* showing the size of the temporal pouch.

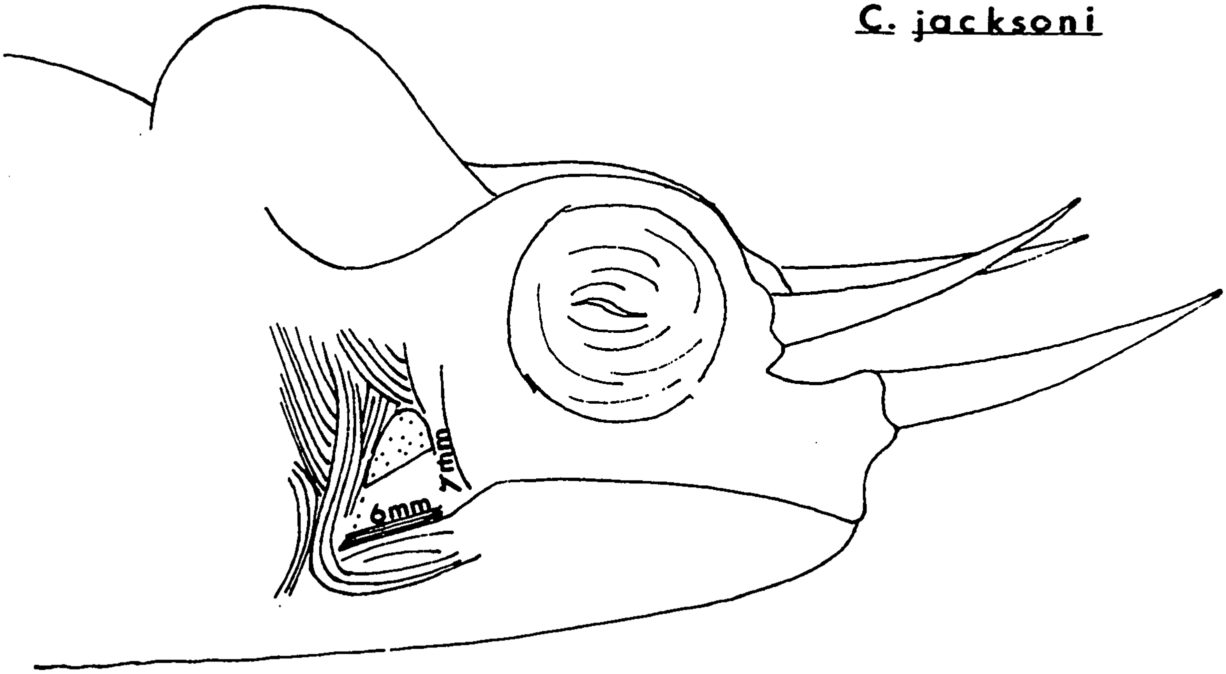

FIG. 8. Drawing of a dissection of *Chamaeleo jacksoni* showing the size of the temporal pouch.

TABLE 3. VARIATIONS IN THE SELECTED HEAD MEASUREMENTS IN A SAMPLE OF *C. HÖHNELII* FROM LIMURU, KENYA. (ALL MEASUREMENTS IN MILLIMETERS.)

MALES				FEMALES			
Length of Lips	Diameter of Orbit	Base Breadth of Pouch	Height of Pouch	Length of Lips	Diameter of Orbit	Base Breadth of Pouch	Height of Pouch
20.3	7.5	4.5	7.1	17.5	7.2	4.6	6.9
14.1	6.3	2.6	5.2	19.1	7.8	5.2	7.4
19.2	7.2	5.2	7.1	18.4	8.4	4.9	7.8
18.0	7.5	5.3	7.3	19.3	7.8	6.2	7.2
19.1	8.2	5.2	7.9	15.7	6.5	4.2	6.1
18.2	7.7	5.2	7.5*	17.4	7.4	4.5	6.4
17.5	7.3	5.7	7.3*	14.9	6.5	3.8	5.5
16.7	7.6	5.6	6.8*	15.4	6.4	4.3	5.6
16.5	7.2	4.8	6.6*	15.6	6.8	3.7	6.6
17.5	7.6	5.1	7.1	15.7	6.7	3.8	6.3
17.0	7.0	4.3	7.1	15.5	6.4	5.4	6.4*
17.3	7.6	5.0	6.7*	16.2	6.9	4.5	5.2*
16.6	6.7	4.8	6.9	13.6	6.3	3.6	4.4
15.2	6.3	4.0	6.1				
14.9	6.7	4.5	6.6				
14.7	6.0	4.3	5.7*				

*Pouches aberrant, bilobed.

familiar. The pouches in these two forms; however, are still quite similar. Table 4 indicates the variation in sixteen individuals of *C. jacksoni* taken from the Nairobi population.

In *Chamaeleo melleri* (Fig. 9), the lightly pigmented pouch was shorter than broad and the zygomatic ligament while overlying the pouch did not completely obscure it.

In *Chamaeleo pumilus* (Fig. 10), the pouch is similar to that found in *C. dilepis*, that is, broader than tall, unpigmented, and completely covered by the broad zygomatic ligament.

There was a very small pouch present in *Brookesia brachyura*, even though it was not seen when the animal was dissected under a binocular dissecting microscope. I believe that the reason for its being so difficult to see is the fact that this pouch is unpigmented and lies between two sheets of non-pigmented tissue. This, together with its small size, makes it extremely difficult to see.

TABLE 4. VARIATIONS IN THE SELECTED HEAD MEASUREMENTS IN A SAMPLE OF <u>C</u>. <u>JACKSONI</u> FROM NAIROBI, KENYA. (ALL MEASUREMENTS IN MILLIMETERS.)

MALES				FEMALES			
Length of Lips	Diameter of Orbit	Base Breadth of Pouch	Height of Pouch	Length of Lips	Diameter of Orbit	Base Breadth of Pouch	Height of Pouch
17.3	7.9	4.6	4.2	19.5	8.2	4.5	4.2
21.5	9.2	6.1	5.4	22.2	9.7	6.4	5.6
18.4	7.8	4.8	3.7	17.8	7.8	4.2	4.4
17.2	7.8	4.3	4.3				
18.9	8.1	5.6	4.1				
18.8	8.0	5.2	4.8				
16.6	8.1	4.8	4.5				
14.5	6.9	4.2	3.4				
18.8	8.4	5.3	4.7				
21.2	9.2	4.8	4.2				
17.8	7.5	4.2	4.1				
16.6	7.5	5.0	4.1				
18.3	8.7	6.2	5.5				

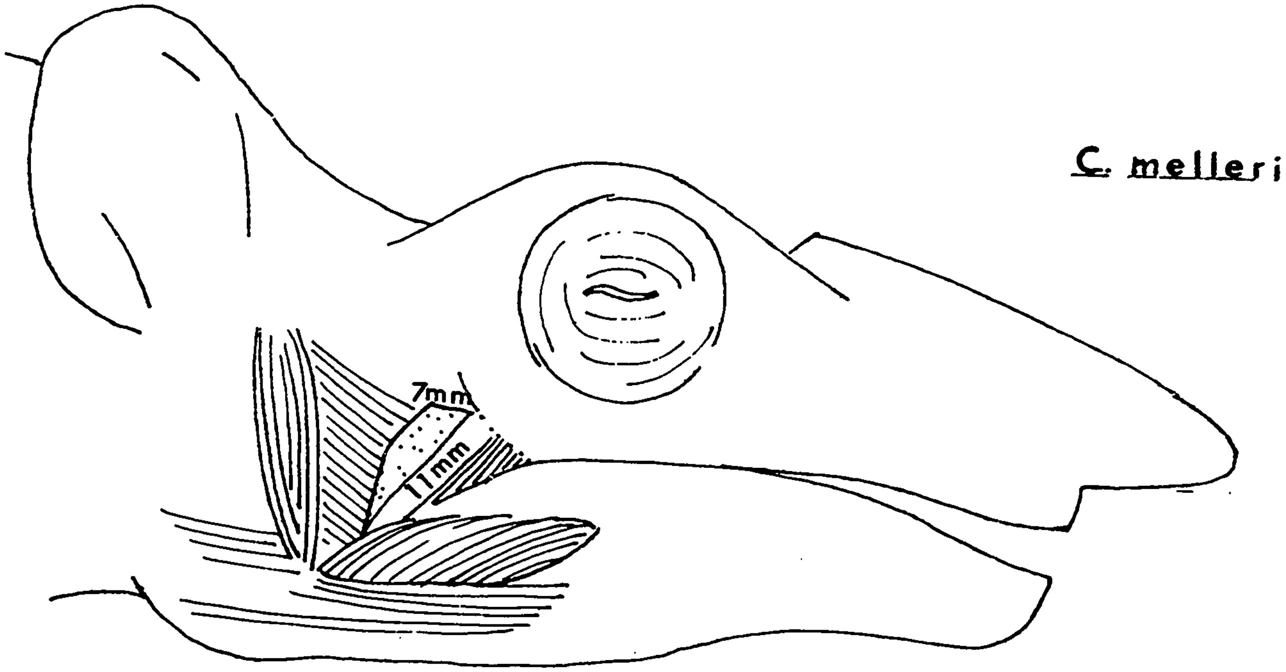

FIG. 9. Drawing of a dissection of Chamaeleo melleri showing the size of the temporal pouch.

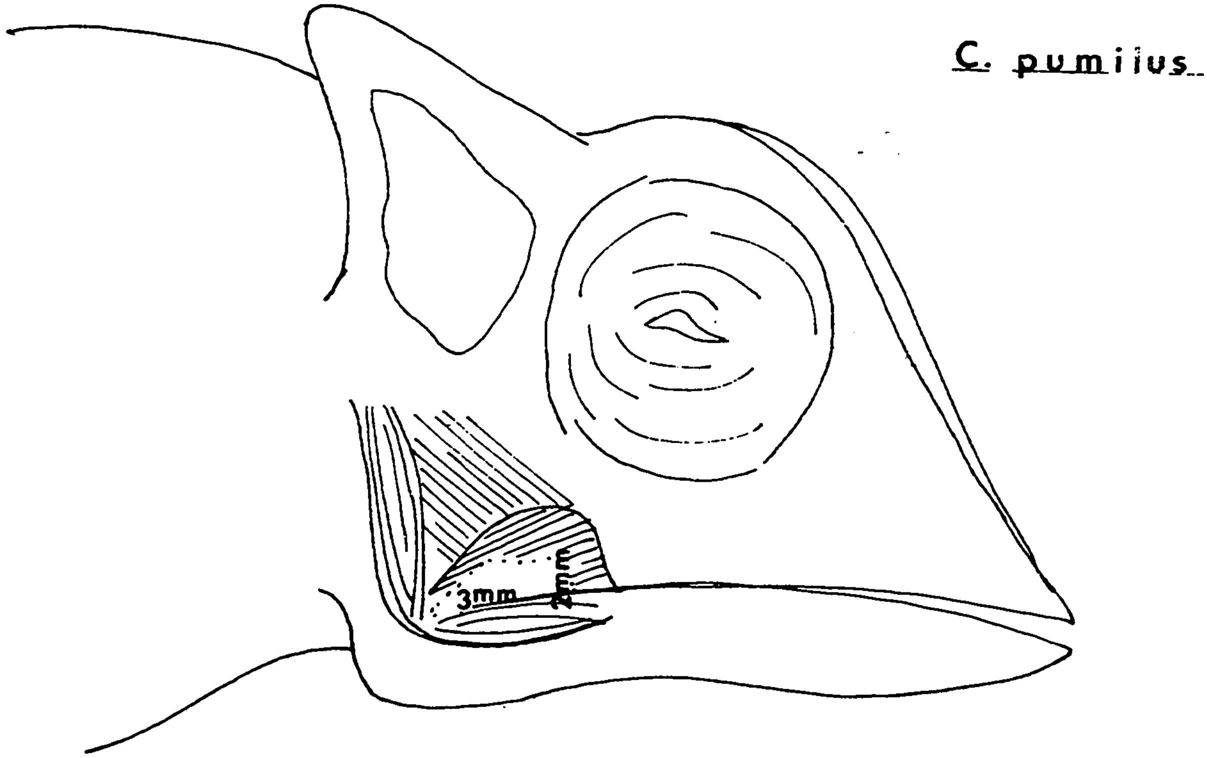

FIG. 10. Drawing of a dissection of Chamaeleo pumilus showing the size of the temporal pouch.

CHAPTER III

HISTOLOGY

Tissue was removed from the left temporal region of examples of both sexes of each of the species examined and was embedded in Tissuemat preparatory to cutting microscopic sections. Due to the brittleness of the tissue, the sections were cut at twenty microns, in order to attempt to preserve the integrity of the tissues.

Sections from each of eleven species examined were stained according to the following techniques: (1) hematoxylin and eosin stain (Armed Forces Institute of Pathology, 1960), (2) Gomori trichrome stain (Gomori, 1950), and (3) Verhoeff's elastic stain (Mallory, 1938). Details of the staining techniques may be found in Appendix B.

The least anticipated information that came from the examination of these sections was the presence of a pouch in Brookesia brachyura, Fig. 11. Sections of the pouch as seen in Chamaeleo bitaeniatus (Fig. 12), C. jacksoni (Fig. 13), and C. melleri (Fig. 14) were selected

FIG. 11. Section through the pouch of Brookesia brachyura. Hematoxylin and eosin stain. Approximately X 103. The following letters are used as abbreviations in figs. 11 through 16: c, commissure of the lips; d, dorsal; l, lateral; m, median; p, temporal pouch; v, ventral; z, zygomatic ligament.

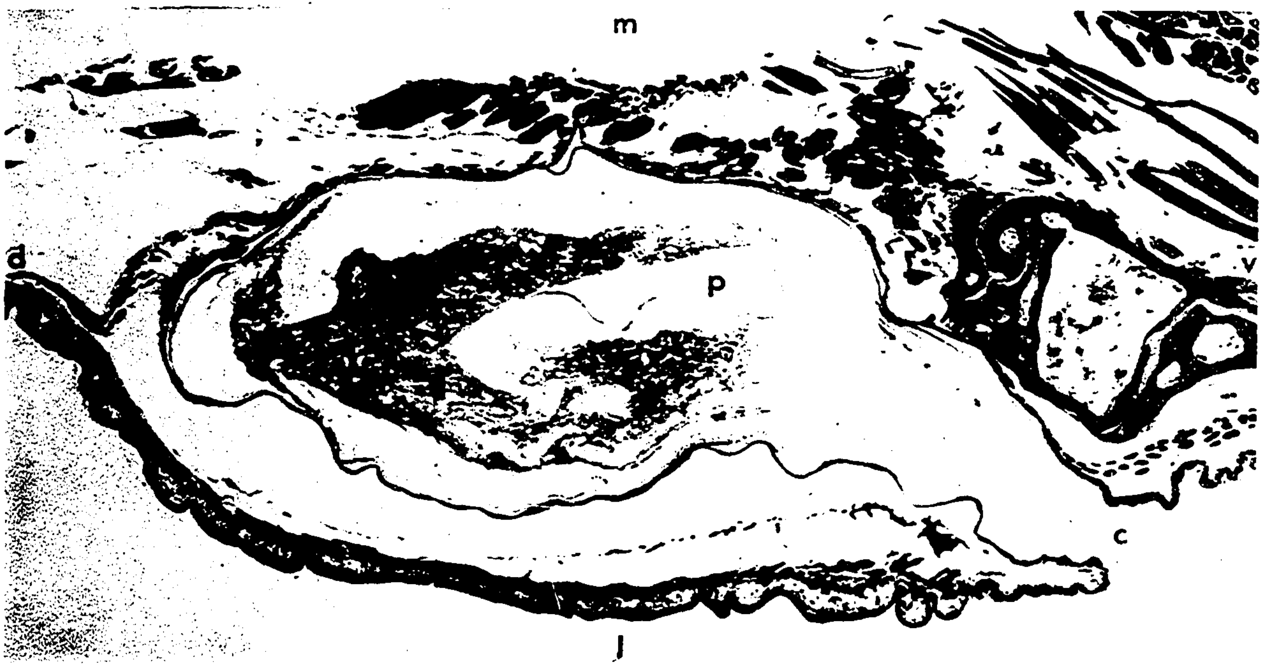

FIG. 12. Section through the pouch of Chamaeleo bitaeniatus. Trichrome stain. Approximately X 44.

FIG. 13. Section through the pouch of *Chamaeleo jacksoni*. Hematoxylin and eosin stain. Approximately X 35. The prominent zygomatic ligament is evident.

FIG. 14. Section through the pouch of *Chamaeleo melleri*. Trichrome stain. Approximately X 42.

as being representative of the range of variation in the pouch as observed in the various species examined. The pouches varied not only in relative dimensions but also in degree of pigmentation and the extent to which they were covered by the zygomatic ligament. C. bitaeniatus represents a species in which the temporal pouch is well developed, C. melleri possesses a proportionally small pouch, whereas C. jacksoni shows an intermediate condition. Fig. 15, C. marshalli, and Fig. 16, C. lateralis, illustrate sections through the temporal region of animals in which the pouch is absent.

The skin within the pouch showed a condition resembling mammalian skin more than typical reptilian skin. The layer of the epidermis immediately above the basal membrane was composed of simple columnar epithelial cells, while the layers lying superficial to this were composed of progressively more compressed stratified squamous epithelial cell, Fig. 17. The cells immediately above the apparently germinal columnar cells, with their enlarged nuclei, were less compact and flattened than the cells lying above them. These first three layers of cells had extremely granular cytoplasm similar to the stratum

FIG. 15. Section through the temporal region of Chamaeleo marshalli. Hematoxylin and eosin stain. Approximately X 104.

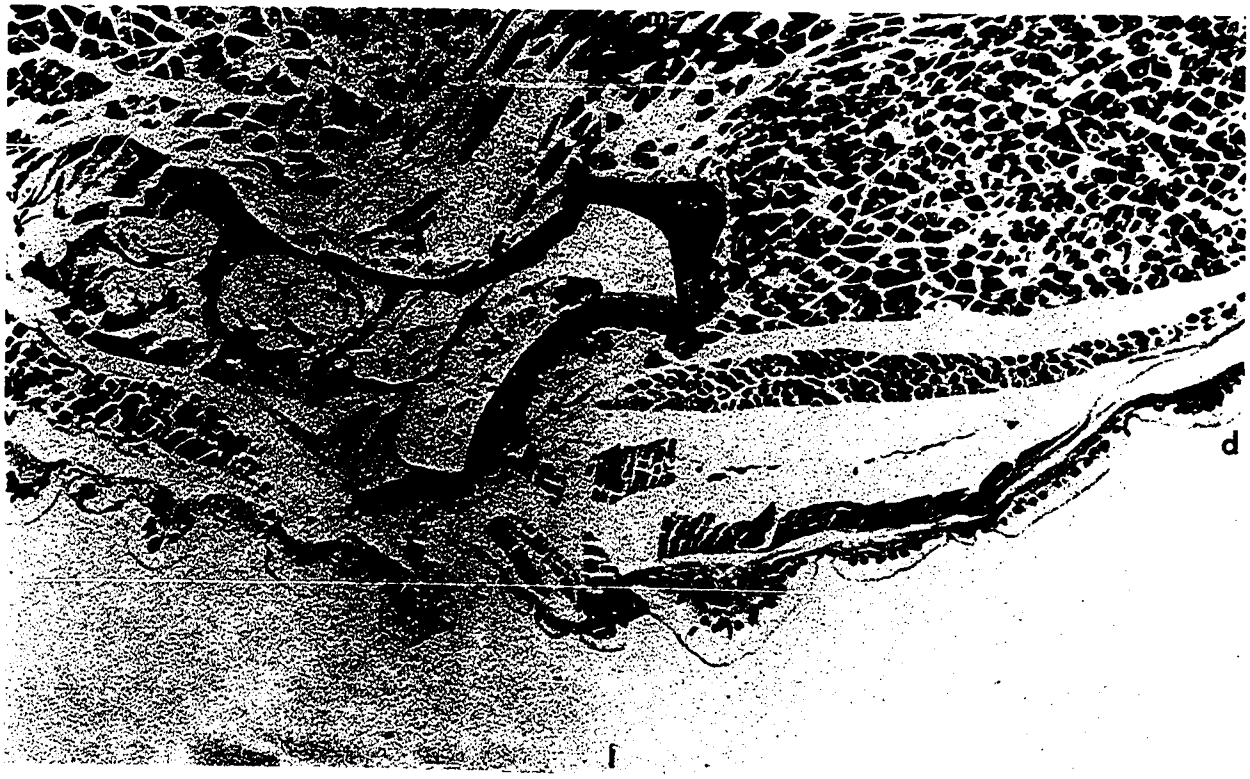

FIG. 16. Section through the temporal region of Chamaeleo lateralis. Trichrome stain. Approximately X 57.

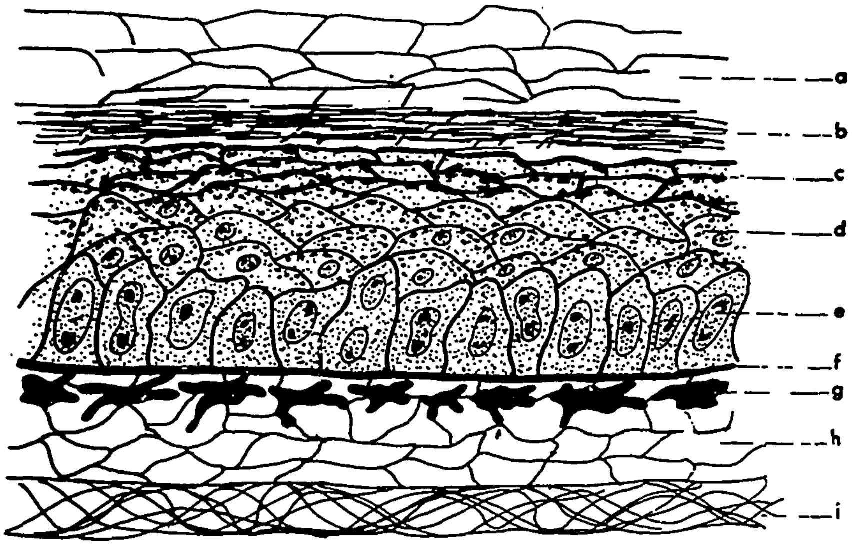

FIG. 17. Section through the pouch wall in Chamaeleo melleri Approximately X 1940. Key: a, sloughing keratinized cells; b, densely compact keratinized layer; c, compressed keratinized layer lacking nuclei; d, granular layer; e, germinative layer; f, basal membrane; g, melanophores; h, dermis; i, subcutaneous connective tissue.

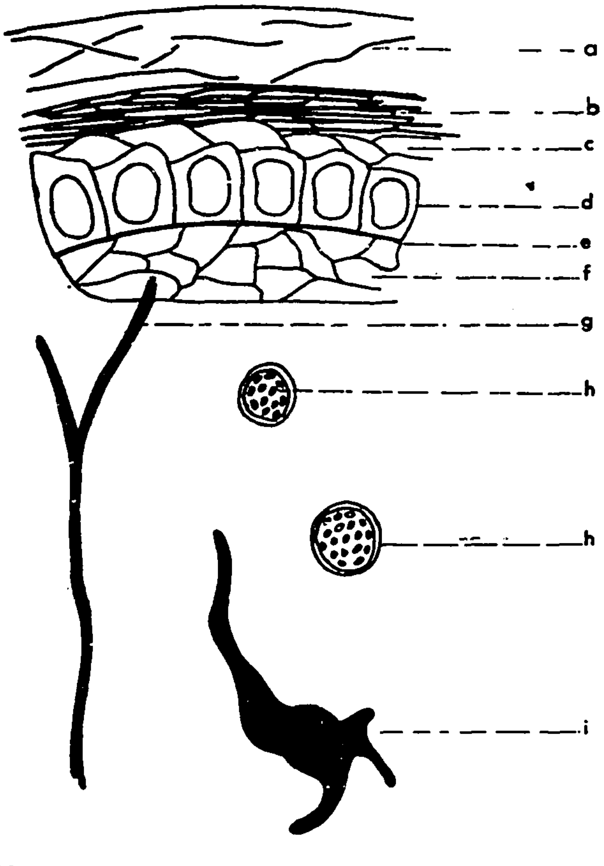

FIG. 18. Diagramatic representation of a section through the skin of Chamaeleo melleri. Approximately X 1940. Key, a, amorphous keratinized layer; b, densely compressed keratinized cells; c, compressed cells; d, germinative layer; e, basal membrane; f, dermis; g, nerve fibers; h, blood vessels; i, melanophores (g, hi, and i all contained within loose subcutaneous connective tissue).

granulosum of human skin. One might presume that these granules are keratohyalin granules leading to the formation of keratin in the more superficial cells. Below the germinative layer there is a thin layer of connective tissue and, beneath this, loose subcutaneous connective tissue. The layers then that can be distinguished in this tissue might correspond to the following layers of thick human skin: the deep layer of columnar tissue would correspond to the stratum germinativum, the more superficial granular layer would correspond to the stratum granulosum, and the yet more superficial compressed layer would correspond to the stratum corneum.

There was no indication of this skin being divided into scale units as there is in the external skin of the chameleon, Fig. 18. Keratin in all cases is confined to the superficial layers and in no instance is found throughout the epidermis. The internal surface of the pouch showed a great deal of sloughing of the keratinized layer and the lumen of the pouch filled with what appeared to be sloughed keratinized skin. In Fig. 13 one can see the extensive elastic connective tissue between the lateral wall of the pouch and the external skin. The broken appearance of the tissues and separation of some of them is due to the method of preservation, since these tissues were taken from animals preserved for taxonomic rather than histological study and had been stored in unbuffered formalin for periods up to five years.

CHAPTER IV

BEHAVIOR

Several behavioral patterns of the chameleon seem to be related to the presence of the temporal pouch. This chapter will describe these behavioral sequences together with the behavior of a prey species when presented with the substance produced in this pouch.

In my repeated field observations of chameleons, I have on numerous occasions, while observing specimens of different species, noted a behavior common to many of them. The animal stiffens its forelegs pushing its body away from the branch, arches its neck forward with the jaws open, and wipes its head from side to side. This series of motions produces the effect of bringing the right side of the mouth in contact with the left side of the branch followed by bringing the left side of the mouth in contact with the right side of the branch. The animal appears to be wiping something from its jaws. This action has been interpreted by Bustard (H. Robert Bustard, personal *communication*) as "removing parts of insects recently ingested and which had remained adhering to the outside of the jaws." If other workers have noticed this phenomenon they have not mentioned it in their publications. I have carefully examined branches immediately after the "jaw wiping" behavior and found the odor of decaying meat characteristic of the substance produced in the temporal pouch. It has, therefore, been my interpretation that the animal was for some reason placing material from this pouch onto a branch.

I have observed this jaw wiping behavior in the following species without any apparent specific variation: *Chamaeleo bitaeniatus*, *C. dilepis*, *C. fischeri*, *C. gracilis*, *C. höhnelii*, *C. jacksoni*, *C. melleri*, *C. pumilus*, and *C. senegalensis*. Dr. Bustard reports having seen this behavior in *C. bitaeniatus*, *C. chamaeleo*, *C. gracilis*, *C. höhnelii*, *C. jacksoni*, and *C. pumilus*. It is probably significant to report that neither of us has seen this behavior in Madagascan species of the genus *Chamaeleo*.

On twenty-three separate occasions, I have observed individual *Chamaeleo bitaeniatus* go through the jaw wiping behavioral sequence, then back off from the point where the jaw wiping took place, and capture flies that landed near the area of the jaw wiping. I have observed similar behavior in C. höhnelii. A different type of behavior associated with jaw wiping and observed in C. melleri may further clarify the function of this pouch. During the months of November and December, the behavior of C. melleri changed from a normally solitary pattern to a gregarious pattern during which time one might find as many as seven individuals in a single tree. On nine separate occasions I observed jaw wiping by individuals when there were several in the tree. These spots were later investigated by other individuals with the tips of their tongues in a manner similar to their drinking behavior, that is, the animal would protrude its tongue a very short distance and manipulate the dorsal and ventral "lips" of the tongue as though picking up something.

In seeking for a hypothesis that might explain this activity in the chameleons, I have investigated the attractiveness of the substance from this pouch to the common housefly, Musca domestica. In order to ascertain the degree of attractiveness of the substance, I constructed a simple T-tube maze of one inch internal diameter glass tubing (Fig. 19). This tube has a short arm (A) four inches in length and a cross tube (BB) twenty-four inches in length. A very low level vacuum was drawn from the short arm, thus producing currents in the cross tube. The currents within the maze as indicated by drawing smoke from either position 1 or position 2 are shown in Fig. 20.

Flies for these tests were collected as wild-caught adults by means of a simple fly trap using decaying meat as bait. For each test ten individual houseflies were selected from the pool of wild-caught adults and introduced into Tube A. The tube was then stoppered restoring the vacuum. The apparatus was then allowed to stand in an evenly lighted room until all of the flies were beyond the point of juncture between tube A and tube BB. During 100 tests, moist cotton was inserted in both of the reagent tubes as blank reagents and served as a control to demonstrate the random movement of the flies. Under experimental conditions, moist cotton was again inserted in both tubes; however, to one plaget of cotton some of the substance was added from the temporal pouch of Chamaeleo bitaeniatus. Between each trial the tube was washed with distilled water and a plug of cotton was forced through

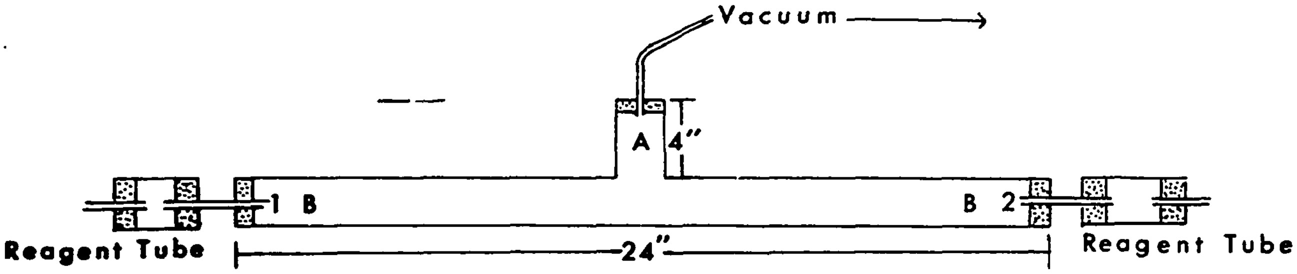

Fig. 19. A simple T-tube maze used in testing the reactions of houseflies, *Musca domestica*.

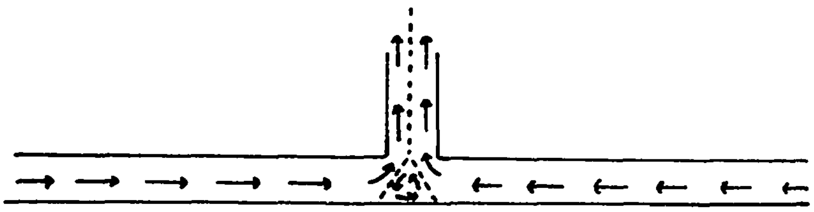

Fig. 20. Diagram of the currents produced in the maze by a low level vacuum as indicated by drawing smoke from either position 1 or position 2.

tube BB. There were as many trials with the substance in position 1 as in position 2. In no instance was the same group of flies used for a second trial. The results of these trials are shown in Table 5. These results indicate that significantly more than half of the flies went toward the tube containing the substance from the temporal pouch.

TABLE 5. REACTION OF FLIES TO THE PRODUCT OF THE TEMPORAL POUCH

	NUMBER OF FLIES CLOSEST TO POSITION 1	NUMBER OF FLIES CLOSEST TO POSITION 2	TOTAL	X^2 (DIXON & MASSEY, 1957)	p
BLANK	502	498	1000	0.016	0.9
EXPERIMENTAL CONDITION 1	813	187	1000	391.876	0.0005
EXPERIMENTAL CONDITION 2	176	824	1000	419.904	0.0005
TOTAL	1491	1509	3000	0.054	0.999

BLANK - moist cotton in both position 1 and position 2.

EXPERIMENTAL CONDITION 1 - moist cotton together with substance from the pouch in position 1; moist cotton only in position 2.

EXPERIMENTAL CONDITION 2 - moist cotton only in position 1; moist cotton together with substance from the pouch in position 2.

CHAPTER V

CONCLUSIONS

The conclusions may be conveniently arranged in three sections: those related to the behavior of the animal, those related to the anatomy of the pouch, and finally certain taxonomic considerations.

The behavior of the smaller chameleons such as _Chamaeleo bitaeniatus_ and _C. höhnelii_, together with the behavior of houseflies in response to the product of the temporal pouch, lead me to conclude that at least in these chameleons the pouch, together with its product, is used as a baiting device in order for the chameleon more easily to secure its food. Both of these animals live in dense populations. I have collected as many as 140 _C. bitaeniatus_ from twenty feet of garden hedge in Kampala, Uganda. I have also seen extremely dense populations of _C. höhnelii_ in the hedges surrounding fields of pyrethrum near Limuru, Kenya. It would seem that in such dense populations a baiting device would prove highly advantageous in securing insect prey. Many of the larger species of chameleons will refuse prey as small as flies. However, in the scats and stomach contents of C. melleri (total length sometimes exceeding twenty-four inches) there were many beetle elytra present. It would seem conceivable that some beetles, particularly those attracted to decaying organic material, might be attracted to the product of the temporal pouch. This must remain in the realm of speculation since none of the African beetle prey species was available for testing.

I think that the pouch may serve another function in these larger species of chameleons. The behavior of these animals, particularly during the breeding season when their local density was much higher than normal, led me to conclude that the product of the temporal pouch may be utilized both in the marking of individual territories and (possibly) in the facilitation of mate location. Most of the larger chameleons and some of the smaller animals are extremely intolerant of other animals in close proximity and when forced together without adequate cover will frequently fight with enough force to inflict fatal bruises on each other. If the product of the temporal pouch gives warning of the presence of a potentially combative animal and avoids the possibly fatal encounter, it is evolutionarily highly advantageous. While it seems most probable that the active agent in the attraction of insects is a product of decomposition, with the current emphasis on animal pheromones I think that it would be valuable in assigning the exact role of the temporal pouch to have a detailed chemical analysis of the substance found in the pouch. It would then be possible to test the various compounds present with regard to the behavioral responses of both chameleons and their prey. It seems probable to me that the most significant contribution of this dissertation is that it apparently presents the first description of an animal structure used in the chemical baiting of its prey.

The anatomy of the temporal pouch is suggestive of that of the femoral glands of many lizards. Camp (1923) described the "femoral organs" as "pseudo-glands proliferating modified epidermal cells." Tölg (1905) considered the secretion as the cellular modified form of the horny layer of the epidermis. Most recently Cole (1966) in an exhaustive study of the femoral glands of Crotophytus collaris carefully described both the macroscopic and microscopic anatomy of them. The similarity of these glands to the temporal pouch is striking. Cole's (1966) description of the microscopic anatomy of this gland illustrates their similarities to the temporal pouch.

> The outer layer of the gland proper consists of densely packed cells of germinative epithelium lying within and lining the envelope and partitions. Nuclei of the germinative cells are spherical to oval, and each nucleus occupies a large part of its corresponding cell. . . . Epithelial cells within the tubes and closer to the femoral pore are larger and have a strikingly granular cytoplasm. . . . Most of the cells at the base of the secretion duct are anucleate and have poorly delimited cell membranes, but nuclei or fragments of nuclei often are observed in the duct, and some cells are easily recognized as distinct entities. Therefore, the innermost part of the secretion plug is granular, and individual cells can be recognized as comprising it; the secretion is less granular the closer it is to the femoral pore, from which the secretion can protrude, and individual cells are not recognizable as comprising the secretion near the femoral pore. This suggests that the secretion is composed of entire cells that undergo a transformation and movement from their points of origins to and through the duct of the gland.

The temporal pouch while similar to the femoral glands in many ways differs strikingly in that, within my experience, there is no seasonal variation in the activity of this structure, whereas there is a marked seasonal activity in the femoral glands of lizards, at least, in species from temperate regions.

Ham (1953) describes the function of a holocrine gland as a "very drastic" process.

> A cell to secrete first accumulates secretory products in its cytoplasm then dies and disintegrates. The dead cell is thereupon

> discharged to constitute the secretion; in holocrine glands (holos=all), all of the cell is secreted.

Ham goes on to point out that the only common holocrine gland of the mammal is the sebaceous gland of the skin. Félizet (1911) remarked on the similarities between the femoral gland of lizards and the mammalian sebaceous glands: "La glande fémorale de l'adulte présente une évolution identique à celle de la peau ou plutôt à celle d'une glande sebacée . . ."

My anatomical investigations of the temporal pouch lead me to conclude that it is structurally similar to the femoral organ of many lizards and that it may be considered a holocrine gland analagous to the sebaceous glands of mammals.

I postulate that this pouch may have originated from an increased expanse of skin at the angle of the jaw and evolved concurrently with the mechanism of aiming the tongue, which requires that the lower jaw be dropped in order that the hyoid mechanism can project forward and allow the animal room to aim the tongue. I feel that this greater expanse of skin may have led to a fold of skin projecting under the zygomatic ligament and that cells sloughed from this skin might collect in such a fold producing a substance similar to the present product of the temporal pouch. Such a condition can be seen in Brookesia brachyura and Chamaeleo fishceri. Those animals that develop a behavioral pattern that could utilize this product would have a decided evolutionary advantage over those animals not utilizing such a structure. This would lead to the selection of those animals with both the better developed anatomical structure and the appropriate behavioral sequence. Of the animals examined, individual species of the Chamaeleo bitaeniatus complex show the greatest development in both of these areas. It is possible that high density of these species may be additional evidence for this hypothesis. This hypothesis might be tested by the examination of a series of chameleon embryos representing different development stages.

The general picture of chameleon taxonomy has remained extremely confused in spite of several major taxonomic works that have attempted to organize this rather complex group. Boulenger (1887) lists three genera of chameleons: Chamaeleon, Brookesia, and Rhampholeon. Werner (1902, 1911) follows a similar classification system; however, Angel (1942) listed four genera: Chamaeleon, Evoluticauda, Brookesia, and Leandria. Loveridge (1951) in a synopsis of the continental African Brookesia indicated that the Evoluticauda of Angel was synonymous with Brookesia and that Rhampholeon should be considered only a subgenus of the genus Brookesia. Loveridge (1957) also substituted the generic name Chamaeleo Laurenti 1768 in place of Chamaeleon Gronovius 1763 since the latter work is a work specifically rejected from taxonomic purposes in rule 89 of International Committee on Zoological Nomenclature. The most recent attempts at taxonomic revision have been by Dirk Hillenius of Amsterdam. His most comprehensive paper appeared in 1959 with a series of supplementary papers appearing in 1963a, b, and 1966. Hillenius' approach is thorough and takes advantage of information supplied by many branches of biology, rather than the classical taxonomic methods. This is best exemplified in Hillenius' (1966) most recent paper in which he suggests that some "species" of Chamaeleo are in reality "hybrids" of two named species.

The only continental animal examined that did not show a pouch was Chamaeleo marshalli. This animal was originally names by Boulenger (1906) as _Rhampholeon marshalli_. Loveridge, however, concluded primarily from the prehensile tail that this animal belonged in the genus _Chamaeleo_ (Loveridge, 1956) and he erected a separate subgenus, _Bicuspis_, for this single species and indicated that he felt that it was midway between the genus _Chamaeleo_ and the subgenus, _Rhampholeon_ of the genus _Brookesia_.

My own examination of this animal together with the examination of several individuals of several species from Hillenius' (1959) "_Chamaeleo nasutus_" group which includes _C. nasutus_, _C. fallax_, _C. gallus_, _C. boettgeri_, _C. linotus_, and _C. guibei_. The above species together with _C. marshalli_ share the following characteristics: They all possess a flexible rostral appendage, weak elongated dorsal-crest-scales, the absence of ventral gular-crests, and make up the smallest species within the genus _Chamaeleo_. The above common characteristics together with the fact that the temporal pouch is missing in _C. marshalli_ as it is in all the Madagascan forms examined has led me to conclude that _C. marshalli_ should be considered with this group of Madagascan chameleons. I take exception to _C. marshalli_ being placed in an intermediate position between the mainland *Brookesia* and the genus *Chamaeleo*, since both the *Brookesia* that I have been able to examine and all of the other mainland species of Chamaeleontidae examined possessed temporal pouches, whereas this structure was absent in *C. marshalli* as it was in all of the Madagascan chamaeleons examined. Hillenius (1959) indicates that he feels *C. fischeri* to be the mainland chameleon most closely allied to the Madagascan group; however, Hillenius up until the summer of 1963 had been unable to examine specimens of *C. marshalli*. It is probably significant that the pouch is extremely reduced in *C. fischeri* and that this animal possesses in common many characteristics with the Madagascan.

I think that the absence of the pouch in a species which appears to be very closely related to a group of Madagascan chameleons lends further credence to Hillenius' (1959) proposed mainland origin of the family Chamaeleontidae. The distribution of both of the mainland species thought to be closest to the Madagascan form, *Chamaeleo marshalli* and *C. fischeri*, is also suggestive of relict populations. Both of these forms are found only in isolated montane habitats. While the current work represents the greatest diversity of species available to me, an examination of all of the species of Chamaeleontidae for the presence or absence of a temporal pouch might serve to clarify the thorny problem of the origin of the Chamaeleontidae.

I have followed Rand's (1963) revision of the Chamaeleo bitaeniatus complex in the consideration of C. höhnelii as a separate species and while the pouches were very similar in these two species, I did not consider that they were any more similar than between other pairs of closely related species.

In summary, this paper presents:

1. An introduction and review of the literature of the anatomy of members of the family Chamaeleontidae.
2. A description of the gross anatomy of the temporal pouch showing that it is an epidermal-dermal structure of some chameleons lying superficially to the muscles filling temporal vacuity and beneath the zygomatic ligament with the entire structure being covered by the skin of the temporal region.
3. The microscopic structure of the temporal pouch indicated it to be a sack of epidermal and dermal tissue surrounded by a subcutaneous connective tissue and secreting by the sloughing of cornified cells into its lumen.
4. The jaw wiping behavior of chameleons was described, together with some of the conditions

that seemed to be related to the chameleons exhibiting this behavior. The behavior of flies in response to the product of the temporal pouch is reported, indicating that the flies are attracted to the substance produced by this pouch.

5. It was concluded that the smaller species of chameleons utilize the pouch together with its product as a baiting device in order to attract flies. It is also suggested that the product of the pouch may have significance with regard to territoriality in these animals. The similarities between this pouch and both the femoral glands of lizards and the sebaceous glands of mammals are discussed. A possible mechanism for the evolution of this pouch is suggested. Finally, the taxonomic significance of the distribution of this structure is discussed.

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APPENDIX A

SPECIES OF SPECIMENS EXAMINED TOGETHER WITH THE LOCALITIES WHERE COLLECTED

Brookesia brachyura	Minaki, Tanzania
Chamaeleo bitaeniatus	Kampala, Uganda
Chamaeleo brevicornis	Foule Pointe, Malagasy Republic
Chamaeleo dilepis	Minaki, Tanzania Johannesburg, Republic of South Africa
Chamaeleo fischeri	Lushoto, Tanzania
Chamaeleo höhnelii	Limuru, Kenya
Chamaeleo jacksoni	Nairobi, Kenya Meru, Kenya
Chamaeleo lateralis	Tananarive, Malagasy Republic
Chamaeleo marshalli	Selinda Mt., Rhodesia
Chamaeleo melleri	Minaki, Tanzania
Chamaeleo pumilus	Johannesburg, Republic of South Africa

MAP 1. Southeast Africa and Madagascar showing collecting localities mentioned in the text.

APPENDIX B

STAINING TECHNIQUES USED IN THE PREPARATION OF TISSUES FOR THIS DISSERTATION

Hematoxylin and Eosin Stain (Armed Forces Institute of Pathology, 1960.)

Solutions:

Harris's Hematoxylin

Hematoxylin crystals	5.0 gm.
95% Alcohol	50.0 ml.
Potassium alum	100.0 gm.
Distilled water	1000.0 ml.
Mercuric oxide	2.5 gm.

The hematoxylin crystals are dissolved in the 95% alcohol and the potassium alum crystals in one liter of warm distilled water. The two solutions are then mixed together. The mixture is then quickly brought to a boil and removed from the heat, at which point the mercuric oxide is added. The solution is reheated until it becomes a deep purple, at which point it is removed from the heat and rapidly cooled in a container of cold water. As soon as the solution is cool it is ready to use.

Acid Alcohol

70% Alcohol	1000.0 ml.
HCl concentrated	10.0 ml.

Ammonia Water

Tap water	1000.0 ml.
Strong Ammonia Water	2.5 ml.

Alcoholic Eosin Solution

Eosin Y, water soluble	2.0 gm.
Distilled water	160.0 ml.
95% Alcohol	640.0 ml.

Mix together in the order listed.

Staining Procedure:

1. (2 min.) Xylol
2. (2 min.) Xylol
3. (1 min.) Absolute Alcohol
4. (1 min.) Absolute Alcohol
5. (1 min.) 95% Alcohol
6. (1 min.) 95% Alcohol
7. (4 dips) Tap water
8. (15 min.) Harris Hematoxylin
9. (4 dips) Tap water

10. (3-10 dips) Acid-Alcohol, until nucleus is distinct and background colorless.
11. (4 dips) Tap water
12. (6 dips) Ammonia water
13. (15 min.) Distilled water
14. (15 sec.-2 min.) Eosin, until counterstain desired.
15. (1 min.) 95% Alcohol
16. (1 min.) 95% Alcohol
17. (1 min.) Absolute Alcohol
18. (1 min.) Absolute Alcohol
19. (2 min.) Xylol
20. (2 min.) Xylol
21. (2 min.) Xylol
22. Mount in permamount

Results:
1. Nuclei, blue
2. Cytoplasm, pink

Gomori's One Step Trichrome Stain (Gomori, 1950)

Solutions:

Bouin's Fluid

Saturated aqueous solution of picric acid - 75.0 ml.

Formalin -25.0 ml.

Glacial acetic acid - - - - - - - - - - - - - - -5.0 ml.

Trichrome Stain

Chromotrope 2R - - - - - - - - - - - - - - - - - 0.6 gm.

Light green -0.3 gm.

Glacial acetic acid - - - - - - - - - - - - - - -1.0 ml.

Phosphotungsic acid - - - - - - - - - - - - - - -0.8 gm.

Distilled water - - - - - - - - - - - - - 1000.0 ml.

Acid Water

Distilled water - - - - - - - - - - - - - 1000.0 ml.

HCl concentrated - - - - - - - - - - - - - - 5.0 ml.

Staining Procedure:

1. (2 min.) Xylol
2. (2 min.) Xylol
3. (1 min.) Absolute alcohol
4. (1 min.) Absolute alcohol
5. (1 min.) 95% Alcohol
6. (1 min.) 95% Alcohol
7. (4 dips) Tap water
8. (1 hr.) Bouin's Fluid at 56°C.
9. Wash well in running tap water
10. (15-20 min.) Trichrome stain
11. (1 min. 30 sec.) Acid water
12. (1 min.) 95% Alcohol
13. (1 min.) 95% Alcohol
14. (1 min.) Absolute alcohol
15. (1 min.) Absolute alcohol
16. (2 min.) Xylol
17. (2 min.) Xylol
18. (2 min.) Xylol
19. Mount in permamount

Results:

1. Muscle fibers, red
2. Collagen, green
3. Nuclei, blue to black

Verhoeff's Elastic Stain (Mallory, 1938)

Solutions:

Elastic Tissue Stain

Hematoxylin	1.0 gm.
Absolute Alcohol	22.0 ml.
10% aqueous solution of ferric chloride	8.0 ml.
Iodine	2.0 gm.
Potassium iodide	4.0 gm.
Distilled water	100.0 ml.

Dissolve the hematoxylin crystals into the warmed alcohol in an open dish, cool and filter. Add the ferric chloride solution. Dissolve the iodine and potassium iodide in the distilled water; then add eight ml. of this solution to the first solution.

Ferric Chloride Solution

Ferric chloride	2.0 gm.
Distilled water	100.0 ml.

Van Gieson's Stain

1% acid fuchsin, aqueous solution	5.0 ml.
Saturated aqueous solution picric acid	100.0 ml.

Sodium Thiosulfate Solution

Sodium thiosulfate	5.0 gm.
Distilled water	100.0 ml.

Staining Procedure:

1. (2 min.) Xylol
2. (2 min.) Xylol
3. (1 min.) Absolute alcohol
4. (1 min.) Absolute alcohol
5. (1 min.) 95% Alcohol
6. (1 min.) 95% Alcohol
7. (4 min.) Distilled water
8. (15 min.) Verhoeff's elastic stain
9. (4 min.) Distilled water
10. (2 min.) Ferric chloride solution, to differentiate.
11. (1 min.) Sodium thiosulfate solution
12. (5 min.) Tap water
13. (1 min.) Van Gieson's stain, to counterstain.
14. (1 min.) 95% Alcohol
15. (1 min.) 95% Alcohol
16. (1 min.) Absolute alcohol
17. (1 min.) Absolute alcohol
18. (2 min.) Xylol
19. (2 min.) Xylol
20. (2 min.) Xylol
21. Mount in permamount

Results:

1. Elastic fibers, blue-black to black
2. Nuclei, blue to black
3. Collagen, red
4. Other tissue elements, yellow