THE COMPARATIVE CRANIAL OSTEOLOGY OF THE SOUTH AFRICAN LACERTILIA (REPTILIA : SQUAMATA)

BY

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VERKLARING

Ek die ondergetekende verklaar hiermee dat die werk in hierdie tesis vervat, my eie oorspronklike werk is wat nog nie vantevore in die geheel of gedeeltelik by enige ander Universiteit ter verkryging van 'n graad voorgelê is nie.

Handtekening Datum

ABSTRACT

There has been a long-standing need to systematically analyze and classify South African fossil Lacertilia. Although extensive assemblages of fossil lizard and amphibian material from Langebaan on the West Coast and elsewhere exist in museum collections, the fragmentary nature of the material has largely prevented in-depth analyses and identification.

In this comparative study the skulls and lower jaws of 7 lizard genera, representing the six extant South African families, were disassembled and the bones analyzed individually. The aim was to compile a comparative database of each bone against which current and future fossil finds could be matched. Detailed descriptions of the isolated elements were given. The results showed that despite some intra-generic variation, unique structural differences do exist in individual bones which may be utilized in the taxonomic assessment of fragmentary fossil material.

OPSOMMING

Daar bestaan lank reeds 'n behoefte vir die sistematiese analise en klassifisering van fossielmateriaal van Suid-Afrikaanse Lacertilia. Alhoewel uitgebreide versamelings van akkedis- en amfibiër-fossiele van Langebaan aan die Weskus en elders in museums bestaan, het die fragmentariese aard van die materiaal grootliks diepgaande analises en identifikasie belemmer

In hierdie vergelykende studie is die skedels en onderkake van 7 akkedisgenera, wat die ses resente Suid-Afrikaanse families verteenwoordig, gedisartikuleer en elke been individueel geanaliseer. Die doel was om 'n vergelykende databasis van elke been saam te stel waarmee huidige en toekomstige fossielvondse vergelyk kan word. Gedetaileerde beskrywings van die geïsoleerde elemente word gegee. Die resultate toon dat desondanks 'n mate van intra-generiese variasie, unieke strukturele verskille tussen individuele bene wel bestaan en dat hierdie verskille gebruik kan word om fossielfragmente taksonomies te analiseer.

Opgedra aan Mariétta, Hein, Lisa en Carla

"To her fair works did Nature link
the human soul that through me ran
And much it grieved my heart to think
what man has made of man."

Anon.

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CONTENTS

INTRODUCTION.

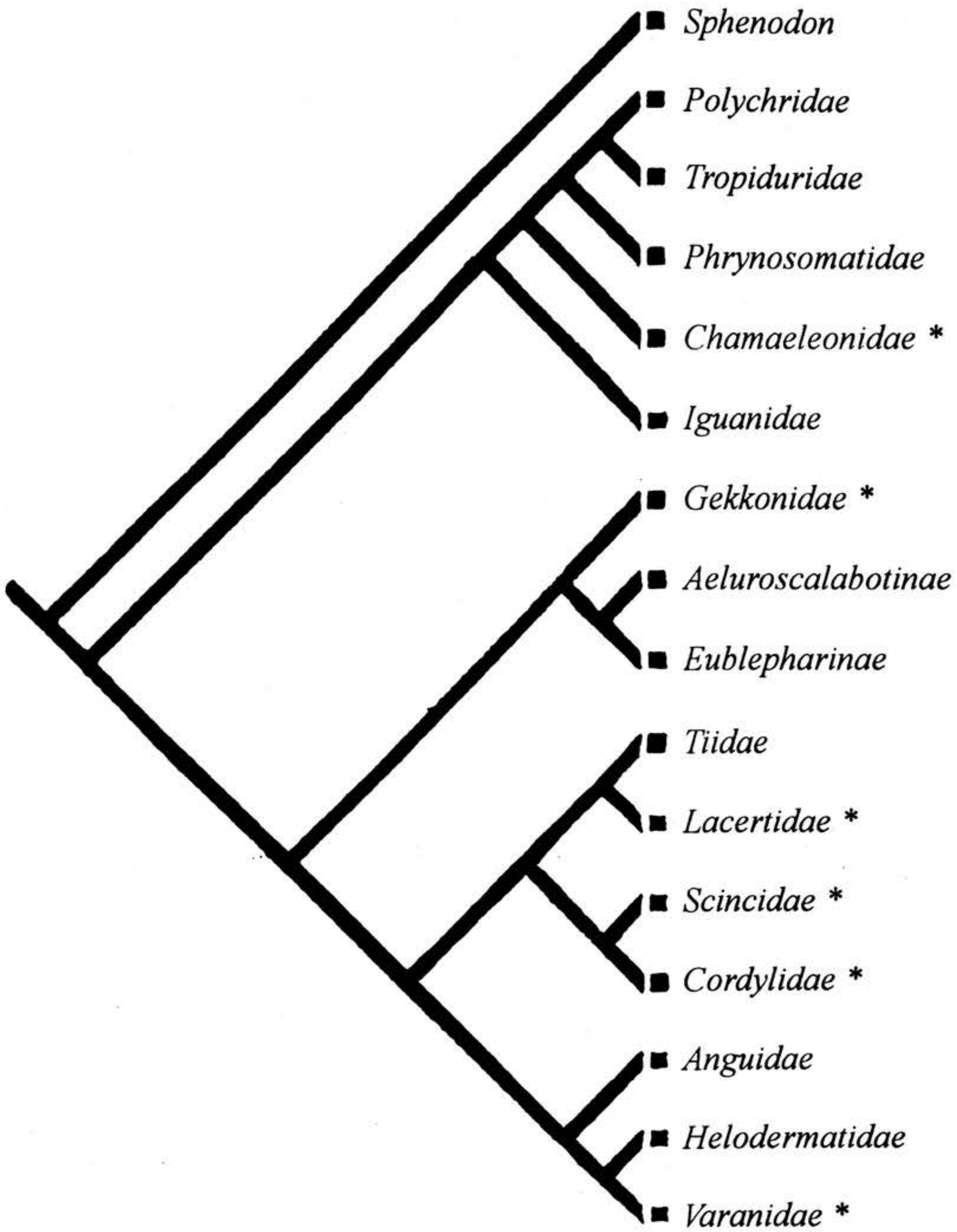
Although a number of comparative osteological studies on the cranial morphology of lizards exist in the literature (Cope, 1892; Camp, 1923; De Beer, 1930; Malan, 1941; Du Plessis, 1944; Webb, 1951; Jollie, 1960; Visser, 1965;), no individual contribution supplies sufficient anatomical detail to assess and identify disarticulated and fragmented faunal remains found in owl pellets and fossil deposits in the South African context. This study therefore attempts to establish a morphological database to assist in the identification of fossil lizard material, particularly from localities such as Langebaanweg on the West Coast and Klasies River Mouth on the South Coast of South Africa. That the data will have a wider application and prove useful in other studies, appear self-evident.

Lizards form the largest group of living reptiles in the world comprising approximately 3700 species. Their fossil record extends back to the Upper Triassic approximately 190 million years ago. As the fossil record of the Lacertilia is relatively incomplete, any additional material form an important link in the unravelling of the prehistory of the taxon. Because fossil material is most often distorted or fragmented, a comparative index based on the cranial osteology of recent taxa against which to evaluate fossil finds, is vital.

The southern African lizard fauna comprises six families i.e. Chamaeleonidae (which includes Agaminae and Chamaeleoninae) (Cooper, 1995), Cordylidae, Gekkonidae, Lacertidae, Scincidae and Varanidae. Although certain families comprise a large number of species on a worldwide basis their distribution in South Africa may be limited. Of these, only the Cordylidae is endemic to southern Africa (Mattison, 1989).

In this preliminary study one species of each family was selected in order to establish a broad morphological base, and then analyzed in detail. In order to identify diagnostic parameters a particular effort was made to assess cranial elements individually.

The following cladogram illustrates the recent classification of the Lacertilia (Cooper, 1995). Each of the taxa utilised in this work are identified by an asterix.


Sphenodon
Polychridae
Tropiduridae
Phrynosomatidae
Chamaeleonidae *
Iguanidae
Gekkonidae *
Aeluroscalabotinae
Eublepharinae
Tiidae
Lacertidae *
Scincidae *
Cordylidae *
Anguidae
Helodermatidae
Varanidae *

MATERIAL AND METHODS

Two lizards of the same species, of each of the six lizard families found in southern Africa, were used in this study. The genera were selected at random due to the general availability of the animals. Most specimens are from the Western Cape (Hermanus, Franskraal region), with the exception of *Chamaeleo dilepis* from the Eastern Transvaal.

Specimens were caught by means of a catching loop and killed by injecting an overdose of Uthenase. After skinning, the skulls were removed leaving the cervical vertebrae intact to aid handling. The material was then stored in a 50% methanol and 10% formalin solution.

Soft tissue was removed with tweezers and modified dental instruments, under a dissecting microscope, as most of the elements are very small and delicate. The cleaned skulls were labelled and left in the sun to dry.

One skull of each genus was placed in a labelled bottle and the other skull placed in a 50% bleach solution for a period of 15 - 30 minutes depending on the size of the skull. The elements were disarticulated at approximately 10 minute intervals, because the skulls tend to become brittle if left in the bleach for too long.

After disarticulation of the second skull of each genus, the elements of the right side of the skull (where possible) were placed in labelled Ependorff vials. The vials were left open to allow the elements to dry.

The elements were then grouped together and photographed from the same angle; eg. all the premaxillaries first seen in a dorsal and then in a ventral view.

During this investigation numerous attempts were made to disarticulate the elements in the skull of *Chamaeleo dilepis*, but due to the sutural interdigitations it was impossible to obtain individual elements without breaking them, with the exception of the few elements that was either disarticulated or removed from the skull of *Bradypodion pumilum*.

Detailled photographs of the isolated elements grouped according to kind and in identical views, are presented. Due to the large number of photographs, a specific labelling system is employed to avoid confusion. The individual elements are labelled with lower-case letters in the skull of *Agama atra atra* only to indicate the respective positions. A list of abbreviations is included.

Note that the upper case letters in the description and on the photographs always indicate the following:

A = *Agama atra atra;*

B = *Chamaeleo dilepis*;

C = *Cordylus cordylus cordylus*;

D = *Pachydactylus bibronii*;

E = *Meroles knoxii*;

F = *Mabuya capensis*; and

G = *Varanus niloticus*.

DESCRIPTION

A synoptic orientation of the bony elements found in an articulated skull is imperative in order to discuss the individual elements found in the different lizard genera described in this work. Most of these elements are closely associated with fenestrae seen in various views of the skull. Only a few elements are not associated with fenestrae.

Basic osteology of the skull of Agama atra atra (Figs. 1 - 3)

A. Elements associated with openings

Dorsal view

1. External naris

The paired external nares are separated by the internasal process of the premaxilla. Each naris is bordered anteriorly by the anterior tip of the maxilla, laterally by the the inner rim of the ascending ledge of the maxilla and posterodorsally by the nasal.

2. Orbit

The orbits are dorsally separated by the fused frontals. The posterior margin of the frontal extends laterally to form the posteromedial border of the orbit. The postorbital and the jugal form the remainder of the posterior border. The maxillary process of the jugal and the posterior process of the maxilla respectively form the posteroventral and anteroventral borders of the orbit. The prefrontal and the lacrimal complete the anterior border of the orbit. The small sclerotic ossicles found in and around the orbit will briefly be discussed later.

3. Supratemporal fenestra

These fenestrae are bordered anteriorly and anteromedially by the fused parietals. Medially and posteromedially the margin of each fenestra is formed by the parietal process, posterolaterally and laterally by the squamosal, the posterior extremity of the jugal and the postorbital, and anterolaterally by the postorbital.

4. Pineal foramen (=parietal foramen)

This foramen is normally present in the midline between the parietal and the frontal. In *Agama* the foramen is prominent and always associated with the parietal. The notched anterior border is formed by the frontal where the latter is syndesmotically attached to the parietal at the coronal suture.

5. Superior nasal fenestra

The two fenestrae, which Rieppel (1981) refers to as the prefrontal fontanelle and found mainly in the Chamaeleontids, are individually covered by the ala nasalis of each nasal. The ala nasalis, which extends laterally to cover this fenestra, is discussed in a following chapter.

Posterior view

1. Posttemporal fenestra

These fenestrae appear triangular and are separated by the median supraoccipital. Dorsomedially the supraoccipital forms the processus anterior tecti(=processus ascendens), a cartilaginous rod, flanked on each side by a small vacuity which in turn is laterally bordered by the processus dorsalis of the supraoccipital. This latter process extends dorsally to attach syndesmotically to the ventral surface of the parietal process. The posttemporal fenestra is bordered dorsally by the parietal process, dorsomedially by the dorsal process of the supraoccipital, ventromedially by the otoccipital and ventrally by the dorsal margin of the processus paroccipitalis of the otoccipital.

2. Middle ear cavities

The paired cavities (Skinner, 1968) are present in the otoccipital region and is bordered dorsally by the ventral margin of the paroccipital process of the otoccipital, laterally by the inner margin of the quadrate and medially by the lateral wall of the otoccipital. Leonard (1973) identified the otoccipital as the fusion product of the opisthotic and the exoccipital. The needle-like stapes extends transversely across the middle ear cavity from the fenestra ovalis towards a point behind the head of the quadrate.

3. Foramen magnum

This foramen is bordered dorsally by the ventral margin of the supraoccipital, ventrolaterally by the otoccipitals and ventrally by the basioccipital. The otoccipitals and the basioccipital contribute to the tripartite occipital condyle, present below the foramen magnum.

Lateral view

1. Infratemporal fossa

The jugal possesses a short posterior process which might be the remains of the quadrato-jugal. Brock (1932) noticed thickened tissue which connected the jugal to the quadrate and suggested that this represented the quadrato-jugal. Romer (1956) refers to this short process as the vestige of the posterior ramus which formed the lower temporal arch in the diapsids. The interruption of the lower temporal arch frees the quadrate and allows a streptostylic condition.

The absence of the quadrato-jugal forms an incomplete infratemporal fossa (Skinner, 1968) which extends in two directions:

i) downwards to reach the absent or imaginary quadrato-jugal (seen in lateral view of the skull). Anteriorly it is bordered by the jugal; anterodorsally by the temporal process of the jugal, which is applied to the posteroventral edge of the postorbital; posterodorsally by the squamosal and posteriorly by the anterior rim of the auditory cup of the quadrate; and,

ii) around the imaginary quadrato-jugal inwards to meet the quadrate process (=quadrate ramus) of the pterygoid (seen in ventral view of the skull).

Anteriorly it is bordered by the transversum (=ectopterygoid) and the transverse process of the pterygoid; anterolaterally by the posterior process of the maxillary and the maxillary process of the jugal; medially by the quadrate ramus of the pterygoid and posteriorly by the quadrate and the tip of the quadrate ramus.

The tooth-bearing maxillary is prominent in this view and extends from the premaxillary backwards where it is applied to the maxillary process of the jugal.

The ascending ledge of the maxillary (Skinner(1968) refers to the latter as the nasal process) is dorsally applied to the nasal and the prefrontal.

Ventral view

At the syndesmotic attachment of the ectopterygoid to the pterygoid, a ventrally directed ectopterygoid tubercle is found.

1. Suborbital fenestrae

These oval fenestrae lie below the orbits. Each is bordered laterally by the posterior process of the maxillary; posterolaterally by the transversum; medially by the lateral edge of the palatine process of the pterygoid and the pterygoid process of the palatine; and anteriorly by the maxillary process of the palatine and the palatine process of the maxillary.

2. Interpterygoid vacuity

In palatal view this single, elongated opening extends anteroposteriorly in the midline between the paired vomers and the basisphenoid. The parasphenoid rostrum protrudes forward into this vacuity. The latter is bordered laterally by the palatine process of the pterygoid, the medial edges of the palatine and the vomer; anteriorly by the syndesmotic attachment of the paired vomers and posteriorly by the basipterygoid process of the basisphenoid and the anterior edge of the basisphenoid.

3. Internal nasal openings

Skinner (1968) and Leonard (1973) refer to these openings as the fenestrae exochoanales. The anterior region of each slit-like opening is referred to as the fenestra vomeronasalis through which the duct of the organ of Jacobson passes into the anterior portion of the choanal grooves. The internal nasal opening is bordered laterally and anteriorly by the anterior section of the palatal shelf of the maxillary, and medially and posteriorly by the vomer.

Additional openings

1. Nasolacrimal foramen

The foramen occurs between the prefrontal medially and the lacrimal laterally.

2. Orbitonasal fenestra

This single, round opening extends from the orbits to the nasal cavity. The ventral edge of the fenestra is incomplete and is confluent with the epipterygoid vacuity. It is bordered laterally by the medial edges of the palatine processes of the prefrontals, dorsally by the frontal and ventrolaterally by the palatines.

B. Elements not associated with openings

The anteriorly situated premaxillary processes of the vomers are syndesmotically attached to the vestiges of the lateral flanges of the premaxilla. The latter will be discussed later.

The epipterygoid is a rodlike element extending vertically from a socket on the dorsal surface of the pterygoid towards the parietal. In *Agama* the dorsal tip of the epipterygoid contacts the anterolateral margin of the prootic. Variations in this attachment is dealt with later.

The prootic is applied to the otoccipital behind it, while the small dorsal process of the prootic is attached to the anterior section of the parietal process. A blade-like ridge on the anteroventral edge of the prootic borders a posteriorly situated groove. This ridge and the groove on the prootic are confluent with the ridge and the groove found on the posterior edge of the paroccipital process of the otoccipital.

The fenestra ovalis, which houses the footplate of the stapes, lies in the lateral wall of the otoccipital, directly beneath the paroccipital process. The groove, present in the ventral side of the latter, houses the stapes.

C. Lower jaw (Fig. 83)

Generally the lower jaw consists of 7 elements which may be fused or partly fused to form a rodlike structure of which the shape varies in the different genera discussed. In some genera elements are absent. Barry (1953) noted that the lower jaw of *Agama hispida* (Linn) consists of five elements only, viz. dentary, coronoid, angular, surangular and gonial (=prearticular). He also refers to the posterior portion of the Meckelian cartilage which "has to ossify yet" to form the articular, thus indicating the existence of a sixth element. The elongated lower jaw is compressed from side to side and is directed in a horizontal plane while the ventral plane is tilted inwards ventrally.

The jaw ramus, apparantly straight along the cheek margin, turns inward anteriorly and is syndesmotically attached to its opposite number at the symphysis (Romer, 1956).

The dentary forms the distal half of the lower jaw with the dorsal margin bearing teeth. Two conical teeth are found at the anterior tip of the dentary, with a number of acrodont teeth occuring directly behind.

The sulcus dentalis (Skinner, 1968) in which the teeth occur, is present, but not very prominent. The canal for the Meckelian cartilage is present on the medial surface of the dentary with the ascending and descending squames bordering the canal dorsally and ventrally (Skinner, 1968). In some families these squames meet to enclose the Meckelian canal completely, while in other the splenial is responsible for completing the canal.

The dorsal process of the coronoid is present behind the last acrodont tooth with the fused prearticular and articular extending backwards to form the retro-articular process.

The surangular (=supra-angular) is fused with the prearticular and articular and consequently is difficult to remove without breaking it. The element is syndesmotically attached to the posterior tip of the dentary. The attachment is shaped, with the middle process bifurcated where it forms the upper and the lower rims of the foramen for the N. auriculo-temporalis (Engelbrecht, 1951). The surangular forms the lateral wall of the pre-articular fossa (Barry, 1953) which occurs behind the coronoid.

The lower two thirds of the coronoid is attached to the medial surface of the posterior tip of the dentary. A small protuberance is present in the posteroventral edge of the coronoid.

The angular is a splint-like element which forms the ventral margin of the prearticular fossa. It extends in an anteromedial direction, curves upwards and passes below the coronoid to cover the posterior portion of the Meckelian canal.

The splenial was not seen and it is either fused to the dentary or absent. Barry (1953) is of opinion that the splenial is absent in *Agama hispida* as in *Sphenodon* (Versluijs, 1924), *Monopeltis* (Kritzinger, 1946) and the Chamaeleontidae (Camp, 1923).

The fused articular and prearticular (=gonial) form the posterior border of the prearticular fossa and is firmly applied to the posterolateral edge of the surangular. The anterior process of the prearticular forms the medial wall of the canal for the Meckelian cartilage. A process occurs on the medial surface of the prearticular (=prearticular process?). The articulation facet, where the lower jaw articulates with the mandibular condyle of the quadrate, is formed on the dorsal surface of the fused articular and prearticular.

The photographs of skulls of the other genera included here are to be used as a counter reference based on this orientation. These are:

B = *Chamaeleo dilepis*	Figs. 4 - 6
C = *Cordylus cordylus cordylus*	Figs. 7 - 9
D = *Pachydactylus bibronii*	Figs. 10 - 12
E = *Meroles knoxii*	Figs. 13 - 15
F = *Mabuya capensis*	Figs. 16 - 18
G = *Varanus niloticus*	Figs. 19 - 21

The dentition is not referred to in this synopsis, but dealt with in the discussion of the individual elements.

Variations in the structure of the individual cranial elements

A. Elements of the skull

1. Premaxilla (Figs. 22 - 25)

Primarily the premaxillary bone is the fusion product of the two elements and the primitive condition is still found in the skinks. Generally this element appears as a single T-shaped structure with the internasal process varying in length in the different genera. Anteriorly a lateral flange bearing the premaxillary teeth is present on both sides.

In *Mabuya* the two elements are unfused, while in *Agama* and *Chamaeleo* the flanges are reduced. The other four genera range between these two extremes.

The total number of premaxillary teeth found in the skulls studied are:
Agama, 1; *Chamaeleo*, 2; *Cordylus*, 7; *Pachydactylus*, 9; *Meroles*, 9; *Mabuya*, 9 (4 left, 5 right); and *Varanus*, 9.

A. **Agama**

The element consists of a single splint-like bone with the processus internasalis extending upwards, but not reaching the frontal. The upper one third of the process is bordered on both sides by the nasals. The middle third forms the septum between the external nares, while the proximal one third is flanked by the maxillae with the remaining portion of the element bearing a single conical tooth. On both sides of this tooth two small projections (remains of the original lateral flanges?) are present.

B. **Chamaeleo**

Two small acrodont teeth are present at the anterior tip of the premaxilla but it lacks lateral projections. Above the teeth the element broadens with a small notch on both sides followed by two small flanges which become narrower as the processus internasalis extends upwards. These flanges underlie the attachment of the maxillae, strenghtening the anterior tip of the snout. The bottom half of the process is flanked by the maxillae, while the remaining half is bordered by the nasals. The distal end of the premaxilla does not reach the frontal.

C. **Cordylus**

The proc. internasalis is confluent with the lateral flanges and gives the premaxilla a wedge-like appearance rather than the T-shape found in other genera.

A shallow groove with small foramina extending across the proximal end of the proc. internasalis. On the posterior edge of the flanges a short posterolateral process forms a supportive shelf for the vomers. The ventral surfaces of these processes are excavated with a small descending projection curving to the front between them. Above the two processes two small foramina are present.

On the ventral surface of the proc.internasalis a small longitudinal ridge is present which shows contact areas for the nasals on each side.

D. **Pachydactylus**

In *Pachydactylus* the proc. internasalis is short and pointed on the dorsal surface of the flanges with the lateral flanges greatly expanded posteriorly to form a supportive shelf for the fused vomers medially and the maxillae laterally. On the dorsal surface of these expanded lateral flanges a small, slanting posterior process is present on both sides of the proc. internasalis which overlies the vomers anteriorly. Below each of the small processes a bigger posterior process is found which underlie the vomers.

E. **Meroles**

The proc. internasalis widens at the distal end forming a rounded tip where it is attached to the nasal elements on both sides of the proximal end of the proc. internasalis with a small foramen in each ridge. The ridges appear to be a strengthening for the narrow base of the proc. internasalis. The lateral flanges curve backwards and expand posteriorly as two small posterior projections supporting the vomers. A deep notch is present between these two processes.

F. **Mabuya**

Two L-shaped elements are present as mentioned. The lateral flange bears the premaxillary teeth and forms a small posterolateral process which underlies the anterior part of the maxilla. The vomers are syndesmotically attached to the posterior rim of the premaxilla. The proximal end of the proc. internasalis possesses a small lateral ridge with a small foramen at the base of the ridge. The two processii internasales taper distally where they are attached to the nasals. The proximal half of the proc. internasalis borders the external nares medially.

Concerning the premaxillary teeth in *Mabuya* one expects to find an even number, but the presence of nine teeth may indicate a tendency towards tooth reduction.

G. **Varanus**

The proc. internasalis is elongated with a small groove on the ventral surface near the distal end. Proximally on both sides two foramina are present which open on the anterior surface of the premaxilla just above the premaxillary teeth. The base of the element is confluent with the lateral flanges, which bears the premaxillary teeth. The lateral flanges expand posteriorly to form two narrow elongated posterior processes which form a supportive shelf for the vomers. On the ventral surface of the two flanges a small ridge is present formed by the two posterior processes. This ridge ends anteriorly in a small anterior process. On both sides of the latter two foramina are present which are continuous with the foramina that opens on the anterior surface of the premaxilla. The distal end of the proc. internasalis is attached to the fused nasal element. The proximal part of the proc. internasalis forms a septum between the external nares.

2. Nasal (Figs. 26 + 27)

The basic structure of the nasal is rodlike and it is situated in the midline of the skull bordering the internasal process of the premaxilla on both sides. Although this element is small in comparison to the other elements situated around it, it serves as a connection between the proc. internasalis of the premaxilla anteriorly and the frontal elements posteriorly. In some cases the proc. internasalis reaches the frontal with the nasal elements on the lateral edge of the proc. internasalis, strengthening the attachment between the latter and the frontal elements. The rodlike nasal varies in length. In *Bradypodion* a broad flange, the ala nasalis, is present on the lateral edge of the element, covering the fossa between the nasal medially and the ascending flange of the maxilla laterally. The ala nasalis is absent in *Chamaeleo*. Skinner (1968) refers to the fossa as the superior nasal fenestra, while Rieppel (1981) prefers to call it the prefrontal fontanelle.

The presence or the absence of the ala nasalis causes the variations found. When the ala nasalis is present, its shape and degree in which it covers the superior nasal fenestra assists in its classification.

A. **Agama**

In dorsal view the nasal appears rodlike with a short, pointed premaxillary process anteriorly. The latter process is attached to the lateral surface of the upper third of the processus internasalis. The anterior premaxillary process extends backwards and outwards to form a small transverse process overlapping a small portion of the inner tip of the ascending ledge of the maxilla.

The posterior tip of the nasal forms the posterior frontal process. The superior nasal fenestra is closed by the ala nasalis, which possesses a small transverse maxillary process.

B. **Chamaeleo**

The nasal is present as a thin rodlike structure with its medial surface attached to the lateral surface of the proc. internasalis. The anterior end of the nasal is in contact with the premaxilla and the posterior end is applied to the frontal. The superior nasal fenestra is present due to the absence of the ala nasalis. In *Bradypodion* the ala nasalis is present, but it does not completely cover the fenestra.

One third of the element at the anterior end is covered by the ventroposterior surface of the ascending ledge of the maxilla. The dorsal surface of the anterior tip mentioned, possesses clear grooves and ridges securing this attachment to the ascending ledge. Whereas the anterior end appears to be flattened, the posterior end is tapered like an arrow head. The latter is overlapped by the anterior end of the frontal. Only the middle third of the element is visible in an articulated skull.

C. **Cordylus**

In dorsal view the nasal shows a well developed ala nasalis which covers the superior nasal fenestra. The medial edge of the nasalis is attached to the lateral surface of the internasal process. The anterior tip of the rodlike splinter ends in a short, tapered anterior process which is syndesmotically applied to the transverse process of the premaxilla. A diagonal groove is present on the dorsal surface extending anterolaterally. A small flange is found in the middle of the lateral surface to secure the attachment of the nasal to the anterior surface of the ascending ledge of the maxilla. The posterior half of the element narrows backwards to form a rounded posterior process where the nasal is syndesmotically attached to the frontal. The ventral surface of the element shows an excavated area in the middle of the element ending in a wide groove anteriorly. This groove forms part of the external nariso opening. Three small foramina are present on the medial side of the above-mentioned flange.

D. **Pachydactylus**

The posterior end of the nasal is rounded and wider than the anterior end, giving the element the shape of a human foot. The lateral side of the "heel" folds downwards to form the posterodorsal rim of the external nostril. The medial surface is smooth and prominent to ensure a firm attachment between the paired nasal elements. The anterior third of the medial surface possesses a small triangular depression where the nasal is attached to the short internasal process of the premaxilla.

The ventral surface shows a prominent wide groove from the ventral side of the "heel", gradually becoming shallow towards the back of the element. The groove, like that of *Cordylus*, forms part of the nasal passage.

The ala nasalis is well developed and completely covers the superior nasal fenestra. The general rodlike appearance of the element is feintly present, but it is dominated by the well developed ala nasalis. The pitted external surface of the element is very characteristic.

E. **Meroles**

Because of the small size of the nasals it was difficult to separate the two elements without breaking them. Although they appear fused, they are syndesmotically attached in the upper half at the midline. A notch is formed by the two elements at the ventral end where they are applied to the distal end of the internasal process. The ala nasalis is well developed and covers the superior nasal fenestra completely.

The ventrolateral end of the ala nasalis forms the upper rim of the external nostril. The ala nasalis widens slightly from the outer end of the external nostril rim towards the back, but from the middle the nasal wing tapers posteriorly to form the posterior process of the nasal. The latter is applied to the frontal.

The anterolateral edge of the ala nasalis is attached to the ascending flange of the maxilla; the middle portion of the lateral edge is applied to the prefrontal with the posterolateral edge connected to the frontal. The dorsal surface is smooth except for a few small irregular grooves and ridges near the anterior tip.

The ventral surface possesses a slight groove indicating the inner nostril passage.

F. **Mabuya**

Skinner (1968) found that in *Mabuya* the nasal covers the superior nasal fenestra. Whereas the dorsal surface is smooth, the anterior two thirds of the ventral surface possesses a large excavated area. The lateral edge is in contact with the nasal process of the maxillary and the anterior process of the prefrontal, while the medial edge rests on the dorsal surface of the nasal septum. The latter was not seen in the complete skull.

The anterior process of the nasal possesses a triangular shaped depression on the medial side where it is aligned to the internasal process of the premaxilla. Behind this, the medial sides of the two nasal elements are straight and are firmly applied to each other on the midline from front to back.

The ala nasalis, present on the posterior two thirds of the nasal, widens backwards to form a rounded posterior tip which is applied to the frontal. The lateral edge of the ala nasalis is attached to the ascending ledge of the maxilla. A small foramen on the posterolateral edge of the ala nasalis is in line with the upper tip of the ascending ledge of the maxilla.

G. **Varanus**

The nasal is narrow and splintlike with the anterior half flattened lateromedially and the posterior half flattened dorsoventrally. Small grooves and ridges are present on the medial surface of the anterior process where the lateral surface of the upper tip of the internasal process is attached to the premaxilla. Although the ala nasalis could not be found, the small winglike process on the lateral side of the upper half may be regarded as a vestige of the ala nasalis. Because of the minuteness of the ala nasalis the large superior nasal fenestra is not covered.

The posterior process of the nasal possesses a flange, more prominent than the vestigial ala nasalis, on the medial side where the nasal elements are attached to each other. The posterior processes of the nasals are firmly attached to the frontal.

In some varanid skulls investigated the posterior half of the two nasals are fused, forming a strong connection between the frontal and the internasal process.

The posterolateral edge of the nasal is not applied to the prefrontal in *Varanus*, as found in the other genera, because the lateral flange on the anterolateral edge of the frontal is wedged between the nasal and the prefrontal.

In lizards generally the nasal is a slender, splintlike element near the midline of the skull, with the shape and structure of the ala nasalis as the only distinguishing mark. Because of the small size of this element it may easily be overlooked if disarticulated material is studied. As variations occur in the general shape, even within the same family, this element should be ignored for purposes of identification.

3. Maxilla (Figs. 28 - 30)

The maxilla consists of a horizontal palatal shelf, an ascending ledge and a posterior process. The anterior tip forms the premaxillary process where it is attached to the premaxilla.

The ventrolateral surface of the palatal shelf bears acrodont maxillary teeth, as in *Agama* and *Chamaeleo*, or pleurodont, as in the other genera. The length of the palatal shelf may vary in the different groups. The ascending ledge shows the differences between the genera discussed below.

A. **Agama**

The ascending ledge is anteriorly situated and its upper end curves inwards and forms a sharp tip where it is attached to the nasal medially, and to the prefrontal posterolaterally. The anterior surface of the ascending ledge forms the posterior border of the external nostril. On the tip of the premaxillary process a short ascending process is present syndesmotically attached to the premaxilla. On the ventral side of the process two conical caniniform teeth are present.

The slightly concave lateral surface of the ascending ledge possesses five small foramina in a horizontal line with the biggest at the end of the line.

In the middle of the palatal shelf a small medially directed process (=palatal process) is present to give support to the fused vomero-palatine.

B. **Chamaeleo**

The ascending ledge of the maxilla of *Chamaeleo* is bisected in an anterior and a posterior part by the external nostril. (A bifurcated ascending ledge is present in *Agama* and *Chamaeleo* only). Is this bifurcation an advanced or a primitive condition from that found in *Agama*? The distal end of the anterior part possesses dermal ornamentation of crests and horns - a typical characteristic of the dorsal skull elements of the Chamaeleontidae (Romer 1956). Only one foramen, in the base of the anterior part, is present on the lateral surface of the maxilla. A horizontal line of foramina is absent.

The posterior process extends backwards as a flat surface dorsally to where the jugal is attached to the maxilla. The horizontal palatal process is adjacent to the posterior part of the ascending ledge. The acrodont teeth on the ventrolateral edge of the maxilla will be discussed under the dentition of the different genera.

C. **Cordylus**

The ascending ledge of the maxilla and the lateral tooth-bearing edge give the element a wedge-like shape. The horizontal line of eight foramina is present at the broad base of the ascending ledge.

The upper edge of the ascending part tapers to form a rounded end, attached to the prefrontal. On the anterior surface of the ascending ledge and near its base, a notched area forms the posterior border of the external nares.

A posterior process tapers to a narrow tip which is attached to the jugal and the transversum. The premaxillary process of the premaxilla widens anteriorly. On the anterior surface it is notched to form a bifurcation which supports the attachment of the premaxilla to the maxilla. The medially situated palatal process of the maxilla forms a small flange extending backward to form part of the orbital floor.

D. **Pachydactylus**

The ascending ledge of the maxilla rises vertically on the palatal shelf with the dorsal surface slanting forwards. A notch in the anterior edge and at the base of the ascending ledge forms the posterior border of the external nostril. The lateral surface of the ascending ledge is pitted. The pits reach down the ledge up to the horizontal line of nine foramina.

The posterior process of the maxilla tapers backward up to a relatively small jugal and the transversum. The prefrontal is attached to the posterior rim of the ascending ledge. The nasolacrimal duct is wedged between the fused prefrontal-lacrimal (prefronto-lacrimal) and the maxilla.

The premaxillary process of the maxilla widens anteriorly and the anterior edge is bifurcated by a wide notch to form two processes. The outer process is firmly attached to the maxillary process of the premaxilla. The prominent inner process is attached to the posterior process of the lateral flange of the premaxilla anteriorly, and to the vomer medially.

The palatal shelf has no palatal process, but possesses a flange covering the anterior portion of the internal nares. On the dorsal surface of the palatal shelf, below the posterior edge of the ascending ledge, a foramen is present extending anteriorly towards the lateral side of the maxilla.

E. Meroles

The ascending ledge is confluent with the toothbearing edge of the maxillary, causing the element to be wedge-shaped. The anterior edge of the ascending ledge bends inward forming a laterally situated protective shield for the nasal capsule. The nasal, protecting the nasal capsule, is attached to the anterior fold of the ascending ledge. The horizontal line, at the base of the ascending ledge, bears 6 foramina with the anterior-most foramen present on the anterior surface of the ascending ledge. The posterior process shows a medially directed flange for the attachment to the transversum. An anteriorly directed foramen is present on the medial surface of the base of the ascending ledge. The premaxillary process possesses an inner process only, with the outer process absent. Due to this the anterior surface is straight for attachment to the premaxilla.

F. **Mabuya**

The ascending ledge of the maxilla is present as a winglike structure with the anterior part forming the apex of the ledge. The edge of the apex is uneven to ensure a firm attachment to the nasal medially, a tip of the frontal dorsomedially and the prefrontal posteriorly. The anterior surface of the ledge bends inwards giving the base of the ledge a widened appearance. On this widened anterior surface two foramina are present, in line with the five horizontally disposed foramina on the lateral surface of the ascending ledge. The middle foramen on the lateral surface is the largest of those found on the horizontal line. The lateral view of the maxilla shows a definite notch anteriorly at the base of the ledge. This notch forms the posterior border of the external nares and is part of the widened base of the ascending ledge. The premaxillary process of the maxilla is bifurcated by a wide notch forming the inner and the outer process for attachment to the premaxilla. The posterior process of the maxilla is also bifurcated with the upper part confluent with the posterior winglike section of the ascending ledge.

The palatal process of the palatal shelf is well developed. A shallow diagonal groove, present on the dorsal surface of the palatal shelf, leads laterally towards a foramen at the base of the inner surface of the ascending ledge.

G. **Varanus**

The ascending ledge of the maxilla is situated near the posterior end of the element. The posteroventral edge of the ascending ledge is confluent with the posterior process of the maxilla. A prominent groove, present on the medial surface of the ascending ledge, extends anteriorly to end in a perforated fossa. The anterior surface of the ascending ledge slants downward, forming a ridge which curves medially to end as the dorsal part of the inner process of the premaxillary process. This latter is bifurcated with a deep, rounded notch. A prominent foramen is present on the inner surface of the ridge formed by the downward slanting ascending ledge.

The palatal process of the palatal shelf is well developed. The palatal shelf extends backward as a narrow flange ending at the posterior process. The posterior view of the posterior process shows two foramina above each other and extending anteriorly. Ten foramina are present in a horizontal line above the tooth-bearing edge of the maxilla.

4. Prefrontal (Figs. 31 - 33)

A. **Agama**

In dorsal view the prefrontal is a triangular shaped element with a bifurcated medial process, the frontal process, where the prefrontal is attached to the frontal. The bifurcation is the result of a groove on the upper, anterior surface of the prefrontal. The bifurcated frontal process is attached to the anterolateral end of the frontal. On the lateral side of the prefrontal is a ridge which borders the anterior surface of the orbit. The anteromedial surface of the prefrontal shows a depressed area. The above-mentioned groove is visible posterodorsally of the depression. The lateral wall of the depression extends downward to form the palatine process of the prefrontal where the prefrontal is attached to the palatine (=processus palatinum prefrontalis).

B. **Chamaeleo**

The dermal ornamentation of crests and horns is present on the dorsal surface of the prefrontal.

The anteromedial depression is shallow. The lateral wall of the depression extends downward to form the palatine process medially and a smaller maxillary process laterally. Between these two processes is a small, concave notch forming the dorsal border of the canal of the nasolacrimal duct. The dorsolateral edge of the prefrontal extends forward towards the anterior part of the ascending ledge of the maxilla. A small notch bifurcates the maxillary process of the prefrontal to form an anterior and a posterior process. This notch forms the dorsal border of the external nares.

The fenestra nasalis is situated between the anterodorsal extention of the prefrontal and the small nasal element. In *Bradypodion* the splinterlike nasal has a lateral wing - shaped flange, the ala nasalis, which covers the fenestra nasalis. This is not the case in *Chamaeleo*.

Posteriorly the prefrontal is attached with sutural interdigitations to the fused postorbitofrontal and medially to the frontal. The posterior surface of the prefrontal forms part of the anterior border of the orbit.

C. **Cordylus**

The anteromedial depression in the prefrontal is bowl-shaped. The lateral wall of the depression extends downward forming the palatine process. The lateral side of the palatine process is attached to the maxilla, while the medial side is attached to the palatine. A long, tapered projection extends dorsoposteriorly towards the lateral side of the frontal.

Anterior to this depressed area a flange is present which underlies the ascending ledge of the maxilla. The lateral side of the prefrontal is visible behind the posterior edge of the ascending ledge. A small horizontal ridge is present on this lateral side of the prefrontal. Halfway between this ridge and the ventral palatine process is a small lateral projection which forms the dorsal wall of the naso-lacrimal duct's passage. A shallow notch below this small lateral projection forms the dorsomedial wall of the canal of the naso-lacrimal duct. The lateral wall of the duct's canal is formed by the maxilla with a vestige of the lacrimal on the medial side of the posterior process of the maxilla. The posterior surface of the prefrontal, below the tapered dorsoposterior projection, forms the anterior wall of the orbit. In the upper medial corner of this anterior wall is a small foramen leading to a small canal that opens medially on the border between the prefrontal and the frontal. Across the medial opening of this canal is a small ridge obscuring it from an anterior view.

D. **Pachydactylus**

The anteromedial depression in the prefrontal is beanshaped with the concavity towards the inside. The depression extends upward and medially to form a flange which underlies the frontal and gives support to the septomaxilla. The lateral wall of the depression extends anteriorly to form a flange which underlies the ascending ledge of the maxilla.

Although the palatine process of the prefrontal is small, it is attached to the palatine medially and the maxilla laterally. An incomplete foramen is present above the palatine process on the ventrolateral side of the prefrontal. A vestige of the lacrimal on the maxilla completes this foramen to form the naso-lacrimal canal. The lateral pitted surface of the prefrontal is not covered by the ascending ledge.

The posterodorsal projection of the prefrontal is attached to the lateral edge of the frontal. The smooth posterior surface of the prefrontal forms the anterior wall of the orbit.

E. **Meroles**

The anteromedial depression of the prefrontal possesses a dorsolateral flange which is overlapped by the ascending ledge of the maxilla. The palatine process, ventrolateral to the depression, is attached to the maxilla laterally and the palatine ventromedially. A small notch, above the palatine process and below the ridge on the lateral side of the prefrontal, forms the dorsal, medial and ventral borders of the naso-lacrimal canal. The lateral wall of the canal is formed by the maxilla and possibly the vestiges of the lacrimal. Below the palatine process a second notch forms the dorsal wall of a foramen with the medial, ventral and lateral walls present on the palatine. The posterior surface of the prefrontal forms the anterior wall of the orbit. The upper medial part of this wall extends backward to form a short posterior projection which is applied to the lateral side of the frontal. A small foramen is found on the ventral side of the posterior projection near the midline .

F. **Mabuya**

The depressed area of the prefrontal is on the anterior surface and not anteromedially as the case in *Chamaeleo*. The edge below the depression extends ventrolaterally to form the palatine process medially and the maxillary process laterally.

The dorsal view of the prefrontal shows a flange that extends forward and underlies the frontal and nasal medially with the ascending ledge of the maxilla laterally. A posterior projection, seen in dorsal view, is applied to the lateral side of the frontal above the orbit.

The posterior surface of the prefrontal forms the entire anterior wall of the orbit. A small notch, lateral to this surface, forms the medial side of the naso-lacrimal canal. A small process on the prefrontal above this notch forms the dorsal border of this canal. In the upper corner and on the medial side of this flat surface, a small foramen is present which extends into the nasal region.

G. **Varanus**

The anteromedial depressed area of the prefrontal has a prominent palatine process ventrally. Because of the size and position of the lacrimal, the prefrontal is not in contact with the maxilla ventrally. The dorsal surface of the prefrontal has a tapered posterior projection attached to the lateral side of the frontal above the orbit. A curved anterior projection is present with a lateral flange which curves downwards. This flange is overlapped by the ascending ledge of the maxilla. A notch, laterally to the palatine process of the prefrontal, forms the medial border of the naso-lacrimal canal.

5. Lacrimal (Figs. 34 + 35)

Skinner (1968) and Leonard (1973) indicate an association between the lacrimal and the posteromedial part of the maxilla. Camp (1923), Jollie (1960) and Romer (1956) find that the lacrimal may be fused to the prefrontal in some genera. Camp (1923), however, notes that small elements such as the lacrimal, is not of great phylogenetic importance because of its sporadic disappearance and fusion with the prefrontal or maxilla, even within the same species. Du Plessis (1944) mentions the absence of the lacrimal in *Chamaesaura anguina*, while Van Pletzen (1946) indicates it to be present in *Cordylus polyzonus*.

A. **Agama**

The agamid lacrimal is a small, flat, C-shaped element with a rounded dorsal tip, attached to the ventral edge of the ridge on the lateral side of the prefrontal. The anterior edge of the lacrimal is in contact with the lower posterior edge of the ascending ledge of the maxilla. The ventral tip of the lacrimal is tapered and curves posteriorly to attach to the maxilla. The medial surface of the lacrimal forms the lateral border of the naso-lacrimal canal.

B. **Chamaeleo**

The rodlike lacrimal has an upward bevelled upper tip attached to the posterior maxillary process of the prefrontal. The ventral half of the lacrimal possesses a lateral flange syndesmotically applied to the posterior edge of the ascending ledge of the maxilla. The upper half of the lacrimal forms the lateral wall of the naso-lacrimal canal.

C. **Cordylus**

A vestige of the lacrimal on the maxilla forms the ventrolateral wall of the naso-lacrimal canal.

D. **Pachydactylus**

The same as in Cordylus.

E. **Meroles**

The same as in Cordylus.

F. **Mabuya**

The lacrimal is triangular in shape with the apex pointing posteriorly. It is attached to the inner surface of the posterior process of the maxilla with the apex of the lacrimal syndesmotically attached to the anterior process of the jugal. A shallow, wide groove extends forward on the inner surface of the lacrimal to form a notch in the anterior edge of the element. This notch forms the ventrolateral wall of the naso-lacrimal canal.

G. **Varanus**

In lateral view the lacrimal is triangular-shaped with the apex pointing anteriorly. The latter is overlapped by the ascending ledge of the maxilla. The section posterior to the apex is not overlapped by the ascending ledge and is visible in the lateral view of the skull.

The posterior view of the lacrimal shows a large notch on the medial surface with a small foramen ventrolaterally to the large notch. The notch forms the lateral wall of the naso-lacrimal canal. The edge of the lacrimal above the notch is attached to the prefrontal and the ventral rim of the notch possesses a small ventral process which is applied to the palatine. Lateral to this process and below the small foramen is a ventral process which is attached to the jugal.

6. Frontal (Figs. 36 - 38)

Generally this element is T-shaped and consists of two fused elements. The condition of two separate elements occurs in *Varanus*, while the T-shape is still maintained with the fusion of the two elements in other forms. The frontal of *Chamaeleo* is shield-like with a sharply tapered projection anteriorly where it is applied to the nasal laterally and touching the internasal process of the premaxilla. Skinner (1968) refers to the suture between the frontal and the parietal, the fronto-parietal suture, as the coronal suture. Both these terms are used in this discussion.

A. **Agama**

The anterior edge of the frontal possesses a small cleft, possibly indicating that the element originated from two fused parts. Lateral to this cleft, and on both sides, a short process is present which is attached to the nasal medially, the tip of the ascending ledge of the maxilla anteriorly and the posterior projection of the prefrontal laterally. A shallow excavation, found on both sides of the cleft, indicates where the nasal covers the anterior edge of the frontal.

The interorbital bridge of the frontal extends posteriorly and widens to form the crossbar of the T-shape with the anterior border of the parietal foramen in the centre of the posterior edge of the frontal.

The ventral view of the frontal shows a shallow groove near the anterior tip. The point of contact with the prefrontal is on both sides of the groove.

B. **Chamaeleo**

The frontal is syndesmotically attached to the surrounding bones with sutural interdigitations and could not be disarticulated without damage.

It is shield-shaped with a small crest of protuberances in the middle near the posterior ridge. A small parietal foramen lies on the mid-line between the crest and the posterior edge of the frontal, but the parietal canal does not exit the frontal ventrally.

In the middle of the anterior edge of the frontal a tapered anterior projection occurs which overlies the posteromedial tips of the nasals. The internasal process of the premaxilla does not reach the anterior process of the frontal. The ventral view of the anterior region of the frontal shows no grooves or folds although traces of folds extending laterally, are present in the posterior region of the element.

C. **Cordylus**

The dorsal view of the frontal shows an anteriorly situated groove parallel to the attachment of the frontal to the parietal. A groove perpendicular to this parallel groove is present in the midline of the bridge between the two orbits. The anterior extremity of this groove diverts towards the orbits. These grooves correspond with the position of the scales found on the head of *Cordylus*. A short anteriorly-directed process is found on the anterolateral side of the frontal with a small semi-lunar shaped excavation between these processes formed by the two nasal elements overlying the frontal.

In the ventral view of the frontal a small fossa can be seen in the posterolateral edge in front of the contact between the frontal and the parietal. The fossa is situated on a ridge of the frontal that extends forward along the edge of the interorbital bridge. The anterior part of the ridge curves downward to form a short ventral palatine process attached to the palatine. The ridge and the ventral palatine process is present on both sides of the frontal forming an incomplete olfactory canal. The latter widens anteriorly in the frontal to be confluent with the canal passing between the palatines. On the lateral side of the descending (ventral) palatine process the contact surface for the posterior frontal process of the prefrontal can be seen. The ridges mentioned can also be seen as folds of the ventral frontal surface contributing to the formation of the olfactory canal (Leonard, 1973).

D. **Pachydactylus**

The dorsal view of the frontal shows a pitted surface with a straight posterior edge where this bone is syndesmotically attached to the anterior edge of the parietal. A shallow groove on the dorsal surface extends from the posterior edge of the element towards the front. Two semi-lunar depressions are visible on the anterior end where this bone is in contact with the nasal elements. Lateral to the anterior end of the frontal a short anterior projection is found, forming support for the attachment of the frontal to the posterior frontal process of the prefrontal. The lateral view of the frontal shows a triangular shaped excavation where the prefrontal is applied to the frontal.

The ventral view of the frontal shows a complete olfactory canal with the prominent descending palatine process on both sides of the anterior opening of the canal. On the midline between the two palatine processes a short tapered anterior process is present forming part of the floor of the olfactory canal. The depressed contact areas of the posterior frontal process of the prefrontal forms tne lateral sides of the olfactory canal. The posterior opening of the canal extends backward as two ridges strengthening the lateral flanges on the posterior edge of the frontal.

E. **Meroles**

The dorsal view shows a short longitudinal groove on the posterior third of the frontal. A short posterior process is present on the lateral sides of the posterior edge where the frontal is in syndesmosis with the parietal. Dermal ornamentation can be seen on both sides of the longitudinal groove, but it is not as prominent as in *Chamaeleo*.

The interorbital bridge widens anteriorly to end in a rounded anterior tip. Lateral to the rounded anterior end a short anterior process is present which borders the posterior third of the nasal laterally. Two U-shaped depressions are present on the anterior end indicating the attachment of the nasals to the frontal.

The ventral view of the frontal shows the descending lateral processes on the posterior edge. These lateral processes support the postfrontals. A ridge found on the ventral surface in the midline of the interorbital bridge extends backward to the posterior edge of the frontal. On the lateral side of this ridge two further ridges are present which gradually expand anteriorly to form ventrally-directed flanges. These flanges do not meet on the midline and an incomplete olfactory canal is therefore present. On the lateral surface of each flange a depressed contact surface for the posterior frontal process of the prefrontal can be seen.

F. **Mabuya**

The dorsal view shows a shallow longitudinal groove on the posterior third of the frontal which diverts anterolaterally towards the orbits. Less dermal ornamentation is found on both sides of this groove than in *Meroles*.

The anterior edge of the frontal ends in a double W-shaped tip which is attached to the nasal elements. The latter overlies the anterior part of the frontal forming a second W-shaped depression posteriorly. The posterior edge of the frontal is straight without any processes. In the posterior half and on the lateral edge of the frontal, a small lateral flange is present.

The prefrontals are attached to the lateral side of the anterior end of the frontal with the posterior frontal process of the prefrontal extending backwards along the lateral edge of the frontal to meet the lateral flange on the frontal.

Viewed ventrally, the frontal shows a lateral ridge extending forward and gradually ascending to form the lateral walls of the olfactory canal. As they do not fuse, the floor of the canal is absent.

G. **Varanus**

Paired frontals are present The dorsal view shows an L-shaped structure with sutural interdigitations on the posterior edge of the short bar of the L. An uneven surface is present on the medial side of the long bar of the L. On the anterior end of the long bar a long medial process is found with a shorter process lateral to the long process. A notch is present between the long and the short process. The notch extends backward on the dorsal surface as a depression indicating the overlap of the nasal on the frontal.

The lateral view shows the contact surface of the postfrontal on the lateral end of the short bar of the L. The contact surface of the posterior frontal process of the prefrontal is on the lateral side of the long bar of the L.

On the posteroventral part of the frontal a descending flange is present which forms the lateral wall of the olfactory canal. The posterior end of the flange meet the adjacent flange to form a complete canal, but the anterior part of the flanges do not meet leaving the canal incomplete. Sutural interdigitations on the posterior part of the flanges prove the contact of the complete part of the olfactory canal.

The ventral view shows a slight excavation in front of the flange which extends towards the notch between the long medial process and the short lateral process on the anterior end of the frontal. A short ridge is present on the lateral surface of the flange extending in an anteroposterior direction.

7. Parietal (Figs. 38 - 40)

A. **Agama**

The dorsal view of the parietal shows an X-shape with the remaining two thirds of the parietal foramen on the anterior edge. Lateral to the foramen the anterior part of the parietal extends outwards to become confluent with the posterior edge of the frontal. A notch is present behind the lateral extention of the anterior edge of the parietal. The inner wall of the notch extends backward along the lateral edge of the parietal process. The walls of the notch forms the anterior and medial walls of the supratemporal fenestra. Behind the parietal foramen the parietal extends posterolaterally to form two long parietal processes. The dorsomedial edge of the parietal process possesses a flange slanting inwards. The distal end of the parietal process is syndesmotically applied to the dorsal head of the quadrate. The squamosal is applied to the lateral side of the tip of the parietal process, while the paroccipital process of the otoccipital is applied to the medial side of the tip of the parietal process.

A small fossa (=parietal fossa) is present at the base of the posterior edge of the parietal behind the parietal foramen. The fossa serves as an attachment for the cartilaginous disc connecting the short supraoccipital spine of the supraoccipital with the parietal.

The ventral view shows that the surface of the parietal surrounding the parietal foramen is excavated to form a slight dome above the brain.

B. **Chamaeleo**

The dorsal view of the parietal shows a T-shaped structure with a long posterior process which meets the squamosals posterodorsally to form the characteristic crest of the chamaeleons. In other genera investigated, the squamosal is in contact with the parietal process and together they are in contact with the cephalic condyle of the quadrate.

Normally the posterolateral end of the parietal extends outwards as the parietal process which is applied to the squamosal. In *Chamaeleo* the opposite is observed. The squamosals extend inward to be dorsally attached to the long posterior process. This indicates that the latter could possibly be fused parietal processes. According to Rieppel(1981) the lateral parietal processes are absent and the ascending parietal process of the squamosal is elongated to meet the parietal to form the parietal crest. This indicates that the posterolateral and lateral borders of the superior temporal fenestra is formed by the squamosal only.

The squamosal and the paroccipital processes are attached to the dorsal surface of the quadrate. The parietal does not reach the quadrate. Near the anterior section of the fused parietal process a ventral extention, the inferior saggital spine, is present which is in syndesmosis with the supraoccipital spine. Skinner (1968) and Leonard (1973) refer to the inferior saggital spine as the processus descendens posterior / processus descendentes posteriores as though this process is composed of two blades of bone. In *Chamaeleo* it was observed as a single, long outgrowth.

Posttemporal fenestrae are present above the parocciptial processes and below the parietal processes (Romer, 1956).

An incomplete infratemporal fenestra is anteriorly bordered by the jugal, dorsally by the squamosal and posteriorly by the quadrate (Skinner, 1968).

A distinctive W-shaped overlap of the frontal with the parietal is present on the anterior edge of the parietal.

The ventral view of the parietal shows the anterior edge of the element with sutural interdigitations where it is attached to the frontal. The ventral extention of the inferior saggital spine appears to be bifurcated at its base near the anterior edge of the parietal to clamp the supraoccipital spine. According to Romer (1956) the "fingerlike process" of the supraoccipital is clamped by the process of the parietal.

On the lateral edge of the parietal the sutural interdigitations between the parietal and the postfrontorbital are present. The posterior end of the fused parietal processes widens to support the overlaying squamosals. According to Rieppel (1981) the lateral parietal processes of the parietal are absent and the ascending parietal process of the squamosal is elongated to meet the parietal to form the parietal crest. This indicates that the posterolateral and lateral borders of the supratemporal fenestra are formed by the squamosal only.

C. **Cordylus**

The dorsal view shows a square-shaped parietal with a longitudinal groove extending from back to front, and a groove extending from left to right perpendicular to the former with a diamond-shaped structure in the centre of the parietal. A triangular dent in the diamond shaped structure is the remnant of the parietal foramen. The ventral view of the parietal clearly shows the position of the parietal foramen. The anterior edge of the parietal forms a straight line where it is connected to the frontal. On the lateral end of the anterior edge of the parietal a slanted fossa is present where the parietal is attached to the frontal.

In the centre of the posterior edge of the parietal a short bifurcated inferior saggital spine is present which is in syndesmosis with the supraoccipital spine of the supraoccipital.

The descending parietal process is present on the posterior and lateral side of the parietal. The two parietal processes and the inferior saggital spine forms a distinctive W-shaped edge giving the posttemporal fossa a rounded dorsal border.

The bifurcated inferior saggital spine extends anteriorly as a flange-like ridge which diverts to reach the ridge formed by the parietal process. A small process, the processus descendens anterior (Skinner 1968; Leonard 1973), is present at this junction. The former is in syndesmosis with the upper tip of the epipterygoid. At the diversion of the ridge of the inferior saggital spine a small fossa is present which slants into the ventral surface of the parietal. Anterior to this fossa the remnant of the parietal foramen is found. The bony plate covering the foramen is very translucent and it may serve as a fixed lens.

The ventral view of the element shows the parietal process extending anteriorly as a longitudinal ridge on the ventral surface of the parietal; the crista cranii parietalis

D. **Pachydactylus**

The dorsal view shows the pitted surface of the parietal and the descending processes posterolaterally.

Above the orbits, the lateral sides of the parietal are slightly dented inwards. The syndesmotic contact between the parietal and the frontal forms a straight coronal suture.

The parietal process on the posterolateral side of the parietal curves backward and downward to reach the dorsal surface of the quadrate. A small shallow notch is present where the inferior saggital spine is supposed to be and instead a thick mass of connective tissue is present connecting the parietal to the supraoccipital spine.

The posttemporal fossae are present with this thick mass of connective tissue forming a septum between them. The dorsal rim of the posttemporal fossa is semi-lunate.

The ventral view shows the crista cranii parietalis with the processus descendens anterior in the centre of the parietal and it is in syndesmosis with a superior process of the prootic. The epipterygoid is syndesmotically applied to the anterior surface of the superior process. A deeply excavated area is present lateral to the crista cranii parietalis. A small broad transverse ridge lies between the crista cranii parietalis, with two small depressions on the posterior side of this transverse ridge.

E. **Meroles**

The dorsal view shows a groove in middle of the posterior edge of the parietal which extends anteriorly. At the centre of the parietal, the groove diverts anterolaterally to form the posterolateral borders of a diamond-shaped structure. The small parietal foramen occurs in the centre of this diamond-shaped structure.

The anterior margin of the parietal is serrated along the transverse contact with the frontal. A small excavated area is present on the posterior edge of the element in line with the longitudinal groove. A transverse excavation is present below the posterior rim of the parietal.

The posterolateral processes extend backward, downward and outward where they are syndesmotically attached to the quadrate heads.

The posteromedial edges of the parietal processes curve upward and inward to form the ventral surface of the transverse excavation mentioned above. The edges do not meet on the midline of the parietal, but form a notch that extends anteriorly on the ventral surface of the parietal.

A series of small crests and grooves are present on the posterior portion of the element.

The ventral view shows the deep notch which extends anteriorly as a foramen leading towards the parietal foramen. The crista cranii parietalis is S-shaped curving outward to reach the lateral edges of the anterior half of the element with two depressed areas on either side of the parietal foramen medially and the crista cranii parietalis laterally. Vestiges of the anterior descendens processes are present on the former.

F. **Mabuya**

The dorsal view shows a triangular impression with the apex of the triangle towards the back of the element. The parietal foramen is present in this V-shaped impression.

The coronal suture is convex towards the front. The lateral ends of the anterior edge of the parietal extends outward and is confluent with the posterior margin of the frontal. The parietal process extends far back, then curves downward and outward. A large V-shaped notch is present posteromedially. Between the notch and the parietal process a tapered flange extends posteriorly and is syndesmotically attached to the dorsolateral side of the supra-occipital. A thick mass of connective tissue extends from a small deep fossa in the base of the V-shaped notch to the supra-occipital spine. A small fossa is present on the laterally at the base of the V-shaped notch.

The ventral surface of the parietal is excavated and the dorsal surface is dome-shaped. The parietal foramen is prominently situated between two very small longitudinal grooves which widens anteriorly. The crista cranii parietalis is near the lateral border of the element with a narrow flange on the lateral side of the crista. A well developed processus descendens anterior is present in the middle of the crista and the former is syndesmatically attached to the superior process of the prootic posteriorly and the dorsal epiphysis of the epipterygoid anteriorly. The anterior tip of the crista forms a broad process which extends beyond the anterior margin of the parietal and contacts the frontal.

G. **Varanus**

The dorsal view shows a X-shaped structure with well developed posterolateral processes. Just below the posterior edge of the parietal a small central fossa is present. A thick mass of connective tissue extends from this fossa and attaches the parietal to the anterior surface of the supraoccipital spine.

An articulation surface is present lateral to the fossa and below the proximal part of the posterolateral parietal process where the parietal is syndesmotically applied to the supraoccipital, adjacent to the supra-occipital spine.

The parietal edge of the coronal suture forms interdigitations to strengthen the contact between the frontal and the parietal. A small, oval parietal foramen is present in the anterior half of the element.

The lateral tip of the anterior edge extends outward and is confluent with the posterior edge of the frontal. The postfrontal is attached to the lateral extention of the anterior edge, completing the supratemporal fenestra laterally. The posterior edge of the lateral extention converge medially to form a V-shaped dorsal surface.

The ventral surface shows the prominent crista cranii parietalis which appears to extend laterally as a winglike flange,the parietal process.

8. Identification of the postorbital, postfrontal and postorbito-frontal.

During the investigation a problem was encountered in correctly identifying the postorbital and the postfrontal. These elements may be present as separate structures, or one may be absent, or the two elements may be fused. Rieppel (1981) referred to this fused element as the postorbitofrontal. Camp (1923) used the term postfronto-orbital, but included elements such as the lacrimal and the jugal as part of the fused postorbital and postfrontal. The discussion of Rieppel (1981) will be used in this work. According to Goodrich (1930) the element present in *Varanus* is the postfrontal, while Romer (1956) stated that the element in *Varanus* is the fused product of the postfrontal and the postorbital. Romer and Parsons (1977) restated the presence of the postorbitofrontal in *Varanus* and Rieppel (1979) seems to agree with them. Romer (1956) described the single element in *Chamaeleo* as "presumably" the postorbital, while in the geckos the single element is "perhaps" the postfrontal. He stated that in agamids the postfrontal is reduced or absent and that both are present in the skinks, but that the postorbital is "generally" absent while in the varanoids it is "thought" to represent a fusion of the two elements.

According to the Henderson's Dictionary of Biological Terms (Holmes, 1979), the elements are given as :

1. postfrontal - "a bone occuring behind the orbit of some vertebrates"; and
2. postorbital - "a bone forming part of the posterior wall of the orbit."

It is obvious from the above that a degree of uncertainty surrounds the definition of the postorbital and the postfrontal. In order to distinguish between these elements an attempt is made to describe them by refering to their different positions in relation to the other elements surrounding them in the temporal region.

Two elements present.

If two elements are present in the position where the postorbital and the postfrontal are supposed to be, it is obviously these elements. The element that does not touch the frontal is the postorbital and the remaining element the postfrontal. Characteristic of the postfrontal is the contact that is established with the jugal. Romer (1956) stated that the developement of the postorbital and the postfrontal vary greatly - partly, but not entirely, in relation to the presence or absence of the temporal arch. Bellairs (1949) states that in more specialised scincid burrowers the temporal arches have been lost as a result of the reduction of the squamosal and jugal and the complete disappearance of the postorbital. In *Scelotes* the postorbital is vestigial. The jugal can close the postorbital arch and in *Cordylus* a small projection is present which may be the vestige of this arch.

An example of the condition mentioned above, can be found in *Mabuya*, and is shown in a simplified sketch (Diagram 1.F). Skinner (1968) stated that the postfrontal begins to ossify in the embryo sooner than the postorbital indicating that two ossification centres must be present. This condition may lead to the different situations present in the remaining genera.

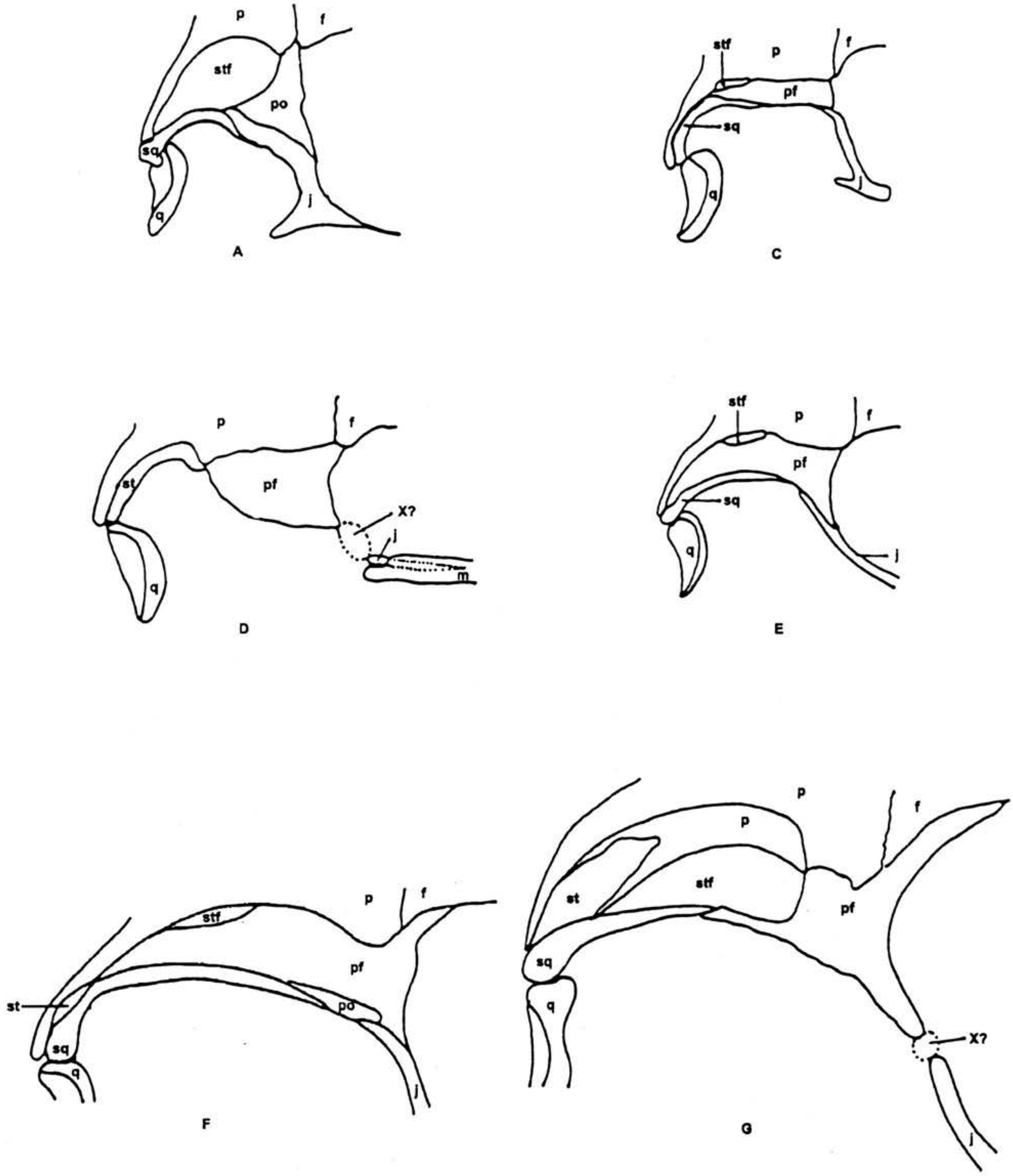


Diagram 1 Temporal region - A, C, D, E, F, G. - Dorsolateral view (Not to scale).

One element present

The decision is impeded if only one element is present, but the following discussion may help identifying the element.

Postorbital

This element is in contact with the parietal anterodorsally or dorsolaterally; with the squamosal posterolaterally or laterally and sometimes with the jugal anteroventrally or ventrally. If however a small anterodorsal projection or process of the element is touching or slightly in contact with the frontal, it can still be regarded as the postorbital. The contact with the jugal in some cases may be seen as an exception in *Mabuya*, if one bears in mind that in the latter, both the elements are present.

Postorbitofrontal

This element contacts the frontal anterodorsally and extends backwards past the middle of the orbit or behind the orbit. It is also in contact with the parietal posterodorsally, the squamosal posteroventrally and sometimes the jugal ventrally.

Postfrontal

This element is anterodorsally in contact with the frontal, which must be extended backwards past the middle of the orbit or behind the orbit. Ventrally it is in contact with the jugal. If a small posterodorsal process is touching or even in the slightest in contact with the parietal, it can still be regarded as the postfrontal. Skinner (1968) mentioned the postfrontal as an element extending far back to reach the squamosal ventrolaterally and extend along the ventrolateral margin of the parietal. Because of this the supratemporal fossa is virtually closed except for a narrow slit at the posterodorsal edge of the postfrontal.

In a situation where the element may or may not be in contact with the frontal or the parietal, consider the definition of the element based on the contact with the frontal or the parietal. If the larger part of the contact is with the frontal, the element in question is the postfrontal. If the larger part of the contact is with the parietal, the element in question is the postorbital. If one examines the sketches supplied, it is noteable that , if the element in question is in contact with the squamosal, one can justifiably identify the element as the postfrontal. An in depth study of the embryology of this area may help to clarify the situation.

To justify the assumptions mentioned above, consider the following different conditions that may prevail and which may influence the decision, eg:

1. The secondary elongation of an element or an adjacent element; or
2. The reduction and/or absence of an element or an adjacent element; or
3. The fusion of the two elements.

Secondary elongation

In the genera investigated it was noted that the squamosal does not extend far forward, but in *Mabuya* it virtually reaches the jugal, while the jugal extends upwards and backwards almost to reach the squamosal. This can explain why contact is established between the postfrontal and the squamosal. The same applies to the postfrontal of *Meroles* where the ossification of the postfrontal extends backwards and this explains why the the supratemporal fossa is nearly closed. Broom(1935) mentioned that in Scincidae and Lacertidae the postfrontal is large and the postorbital reduced or absent.

In *Agama* the element appears to be the postorbital or the postfrontal. The firm contact with the jugal indicates that it must be the postfrontal. The contact dorsally with the parietal makes it the postorbital, because it does not reach the frontal. An investigation of the jugal shows that it extends exceptionally far upward and backward, which explains the lack of contact between the jugal and the squamosal. This indicates that the element must be the postorbital. Brock (1932) and Barry (1953) claim that in *Agama hispida* the postorbital is large and that it completes the postorbital arch, while the postfrontal is absent.

In *Cordylus* the jugal extends exceptionally far upward to reach the element. The latter extends backward to reach the squamosal and in doing so it closes the supratemporal fossa. From the deductions discussed here it became obvious that the only element which can close off the supratemporal fossa is the postfrontal. This is due to the presence and the position of the ossification centre of the postfrontal. According to Van Pletzen (1946) two elements are present in the temporal region of *Cordylus polyzonus*. A large postorbital, extending backward to close off the supratemporal fossa except for a very small slit at the posterodorsomedial margin of the postorbital, and a very small postfrontal present on the posterolateral edge of the frontal extending backwards to contact the anterolateral edge of the parietal. The same condition is present in *Cordylus* used in this study and a detailled discussion is presented when the individual elements are described.

In *Meroles* the condition resembles that of *Mabuya* except that the postorbital is absent.

In *Pachydactylus* the absence of a supratemporal fossa indicates that the element which closes the supratemporal fossa must be the postfrontal. Furher details regarding the gecko discussed here will be referred to during the discussion of the reduction of elements.

In *Varanus* it was found that although a large supratemporal fossa is present and the squamosal shows an anterior elongation, something was missing. Comparing *Varanus* and *Pachydactylus* it was soon discovered that an element was either reduced or absent. Rieppel (1979) however, states that the element found in *Varanus* is the postorbitofrontal, but from the present investigation it is clear that one element is absent.

Thus the bridge between the jugal and the squamosal, and between the jugal and the parietal and/or the frontal is formed by the postorbital.

Therefore, if the postfrontal extends downward to meet the jugal, it also extends backward to close the supratemporal fossa and the postorbital seems to be absent. Alternatively, if the postorbital extends upward to meet the parietal and/or the frontal and leaves the supratemporal fossa open, it seems that the postfrontal is absent. Exceptions may occur regarding these two conditions, because in certain instances the posterior wall of the orbit may be incomplete. (X? in Diagram 1 D,G)

Reduction and/or Absence

During this investigation it was found that "something" was missing in the posterior wall of the orbit in *Varanus* and *Pachydactylus*. It was assumed on embryological grounds that during the ossification of the posterior wall elements, the presence of only one ossification centre is present (Skinner, 1968). This ossification does not extend downward to reach the jugal, resulting in an incomplete posterior wall of the orbit. Romer (1956) stated that the squamosal is absent in the gekkonidae and that only the supratemporal is present.

Fused elements

In *Chamaeleo* (Diagram 2) the element in question is applied to the frontal, the parietal, the jugal and the squamosal. It also appears as though it covers the skull behind the orbit in a horizontal and a vertical plane. This means that if only one element was present, it had to lengthen backwards and downwards to reach the squamosal posteriorly and the jugal ventrally,thus completing the temporal arch and the posterior orbital wall. It also had to extend forwards to contact the prefrontal and complete the dorsal rim of the orbit. Rieppel (1981) regards the element in *Bradipodion* and *Chamaeleo* as the postorbitofrontal implying that two ossification centres were present, but that the elements fused during development. Bearing in mind that exceptions may occur, the above discussion could help to identify the element in question. Embryological studies of the genera discussed may further assist in the positive identification of the elements.

The absence of the squamosal in *Pachydactylus* makes it difficult to indicate the exact position of the supratemporal fossa, but with reference to the condition found in some of the genera discussed, the postfrontal appears not to extend far back to close the incomplete supratemporal fossa. This is due to the fact that the fossa is situated laterally to the supratemporal and dorso-anteriorly of the quadrate. Webb (1951) mentioned that either the postfrontal or the postorbital is absent or these two elements are fused to form an element situated on the lateral border of the fronto-parietal suture and fringing the frontal. Camp (1923) stated that the disappearance of the supratemporal fenestra in geckos is caused by the fusion of the squamosal to the lateral border of the parietal.

According to Webb (1951) the pattern of the skull is normal in *Palmatogecko rangei* and *Oedura karroica* , but a considerable reduction of the bone of the temporal region in the vicinity of the orbit is found. A supratemporal arch is absent. In the orbital region the jugal, lacrimal and postorbital are missing, the latter of these possibly fused with the postfrontal to form the postfronto-orbital. According to Romer (1956), if one element remains at the posterior end of the temporal region, it is presumably the supratemporal. This indicates that the element absent in the temporal region *of Pachydactylus* must be the squamosal. Camp (1923), Brock (1932) and Broom (1935) have all discussed the temporal region of the geckos and they have all reached the same conclusion (Webb, 1951).

With these guidelines in mind, it is now possible to identify and describe the elements present in the genera discussed.

8.1 **Postorbital** (Figs. 41 - 43)

A. **Agama**

The element is triangular in shape with the apex extending upwards where it fits into a small triangular notch on the fronto-parietal suture. The notch lies on the fronto-parietal suture.

The ventral edge of the element is attached to the dorsal rim of the posterodorsal elongation of the jugal. The posterodorsal edge of the postorbital forms the ventrolateral margin of the supratemporal fenestra. The anterior edge of the element links the frontal and the jugal, completing the posterior wall of the orbit. Viewed anteriorly, the upper half of the anterior margin of the postorbital is thicker than the lower half.

B. **Chamaeleo**

The element is absent as a single structure, but it is fused with the postfrontal.

C. **Cordylus**

The supratemporal fenestra is present as a small slit posteromedial to the postorbital and is closed off posteriorly by the overlaying postfrontal. In dorsal view the surface of the element is rugose and corresponds with the overlaying scales. It has a narrow, blade-like structure with a sharp tip directed posteriorly and which is attached to the anterodorsal surface of the squamosal. The tapered tip of the postorbital is covered by a small rectangular postfrontal. Anteriorly a small, short anterior process is present. Lateral to this a short projection extends downward to the anterodorsal tip of the jugal. The medial edge of the element tapers posterolaterally and is applied to the lateral edge of the parietal.

The ventral view shows an anteroposteriorly directed ridge with a slight recessed area anteromedial to the latter. The anterior aspect of the ridge is confluent with the short ventrolaterally directed process which contacts the jugal. A very short, but prominent transverse ridge extends from the short ventrolaterally directed process and is continuous with the anterior edge of the parietal.

D. **Pachydactylus**

The element is absent.

E. **Meroles**

The element is absent.

F. **Mabuya**

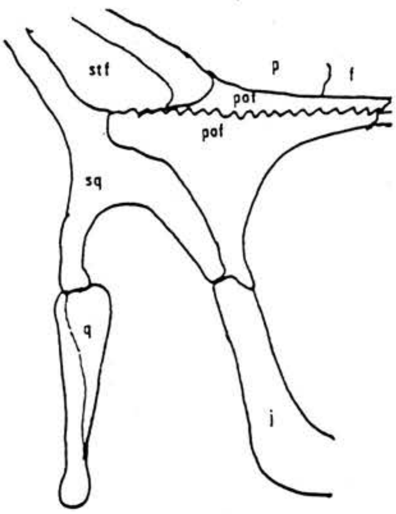
The bone is present as a small splint joining the posterodorsal tip of the jugal to the anterior tip of the squamosal. The dorsal edge of the element is syndesmatically applied to the ventral edge of the large postfrontal. (Skinner, 1968)

G. **Varanus**

The element is absent.

8.2 **Postorbitofrontal** (Diagram 2)

This element is present in *Chamaeleo* only and it is identified by Rieppel (1981). It is present in two planes: laterally it extends backwards behind the orbit and dorsally forwards above the orbit to reach the prefrontal. Ornamentation occur on the dorsolateral edge of the element as slight crests and horns. It forms the posterior wall of the orbit and it extends backward to reach the squamosal. The latter has an anteroventral ramus which contacts the dorsal end of the jugal.



B

Diagram 2 Temporal region - B - Dorsolateral view (Not to scale).

The postorbitofrontal also extends downward to reach the jugal. It is therefore in contact with the jugal ventrally, is applied to the anterior surface of the anterior ramus of the squamosal and borders the supratemporal fenestra anterolaterally.

The peculiar shape of this element is a characteristic of chamaeleons.

Rieppel (1979) states that *Varanus niloticus* possesses a postorbitofrontal; but from the discussion prior to this section it is clear that this element is not present in *Varanus*.

8.3 **Postfrontal** (Figs. 43 - 46)

A. **Agama**

The element is absent

B. **Chamaeleo**

The fused postorbitofrontal is present.

C. **Cordylus**

The dorsal view shows a small rectangular element with a slightly recessed posterior edge. The anterior portion of the element tapers anteriorly to form a narrow anterior edge where the element is applied to the larger postorbital. The dorsal surface is rugose and may also be slightly pitted.

The ventral view shows an anteroposteriorly directed groove where the element is attached to the sharp posteriorly directed process of the postorbital and the anterodorsal surface of the squamosal.

D. **Pachydactylus**

The dorsal view shows a triangular element tapering slightly towards the back. The anterior edge is slightly curved to form the posterior rim of the orbit. The upper tip of the edge folds inwards underneath the fronto-parietal suture to form a syndesmatic attachment to the latter. Behind this inward fold (=fronto-parietal process), a small notch is present on the dorsal edge where the parietal contacts the postfrontal. A small flange extends backward behind the notch for further attachment between the lateral edge of the parietal and the dorsal edge of the postfrontal. No contact is found between the postfrontal and the supratemporal. The outer surface of the element is pitted and slightly dome shaped, while the inner surface appears smooth. The ventral edge of the element is smooth and rounded with no contact with any other element.

E. **Meroles**

In dorsal view the element appears rectangular with a prominent, rounded anterior edge which forms the posterior rim of the orbit. The tips of the rim extend upward and downward as narrow processes. The upper process is attached to the anterolateral surface of the wider posterior end of the frontal. The ventral process is in contact with the upper tip (=temporal process) of the jugal to complete the posterior wall of the orbit. The ventral margin of the bone curves upwards and ends in a short posterior process. The ventral side of the process is attached to the anteromedial surface of the squamosal. A notch is present dorsally to the short posterior process which forms the anterolateral border of the small supratemporal fenestra. The dorsal edge of the element is syndesmatically attached to the lateral edge of the parietal. The dorsal surface of the element shows slight ornamentation with a very prominent groove just above the ventral edge of the element. The inner surface is smooth and appears to be slightly excavated, leaving a slightly dome-shaped outer surface.

F. **Mabuya**

The element resembles that of *Meroles* as far as shape is concerned. The anterior edge forms the posterior rim of the orbit. The tips of the anterior edge extend upward and downward as sharp processes. The upper process is attached to the anterolateral surface of the wider posterior end of the frontal. A notch is present behind the upper process and the latter curves inwards and backwards to form a small flange visible in this notch. The frontal and the parietal extend laterally at the fronto-parietal suture which is firmly attached to the postfrontal at the notch with the flange applied to the frontal. The dorsal edge of the postfrontal is attached to the lateral edge of the parietal.

The ventral process is attached to the temporal process of the jugal to complete the posterior wall of the orbit. A small depressed area is present on the posterior surface of the ventral process to accomodate the small postorbital element. The ventral edge of the postfrontal is applied to the dorsal edge of the squamosal. This means that the ventral side of the postfrontal is attached to three elements - anteriorly to the jugal; medially to the postorbital and posteriorly to the squamosal. The ventral edge extends backwards to form a small splintlike process. The latter is applied to the squamosal ventrally and the parietal process of the parietal dorsally. The posterior edge of the postfrontal forms the anterior border of a small supratemporal fenestra. The dorsal surface of the element is smooth and not as dome-shaped as the element present in *Meroles*.

Although the shape of the element in *Mabuya* and *Meroles* appears to be similar, the distinctive difference described here will ensure easy identification.

G. **Varanus**

The dorsal view shows a triangular element with the apex of the triangle extending backwards to form an elongated posterior process. The latter is attached to the anteromedial surface of the squamosal. The lateral tip of the triangle forms a short ventrolateral process. The latter is not attached to the temporal process of the jugal. The medial tip of the triangle is elongated and is attached to the anterior surface of the wide end of the frontal. The medial process of the postfrontal and the posterior process of the prefrontal virtually touch each other on the lateral edge of the frontal above the orbit.

Between the elongated posterior process and the elongated medial process of the postfrontal, a knoblike structure is present. The back of this structure and the medial surface of the elongated posterior process form the anterolateral border of the supratemporal fenestra. The anterolateral end of the parietal and the posterolateral end of the frontal, syndesmatically attached at the fronto-parietal suture, extend outward and contact the postfrontal in an area between the knoblike structure and the medial process.

The dorsal surface of the bone is smooth except for 2 - 3 small ridges on the ventrolateral process and a small foramen in the middle of the element. The ventral surface shows a distinctive ridge between the ventrolateral process and the knoblike structure mentioned previously.

9. Jugal (Figs. 47 + 48)

Generally the jugal is a rodlike L-shaped structure, but variations do occur. In *Cordylus* the bone is T-shaped whereas in *Pachydactylus* it is rod-shaped.

A. **Agama**

In lateral view the jugal is rodlike and L-shaped. The temporal process extends far upwards and backwards and is syndesmotically attached to the ventral edge of the postorbital and the anterodorsal edge of the squamosal. The broad central portion tapers towards the temporal and the maxillary processes.

Anteriorly a rounded edge is present, forming part of the posteroventral wall of the orbit, with a medial flange extending inwards to meet the lateral tip of the transversum. The anterior end of the element (maxillary process) is applied to the dorsal surface of the posterior process of the maxilla, completing the orbital rim.

A small posterior process, which may represent the remains of the posterior ramus, is present on the posterior edge of the element. The latter forms the lower temporal arch in the diapsids (Romer,1956, p.115)

B. **Chamaeleo**

The element is L-shaped in lateral view with the anterior maxillary process attached to the dorsal surface of the posterior process of the maxilla. The maxillary process extends posterodorsally to form the posteroventral wall of the orbit. The temporal process of the jugal extends upwards and contacts the posterior edge of the ventrolateral flange of the postorbito-frontal and the ventral tip of the squamosal. Ornamentation occurs on the lateral surface of the jugal which forms the rim of the orbit. Two foramina are present on the anterior surface of the jugal lateral to the transversal-jugal contact.

The posterior margin of the jugal forms a thin flange extending backwards. The latter does not possess any vestige of the posteriorly directed process refered to in *Agama*. The transversum is attached to the medial surface of the jugal.

The maxillary process touches the lacrimal, but it is not applied to the latter. The ornamentation on the lateral edge of the jugal is confluent with the ornamentation occuring on the anterior edge of the ventrolateral flange of the postorbitofrontal.

C. **Cordylus**

The element resembles an inverted T in lateral view with a long, slender temporal process extending upwards to meet the postfrontal, whilst a short maxillary process is present anteriorly which is applied to the posterior process of the maxilla, completing the posteroventral orbital wall. A well developed posterior ramus is present. A medial flange, extending inwards, is syndesmotically attached to the transversum. A small dent is present on the posterior surface of the element medial to the posterior ramus.

D. **Pachydactylus**

The element is rod-shaped with a small protuberance at the posterior tip. A temporal process is absent. A thin blade-like maxillary process extends anteriorly and is applied to the posterior process of the maxilla. Because of the shape of the element, an incomplete posterior orbital wall is present.

E. **Meroles**

In lateral view the bone shows a slender temporal process of which only the upper third is applied to the posterior margin of the ventral process of the postfrontal.

The maxillary process possesses a well defined ventral flange which contacts the posterodorsal process of the maxilla. This flange forces the ventral rim of the orbit upwards resulting in a firm attachment of the anterior end of the maxillary process to the ascending flange of the maxilla. A vestige of the posterior ramus is present behind the maxillary process. A single foramen is present on the ventral edge of the ventral flange. The transversum is applied to the inner surface of the jugal. The jugal completes the posteroventral orbital wall.

F. **Mabuya**

In lateral view the jugal shows a well developed temporal process which extends markedly higher towards the postorbital and the postfrontal than in the other genera under discussion. The anterodorsal surface of the jugal is syndesmotically attached to the posteroventral margin of the ventral process of the postfrontal and the anteroventral surface of the small postorbital. The anterior tip of the squamosal barely touches the dorsal end of the temporal process.

In an articulated skull the jugal appears rodlike in lateral view because its maxillary process is obscured by the well developed ascending flange of the maxilla. The short, splintlike maxillary process is firmly attached to the dorsal surface of the posterior process of the maxilla.

The posterior margin of the orbit is formed by the postfrontal and the temporal process of the jugal whereas the ventral margin is formed by the ascending flange of the maxilla.

A nodular structure with a single foramen is present at the junction of the temporal and posterior processes, the medial surface of which is firmly attached to the ectopterygoid. A vestige of the posterior ramus is visible.

G. **Varanus**

Seen laterally the jugal is a horizontal bar on the posterodorsal surface of the maxilla. The posterior tip of the jugal curves upwards to form a short temporal process which does not contact the postfrontal. The maxillary process of the jugal is prominent. The anterior surface of the process is firmly attached to the lacrimal, whilst the anteroventral surface is laterally applied to the posterior process of the maxilla and medially to the maxillary process of the palatine. The posteroventral surface contacts the dorsal surface of the transversum. The jugal forms the ventral rim of the orbit.

10. Squamosal (Figs. 49 + 50)

Generally the squamosal has a curved, rodlike appearance and is pointed anteriorly. It forms the posterior half of the supratemporal arch, the posterolateral rim of the supratemporal fenestra and the posterodorsal margin of the incomplete infratemporal fenestra. Skinner (1968) and Leonard (1973) refer to the latter as the infratemporal fossa. The squamosal is normally in syndesmosis with the cephalic condyle of the quadrate ventrolaterally and the parietal medially. If a supratemporal is present, it invariably lies between the squamosal and the processus parietalis. The tabular, if present, is found behind and medial to the parietal wing (Romer, 1956).

The tapered anterior portion of the squamosal is applied to the posterior temporal process of the jugal or to the ventrolateral margin of the postfrontal and/or the postorbital as discussed previously. In *Chamaeleo* the element is attached to the postorbitofrontal.

A. **Agama**

The posterior hook-shaped extremity of the element possesses a small medially directed T-shaped process which is firmly attached to the lateral edge of the processes parietalis and the processus paroccipitalis of the otoccipital. The position of the T-shaped process indicates that it may represent a vestigial supratemporal, as the bone appears to be absent in the *Agama* skulls studied . This may be the reason why the squamosal of *Agama* differs from that of the remaining genera, excluding *Pachydactylus* and *Chamaeleo*.

Posteroventrally the squamosal is syndesmotically attached to the cephalic condyle of the quadrate. A small dent is present anterodorsally where the bone is firmly applied to the elongated temporal process of the jugal (as is implied in the description of the jugal).

B. **Chamaeleo**

The squamosal is shaped like an inverted Y. Posteriorly it forms a hook which extends downwards and attaches syndesmotically to the cephalic condyle of the quadrate. The anterolateral surface is excavated.

Anteriorly the bone is tapered and extends downwards to contact the temporal process of the jugal. Anterodorsally it is firmly attached to a groove in the posterovental margin of the postorbitofrontal. Ornamentation of 2 - 4 horns and crests occur on the anterodorsal surface. The posterior hook-shaped extremity extends upwards and inwards. It is in syndesmosis with the fused parietal processes, forming the prominent crest of the chamaeleons.

Because it was not possible to disarticulate the different skull elements of *Chamaeleo*, a detailed description of most elements is not always possible.

C. **Cordylus**

The bone is gently curved and tapers anteriorly. The anterior portion contacts the postfrontal posteroventrally to form the dorsal margin of the infratemporal fenestra. The posterior tip of the bone contacts the posterolateral edge of the cephalic condyle of the quadrate. A small flange extending inwards is present on the mid-third of the element, covering the posterolateral portion of the minute supratemporal fenestra. Posteromedially the squamosal contacts the lateral surface of the parietal process. The small posteriorly situated supratemporal is wedged between the squamosal and the parietal process.

D. **Pachydactylus**

The squamosal is absent.

E. **Meroles**

The posterior hook-shaped portion is well developed and curves ventrally to contact the cephalic condyle of the quadrate and the lateral surface of the parietal process. Anteriorly it tapers dorsoventrally with a shallow groove near the anterior tip into which the posteroventral margin of the postfrontal fits. The squamosal does not contact the jugal.

F. **Mabuya**

The squamosal is typically C-shaped. The posterior extremity curves downwards and contacts the head of the quadrate posterodorsally. The small, splintlike supratemporal is wedged between the medial surface of the squamosal and the lateral surface of the parietal process. A small medial flange is present posterodorsally which contacts the lateral surface of the parietal process. A shallow groove on the medial surface extends between the small medial flange and the anterior tip of the bone.

Anteriorly the dorsomedial margin of the tapered portion of the bone contacts the ventrolateral margin of the postfrontal, whilst the tip of the squamosal is in contact with the small postorbital.

G. **Varanus**

The element appears to be an enlargement of that found in *Mabuya* with only the vestigeal flange absent. The hook-shaped posterior extremity is syndesmotically attached to the cephalic condyle of the quadrate, while the medial surface of the posterior extremity is applied to the lateral surface of the supratemporal. The latter in turn is applied to the parietal process as well as the paroccipital process. The medial surface of the tapered anterior end of the squamosal is attached to the lateral surface of a posterior bar-shaped projection of the postfrontal. A short but shallow dorsomedial groove is present on the medial surface of the bone to secure a firm attachment for the postfrontal. The lateral border of the supratemporal fenestra is formed by an arch consisting of the squamosal and the postfrontal. A small C-shaped element is attached to the hook-shaped portion of the squamosal. It is part of the cephalic condyle of the quadrate.

11. Quadrate (Figs. 51 + 52)

Basically the element consists of a bar of bone comprising a mandibular condyle, a curved body and a dorsal cephalic condyle. The mandibular condyle articulates with the fused articular and prearticular of the lower jaw. The articular surface of the mandibular condyle is bisected by a shallow groove forming a lateral and a medial articular area. The cephalic condyle does not possess an articular surface. The curved body of the quadrate may be present as a rodshaped bar of bone or it may possess a small medial and a larger lateral flange. The latter is referred to as the auditory cup by Smith (1938) as quoted by Leonard (1973). The anterior part of the tympanum (=tympanic membrane) is firmly attached to the lateral rim of the auditory cup.

A. **Agama**

The cephalic condyle is bigger than the mandibular condyle and the lateral flange is much bigger than the medial flange. The former extends in an anterolateral direction while the latter extends in a anteromedial direction. The dorsal end of the lateral flange extends outward from the middle of the cephalic condyle, bisecting the latter in an anterior and a posterior "head". A deep notch is formed between the lateral flange and this posterior head. The lateral flange tapers down towards the mandibular condyle and becomes confluent with the smaller lateral portion of the mandibular condyle. The posterior tip of the quadrate ramus of the pterygoid is syndesmotically attached to the ventromedial surface of the quadrate above the medial articular facet of the mandibular condyle.

The ventral surface of the paroccipital process is attached to the medial half of the cepahlic condyle while the posterior process of the squamosal is applied to the lateral half.

B. **Chamaeleo**

The rod-shaped element possesses a small cephalic condyle and a larger mandibular condyle. Although vestiges of the lateral and medial flanges are present, the dorsal tip of the medial flange tapers inwards in a dorsomedial direction to form a process raised above the cephalic condyle. This raised process is firmly applied to the anterolateral surface of the paroccipital process forming a prominent foramen between them. The posterior process of the squamosal (=cephalic process) is syndesmotically attached to the cephalic condyle of the quadrate. The anterior surface of the element appears to be flat near the mandibular condyle, but the surface near the cephalic condyle is slightly grooved due to the vestigial flanges. The posterior surface shows a ridge which is confluent with the cephalic condyle but disappears as it extends towards the mandibular condyle. A foramen is present on the posterolateral surface of the medial flange in front of the cepahlic condyle. The mandibular condyle shows the lateral and medial articulation areas.

C. **Cordylus**

The element possesses a smaller medial and a larger lateral flange. The medial flange is confluent with the anteromedial portion of the cephalic condyle. The cephalic condyle is excavated anteroventrally. The middle section of the medial flange is concave in relation to the proximal and distal ends. The bisected mandibular condyle is prominent, with the lateral articulation surface continuous with the rod-shaped body of the element. The posterior view of the latter shows a definite ridge which is confluent with the posterior portion of the cephalic condyle. The posterior surface of the auricle-shaped lateral flange is excavated producing a prominent ridge on the rim of the flange. The proximal end of the lateral flange extends anterolaterally and tapers inwards towards the mandibular condyle. The dorsal view of the upper edge of the lateral flange is wide in comparison with the remaining ridge which makes the cepahlic condyle appear bigger than it actually is.

D. **Pachydactylus**

The rod-shaped body possesses a vestige of the medial flange with an exceptionally big auricle-shaped lateral flange. The cephalic condyle is smaller than the bisected mandibular condyle. The cephalic condyle, the curved body and the mandibular condyle appear to be vertically in line with one another in the genera used in this study. The only genus which seems to be different is *Pachydactylus*, as the curved body portion slants inwards above the mandibular condyle, placing the cepahlic condyle in a position closer to the midline of the skull.

The posterior surface of the lateral flange is extensively excavated giving the anterior surface a dome shape. The recessed area extends posteromedially underneath the curved body of the element. The lateral margin of the flange is well defined and faces anterolaterally. The dorsolateral tip of the lateral flange seems exceptionally brittle and is probably cartilaginous. A foramen is present in the ventral tip of the lateral flange directly above the lateral articulating surface of the mandibular condyle. A small tubercle is found on the medial surface of the curved body adjacent to the medial articulating surface of the mandibular condyle. Dorsally the lateral flange is confluent with the cepahlic condyle.

E. **Meroles**

The upper half of the curved body portion slants inwards towards the midline of the skull. The narrow medial flange is present and the lower tip extends anteromedially to form a small winglike process on the medial articulation facet of the mandibular condyle. The upper tip of the medial flange is confluent with the cepahlic condyle and it extends posteriorly to the back of the cephalic condyle. A prominent groove on the anterior surface of the curved body forms a distinctive border between the small medial flange and the large auricle-shaped lateral flange. The latter extends anterolaterally and tapers ventrally towards the lateral articular facet of the mandibular condyle, with the lateral rim of the auditory cup folding backwards to form a prominent ridge for the attachment of the tympanic membrane. The lateral flange is deeply recessed with a dorsomedial excavation below the cephalic condyle.

The roof of the deep recess extends anterolaterally giving the impression that the cephalic condyle consists of the entire dorsal surface of the element.

F. **Mabuya**

The rod-shaped body appears more curved backwards than in the other genera. A prominent groove on the anterior surface of the body separates the small anteromedial flange from the auricle-shaped lateral flange. A small foramen is present in the middle of the posteromedial surface of the medial flange. It extends downwards towards the mandibular condyle. A shallow notch is present between the dorsal end of the medial flange and the cephalic condyle. The large lateral flange initially extends anterolaterally, but towards the middle it curves posterolaterally giving the anterior surface a dome shape. A deep notch is present in the dorsomedial edge of the lateral flange anterolateral to the cephalic condyle. The notch makes the posterior tip of the cephalic condyle appear larger than it really is.

The lateral flange extends outwards from the notch but tapers inwards until it reaches the larger lateral articulation facet of the mandibular condyle. Posteriorly the lateral flange is deeply recessed with a small excavation ventrolaterally to the cephalic condyle. A foramen is present in this recessed area whilst a second small foramen is located above the lateral articulation facet of the mandibular condyle where the body and the lateral ridge of the larger flange meet. The notches referred to in the above give the cepahlic condyle a diamond-shaped appearance.

G. **Varanus**

The element is short and relatively broad. A ridge is present on the upper posterior surface of the body. The ridge tapers ventrally towards the lateral facet of the mandibular condyle. The narrow lateral flange extends dorsally from the side of the lateral articulating surface of the mandibular condyle towards the anterior aspect of the cepahlic condyle. A deep recessed area is present between the lateral flange and the curved body. A well developed foramen is present in the ventral half of this recessed area.

The medial articulation facet of the mandibular condyle projects anteromedially. The narrow, medial flange extends between this facet and the posterior aspect of the cephalic condyle. An excavated area is present anterior to the medial flange in the upper half of the body. A shallow dorsoventral groove is present on the anterior surface of the medial flange. This groove extends ventrally and curves backwards to end in a depression on the anterior surface of the middle articulation facet of the mandibular condyle. A number of foramina (4 - 6) occur in this groove. The prominent anterior head of the cephalic condyle tapers ventrally as an anterior ridge. A foramen is present at this point on the anterior surface.

In ventral view the mandibular condyle is sigmoid-shaped with an anteroposteriorly orientated groove bisecting the two articulation surfaces.

In dorsal view the the large articulation surface of the cephalic condyle extends anteroposteriorly. The posterior portion of the condyle is bisected by a groove, dividing it into a medial and lateral portion with a flattened posterior edge.

12. Vomeropalatine (Fig. 53)

This fused element is present in *Agama* only. In ventral view it shows an elongated anterior process which contacts the anteromedial tip of the maxilla.

The interpterygoid vacuity separates the vomeropalatines except for the anterior halves of the anterior processes which are syndesmotically attached. A short maxillary process is present on the lateral margin of the element. The lateral edge of the maxillary process is depressed bisecting the process to form an upper and a lower flange. The lower flange is confluent with and attached to the palatal shelf of the maxilla. The upper flange possesses a dorsolaterally directed prefrontal process where the vomeropalatine is attached to the prefrontal. The upper flange possesses a small anterior process which is absent in the lower flange. This small anterior process secures the attachment between the vomeropalatine and the palatal shelf of the maxilla. The internal naris lies in a deep notch between the anterior process and the maxillary process. The anterolateral border of the internal naris is formed by the anteromedial edge of the palatal shelf of the maxilla. Posteriorly the pterygoid process contacts the palatine process of the pterygoid.

In dorsal view the lateral prefrontal process extends towards the medial edge of the element as a transverse ridge. This ridge bisects the vomeropalatine in an anterior and a posterior surface which slant towards the anterior process anteriorly and the pterygoid process posteriorly. The palatal shelf of the maxilla is not a prominent part of the palate.

13. Vomer (Figs. 54 + 55)

The vomers may be present as separate elements, partially fused or complete fused. The vomer consists of a splintlike body with a lateral flange which may be vestigial as in *Chamaeleo* or well-defined as in *Cordylus*.

A. **Agama**

The element is absent.

B. **Chamaeleo**

The two blade-like elements are partially fused with the palatine processes. The anterior process is syndesmotically applied to the palatal shelves of the two maxillaries, while the dorsal aspect of the anterior process contacts the internasal process of the premaxilla. The ventral surface is depressed with a medial foramen in the anterior area of the depression. The medial portions of the palatal shelves of the maxillaries are situated well below the vomers. In dorsal view the element shows a small excavation behind the anterior process to ensure firm contact with the palatal shelf.

C. **Cordylus**

The elements are not fused. The splintlike body is present with a small toothlike anterior process which projects ventrally directly behind the middle tooth in the premaxilla. A small recessed area is present midway along the medial margin. A spiky palatine process is present at the posterior tip of the body.

In ventral view the lateral flange extends dorsolaterally with an excavated area along the posterior tip of the flange adjacent to the spiky process. This recessed area forms a syndesmotic attachment with the anterior process of the palatine. The posterior half of the flange slants inwards towards the body of the vomer. Anteriorly the margin of the flange is notched, forming a minute perforated flange adjacent to the anterior process.

In dorsal view the element shows the laterally compressed splintlike body. Dorsally the lateral flange possessess an auricle-shaped depression bordered anteriorly and posteriorly by a blade-like transverse ridge, the crista transversalis, and medially by the body of the vomer. The dorsal surface of the small flange, adjacent to the anterior process, is depressed formong a shallow excavated area lateral to the body. The ridge on the dorsal surface of the body is referred to as the crista longitudinalis.

A narrow groove occurs between the lateral margin of the body and the posterior ridge. This posterior ridge extends from the posterior palatine process towards the auricle-shaped depression.

The palatal shelf of the maxilla is vestigial and on the same level as the ventral surface of the vomer.

D. **Pachydactylus**

The elements are fused into a single structure. The narrow anterior tip is deeply notched forming two anterior processes which attach anterolaterally to the palatal shelves of the two maxillaries and anteriorly to the posterior flange of the premaxilla.

Posterolaterally a distinct, curved process is present on both sides of the element. Between these processes the posterior margin of the element is rounded. A small recessed area with a foramen on its lateral margin is present on each side of the midline.

In dorsal view a medial groove extends from the deep anterior notch to the middle of the element.

The dorsal tip of the posterolateral process is flattened where it is contacts the prefrontal laterally and the septomaxilla medially.

The palatal shelf of the maxilla is well developed and extends inwards slightly below the ventral surface of the fused vomers.

E. **Meroles**

The body of the unfused element is splintlike with a spiky anterior process. The posterior tip of the element is slightly serrated where it attaches to the anterior process of the palatine. The lateral flange extends outwards from the anterior tip and tapers inwards to reach the posterior process. Medially the flange forms a recess within which a foramen is present.

The palatal shelf of the maxilla is vestigeal and it lies sligthly below the ventral surface of the vomer.

F. **Mabuya**

In ventral view the blade-like laterally compressed body has a sharp anterior process which contacts the posterolateral flange of the premaxilla. The anterior process extends posterolaterally and is firmly attached to the anteromedial edge of the palatal flange of the maxilla. A shallow notch is present behind the contact between the vomer and the maxilla. The lateral flange extends outwards from the notch and tapers inwards towards the back of the element. The posterior palatine process is bifurcated to ensure a firm attachment to the palatine.

A number of foramina occur on the edge between the body and the lateral flange. The posterolateral portion of the latter is slightly vaulted to form the medial border of the internal naris.

In dorsal view a narrow depression is present anterolaterally behind the anterior process. A narrow groove extends from the posterior process towards the depression.

The narrow anterior part of the palatal shelf of the maxilla curves ventrally while the posterior part of the shelf extends medially to contact the palatine. This indicates that the anterior part of the palatine is connected to both the palatal shelf of the maxilla and the vomer.

G. **Varanus**

The unfused element is splintlike with various ornamentations on the dorsal surface not found in the other genera discussed here.

A pointed anterior process is present which contacts the prominent posterior flange of the premaxilla. The flat medial surface extends ventrally as a thin blade-like ridge on the anterior half of the element. A well developed groove containing 4 - 5 foramina lies immediately lateral to this ridge. A more prominent ridge forms the lateral border of this groove in the anterior third of the bone.

The lateral flange is syndesmotically attached to the palatal shelf of the maxilla. A short anteroposteriorly directed groove extends along the ventral surface of this process. A small notch on the anterior margin of the maxillary process forms the posterior border of the opening leading to the Organ of Jacobson.

The posterior half of the element extends posterolaterally. The palatine process is divided by a groove which extends anteromedially forming a ventrolateral and a dorsomedial aspect of the palatine process. The ventrolateral aspect occurs more to the front than the dorsomedial aspect making both visible in a ventral view of the vomer. A foramen is present on the ventral surface of the dorsomedial aspect of the palatine process.

In dorsal view a groove extends anteriorly on the palatine process. A deep, narrow slit is present on the medial edge of the palatine process which forms part of the posterior section of the groove mentioned above. The ridge bordering the groove laterally is dorsolaterally flattened, partly covering the groove. A foramen which opens on the ventral surface of the bone lies in this section of the groove.

Anteriorly the groove slants anterolaterally to a hook-shaped dorsal process. The tip of the hook extends dorsolaterally. A small, ridge-like process is present in the anterior section of the groove, bisecting it into a medial and a lateral portion. The ridge-like process folds dorsomedially giving the medial groove a tube-like appearance. Directly below the hook-shaped process a notch is present on the lateral edge of the element. Anterior to the hook-shaped process a shallow, excavated area is visible.

14. Palatine (Figs. 56 + 57)

The paired palatines are present, each consisting of a slender splintlike body with a lateral flange which may vary in size in the different genera. The anterior section forms the vomerine process (Leonard, 1973), the lateral edge of the lateral flange forms the maxillary process, and the posterior edge forms the pterygoid process. The lateral and posterolateral sides of the vomerine process borders the internal nares. The posterior margin of the palatine forms the anterior border of the suborbital fenestra.

A. **Agama**

The elements are absent.

B. **Chamaeleo**

The vomerine process is present as an elongated anterior extention of the body. The medial edge of the latter is serrated where the element is firmly applied to the adjacent palatine. The posterolateral edge of the process extends laterally, folds downwards and then it extends posteriorly and laterally to form a large flat lateral flange. The lateral edge forms the maxillary process where the palatine is applied to the palatine process found on the posteromedial edge of the palatal shelf of the maxillary. The posterior and posteromedial edges of the flange extends posteroventrally to form the pterygoid process where the palatine is applied to the pterygoid. The interpalatal vacuity (Leonard, 1973) separates the posterior sections of the palatines. A foramen is found near the medial edge in the middle of the lateral flange.

In dorsal view the lateral flange shows a transverse ridge bisected by a V-shaped notch to form the lateral maxillary process and medially the serrated area where the paired palatines are applied to each other. The extremity below the anteromedial edge of the lateral flange is vaulted to form a trough for the internal naris.

C. **Cordylus**

The anterior tip of the body extends anteroventrally to form the flattened medial surface of the vomerine process which is applied to the lateral palatine process of the vomer. Posteriorly the body forms a bifurcated, posterior pterygoid process. The inner margin of the body is gently concave. The lateral flange extends both anteroventrally and posterodorsally to form the flattened surface of the maxillary process which is applied posteromedially to the palatal shelf of the maxilla. A foramen is present on the flattened surface of the maxillary process of the palatine. The anterior margin of the element is deeply grooved with excavated inner walls, giving the posterior border of the internal naris a bulbuous appearance. The groove is bordered laterally by the maxillary process and medially by the vomerine process. The groove shallows towards the pterygoid process.

In dorsal view a prominent ridge is present on the anterior margin of the palatine. A small groove is present on the medial edge of the lateral flange in the anterior half of the element. A small foramen is found on the medial edge of the pterygoid process.

D. **Pachydactylus**

In ventral view the anterior portion of the rod-shaped body of the palatine curves laterally. At its anterior tip it extends anteroventrally to form a narrow, spiky vomerine process. Anterolaterally the well developed maxillary process is applied to the large posteromedial edge of the palatal shelf of the maxilla. Anteriorly the maxillary process is drawn out to a needle-like anterior extension whilst posteriorly it forms a sharp posterolateral spike. Posterior to this spike a small notch is present on the lateral margin of the lateral flange, whereas further back a small foramen is present on the posteromedial margin of the lateral flange.

A deep, well-defined notch is present at the anterior margin of the palatine, bordered medially by the vomerine process and laterally by the needle-like anterior extension of the maxillary process. The area posterior to this notch is excavated and in dorsal view forms a dome. The notch forms the posterior extremity of the internal naris.

The lateral flange is wing-shaped and its straight posterior margin forms a wide pterygoid process. Posteromedially a small recessed area is present near the edge of the pterygoid process.

E. **Meroles**

The anterior tip of the body extends anteroventrally to form a thin, blade-like vomerine process, which is dorsally excavated. Posteriorly the slender body forms a narrow pterygoid process. The lateral flange widens anterolaterally from the pterygoid process to the maxillary process. A small notch is present on the lateral margin of the maxillary process. Between the vomerine and maxillary processes a well developed anteroposteriorly directed groove is present.

In dorsal view the recessed area above the vomerine process and a small ridge bordering the recess anterolaterally is visible.

F. **Mabuya**

The structure of the element is totally different compared to the other genera. In ventral view the bone has a flat rectangular surface. A spiky vomerine process is present extending anteriorly from underneath the large flat surface. Anterolaterally the maxillary process possesses a small groove ensuring a firm contact with the palatal shelf of the maxilla. The lateral margin of the flat surface extends posteriorly to the lateral edge of the pterygoid process. The latter is formed by the serrated posterior edge of the flat surface. A short, pointed posterior process protrudes from underneath the serrated edge. The former is actually the posterior tip of the slender body of the palatine which forms part of the pterygoid process medial to the maxillary process.

In dorsal view a dorsomedial flange is present tapering posteroventrally. A small, shallow groove is present dorsolaterally on the dorsomedial flange which extends towards the vomerine process. The area between the large flat surface and the dorsomedial flange is excavated to form a tube-like groove which is continuous with the opening encircled by the vomerine and the maxillary processes. The "tube" is the internal naris.

A foramen is present on the posterior surface of the anterodorsal ridge of the "tube". The area behind the foramen is depressed to form a blade-like lateral edge of the large flat surface. The latter appears a modification of the lateral flange seen in the other genera.

G. **Varanus**

In ventral view the bone has a slender, inverted S-shaped body. Anteriorly the vomerine process borders the internal narial groove medially. The posterior portion of the body curves medially as the medial aspect of the pterygoid process. The lateral margin of this process possesses 4 - 5 foramina. Posteriorly the pterygoid process is bifurcated to ensure a firm attachment to the pterygoid.

The lateral surface of the maxillary process possesses a ventral, a medial and a dorsal ridge to ensure a firm attachment to the palatal shelf of the maxillary. The posterior margin of the maxillary process extends posterolaterally to form the anterior border of a notch in the lateral edge of the small lateral flange. The latter forms the anterior border of the suborbital fenestra. The area between the ventral and the medial ridges of the maxillary process possesses 4 - 5 foramina, while the area between the medial and dorsal ridges possess a large posteromedially slanting foramen which extends towards the dorsal surface directly behind the maxillary process.

In dorsal view a narrow ridge is present on the anterior edge of the small lateral flange. The lateral margin of the maxillary process slants ventrolaterally forming a rounded ridge medial to the latter, delimiting the dorsal border of the large foramen in the maxillary process.

15. **Septomaxilla** (Figs. 58 + 59)

The septomaxilla is very thin, membranous, and found inside the nasal cavity. It consists of a rodlike body with various projections to cover the organ of Jacobson and to form part of the nasal septum. (De Beer, 1937; Malan, 1946; Jollie, 1960).

A. **Agama** (No photograph)

Barry (1953) mentions that a cartilaginous dermal roof is absent except for a small part which is covered by a triradiate septomaxilla in *Agama hispida*. Malan (1946) found the element in *Agama atra atra* to be bisquamous of nature due to the medial migration of the anterior section of the true nasal cavity.

The dorsal surface of this extremely thin element shows a shallow excavated area near the anteroposteriorly directed ridge which flattens out anteriorly. The surface slants ventromedially to form the wall of the vestibule (Malan, 1946). The anterior section of the dorsal surface is dome-shaped with the anterior edge curving anterolaterally towards the external nostril. The dorsolateral edge of the element is syndesmotically applied to the dorsomedial surface of the prefrontal. The ventromedial edge is attached to the dorsomedial surfaces of the vomer and the palatine, as well as to the ventral edge of the cartilagenous septum nasi.

The posterior section of the ventral surface is dome-shaped due to the dorsal excavation, while the anterior part possesses a prominent recessed section which covers the organ of Jacobson (Malan, 1946). The anterior margin of the recessed area extends anterolaterally as a narrow process which becomes confluent with the ventral border of the external nostril. A prominent, transverse flange-like ridge separates the recessed area from the posterior dome-shaped section. The dorsal tip of the ridge split medially to form a widened section where the ridge becomes confluent with the dorsolateral margin of the septomaxilla.

B. **Chamaeleo**

The element is absent (Camp, 1923; Engelbrecht, 1951 and Jollie, 1960).

C. **Cordylus**

The bone has a triangular shape and is reinforced by the crista transversalis posteriorly and the crista longitudinalis medially. The anteromedial and lateral edges of the element are ridged with the medial surface membranous. The wide posterior edge slants downwards where it is applied to the crista transversalis. A dorsal process is present on the posterolateral margin of the lateral ridge. In ventral view the excavated middle surface is present, with the ridged edges slanting outwards.

D. **Pachydactylus**

The two septomaxillaries are in syndesmotic contact in the midline. Although they are not disarticulated, the elements are slightly damaged due to their fragility. (Fig. 58 D, left front and right rear). The dorsal surface of the vomer possesses cristae and it appears as if these structures also occur on the ventral surface of the septomaxilla.

In dorsal view a deep, longitudinal depressed area is present between the medial crista longitudinalis and the prefrontal process on the lateral margin.

In ventral view the anteromedial portion of the bone is thin and flat. This area is bordered medially by the body and anteriorly and laterally by a swollen ridge. Anteriorly the body forms a short anterior process and posteriorly a blade-like posterior process. A thin blade-like ridge, which resembles the crista transversalis of the vomer, extends obliquely between the body and the lateral ridge. A deep groove is present between the posterolateral and the posteromedial processes.

The lateral surface of the posterolateral process contains a groove which extends anteriorly and becomes confluent with the deep grooved area referred to previously. A very small lateral process divides the groove where it joins the deep groove.

E. **Meroles**

The two elements are unfused, but are extremely small (1mm). The dorsal surface is dome-shaped with the anterior and posterior edges bent downwards. An anterolateral process, present on the margin of the bone, contacts the medial surface of the ascending ledge of the maxilla. A smaller dorsal process lies directly behind the anterolateral process on the lateral margin of the element. A larger dorsal process is situated in line with the smaller dorsal process on the medial margin of the bone. The anterior edge of the larger dorsal process extends anteriorly with a small depressed area present between the smaller dorsal process and the anterior section of the anterolateral process. The ventral surface is vaulted and covers the organ of Jacobsen (Malan, 1946; Jollie, 1960). The anteroventral margin appears rounded with a small lateral notch.

F. **Mabuya**

The dorsal surface is dome-shaped with a narrow anterior and a wider posterior margin. Anteromedially it contacts the premaxillary process of the maxilla and posteriorly the crista transversalis of the vomer.

The anterolateral margin flares upwards and forms a smaller anterior and a larger posterior process. Medially the bone forms a vertical flange which is confluent with its anterior border and extends behind the body of the element as the posterior process (Skinner, 1968). A canal for the ramus medialis ethmoidalis nerve (Skinner, 1968) is present dorsomedially immediately lateral to the vertical flange. The canal extends anteriorly and emerges through an anteromedial foramen.

In ventral view the vaulted surface is bordered by a thin, blade-like ridge. Posterolaterally the ridge is less prominent and extends outwards as a lateral process confluent with the dorsal process mentioned above.

G. **Varanus**

In dorsal view a vertical, medial ridge extends forwards as a short anterior process. Posteriorly it forms a posteromedial process. The lateral margin of the element extends outwards from the anterior process and continues backwards parallel to the medial ridge. The anterior half of the area between the medial ridge and the lateral margin is dome-shaped with a small ascending flange in the middle of the dome. Lateral to the small ascending flange, a blade-like lateral process is found which extends backwards to form a ridge ending as the posterolateral process. Ventral to the lateral process a groove is present.

The lateral process becomes confluent with the dorsal surface of the posterolateral process. The posterior half of the dorsal surface is deeply recessed with an anterolateral excavated area below the small, medial ascending flange. The posterior margin of this recessed area undulates unevenly. The dorsal surface of the posterolateral process folds ventromedially towards the depressed area. Lateral to the medial vertical flange a prominent groove is present laterally, bordered by a ridge.

In ventral view a round anterior recessed area corresponds to the dome seen in dorsal view. A well developed ridge borders the recessed area. A wide, shallow groove emerges posteromedially from the recessed area towards the posteromedial process. The latter covers the "...blind pocket of unknown function situated behind the organ of Jacobson"... (Malan, 1946). A groove is present lateral to the ridge bordering the anterior depressed area. Anterior to the groove a flattened surface extends towards the short anterior process.

The posterolateral section of the element is vaulted corresponding to the dome-shaped area seen in dorsal view. The surface of the former is uneven with shallow grooves and flattened ridges.

16. Pterygoid (Figs. 60 + 61)

Generally the element consists of a curved, rodlike body with an anterior palatine process and a posterior process(=quadrate ramus). A small ridge is present on the dorsal surface of the posterior portion of the quadrate ramus. The position and shape of the laterally placed transverse process (=ectopterygoid process) varies considerably. In certain genera, pterygoid teeth may occur on the ventral surface of the element.

A. **Agama**

In ventral view the curved body extends anteriorly as the dorsoventrally flattened palatine process. It tapers anteromedially and has a ridge near the medial edge of the element. The ridge extends posterolaterally to form the ventral margin of the laterally compressed quadrate ramus. The posterior half of the ramus is excavated, narrowing the portion which syndesmotically contacts the quadrate. A vertical, transverse process is present midway along the lateral margin of the body. The posterolateral margin of the transverse process is widely notched and forms part of the infra-orbital fenestra. The basipterygoid process of the basisphenoid is syndesmotically attached to the medial surface of the pterygoid, in line with the transverse process.

The medial surface of the quadrate ramus is excavated and narrows anteriorly to form a shallow groove. In dorsal view 2 - 4 small foramina are seen on the surface of the palatine process. A shallow collumellar fossa is present on the anterior margin of the quadrate ramus, behind the transverse process where the epipterygoid is in syndesmosis with the pterygoid. The fossa is in line with the posterior margin of the basipterygoid process of the basisphenoid. The dorsal margin of the quadrate ramus is blade-like.

B. **Chamaeleo**

Note: The element illustrated is that of *Bradypodion* to show the general structure. The discussion pertains to the articulated pterygoid of *Chamaeleo*.

The pterygoid process of the palatine extends far back to form the anteroventral wall of the orbit, making the palatine process of the pterygoid rather short as seen in dorsal view. The ventral margin of the process extends more to the front covering the ventral surface of the pterygoid process. The medial extremity of the palatine process extends anterodorsally and is firmly applied to the medial edge of the pterygoid process. The dorsal half of the transverse process is short and is overlapped by the dorsal edge of the pterygoid process of the transversum. The remaining ventral portion of the transverse process extends laterally for a distance and then bends ventrolaterally to form a large, winglike flange of which the posterior edge extends backwards. The ventral portion of the bisected pterygoid process of the transversum is applied to the anteroventral edge of the winglike flange of the transverse process.

The laterally compressed quadrate ramus is a large, winglike process of which the ventral margin is confluent with the posterior border of the ventral flange of the transverse process. A shallow but wide groove is present on the lateral surface between the flange of the quadrate ramus and that of the transverse process. The posteroventral rim of this big "double flange" is even and rounded posterodorsally.

In ventral view a short, triangular medial process tapers downwards and posteriorly to form a small longitudinal ridge on the medial surface of the quadrate ramus. The dorsal surface of the medial process - possibly the basisphenoid process of the pterygoid - supports the basipterygoid process of the basisphenoid where the latter is in syndesmotic contact with the pterygoid. The blade-like dorsal margin of the flange of the quadrate ramus extends dorsomedially into the middle ear cavity.

C. **Cordylus**

The ventral view shows a broad anterior palatine process which tapers anteromedially with a small foramen in the middle of the body of the process. The latter extends posterolaterally to form the long lateromedially flattened quadrate ramus. The blade-like ventral edge of the latter shows a small depressed area near its contact with the quadrate.

The medial surface of the quadrate ramus is anteroposteriorly grooved. Anteromedially an uneven area indicates the position where the basipterygoid process is applied to the pterygoid.

The transverse process extends laterally for a considerable distance and ends in a narrow, anterolaterally directed process, which is applied to the pterygoid process of the transversum. The anterolateral border of the area between the palatine- and transverse processes is excavated to form the posteromedial rim of the suborbital fenestra. A foramen is present on the posterior edge of the long transverse process.

In dorsal view a very prominent collumellar fossa is present lateral to the uneven surface where the basipterygoid process attaches.

D. **Pachydactylus**

In ventral view the long rodlike quadrate ramus extends further posterolaterally than in the other genera. A deep fossa is present in the anteromedial surface of the quadrate ramus indicating the contact between the basipterygoid process and the pterygoid.

The palatine process is broad posteriorly and tapers to a medially directed tip. The transverse process extends laterally ending in a sharp, spiky tip, medial to which the bone is excavated to form the posteromedial border of the suborbital fenestra. The posterior margin of the transverse process flares ventrally to form a winglike flange with a recessed anteroventral surface.

In dorsal view a shallow groove is present on the quadrate ramus with a prominent collumellar fossa situated anteriorly. A raised area in front of the depression probably acts as a buttress for the contact. A small foramen is present on the anterior margin of the raised area, with a slight depression lateral to it.

E. **Meroles**

In ventral view a long spiky palatine process is present which tapers anterolaterally. Four prominent pterygoid teeth are present in the middle of the process. A short, sharply pointed transverse process lies near the middle of the element. Between these processes the bone is excavated to form the posteromedial and posterior margins of the suborbital fenestra. The slender, splintlike quadrate ramus is shallowly grooved along its posteromedial surface. In dorsal view a groove on the quadrate ramus terminates in the collumellar fossa. The medial edge of the fossa is raised, indicating the position where the basipterygoid process contacts the pterygoid. A small foramen with a recessed area anterior to it is present immediately in front of the fossa.

F. **Mabuya**

In ventral view the quadrate ramus is long and slender with a grooved medial surface. A small depression lies dorsolaterally on the anterior margin of the ramus. The thin, anterolateral transverse process has a small, ventral flange on its posterior edge. The area between the transverse- and palatine processes is excavated to form the posteromedial margin of the suborbital fenestra. The palatine process is anteriorly bifurcated and the medial prong shows definite serrations. The lateral prong is spiky and extends further forward than the medial prong. Posteroventrally the palatine process contributes to the bony palate and it bears 1 - 2 pterygoid teeth.

The dorsal border of the quadrate ramus is blade-like and it terminates at the collumellar fossa. Anteromedial to the fossa a raised area indicates the position of the articulating facet for the basipterygoid process. A small depression lies lateral to the raised area with a foramen at its base.

G. **Varanus**

In ventral view the long rodlike quadrate ramus has a sharp ventral edge. Posteriorly the ventral margin is depressed and a shallow groove is present on the medial surface of the element. Anteriorly the palatine process is bifurcated with a longer medial prong. A small anterior process lies within the excavated anterior margin of the bone between the palatine- and transverse processes. The well developed transverse process is covered ventrally and dorsally by the bisected pterygoid process of the transversum. The small anterior process contacts the medial surface of the transversum where the perygoid process bifurcates. The articulation surface of the basipterygoid process lies on the medial surface of the pterygoid. The dorsally situated columellar fossa, lateral to articulation surface, has a raised medial border forming a small ridge making the fossa appear deeper than it actually is. A recessed area posterior to the small anterior process contains 2-3 small foramina. A small dorsal process lies on the posterior margin of the transverse process. Dorsally the palatine process is grooved between its lateral and medial prongs.

17. Transversum (=ectopterygoid) (Figs. 62 + 63)

The transversum forms the bony bridge between the posteromedial surface of the posterior process of the maxillary and the transverse process of the pterygoid. The element essentially consists of a short, thick body with a laterally and a medially directed process.

The lateral process (=maxillary process) of the transversum is often present in the genera discussed as three projections; one posteroventrally; one anteroventrally or anteromedially; and the third posterodorsally.

The ventral process contacts the transverse process of the pterygoid. Its ventral tip is shaped like a tubercle.

A. **Agama**

In ventral view the body exhibit an elongated medial process which is ventrally grooved. Lateral to this process a posteroventral process extends a considerable distance from the body to firmly contact the pterygoid. The lateral maxillary process has three prongs. A small posterodorsal projection contributes to the posterolateral floor of the orbit. A small anteroventral projection borders the posterolateral margin of the suborbital fenestra, and a large posteroventral projection.

The tip of the posteroventral process is broad to support the medial surface of the posterior process of the maxilla and the maxillary process of the jugal. The three projections are in syndesmosis with the medial surface of the posterior process of the maxilla. A deep, wide notch is present between the large posteroventral projection and the posteroventral process.

B. **Chamaeleo**

In ventral view the elongated medial process overlaps the transverse process of the pterygoid dorsally. A ventral process lies lateral to the medial process and ensures a firm attachment between the former and the anterolateral margin of the large winglike flange of the transverse process of the pterygoid.

The lateral maxillary process is also present with three definite prongs - one anteroventrally to support the medial surface of the jugal and the posteromedial surface of the posterior process of the maxilla; one posteroventrally to support the medial surface of the posteroventral margin of the jugal, and a much shorter posterodorsal prong which contributes to the posteroventral wall of the orbit. The posterodorsal margin of the surface connecting the posterodorsal and the posteroventral processes, contains a small recessed area near the latter indicating a confluency between these two processes. The ventral margin of the body, between the long, ventral process and the short anteroventral projection is not recessed as in *Agama*, but forms the dorsal border of a passage between the ventral process and the posteromedial edge of the maxilla.

C. **Cordylus**

In ventral view the body has a concave anteromedial margin with a long posteromedial process and a long anterolateral process. The long posteromedial process covers the transverse process of the pterygoid dorsally whilst a short ventral process contacts the lateral surface of the transverse process. The long anterolateral process is confluent with the posterior tip of the palatal shelf of the maxilla. The lateral surface of the long anterolateral process is grooved for firm contact to the posteromedial surface of the posterior process of the maxilla. The posterior tip of this lateral surface extends posteromedially towards the short ventral process which supports the medial surface of the jugal. A shallow depression occurs in the ventral surface of the body between the short ventral process and the posterior tip of the lateral surface.

D. **Pachydactylus**

In ventral view the body is very small with a small medial process which overlaps the transverse process of the pterygoid dorsally. Its ventral surface is grooved and it lies at the level of the body of the element. The reason why the body of the element seems to be so small is because the transverse process of the pterygoid extends a considerable distance laterally. The ventral process is less prominent than the medial process and it extends in a ventromedial direction to underlie the transverse process of the pterygoid ventrally.

The maxillary process of the transversum has a long anteroventral projection which contacts the dorsomedial surface of the posterior process of the maxilla.

E. **Meroles**

In ventral view the body has a long medial process which overlies the dorsal surface of the transverse process of the pterygoid. A very small ventral process extends ventromedially and contacts ventrolateral surface of the transverse process. The posterior margin between the medial and the small ventral processes is recessed and contacts the anterior margin of the transverse process of the pterygoid. The maxillary process is present as an elongated anteroventral projection. The lateral surface of the maxillary process is grooved to ensure firm attachment to the dorsomedial surface of the posterior process of the maxilla.

F. **Mabuya**

In dorsal view a very small medial process with a deep, recessed area in its posterior surface is visible. The anterior margin of the transverse process of the pterygoid fits into this recess. The ventral process is a winglike flange expanding posteroventrally to underlie the transverse process. The flange makes the ventral process appear much larger than the medial process. The maxillary process is very small and it extends anteriorly. It is firmly applied to the posteromedial surface of the posterior process of the maxilla. According to Skinner (1968) the element consists of a bifurcated medial and an anterior process. However, it seems rather that the bifurcated medial process of Skinner (1968) are in fact two separate processes if the structure of the element in the other genera is considered.

G. **Varanus**

In ventral view a broad medial process with its posterior edge tapering anteromedially overlies the transverse process of the pterygoid. The posterior margin of the medial process has a small medial projection with a deep, narrow slit between the process and the projection. The ventral process, smaller than the medial process, extends ventromedially to underlie the transverse process of the pterygoid. A deep recess is present in the posterior surface between the medial and ventral processes ensuring a firm contact between these processes and the transverse process of the pterygoid. The maxillary process has a long anteroventral projection. The lateral surface of the projection possesses a deep recess which bifurcates the anterior tip of the projection to overlie and underlie the posterior process of the maxilla. The posterolateral surface of the maxillary process has 3 - 4 small foramina with an excavated area dorsolaterally to the surface. The depressed dorsolateral surface of the upper ledge of the bifurcated anterior tip of the anterior projection is in syndesmosis with the posteroventral margin of the maxillary process of the palatine. The dorsolateral surface of the maxillary process supports the jugal. A shallow, wide groove is present between the ventral process and the maxillary process.

In dorsal view a convexed posterolateral margin of the body flares upwards as part of the ventrolateral floor of the orbit.

18. Epipterygoid (Figs. 64 + 65)

Generally the element is present in the different genera as a long, rodlike structure varying in length. Ventrally it fits into the columellar fossa on the dorsal surface of the pterygoid and dorsally it articulates with different structures in the different genera. According to Engelbrecht (1951) the element is absent in *Bradypodion pumulis* and Romer (1956) found it to be absent in Chamaeleons and Amphisbaenids, and reduced in Agamids and Masosaurs. The structure of this element is such that it cannot be profitably utilised for purposes of identification. Consequently the following description is presented for the sake of completeness only.

A. **Agama**

Dorsally the bone curves backwards and contacts the bulbous anteroventral portion of the prootic. The ventral tip is embedded in the columellar fossa of the pterygoid.

B. **Chamaeleo**

Engelbrecht (1951) indicated that the absence of an epipterygoid is a constant characteristic throughout the Chamaeleontidae, but note that Brock (1941) detected a rudiment of what seemded to be an epipterygoid in the embryo of *Microsauria ventralis*. Camp (1923) states that the element is absent in chamaeleons. He also refers to Dollo (1884) who apparently discovered the bone in *Chamaeleo vulgaris*, but Siebenrock (1892) concluded that Dollo mistook the orbitosphenoid for the epipterygoid. Skinner (1968) mentions the orbitosphenoid as an element found in the membrane separating the orbits. According to Camp (1923) the orbitosphenoid can be traced within the membrane which closes the brain-case in front of the paroccipital. The position in which the element was found in *Chamaeleo dilepis* corresponds with that mentioned by Camp (1923), indicating that the element present must be the orbitosphenoid and not the epipterygoid. A similar bony element was seen in two *Bradypodion pumulis* skulls used as reference. The broad ventral tip of the element contacts the dorsolateral edge of the anterodorsal process of the basisphenoid, which may be the reason why a columellar fossa is not present on the pterygoid. The element is not rodshaped as in the other genera, as its ventral extremity is laterally compressed. The dorsal portion is rod-shaped and curves backwards. The apex of the bone forms a rounded head which is secured by means of ligaments to the anteroventral margin of the prootic.

C. **Cordylus**

The rod-shaped element extends posterodorsally from the columellar fossa in the pterygoid to a ligamentous attachment to the anterodorsal surface of the prootic (=taenia tecti marginalis, Van Pletzen, 1946). The dorsal epiphysis of the epipterygoid reaches the ventral surface of the parietal where it is syndesmotically applied to the processus descendens anterior. (Skinner, 1968)

D. **Pachydactylus**

The rod-shaped epipterygoid extends posterodorsally from the columellar fossa to the taenia tecti marginalis to which it is applied by a ligament. The pterygoids are situated in a more lateral position than in the other genera so that the epipterygoid also slants inwards. The dorsal epiphysis is connected to the processus descendens anterior of the parietal by a ligament.

E. **Meroles**

The element extends posterodorsally from the columellar fossa to a ridge on the ventral surface of the parietal where it attaches by a ligament. The element does not contact the prootic. Skinner (1968) refers to the ".. thickened lateral margin of the parietal" as the crista cranii parietalis, while Leonard (1973), on the other hand, refers to the ridge on the ventral surface of the parietal as the crista cranii parietalis with its ventrally directed processus descenens anterior. Although Skinner and Leonard seem to descibe something different, they both refer to the same structure.

F. **Mabuya**

The element extends posterodorsally from the columellar fossa to the processus descendens anterior of the parietal and the upper tip of the taenia tecti marginalis to which it is applied by a ligament. The processus descendens anterior is very small and should be seen as the crista cranii parietalis, but for identification purposes the former is applicable.

G. **Varanus**

The element extends posterodorsally from the columellar fossa to the upper tip of the taenia tecti marginalis as well as the crista cranii parietalis.

19. Basisphenoid (Fig. 66)

A. **Agama**

In dorsal view the bone has a rectangular surface with two small excavated areas, separated by a small longitudinal medial ridge. The anterolateral margin is raised to form a anterodorsal process which supports the anteroventral process of the prootic. A small anterolaterally directed foramen is present in the medial surface of the anterodorsal process. The latter tapers downwards posteriorly and becomes confluent with the posterolateral margin of the element. The posterior margin is a straight transverse line with two laterally situated articulation areas in posterior view. A small posteriorly directed process is present below the posterolateral margin of each articulation area, supporting the contact between the basisphenoid and the basioccipital. The lateral margin of each process extends anteriorly as a small, winglike flange which becomes confluent with the lateral margin of the basipterygoid process. A foramen is found on the dorsal surface of the proximal basipterygoid process. The lateral surface below the anterodorsal process is excavated and an anteromedially directed foramen lies within the posterior portion of the excavated area. The anterior margin (=crista sellaris, Skinner, 1968) of the dorsal surface is convex posteriorly with a narrow recessed area (fossa hypophyseos) directly below the small, longitudinal medial ridge. A small anterior process which forms the posterior part of the parasphenoidal rostrum, occurs below the fossa hypophyseos. The margin lateral to this process extends anterolaterally as the anterior border of the basipterygoid process. The ventral surface shows a medial recessed area with the basipterygoid processes extending ventrolaterally and obliquely forward.

B. **Chamaeleo**

The element is present as part of the "fused braincase" and will be discussed later.

C. **Cordylus**

The same as in B.

D. **Pachydactylus**

The same as in B.

E. **Meroles**

The same as in B.

F. **Mabuya**

In dorsal view the bone has a rectangular, recessed surface, bordered laterally by a longitudinal ridge. The anterolateral tip of each ridge forms an anterodorsal process. Posterolaterally the ridge is in syndesmotic contact with the medially directed anteroventral process of the prootic. A small anterolaterally directed foramen is present on the medial surface of the ridge directly behind the anterodorsal process. The posterior margin of the bone has two laterally placed articulating areas lacking the connecting transverse line as seen in *Agama*. A blade-like posteriorly directed margin is present below the articulating areas. The middle section extends further backwards giving it a distinctive W-shape. The lateral extremity of the margin forms a spiky posterior process on both sides of the element. These structures ensure a firm attachment to the anterior margin of the basioccipital. The concave crista sellaris is not as prominent as in *Agama*. The lateral surface of the anterodorsal process is excavated to form a small fossa.

The ventral margin of the anterodorsal process extends downwards to form a notch and then continues anterolaterally as the anterior margin of the basipterygoid process. The descending ventral margins of the anterodorsal processes form the lateral walls of the fossa hypophyseos. Two foramina are present in the medial surface of each lateral wall, with a third foramen near the base of each wall. A small anteromedial process, which represents the posterior portion of the parasphenoidal rostrum, extends from the middle of the anterior margin below the fossa hypophyseos. Distally the basipterygoid process is spatulate with a slightly eroded dorsal surface where it articulates with the medial surface of the quadrate ramus of the pterygoid.

The lateral surface of the basisphenoid below the anterodorsal process contains an anteroposterior groove, which is ventrally confluent with the foramina in the fossa hypophyseos. The dorsal border of the groove forms a small blade-like ridge. The ventral border of the groove is confluent with the posterior margin of the basipterygoid process. Posteroventrally the surface of the basisphenoid is slightly excavated with a small foramen on either side of the midline. The posterior margin is W-shaped where the bone contacts the basioccipital. The parasphenoidal rostrum forms a small anteroventral ridge in the midline.

G. **Varanus**

The bone has an almost squarely excavated dorsal surface with 2 - 3 very small foramina on the mid-line. A small dorsal tubercle occurs on the mid-line near the posterior edge of the depressed surface. The lateral margins of the depressed surface are wide and raised to form prominent lateral ridges. A large anteroventrally directed foramen is present in the medial surface of both lateral ridges in close proximity to the concave crista sellaris. The dorsal surface of the lateral ridge directly behind the anterodorsal process contains a small longitudinal groove for firm attachment to the ventral edge of the prootic. Posterolaterally the bone forms a winglike flange which contacts the anterolateral margin of the basioccipital. The area of contact is slightly eroded to ensure a firm attachment. The prominent basipterygoid process extends ventrolaterally from the anteroventral margin of the basisphenoid. Proximally, its anterior border is confluent with the notch below the anteroventral process of the prootic. Its posterior border is confluent with the ventral margin of the posterolateral flange. The dorsolateral surface of the basipterygoid process is perforated and slightly excavated where it forms a syndesmotic contact with the quadrate ramus of the pterygoid. The lateral surface of the basisphenoid, is pierced by a large, medially directed foramen in front of the posterolateral process. The dorsal border of the foramen is a winglike ridge which is part of the lateral margin of the depressed dorsal surface.

In anterior view the fossa hypophyseos, below the crista sellaris, is well developed. The middle section is deeply excavated and the lateral walls of the excavation are in line with the large foramen seen in lateral view. The lateral margins of the excavation extend anteroventrally as winglike ridges on the dorsal surface of the base of the parasphenoidal rostrum. The surfaces lateral to these winglike ridges are excavated towards the back to form deep pockets. Lateral to each pocket a foramen is found with a second foramen present directly above first. This first foramen is confluent with the large, medially directed foramen seen in lateral view. The second foramen is confluent with the large anteroventrally directed foramen seen in dorsal view. The anterior surface of the parasphenoidal rostrum forms two posteriorly converging articulation surfaces dissected by a narrow trench. A small dorsally directed projection is visible within this trench.

20. Fused brain-case (Figs. 67 - 70)

Although the different cranial elements of the skulls used in this invstigation were disarticulated, it was not possible to do so with the skulls of *Chamaleo, Cordylus, Pachydactylus* and *Meroles* without breaking them, especially the elements of the brain-case. In *Chamaeleo* the suture lines between the elements can be clearly seen, but due to the numerous interdigitations, the respective bones cannot be disarticulated. The elements of the fused braincase or "fused unit" are the basisphenoid, basioccipital, supraoccipital, exoccipital, opisthotic and prootic. The structure of the elements of the fused braincase will not be described individually, but only the general structure of the fused unit itself.

A. **Agama**

The elements of the braincase are easily disarticulated except for the otoccipital and they are individually described.

B. **Chamaeleo**

In ventral view the fused unit shows distinctive suture lines. The basisphenoid is clearly visible with a deep recess in the middle of the element. The lateral walls of the recess extend anterolaterally to form the two basipterygoid processes. The anterodorsaly directed parasphenoidal rostrum is present between the two basipterygoid processes on the anterior edge of the basisphenoid. The blade-like lateral margins of the basisphenoid extends posteriorly and become confluent with the anterior surface of the spheno-occipital tubercle. The transverse suture between the basisphenoid and the basioccipital is ridge-like. The lateral surface of the element is excavated and bordered ventrally by the blade-like edge mentioned above. The dorsal margin of the lateral excavation contacts the anteroventral margin of the prootic. An anteromedially directed foramen lies on the posterior edge of the lateral excavation. The basioccipital is small and triangular. The apex forms a portion of the tripartite occipital condyle. Directly behind the suture with the basisphenoid, the middle section of the basioccipital is slightly recessed. The lateral portion of the recess extends outwards to the spheno-occipital tubercle antero- laterally, and the occipital condyle posteromedially.

In posterior view the otoccipital possesses a short, horizontally orientated paroccipital process. The proximal portion of the paroccipital process forms a dorsomedially extended process which is syndesmotically applied to the posteroventral margin of the supra-occipital cup (vide supraoccipital). This cup encloses the membranous portion of the inner ear. The medial border of the otoccipital extends ventrally from the inner margin of the supra-occipital cup as the lateral rim of the foramen magnum. Ventromedially the otoccipital contributes to the occipital condyle. Three foramina are present on the posterolateral surface below the proximal portion of the paroccipital process. The middle foramen is the larger. Posterodorsal to the spheno-occipital tubercle, a small foramen extends anteromedially. The unpaired supra-occipital forms dorsal rim of the foramen magnum. The ventrolaterally extending supra-occipital cups meet the otoccipitals laterally. The tip of the processus anterior tecti extends anterodorsally to meet the saggital crest of the parietal (Rieppel, 1981). The dorsal surface of the processus anterior tecti is bifurcated ensuring a firm attachment to the saggital crest of the parietal. The anterior portion of the supra-occipital cup contacts the anterodorsal edge of the prootic completing the otic-capsule which encloses the inner ear. A small, anterodorsally directed rodlike process lies on the anterior margin of the supraoccipital cup ventrolateral to the processus anterior tecti.

The prootic has a large laterally placed fenestra ovalis, bordered posteriorly by the otoccipital and anteriorly by the prootic. A small foramen, directly anterior to the large oval window, is situated in a groove ventrally bordered by the crista prootica on the anterolateral margin of the prootic. The crista sellaris of the basisphenoid is visible in anterodorsal view. A foramen lies near the lateral margin directly behind the crista sellaris. Anteroventral to the crista sellaris the floor of the fossa hypophyseos is perforated by two large juxtapositioned foramina, lateral to which a smaller foramen occurs. A tiny foramen lies anteromedial to the larger foramina.

C. **Cordylus**

No sutures are visible between the different elements. In ventral view the unit shows an even surface extending posteriorly from the base of the parasphenoidal rostrum to the occipital condyle. The slender basipterygoid process extends anterolaterally and slightly ventrally. The lateral margin of the basipterygoid process extends posteromedially towards the body of the basisphenoid and continues posterolaterally to the spheno-occipital tubercle. Posterolateral to this tubercle the ventral surface is deeply excavated, with a large foramen present in the roof of the excavation. The large fenestra ovalis lies lateral to this foramen, from which it is separated by a rodlike bridge of bone. The posterior edge of the spheno-occipital tubercle extends downwards to a notch in the lateral margin of the occipital condyle. The lateral edge of the notch extends posterolaterally towards the tip of the paroccipital process. Three small foramina, forming a vertical line, occur in the notch, lateral to which a large slitlike foramen is present. The dorsal margin of the notch forms the ventromedial border of the foramen magnum. An anteromedially directed foramen is present laterally on the basisphenoid, at the base of the basipterygoid process. The crista prootica is a thin blade-like ridge forming the anterolateral border of a deep groove which extends posterolaterally from a small recess at the base of the basipterygoid process, passes the oval window dorsolaterally and terminates as a wide shallow excavation on the ventral surface of the paroccipital process. A small foramen is present in the groove, slightly anterior to the oval window. The anterior portion of the groove extends anterolaterally from the small recess and becomes confluent with a well developed notch on the dorsal edge of the basipterygoid process, visible in lateral view.

In lateral view the braincase shows the above mentioned notch as well as the prominent incisura prootica. The anterior superior process of the prootic extends upwards, its lateral surface becoming confluent with the anterior surface of the paroccipital process. Anteromedially the anterior superior process is slightly recessed, while the posterior portion of the medial surface extends inwards becoming confluent with the supra-occipital cup. A narrow notch, flanked by the supraoccipital cups, forms the roof of the brain, but widens ventrally to enclose the larger part of the brain. The medial surface of the otoccipital, which forms the lateral wall of the braincase, possesses two large foramina leading into the inner ear cavity. The supraoccipital spine (= proc. ascendens) is present on the dorsal surface of the supraoccipital and it extends posterodorsally terminating in a small bifurcated tip. In anterior view, the fossa hypophyseos is bordered laterally by the anterior inferior process, dorsally by the crista sellaris and ventrally by the anterior margin of the basisphenoid. The anterior margin of the basisphenoid possesses a small, narrow notch bordered ventrally by a small, short, rodlike process. This rodlike process is confluent with the posterior portion of the parasphenoidal rostrum. The fossa hypophyseos is perforated by six foramina - four foramina juxtapositioned directly below the crista sellaris, and the two remaining foramina are situated on the ventral edge of the fossa hypophyseos on either side of the parasphenoidal rostrum.

In posterior view the rim of the foramen magnum evinces no suture lines with other elements. The occipital condyle is solid, without the lines indicating a tripartite occipital condyle. The middle portion of the posterior surface of the occipital condyle is slightly recessed.

D. **Pachydactylus**

Suture lines between the different elements of the braincase are absent. In ventral view the anteriorly positioned basisphenoid has a deep recess in the middle of the element. The posterior wall of the recess rises to form a ventrally directed dome-shaped central part of the basioccipital in the area between the two spheno-occipital tubercles. The posterior margin of the "dome" curves posteroventrally towards the occipital condyle. The recess extends anterolaterally into the proximal part of the long slender basipterygoid process as a shallow groove . The groove terminates in a wide, flattened tip which is syndesmotically applied to the pterygoid.

A short, rodlike process, forming the posterior section of the parasphenoidal rostrum, is present on the anterior edge of the basisphenoid. The lateral edge of the basipterygoid process extends posteriorly along the lateral margin of the basisphenoid to reach the anterior surface of the very prominent spheno-occipital tubercle. The posterolateral surface of the spheno-occipital tubercle is very deeply recessed and lacks any foramina. The posterior edge of the tubercle forms a ridge which slants upwards towards the lateral tip of the occipital condyle. In posterior view the condyle has a wide V-shape with a deep notch in the middle of its wide posterior edge. A very prominent, wing-shaped crista prootica is present. It extends posteriorly from the middle of the dorsolateral margin of the basipterygoid process, curves laterally and becomes confluent with the ventral tip of the anterior superior process of the prootic, and then it slants posteromedially towards the proximal part of the paroccipital process. The crista prootica forms the lateral rim of a groove which extends from a deep recess at the base of the basipterygoid process towards the anteroventral surface of the paroccipital process. The oval window is positioned posterolaterally directly above the deep excavation in the spheno-occipital tubercle. The anterior margin of the oval window forms a laterally directed protuberance, anterodorsal to which a groove, containing a foramen, is present. The foramen is situated anteromedially on the antero-superior process. The anteroventral margin of the protuberance has a narrow groove which extends anteromedially towards a foramen in the base of the basipterygoid process. The ventral margin of the paroccipital process forms a rounded ridge extending from the narrow distal tip of the process towards the ventral rim of the oval window. A small, round excavation is present proximally on paroccipital process posterior to the ridge.

In dorsal view a rather small supraoccipital with a vestigal supraoccipital spine is visible. The posterior edge of the supraoccipital is smooth and confluent with the rim of the foramen magnum. The paroccipital processes extend laterally and are in line with the posterior edge of the supraoccipital. The crista sellaris forms a thin, but prominent, V-shaped ridge which extends posterolaterally on the anteromedial surface of the anterior superior process. A small excavation is present between the ridge and the middle of the anteromedial surface. The incisura prootica is less prominent than in the other material, but extends inwards to become confluent with a foramen in the anterolateral portion of the ridge mentioned above. The anterior inferior process extends laterally to form the anterior portion of the wing-shaped crista prootica. The fossa hypophyseos is small with an anterolaterally directed foramen in its lateral wall. A small foramen is present below the crista sellaris and on the lateral edge of the fossa hypophyseos. A foramen, partially concealed by the anterior edge of the laterally directed anterior inferior process, extends posteromedially towards the fossa hypophyseos, does not enter the fossa directly, but becomes confluent with the foramen present within the fossa. A ventrolaterally directed foramen is present on the medial surface of the anterior superior process below the fusion of the supraoccipital cup and the dorsal edge of the anterior superior process. The ventral margin of the bulbous posterior section of the anterior superior process is perforated by three juxtapositioned foramina which extends laterally into the inner ear cavity.

In posterior view a collar-like flange extends ventrolaterally from the vestigal supra-occipital spine towards the base of the paroccipital process. The posterior margin of the supraoccipital extends posteroventrally as the thin, blade-like upper rim of the foramen magnum. The posterior surface of the collar-like flange has two to three small excavations for the attachment of the dorsal neck muscles.

In lateral view the anterior edge of the anterior superior process is vertical. The ventral tip of this process extends anterolaterally to form the anterolateral portion of the wing-shaped crista prootica. The dorsal tip of this process extends upwards to form a short process which is syndesmotically applied to the processus descendens anterioris of the parietal. The dorsal epiphysis of the epipterygoid is in syndesmosis with the processus descendens anterioris of the parietal and the dorsal tip of the anterior superior process of the prootic. The posterior margin of the dorsal tip of the anterior superior process slants posteroventrally towards a small process, which possibly indicates the fusion between the prootic and the supra-occipital cup. The margin posterior to this juncture extends posteromedially as the anterior edge of the supraoccipital.

E. **Meroles**

Suture lines are clearly visible, but individual elements could nnot be disarticulated. In ventral view the smooth, flat surface of the basisphenoid is visible with a small recess in the middle of the anterior section of the element. Short stubby basipterygoid processes are present, terminating in large, distal extremities firmly attached to the pterygoids. The lateral edge of the basipterygoid process extends backwards, but slants towards the prootic and not towards the spheno-occipital tubercle as in the other genera discussed here. The two spheno-occipital tubercles indicate the fusion line between the basisphenoid and the basioccipital. The basioccipital extends from this point towards the tripartite occipital condyle and forms a vaulted posterior neurocranial floor. A ridge, extending from the posterolateral edge of the spheno-occipital tubercle, extends posteromedially towards the lateral edge of the occipital condyle. This lateral edge forms the lateral margin of a recess found directly behind the spheno-occipital tubercle. Two small foramina occur lateral to the upper margin of the occipital condyle and medial to the bulbous portion of the otoccipital. The bulbous part of the otoccipital extends dorsolaterally from the ridge mentioned above to the ventral surface of the proximal portion of the paroccipital process. The latter is very short and a lateral extension is in line with the occipital condyle. A deep recess on the upper lateral edge of the spheno-occipital tubercle is perforated by two foramina. The upper foramen extends medially into the inner ear cavity, while the lower one proceeds medially into the neurocranial cavity. The lower foramen is visible on the ventral margin of the bulbous medial surface of the anterior superior process of the prootic. The oval window is present directly above the deep recess mentioned above.

The lateral surface of the prootic slants dorsolaterally towards a narrow crista prootica forming a wing-like flange. A shallow groove extends posteriorly from the base of the basipterygoid process and terminates in a wide flattened area on the ventral surface of the paroccipital process. The groove is laterally bordered by the crista prootica. The flattened ventral surface of the paroccipital process extends posteriorly towards a recess in the anterolateral surface of the bulbous portion of the otoccipital mentioned above. A small anteromedially directed foramen is present on the ventrolateral edge of the basisphenoid close to the base of the basipterygoid process.

In dorsal view the large supraoccipital has a median, longitudinal ridge treminating anteriorly in a vestigial supra-occipital spine. The posterior margin of the supra-occipital forms the dorsal rim of the foramen magnum and possesses a wide notch of which the lateral borders extend posteroventrally towards the base of the paroccipital processes. The anterior margin of the suproccipital extends anterodorsally and becomes confluent with the dorsal edge of the anterior superior process of the prootic. The anterior edge of the latter extends downwards and slightly backwards to the incisura prootica. The ventral margin of the latter curves anteromedially and forms a small anterior inferior process which borders the fossa hypophyseos dorsolaterally. The crista sellaris borders the fossa dorsally and the anterior edge of the basisphenoid ventrally. The ventral portion of the fossa is perforated by four juxtapositioned foramina while two laterally placed foramina are present dorsally. Both the latter foramina are visible on the anterior margin of the neurocranial floor.

21. Basioccipital (Fig. 71)

This element forms the posterior floor of the cranium and contributes to the tripartite occipital condyle. It is present in *Agama*, *Mabuya* and *Varanus* as an individual element with distinctive suture lines where it contacts adjacent bones.

A. **Agama**

In dorsal view an excavated central portion with raised lateral edges is visible. The edges extend backwards to form a raised posterior wall terminating in the central portion of the tripartite occipital condyle and the ventral rim of the foramen magnum. The straight anterior edge contacts the posterior margin of the basisphenoid to complete the cranial floor. Near the middle of the anterior edge two small anteriorly directed processes occur, with a small notch lateral to each process. The latter presumably strengthens the contact between the basioccipital and the basisphenoid.

In ventral view the prominent middle portion of the occipital condyle is evident. The lateral edge of the condylar process extends anterolaterally to form the margin of the excavated area seen dorsally. This ridge extends ventrally to form a prominent projection, the spheno-occipital tubercle. A small foramen is present on the medial surface of the tubercle and another on the midline anterior to the condylar process. The anterior surface of the tubercle slants anterodorsally towards the anterior margin of the element.

B. **Chamaeleo**

The element is present as part of the "fused brain-case".

C. **Cordylus**

The same as for B.

D. **Pachydactylus**

The same as for B.

E. **Meroles**

The same as for B.

F. **Mabuya**

In dorsal view an excavated central portion resembles that founnd in *Agama*. A small rounded notch is present in the middle of the straight anterior edge. The spheno-occipital tubercle is prominent and forms part of the lateral margin of the element. Anterior to the tubercle a shallow notch is visible. The anteromedial margin of this notch appears to be slightly thickened and it supports the posteroventral tip of the otoccipital. A small, shallow groove lies on the dorsal surface of the tubercle extending from the excavated central area towards the lateral tip of the spheno-occipital tubercle. The posterior margin of the tubercle extends inwards and contributes to the lateral edge of the condylar process.

In ventral view the thin bulbous central area with the distinctive notch in the anterior edge is clear. The notch in the lateral margin, anterior to the ventrolaterally directed spheno-occipital tubercle, slants posterolaterally to form a small pointed posterodorsally directed process. A vestige of a small foramen is present in the ventromedial surface of the tubercle.

G. **Varanus**

In dorsal view the triangular-shaped element has an excavated central area, laterally bounded by several foramina. A small recess is present dorsomedially on the occipital condyle. The anterior margin of the element is straight, but seen in an anterior view appears medially depressed with its lateral margins extending dorsally. The anterior edge is thickened dorsoventrally to ensure a firm contact with the basisphenoid. A shallow anteromedially directed groove is present on the dorsolateral edge of the large excavated area in the anterior half of the element.

In ventral view an amphiplatyan central area with a slight median ridge is present. The central area is perforated by a number of foramina. The straight anterior edge possesses a wide, but shallow notch medially and a deep, narrow notch laterally. This notch lies between the spheno-occipital tubercle and the straight anterior edge. The spheno-occipital tubercle extends laterally with a shallow groove separating it from the thicker anterior edge. A small posteriorly directed foramen is present in this groove. The posterior edge of the tubercle slants posteromedially to form a narrow posterior half of the element. The lateral wall of the posterior half is serrated to firmly attach to the dorsolateral edge of the otoccipital. The surface of the anterolateral edge of the tubercle possesses 6 - 8 small shallow grooves. A small ventrolaterally directed flange is present on the posterolateral edge of the tubercle. The posterior margin of the tubercle extends medially to separate the wide anterior half from the narrower posterior half. The lateral edge continues backwards to reach the basioccipital portion of the occipital condyle. A transverse groove separates the condyle form the rest of the basioccipital. The posterior surface of the basioccipital portionof the condyle is slightly recessed.

The criteria mentioned in 20, the fused braincase, can also be applied to identify the basioccipital in those genera where complete disarticulation of the elements occur.

22. Supraoccipital (Fig. 72)

This unpaired element forms the roof of the cranium behind the prootic (Leonard, 1973). The posterolateral edge of the supraoccipital is syndesmotically applied to the dorsomedial surface of the paroccipital process of the otoccipital and it contacts the posterior margin of the parietal. The posterior margin of the supra-occipital forms the dorsal rim of the foramen magnum. The dorsal surface is arched with an anteromedial processus anterior tecti (= processus ascendens of Jollie, 1960; supra-occipital crest of Du Plessis, 1944)) or the vestige thereof.

A. **Agama**

In dorsal view the arched surface has a small anteroposterior ridge (processus anterior tecti) on the midline. The surface lateral to the proc. anterior tecti is slightly recessed and extends outwards to form the lateral margin of the element. Anteriorly this edge forms a small anterior process which bends downwards. The latter is syndesmotically applied to the anterior half of the ventral surface of the parietal process. Laterally the element extends outwards to form a prominent posterolateral margin which contacts the anteromedial edge of a dorsally directed process on the dorsal surface of the otoccipital. The tip of the proc. anterior tecti is recessed for the insertion of a ligament which attaches the supra-occipital to the parietal. The anterior margin on both sides of the proc. anterior tecti curve gradually, backwards. A very small projection is present on this edge to ensure firm attachment to the otoccipital. The posterior edge of the element forms the dorsal rim of the foramen magnum and is gently rounded. The dorsal margin of the foramen magnum may be notched, but is not regarded as a criterium for identification.

In ventral view the bone has a narrow, medially curved surface, bearing the dorsally directed process on either side. The tip of each process is deeply recessed to form the supra-occipital cup (Leonard, 1973). This cup covers the posterodorsal section of the membranous labyrinth (Leonard, 1973). The anterior edge of the cup is firmly applied to the posterodorsal edge of the prootic, while the posterior portion is attached to the anterior rim of the posterodorsal margin of the otoccipital. A small foramen (Leonard, 1973) is present in the anterolateral rim of the cup. The anteromedial surface of the cup is perforated by two small foramina, whilst another small foramen is present on the posteromedial surface. A small anteromedially directed foramen is present in the posterolateral rim of the cup and viewed dorsally, it is visible below the surface of the translucent bone.

B. **Chamaeleo**

The element is present as part of the "fused brain-case".

C. **Cordylus**

The same as for B.

D. **Pachydactylus**

The same as for B.

E. **Meroles**

The same as for B.

F. **Mabuya**

In dorsal view a small proc. anterior tecti, with a small winglike flange on each side, gives the anterior margin of the element a notched appearance. The small anterior process on the lateral edge curves upwards, with a triangular recessed area behind it. The small anterior process contacts the crista cranii parietalis (Skinner, 1968; Leonard, 1973) and the dorsal epiphysis of the epipterygoid. The processus descendens anterior is found where the above mentioned elements meet the crista cranii parietalis. The tubular structure seen underneath the dorsal surface is raised to form a wide ridge. The blade-like posterior margin is convex and forms the dorsal rim of the foramen magnum.

The ventral and posterior views of the element show it identical to that of *Agama*, except for the wing-like flanges mentioned above.

G. **Varanus**

In dorsal view a very prominent longitudinal ridge (proc. anterior tecti) extends anteroposteriorly. The posterior edge forms the dorsal rim of the foramen magmnum and the surface lateral to the ridge is recessed. Dorsal to the short proc. anterior tecti, a small pointed anterior process is present on both sides of the former. A small and less prominent anterior process is present ventrolaterally on the rim of the proc. anterior tecti. The anterior surface of the proc. anterior tecti is wide to ensure a firm ligamentous attachment to the parietal. Lateral to the proc. anterior tecti the anterior margin of the bone curves downwards to a small indented anterior process. This process is syndesmotically applied to the proc. descendens anterior of the crista cranii parietalis and to the dorsal tip of the epipterygoid. The lateral edge of extends posterolaterally to form the posterolateral margin which contacts the dorsomedial edge of the otoccipital. The lateral tip of the posterolateral edge curves upwards as a spiky process. The remainder of the edge is fairly uneven due to interdigitations.

In ventral view the medial body of the element has a dorsally directed process on each side. The body widens posteriorly towards the rim of the foramen magnum. The tip of each process is recessed to form the supra-occipital cup (=otic cup, Leonard, 1973), covering the membranous labyrinth posterodorsally. The posterior edge of the cup extends posterolaterally to form a wing-like flange ending in the pointed process mentioned above. An excavated area, present directly behind the supra-occipital cup, extends posteriorly with a blade-like medial margin. An anteriorly directed foramen is present halfway along the latter. The lateral margin of the cup is confluent with the pointed process. The anterior rim of the cup narrows dowm in an anterior direction and is confluent with the small, notched anterior process. The medial edge of the rim extends upwards as a winglike flange which overlaps the dorsomedial edge of the otoccipital. One foramen is present in the middle of the anterior rim, whilst a large foramen lies on the medial surface of the supra-occipital cup. A third, smaller foramen occurs anterior to the cup and pierces the bone, appearing anteromedially on the dorsally directed process.

23. Exoccipital

Jollie (1960, p.7) states: "The exoccipital arises in the occipital arches of the cranial vertebrae (posterior to the metotic fissure) and fuses almost immediately and completely (no suture lines) with the opisthotic; the combined bone can be called the otoccipital." Skinner (1968) mentions that during the early ontogeny of *Mabuya capensis*, complete fusion between the exoccipital and the opisthotic takes place to form the otoccipital. The exoccipital and the opisthotic could therefor not be disarticulated as individual elements in this investigation, as both occur as the otoccipital in *Agama*, *Mabuya* and *Varanus*.

24. Opisthotic

This element is not distinguishable in the three genera mentioned above as it is fused with the exoccipital. Romer (1956) mentions an otic capsule which forms from two ossification centres, the opisthotic and the prootic. The supraoccipital completes the capsule in a dorsoposterior position. Skinner (1968) refers to the same structure as the otic capsule, while Leonard (1973) prefers the otic cup.

25. Otoccipital (Fig. 73)

This fused element occurs in reptiles and birds although a suture line may delimit the bones in the adult (Jollie, 1960). It is located laterally in the occipital ring and contributes to the lateral wall of the foramen magnum as well as the lateral element on each side of the tripartite occipital condyle (Leonard, 1973). It contacts the supra-occipital dorsally, the prootic anteriorly and the basioccipital ventromedially. The sutures between the different elements are clear, especially between the otoccipital and the occipital condyle. Laterally the element possesses a posterolaterally directed paroccipital process, syndesmotically applied to the supratemporal, squamosal and the cephalic condyle of the quadrate as well as the parietal process of the parietal.

A. **Agama**

The ventral view of the L-shaped element shows a posterolaterally directed paroccipital process. The anterolateral surface of the tip of the process is syndematically applied to the squamosal , the cephalic condyle of the quadrate and the parietal process of the parietal. The anteroventral surface of the process possesses a groove which is bordered posteriorly by a flange. The latter becomes more prominent medially to end in a recessed area. The rim of the recessed area forms the posterior border of the fenestra ovalis which lies between the otoccipital and the prootic. The posterior surface of the flange extends medially to reach a slightly recesed area. A small ridge on the posterior edge of the paroccipital process extends medially to form the dorsal border of the above mentioned recessed area. Dorsally to the recessed area the paroccipital ridge extends posteromedially to become confluent with the lateral wall of the foramen magnum. The lateral wall extends downwards to reach the otoccipital portion of the tripartite occipital condyle. A small excavation is present ventrolaterally to the condyle. The medial edge of the excavation is applied to the dorsoposterior edge of the spheno-occipital tubercle. The lateral edge of the recessed area is blade-like. The latter forms the ventral rim of a very large foramen which is seperated from the fenestra ovalis by a narrow ledge-like portion of the otoccipital, the crista interfenestralis (Leonard, 1973). The medial edge of the otoccipital, extending from the occipital condyle towards the front, is attached to the lateral edge of the basioccipital.

The dorsal view shows a flattened surface towards the middle of the element which widens towards the middle. The posteromedial edge of the flattened surface extends upwards as a dorsal flange. The dorsal edge of the flange extends medially to form a dome-shaped structure which becomes confluent with the otoccipital contribution of the occipital condyle. A vertically directed tubular structure is visible beneath the surface of the dorsal edge of the flange. The anterodorsal edge of the dome-shaped structure is attached to the posterior edge of the ventrally directed lateral process of the supra-occipital which becomes the supra-occipital cup. A foramen, which extends downwards as the vertical tubular structure, occurs on the anterodorsal surface of the dome. Medial to the foramen a larger foramen is present with an even bigger foramen medial to the former. The three above-mentioned foramina converge ventrally inside the dome-shaped structure. The ventromedial edge of the third foramen is formed by a blade-like flange. The latter forms the posterior wall of the fenestra ovalis. The posterodorsal edge of the third foramen is present as a blade-like medially directed flange. The medial edge of the dome-shaped structure is curved laterally and forms the lateral wall of the foramen magnum. Anterior to the curved lateral wall a very narrow slitlike groove is found. The latter occurs at the base of the posterior wall of the large third foramen. Two small foramina are present in the middle of the narrow groove. A foramen is found in the lateral surface below the big third foramen, anterior to the narrow slit-like groove. A second foramen, posterior and in line with the first, occurs behind the mentioned narrow groove. The foramina referred to above, extend laterally towards the outer surface anterodorsally to the condylar portion of the otoccipital. Only three well-defined foramina are seen on this surface. The lateroventral edge of the surface forms the dorsolateral aspect of the spheno-occipital tubercle. The lateral edge of the surface forms the posterior border of the large foramen seperated from the fenestra ovalis by the crista interfenestralis. A large posteriorly directed foramen is found on the anterior surface of the paroccipital process above the fenestra ovalis. The former is covered by the posterolateral extention of the prootic.

B. **Chamaeleo**

The element is fused to form part of the fused brain-case.

C. **Cordylus**

The element is fused to form part of the fused brain-case.

D. **Pachydactylus**

The element is fused to form part of the fused brain-case.

E. **Meroles**

The element is fused to form part of the fused brain-case.

F. **Mabuya**

In ventral view the element shows a very short, laterally directed paroccipital process which is rather wide compared to the rest of the element. The tip of the paroccipital process contacts the parietal process of the parietal, the cephalic condyle of the quadrate, the squamosal and the supratemporal. A feint ridge on the anterolateral surface of the parocciptial process indicates where the latter is in syndesmosis with the medial surface of the quadrate. A small recessed area with a very shallow, laterally directed groove is present on the anteroventral surface. The groove extends medially towards a notch which represents the dorsal and posterior borders of the fenestra ovalis.

Anteroventrally the rim of the fenestra is completed by the prootic. Posterior to the fenestra ovalis the crista interfenestralis forms its posterior wall and seperates it from the large foramen behind it. The lateral tip of the paroccipital process possesses a small posteroventrally directed flange which ensures a firm contact with the cephalic condyle of the quadrate and the supratemporal. The posterior margin of the small flange is confluent with the posterior ridge-like edge of the paroccipital process. The latter extends medially towards a prominent dorsoventrally directed ridge which forms the posterior border of the large foramen behind the fenestra ovalis. The ventral tip of the ridge forms the dorsolateral portion of the spheno-occipital tubercle. The surface behind the ridge is recessed and it extends posteriorly terminating in the portion of the otoccipital contributing to the tripartite occipital condyle. The ventral border of the recessed surface forms a continuous ridge between the condyle and the spheno-occipital tubercle. A foramen is present on the lateral margin of the recessed surface mentioned above. A prominent notch with two small, ventrally situated foramina lies on the dorsal margin of this surface. The former is situated anterior to that portion of the otoccipital which contributes to the occipital condyle. The tip of the ridge which contributes to the spheno-occipital tubercle extends anteriorly as a blade-like flange. A small, narrow notch is present on the posterior margin of this flange which also forms the medial border of the large foramen mentioned previously. The medial surface of the flange and the inner surface of the recessed area anterior to the occipital condyle extend posteriorly to reach the rim of the foramen magnum. Three foramina occur successively on the inner surface of the recessed area. One foramen is present in the dorsolateral margin of the foramen magnum with a second foramen directly anterior to the former. A bony bar seperates the two foramina. The medial border of the element extends from the occipital condyle anteriorly and is applied to the lateral margin of the basioccipital.

In dorsal view the paroccipital process is short with a recessed surface posterodorsally of which the anterior portion is raised to form the posterodorsal roof of a dome-shaped structure. The anterior surface of the dome is excavated into a large cup-shaped recess enclosing the posterior portion of the inner ear. A large medially situated foramen is present inside the cup-shaped excavation. Two foramina, one laterally and the other medially, lie on the anterior margin of the dorsal roof. A small dorsal ridge, extending anteroposteriorly, lies on the roof of the dome. It curves backwards and downwards to a small recessed area which terminates on the dorsolateral margin of the foramen magnum. The anterodorsal margin of the dome contacts the posterior margin of the supra-occipital cup. The ventral border of the cup-shaped recess is indicated by the fenestra ovalis, the crista interfenestralis and the large foramen mentioned earlier. The ventral border of this cup-shaped recess is formed by a ridge with a transversely extended tubular structure visible beneath its surface. The ridge also forms the dorsal border of a narrow groove on the posterior surface of the paroccipital process. The groove extends medially from the tip of the process towards the foramen magnum.

G. **Varanus**

In ventral view the element is L-shaped with the paroccipital process directed posterolaterally. The tip of the smaller arm of the L forms part of the occipital condyle. The condylar portion extends anteriorly and slightly laterally to form a recessed surface. The anterior flange of this recess forms the posterior border of the longitudinal groove which is present on the anteroventral surface of the paroccipital process. The groove extends medially to a deep notch which forms the dorsal, posterior and ventral borders of the fenestra ovalis. The tip of the crista interfenestralis, which seperates a large foramen from the fenestra ovalis, curves backwards to enclose this large foramen. This foramen is bifurcated with one foramen leading into the inner ear, while the other extends inwards to open as a slit-like foramen in the lateral wall of the brain cavity. The medial tip of the flange is excavated and forms a small posterior portion of the spheno-occipital tubercle. Three small, consecutively situated foramina are found near the posterolateral margin of the recessed area. The posterolateral border of the recess forms the ventral border of a groove. This groove extends medially terminating in a large foramen inside a socket-like excavation on the lateral wall of the foramen magnum. A small foramen lies above, and a slightly larger foramen lies posterior to this large foramen. The three foramina mentioned open on the inner surface of the lateral wall of the foramen magnum.

The medial border of the element extends from the occipital condyle anteriorly and is firmly applied to the lateral margin of the basioccipital.

In dorsal view a broad ridge on the paroccipital process extends medially to a small vertical flange with a prominent foramen. The flange extends posteriorly, curves inwards and continues anteriorly forming the U -shaped posterior wall of the otic cup. The posterior section of the flange, directly behind the prominent foramen, narrows posteriorly to form a tubercle-like structure. This structure is applied to the posteroventral wall of the supra-occipital cup. The surface lateral to the foramen shows a > -shaped uneven surface for the firm attachment to the lateral wall of the supra-occipital cup. The medial surface of the U-shaped wall, as well as that of the tubercle-like structure, form the lateral wall of the brain case. The wall extends posteriorly to the lateral margin of the foramen magnum.

In anterior view the upper section of the posterior wall of the otic cup shows a large aperture consisting of a smaller dorsolateraly directed foramen and a much larger ventrolaterally directed foramen. Ventromedially to the large aperture a smaller aperture is found which is connected to the large foramen found posteroventrally to the fenestra ovalis. Ventro-laterally to the large aperture a deep posteriorly directed notch, which forms the dorsal, posterior and ventral borders of the fenestra ovalis, is visible. The anterolateral wall of the otic cup extends ventromedially as the anterior surface of the crista interfenestralis. This surface is interrupted ventromedially by the incomplete fenestra ovalis. A foramen is present above the notch of the fenestra ovalis. The anteromedial wall of the otic cup extends ventrally to a shallow groove on the dorsal margin of the crista interfenestralis. The anterolateral and anteromedial walls are attached to the lateral and medial walls of the prootic respectively. The anterolateral surface of the paroccipital process possesses two distinct contact areas with a longitudianal ridge along the anterior surface of the process which seperates these areas. The dorsal contact surface extends over the length of the paroccipital process where the latter is applied to the prootic medially and the parietal process and the supratemporal lateraly. The ventral contact surface is in syndesmosis with the cephalic condyle of the quadrate.

26. Prootic (Fig. 74)

According to De Beer (1937) the element arises in the anterior part of the wall of the auditory capsule and spreads forward in the membranous sidewall of the skull. Leonard (1973) states that the paired bones contribute to the lateral and the dorsolateral wall of the otico-occipital region. The anterior margin of the bone is deeply notched, forming the incisura prootica. The latter divides it in three portions: the anterior superior process above the notch, the anterior inferior process below the notch and the posterior process behind it. The anteroventral margin of the anterior inferior process is in contact with the posterior surface of the alary process of the sphenoid. The upper edge of the anterior inferior process and the upper edge of the alary process border the incisura prootica ventrally. A suture seperates the ventral part of the posterior process from the otoccipital and the basioccipital. The anterior superior process articulates with the head of the epipterygoid. This articulation is discussed in the description of the epipterygoid. The prootic houses the anterior portion of the membranous labyrinth and can be divided into an inner and an outer capsular wall collectively known as the prootic capsule. The outer wall extends to the middle of the fenestra ovalis. The outer surface of the prootic bears a longitudinal crest, the crista prootica, which continues anteriorly onto the sphenoid (Leonard, 1973). A deep groove lies below the crest and a excavated area is present above the crest.

A. **Agama**

In dorsal view a blade-like, vertical flange tapers dorsally. This flange is a dorsal extention of the anterior superior process. Anterolateral to the base of the flange a wide ridge is present, which possesses an anteroposteriorly directed canal visible directly below the surface. The anterior tip of this wide ridge curves downwards towards the incisura prootica. The posterodorsal surface of the epipterygoid articulates with the anterolateral tip of the anterior superior process and the anteromedial edge of the dorsally directed flange. A ridge, the crista prootica, (Leonard 1973) extends posterolaterally from the anterior tip of the anterior superior process. This ridge possesses a subsurface tubular structure which is confluent with the canal mentioned above. The tube tapers posterolaterally and terminates in the tip of a lateral process, which is syndesmotically attached to the anterior surface of the paroccipital process. The surface above the crista prootica extends backwards and becomes narrower. The medial portion of this surface represents the outer capsular wall of the prootic capsule. A small, slitlike foramen is present near the dorsomedial margin of the outer capsular wall. The medial margin of this surface extends upwards as the dorsally directed anterior superior process. A wide, transverse groove, present below the crista prootica, becomes confluent with the incisura prootica. The incisura prootica curves backwards below the anterior superior process forming a prominent notch medially on the ventromedial surface of the anterior superior process. A small medially directed process forms the dorsal border of the medial notch mentioned above. The area below the transverse groove forms the anterior inferior process. This process extends anteromedially towards the syndesmotic contact between the prootic and the basisphenoid. The medial surface of the anterior inferior process extends anteroventrally as a blade-like flange.

This flange forms the anteroventromedial border of a prominent groove visible only in ventral view of the anterior inferior process. The margin of this anteroventromedial flange is applied to the basisphenoid anteromedially, to the basioccipital medially and to the otoccipital posteromedially and posterolaterally. The posteroventrolateral border of the groove is formed by the narrow, lateral surface of the anterior inferior process. The dorsolateral portion of the groove is bordered by the ventral surface of the lateral process which is applied to the anterior surface of the paroccipital process. A small foramen is present in the lateral portion of the groove. The medial surface of the anterior superior process is recessed and it extends upwards along the medial surface of the blade-like, dorsally directed flange. The ventromedial portion of the recessed area possesses three to four small foramina located on an anteroposteriorly directed line. The ventromedial margin of the recess extends inwards to form a large anteroposteriorly directed ridge. The posterior portion of the ridge and the posterior margin of the recessed surface represent the inner capsular wall (Leonard, 1973). The anterior tip of the ridge forms the small medially directed process which represents the dorsal border of the previously mentioned medial notch. The anterior and the posterior margins of the excavated area below this ridge possess a large foramen each. The surface ventral to the excavation extends ventromedially as the posterior border of the ventral groove referred to above. The posterodorsal edge of the prootic capsule is attached to the anteroventral edge of the supra-occipital cup.

The posterior view of the element shows the prominent prootic capsule. An anteriorly directed foramen is present in the posterodorsal tip of the anterior superior process. The former represents the canal visible in the dorsal edge of the latter. An anteromedially directed foramen is found in the posterior surface of the lateral process. A large foramen is present in the middle of the inner capsular wall with a smaller foramen directly below the former. A narrow deep groove extends downwards as a continuation of the ventral prootic capsular floor. The former occurs in the posterior surface of the posterior process. The medial and lateral edges of this groove are attached to the otoccipital completing the enclosure of the membranous labyrinth (=inner ear cavity).

B. **Chamaeleo**

The element forms part of the fused brain case and is not discussed individually.

C. **Cordylus**

The same as for B.

D. **Pachydactylus**

The same as for B.

E. **Meroles**

The same as for B.

F. **Mabuya**

The general structure of the element resembles that of *Agama* in many aspects with only a few differences.

In dorsal view a thin, blade-like dorsally directed flange is present. The smooth, dorsal edge of this flange is vaulted and extends longitudinally. Anterolateral to the base of the flange, which represents a dorsally directed extention of the anterior superior process, a ridge is found. The ridge possesses an anteroposteriorly directed canal visible below its surface. The anterior tip of the ridge curves downwards towards the incisura prootica. The tip of the dorsally directed flange articulates with the dorsal epiphysis of the epipterygoid. A prominent ridge, the crista prootica, extends in a posterolateral direction from the tip of the anterior superior process towards the tip of the lateral process. A tubular structure is visible below the surface of the crista prootica and it is confluent with the canal found below the surface of the anterior superior process. The lateral process is syndesmatically attached to the anterior surface of the paroccipital process. The surface above the crista prootica extends backwards with a small recessed area near the posterior edge. A small but wide process extends backwards on the posterior edge in line with the recessed area. The surface tapers laterally to reach the tip of the lateral process. The medial portion of the surface represents the outer capsular wall. A small slit-like foramen is present dorsomedially to the recessed area near the edge of the outer capsular wall. A lateromedially directed groove is found below the crista prootica and medially it becomes confluent with the incisura prootica. A very small dorsoventrally directed flange indicate the border between the groove and the incisura prootica. A small foramen is present in the medial surface of the former. The incisura prootica curves backwards below the anterior superior process towards a notch near the base of the ventromedial surface of the anterior superior process. A small medially directed process forms the dorsal border of the "inner" notch referred to above. The anterior inferior process is found below the lateromedially directed groove and the incisura prootica. The former extends anteromedially to reach the syndematic attachment between the prootic and the basisphenoid. The edge of the anterior inferior process extends anteroventrally as a blade-like flange. The flange forms the anterior border of a large groove present in the ventral surface of the anterior inferior process. The groove is visible in the ventral view of the prootic only. The posterior border of the groove extends ventrally to be below the edge of the anterior border. The former is applied to the basisphenoid anteromedially, to the basioccipital medially and to the otoccipital posteromedially and posterolaterally. The dorsolateral portion of the groove is bordered by the ventral edge of the lateral process. A small foramen is present in the middle of the roof of the groove. A small excavated area can be seen laterally to the foramen and in the middle of the ventral surface of the lateral process. A small ridge forms the medial border of the excavation.

The medial surface of the anterior superior process is recessed and it extends upwards along the medial surface of the blade-like dorsally directed flange. The ventromedial portion of the recessed area possesses three to five small foramina spaced out in an anteroposteriorly directed line. The ventromedial edge of the recess extends inwards to form a large anteroposteriorly directed ridge. The posterior section of the ridge and the posterior edge of the recessed surface form the inner capsular wall (Leonard, 1973). The anterior tip of the ridge forms the small medially directed process representing the dorsal border of the smaller "inner notch". The surface below the ridge shows a deep recessed area which possesses two large foramina: one in the anterior edge and one in the posterior edge respectively. The surface below the recess extends anteromedially and slightly ventrally to form the posterior border of the groove in the ventral portion of the anterior inferior process mentioned previously. The posterodorsal edge of the prootic capsule is applied to the anteroventral edge of the supra-occipital cup.

The posterior view shows the prominent prootic capsule. An anteriorly directed foramen is found in the posterodorsal tip of the anterior superior process. The former represents the canal visible in the dorsal edge of the anterior superior process. An anteromedially extending foramen is present in the middle of the posterior surface of the lateral process. A large foramen is found in the middle of the inner capsular wall. A small anteriorly directed foramen is found directly below the large foramen. A narrow deeply recessed groove extends downwards from the ventral prootic capsular floor. The deep groove is found in the posterior surface of the posterior process. The medial and the lateral edges of the deep groove are applied to the otoccipital to form the enclosure of the membranous labyrinth.

G. **Varanus**

The dorsal view shows an anteromedially directed flange situated on the dorsal ridge of the anterior superior process. A small shallow notch is present near the anterior tip of the flange. A small dorsally directed protuberance forms the posterior border of the notch. The anterior tip of the flange is syndesmatically attached to the posterior edge of the dorsal epiphysis of the epipterygoid. The anterodorsal section of the flange is applied to the anteroventral portion of the crista cranii parietalis. The posterodorsal section of the medial surface of the flange possesses a small anterodorsally directed oval-shaped structure. A membrane is applied to the structure closing a small opening present below the proximal end of the parietal process. An anteroventrally directed foramen is present directly behind the oval-shaped structure. The surface medially and posteriorly to the foramen shows a few recessed areas which ensure firm contact between the element ant the anteroventral edge of the supra-occipital cup. The dorsal surface of the outer capsular wall is widely spread for firm syndesmatic attachment to the lateral portion of the anteroventral edge of the supra-occipital cup. The lateral surface of the flange extends backwards to reach the anterior surface of the lateral process forming a rectangle between the two surfaces. The dorsal edge of the angle slants anterolaterally to form a small ridge with a small recessed area below the ridge. The posterior edge of the anteromedially directed flange possesses a deep U-shaped recess representing the inner and outer capsular walls. The medial surface of the anteromedially directed flange extends posteroventrally towards a widened ridge present on the medial surface of the inner capsular wall. The anteroventral tip of the ridge extends towards the incisura prootica. The dorsal surface of the tip possesses a small protuberance which forms the posterodorsal border of a groove present in the ventromedial edge of the anteromedially directed flange. The area below the ridge is recessed with two foramina present inside the recess. The dorsally situated foramen extends anterolaterally towards the inner ear cavity. Directly below the former, the second foramen occurs which extends posterolaterally towards a foramen found in the distal portion of a groove present in the ventral edge of the lateral process. The anterior edge of the recess is confluent with the medial edge of the incisura prootica. The latter is rather wide in comparison to the incisura prootica found in the other genera discussed here, resulting in a much smaller anterior inferior process. The surface below the recess curves inwards to reach the ventromedial edge where the element is applied to the basisphenoid anteriorly and medially, and the basioccipital posteriorly. The surface of the ventral edge is thick and uneven for firm attachment to the element mentioned above. The anterior tip of the ventral edge extends forwards to form a sharp-tipped anterior process. The ventromedial edge of the latter is syndesmatically applied to the dorsolateral edge of the basisphenoid. A shallow groove is present in the anteroventral edge of the lateral process and it extends medially towards the incisura prootica. Three small foramina occur in the proximal end of the groove which curves anteriorly to become confluent with the lateral edge of the incisura prootica. A small lateral extending process forms the ventral border of the proximal portion of the groove. A large foramen is found directly behind the small lateral process, the processus lateralis inferior. The former is confluent with the foramen found in the recess referred to in the medial surface of the element. The ventral edge of the inferior lateral process is uneven and it extends anteroventrally to reach a small ventrally directed process. The ventral edge forms the anterior border of a groove present in the ventral surface of the inferior lateral process. Two foramina are present in the middle of the groove. The latter extends in a dorsolateral direction to reach the large foramen found behind the inferior lateral process. The posterior border of the groove extends downwards to form a blade-like ridge, which becomes thicker ventrally. The thick ventral portion of the ridge is applied to the basioccipital.The ventral edge continues from the small ventrally directed process towards the tip of the sharp-tipped anterior process.

The posterior view shows the prootic capsule with a very large anteriorly directed foramen in the dorsal portion of the capsule. The posterior surface of the lateral process is very uneven and shows the area where the former is applied to the anterior surface of the paroccipital process. A number of small foramina (10-14) is present in the posterior surface referred to above. An anteromedially directed foramen is found in the middle of the outer capsular wall at the proximal end of the posterior surface. A prominent notch occurs in the innner capsular wall in line with the foramen found in the outer capsular wall. A foramen is found in the middle of the anterior border of the notch. Two recessed areas occur in the surface of the lower portion of the prootic capsule. A number of small foramina are present in each recessed area. The posterior edge of the prootic capsule is thick and well-developed to ensure firm contact with all its adjacent elements.

27. Stapes (=columella auris) (Figs. 75 + 76)

According to Goodrich (1930) the columella auris consists of a proximal or stapedial region and a distal extrastapedial region. The latter is also referred to as the extrastapes or 0extracolumella. Jollie (1960) notes that the columella auris consists of the proximal bony stapes and the distal cartilaginous extracolumella. Romer (1956) mentions that the basal end of the rodlike bone possesses a footplate which fits in the fenestra ovalis. Near the base a foramen for the stapedial artery may occur, but the foramen is rare in modern lizards. Versluijs (1903), quoted by Goodrich (1930), indicates that the stapedial region may be pierced by the facial (stapedial) artery in some Geckonids. According to Romer (1956) the shaft extends towards the eardrum but fails to reach it. It does, however, reach the cartilaginous extracolummella. He also refers to the fact that the extracolummella possesses two processes: a dorsal process which is attached to and articulates with the paroccipital process, and a ventral process which is attached to the quadrate. Jollie (1960) mentions that near the tip of the bony stapes a dorsal process is found which extends upwards between the paroccipital process and the temporal bones to form the intercalare. Ventral to the dorsal process the internal process (=quadrate process) extends forwards and attaches by a ligament to the quadrate (Jollie, 1960). The columella develops from the dorsal end of the hyoid arch, which is bent so as to abut against the auditory capsule at the fenestra ovalis (Goodrich, 1930). The structure of the columella of the genera discussed in this work is basically identically as noted by Goodrich (1930, p. 454). The bone is also very small. It is therefore possible to either lose or accidentally remove the element when preparing material. Romer (1956; p.417): "Furthermore, even an ossified stapes is a small structure and not firmly attached to adjacent elements; it may be lost from the skeleton and, if preserved during fossilization, may be destroyed before recovery or by accidents of preparation."

A. **Agama**

The proximal footplate is oblong with a rounded margin and a smooth medial surface. The shaft extends from the centre of the footplate in a posterolateral direction. The middle portion of the shaft is not straight. The distal tip is rounded and is not cartilaginous. A stapedial foramen is absent.

B. **Chamaeleo**

The proximal footplate is large in relation to the length of the shaft. It is oblong in shape with rounded edges while its medial surface is slightly recessed. The shaft extends from the centre of the footplate in a lateral and slightly posterior direction. The distal tip is not cartilaginous. A stapedial foramen is absent.

C. **Cordylus**

The proximal footplate is oblong and with rounded edges. The medial surface is slightly recessed. The straight shaft extends from an off-centred position from the footplate in a posterolateral direction. The tip of the shaft is slightly elongated. A stapedial foramen is absent.

D. **Pachydactylus**

The medial surface of the oblong footplate is not recessed. Its margin is rounded and the shaft extends from the center of the footplate in a posterolateral direction. The shaft is straight and the tip slightly elongated. A small foramen for the stapedial artery is present at the base of the shaft.

E. **Meroles**

The element is extremely small and very brittle. The circular footplate has a deeply recessed medial surface. The curved shaft extends posterolaterally from the center of the footplate terminating in an elongated tip. A stapedial foramen is absent.

F. **Mabuya**

The element is very small and brittle. The footplate is oval and its medial surface is slightly recessed. The shaft extends from the center of the footplate in a posterolateral direction terminating in an elongated tip. The shaft is uneven and slightly curved. A stapedial foramen is absent.

G. **Varanus**

The footplate is small and circular. It is confluent with the shaft except for a suture-like groove which seperates it from the rest of the shaft. The medial surface of the footplate possesses a small recess. A small foramen lies on the narrow edge near the end of the tip. A stapedial foramen is present near the base of the shaft, which is curved and terminates in an elongated tip.

28. Supratemporal (Figs. 77 - 79)

Jollie (1960) states that whether the element is the supratemporal or the tabular is a question that cannot be resolved. Romer (1956) however, regards the relative position and relationships of the bone in lizards as well as its presumed phylogenetic history, to support the use of the term supratemporal. According to Jollie (1960) the supratemporal is present as a small splint of bone wedged between the squamosal and the parietal. Van Pletzen (1946) finds the bone to assist in the support of the quadrate and that it may even invade the intercalare cartilage of the articular region. Romer (1956) mentions three elements extending along the edge of the skull, from the postfrontal towards the back. The bones are, in this order, the intertemporal, the supratemporal and the tabular, but they are destined to early reduction or loss in most reptiles. The difference between the supratemporal and the tabular is based on their respective positions in the skull. Illustrations given by Romer and Parsons (1977, pp 218 - 232) and some simplified sketches in diagram 3 shows that the supratemporal occurs on the lateral margin of the parietal process. The tabular is found on the posteromedial edge of the parietal process. Jollie (1960) pointed out that the supratemporal is much reduced and concealed by the squamosal in some chamaeleons. According to Rieppel (1981) the supratemporal is reduced to a small splint of bone in chamaeleons and lies along the posteromedial edge of the ventral ramus (=quadrate process) of the squamosal. The element is present in *Bradypodion pumilus* (Engelbrecht, 1951) but absent in *Chamaeleo dilepis* (Rieppel,1981). Jollie (1960, p.21) states : "When only the supratemporal occurs, as in most geckos, it is shaped much the same as the squamosal of the typical lizard with a temporal arch; that is, there is a long, pointed parietal process and a short, rounded, somewhat downwardly and outwardly bent quadrate process."

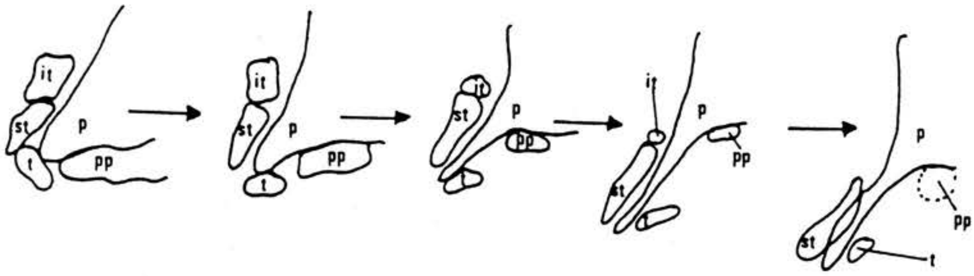


Diagram 3 The change in the position of the supratemporal and the tabular (after Romer and Parsons, 1977) (Not to scale).

A. **Agama**

The element is absent.

B. **Chamaeleo**

The element is absent, but present in *Bradypodion pumilus* (Engelbrecht, 1951).

C. **Cordylus**

The element is present as a small, flattened splint wedged between the posteromedial tip of the squamosal, the posteromedial tip of the cephalic condyle of the quadrate, the posterolateral tip of the parietal process and the posterolateral tip of the paroccipital process. The medial surface has an anteriorly directed excavated area where the element is attached to the tip of the paroccipital process. Posteriorly the excavation is bordered by a ridge which is confluent with the tip of the paroccipital process. Above the excavation a small anterodorsally directed process is present. This process is slightly recessed and contacts the posterolateral margin of the parietal process. The lateral surface of the element is smooth.

D. **Pachydactylus**

In dorsal view the element has a long, flattened, anteriorly directed process, the parietal process (Jollie, 1960). The medial border of this parietal process forms a thin blade-like flange, which is overlapped by the parietal process of the parietal. The anterior tip of the parietal process of the supratemporal abuts against the posterolateral margin of the parietal. The thin blade-like flange tapers backwards as a small ridge before it bends downwards towards the cephalic condyle as the pointed quadrate process. The excavated medial border indicates where it overlaps the parietal process. Anteriorly the ventral surface is slightly excavated with a smaller recessed area at the point where the posterior extremity bends downwards to form the quadrate process. A small foramen is present in the smaller recess.

E. **Meroles**

The small, splintlike element possesses a sharp anterodorsally directed parietal process and a thicker, rounded, posteroventrally directed quadrate process. The anteromedial surface of the element is attached to the lateral margin of the parietal process. The remainder of the medial surface contacts the tip of the paroccipital process. The posterior half of the anterolateral surface is in syndesmosis with the cephalic condyle. The lateral and medial borders of the parietal process of the element indicate where the latter is overlapped by the squamosal and the parietal process of the parietal respectively.

F. **Mabuya**

The structure of the element resembles that of *Meroles*. It is wedged between the parietal process of the parietal and the paroccipital process medially, and the squamosal laterally. The lateral surface of the long, tapered parietal process shows a recess where it is overlapped by the squamosal. The thicker and more prominent quadrate process gradually bends downwards to reach the cephalic condyle. The medial surface of the quadrate process shows a small recess where it is attached to the tip of the paroccipital process.

In ventral view the margin of the parietal process is thin and blade-like whilst the quadrate process has a more rounded margin. A small tubercle-like structure is present where these two margins meet.

G. **Varanus**

In lateral view the large, wing-shaped element shows a tapered parietal process. Its ventral margin is smooth and extends posteriorly and bends downwards to the quadrate process. The uneven dorsal margin of the parietal process extends backwards forming an ascending flange. This flange ends as a small antero-dorsally directed process. The edge behind this process curves downwards to the quadrate process. A second, smaller and anterodorsally directed process lies lateral and slightly posterior to the first anterodorsally directed process. Four to five small foramina occur in the notched area between these processes. The surface behind the smaller anterodorsally directed process is slightly recessed and uneven indicating the position where it contacts the squamosal. A shallow, posteroventrally directed groove lies below the recessed area. A small foramen is present at the point where it reaches the quadrate process.

In medial view the uneven medial surface of the element is applied to the lateral surface of the parietal process of the parietal. The ventral margin of the supratemporal bends inwards and upwards towards the back forming a deep groove which supports the ventral margin of the parietal process of the parietal. The paroccipital process contacts the medial surface of the supratemporal below the groove. Two small foramina lie on the medial surface of the quadrate process.

29. Supraorbital (Figs. 80 + 81)

De Beer (1937) refers to dermal ossifications (osteoscutes) in the skin, while Romer (1956) uses the term osteoderms. Camp (1923) noted that these bony dermal scutes are developed just under the pigment zone of the uppermost layer of the dermis and that the epidermis is not involved in their formation. De Beer (1937) refers to these elements as additions to the "standard" bones found in the lacertilian skull. "A single prominent element of this sort is found in a few geckos, some scincids, *Shinisaurus, Varanus,* ..."; "and paired supraorbitals are found in *Phrynosoma* and a few agamids." "... a whole complex of these dermal elements may cover the orbits, arranged in two longitudinal rows in many lacertids and the Cordylidae" (Romer, 1956, p.121). Two examples are included to illustrate the single element as in *Varanus* and the complex of dermal elements found in two rows as in *Mabuya*.

The reasons why the supraorbital(s) are not discussed in this comparitive study, are :

1. the fact that these elements are not true bony components of the skull, as indicated above; and
2. the number of elements are highly variable, even within a single genus; and
3. the elements may be removed, disarticulated or even lost during the course of

preparation.

30. Sclerotic ossicles (Fig. 82)

According to De Beer (1937) these elements vary in number and surround the rim of the sclerotic cartilage. Romer(1956) noted that in lizards the shape of the eyeball is maintained by its external covering which he refers to as the sclerotic coat. This is primarily a layer of connective tissue, which may be strengthened with cartilaginous or bony skeletal structures developing within the sclerotic coat. The scleral ring occurs further outward in the eyeball and consists of a number of flattened plates surrounding the pupil (Romer, 1956). He also mentions that these plates, which may vary from 10 - 17 or sometimes even more, are rarely preserved in fossils. These elements are not discussed, but merely mentioned due to their presence in the genera used in this work.

31. Hyoid apparatus

It is found in the floor of the mouth and the pharynx and it is concerned with the support and the movement of the tongue, and to a lesser degree, of the larynx (Romer,1956). " The hyoid apparatus of typical living reptiles is derived from the hyoid arch and the two succeeding visceral arches" (Romer, 1956, p. 420). The apparatus is mostly cartilaginous, but ossification may occur in certain areas such as the first branchial arch and the corpus. Although these ossifications may occur, the ossified structures are not discussed, because they too are additional structures to the "standard" elements found in the skull. In *Agama* (Harris, 1963) the first branchial arch ossify as two rod shaped bones, while the rest of the hyoid apparatus remains cartilaginous. The whole hyoid apparatus of *Cordylus* remains as a cartilaginous structure.

B. Elements of the lower jaw (Figs. 83 - 116)

Romer (1956) describes the typical reptilian lower jaw as laterally compressed and directed horizontally, lying in a vertical plane which is slightly tilted inwards ventrally. The jaw is fairly straight with the anterior tip turning inwards towards a symphysis with its counterpart. Posteriorly the jaw increases in both depth and width. The elements present are the dentary, coronoid, splenial, angular, surangular, articular and prearticular. The number of elements in the lower jaw varies markedly due to the fusion between certain elements. Cope (1892) states that the angular fuses with the articular(=articular + prearticular (=gonial)) in the Gekkonidae, Liniidae, *Acontias*, *Aniella* and the Amphisbaenidae. Barry (1953) finds only five elements in *Agama* - viz. the dentary, prearticular (=gonial), angular, surangular and coronoid, with the splenial being absent. He also refers to the fact that the articular is not yet ossified, indicating the excistence of six elements. In some genera the splenial are present. Jollie (1960) states that when the splenial is reduced or lacking, the angular extends up on the medial surface of the mandible in agamids and amphisbaenids. He further notes that the angular is presumed to be absent (or fused to the prearticular and surangular) in most geckos, while the splenial is presumed to be present. Engelbrecht (1951) finds six elements in the Chamaeleoninae with the splenial absent. The retro-articular process is also absent. Du Plessis (1944) and Van Pletzen (1946) record seven elements in the lower jaw of *Cordylus* as described by Versluijs (1936). Webb (1951) notes the position of the elements in two geckos, *Palmatogecko rangei* (Anderson) and *Oedura karroica* (Hewitt). The former has five elements, while the latter possesses four elements only. In *P. rangei* the elements are the dentary, coronoid, splenial, prearticular (=gonial) and a compound bone. The compound element consists of the fused articular, angular and supra-angular (=surangular). In *O. karroica* however, the elements are identical except for the prearticular which is fused to the compound bone. Webb (1951) assumed that the composite bone is the fused prearticular (=gonial), angular, supra-angular and articular. It is clear, however, that apart from the fused bones, there are a total of seven elements in the lower jaw of the geckos. A large enclosed fossa prearticularis occurs dorsomedially on the posterior half of the lower jaw with the articulating surface directly behind. An anteriorly directed groove, the Meckelian canal (=premordial sulcus of Romer, 1956) extends from the fossa prearticularis along the medial surface of the dentary towards the symphysis. The canal is bordered by the dentary dorsally and laterally, while the anterior and posterior portions of the ventral border is formed by the splenial and the angular respectively. The splenial, coronoid and prearticular may, in some cases, enter the medial border (Romer, 1956). The posterior tip of the lower jaw is formed by the angular and prearticular (Romer, 1956). Cope (1892), quoted by Camp (1923), notes that the angular fuses with the articular. Camp (1923) referred to the latter as the fused product of the articular and the prearticular. According to Jollie (1960) the articular, which ossifies in the Meckelian cartilage, forms the articular region of the lower jaw where it fuses with the surangular and the prearticular to form a compound bone. The latter is often identified as a single element (Parker, 1879; Cope, 1892; Oelrich, 1956).

The angular was completely disarticulated in the genera used in this work, indicating that the articular region consists of the surangular, the prearticular and the articular only. Du Plessis (1944) finds that in *Chamaesaura anguina*, the gonial (= prearticular) and the surangular (=supra-angular) are fused to the articular, but not to each other, and it confirms the statement by Jollie (1960) that some variations may be induced by fusion of the supra-angular, prearticular and the articular. Jollie (1960) furthermore notes that the interrelationship of the bones of the lower jaw remains fairly constant except for the angular and the splenial, which shows variations in size and may even be absent.

1. Dentary (Figs. 89 - 102)

The dentary is the largest mandibular element and forms the anterior half of the mandibular ramus. The longitudinal sulcus dentalis, which houses the teeth, occurs along the dorsomedial surface. The lateral surface is pierced by a number of foramina (=mental foramina; Leonard, 1973). Ventromedially the Meckelian groove or canal (=sulcus cartilaginous Meckelii) may be open as in agamids and chameleons (Jollie, 1960) or partially closed. The closure may be effected by the splenial or the fusion of the dorsal and the ventral margins of the sulcus. Skinner (1968) refers to these margins as the ascending and the descending squames respectively. Jollie (1960) mentions that the sulcus is closed in those forms in which the splenial is greatly reduced or absent. In agamids and chameleons, the sulcus is open, although the splenial is reduced or absent. Jollie (1960) indicates that within the genus *Lygosoma* the groove may be open or closed. The broad posterior tip of the dentary forms various lateral and medial processes overlapping or fusing with the elements in the proximal half of the jaw.

A. **Agama**

The lateral surface is smooth with five mental foramina on the ventrolateral edge of the anterior third of the dentary. The anterior tip curves upwards and slightly anteromedially and is syndesmotically attached to its fellow at the mandibular symphysis. The element widens posteriorly with its dorsal margin extending upwards. This margin bears the acrodont teeth with one or two conical teeth present at the anterior tip.

The posterior tip is flattened from side to side forming two posteriorly directed processes. The lower posterior process (=posteroventral process) is smaller than the upper (=posterodorsal process) and separated from it by a deep notch. The posterodorsal process (=coronoid process) forms the anterior and anterodorsal rim of a large foramen present on the lateral surface of the dentary. The foramen is bordered posteriorly and ventrally by the bifurcated anterior tip of the lower process of the surangular.

The dorsal margin of the dentary is grooved between consecutive teeth to receive the overlapping teeth of the upper jaw. The medial surface of the dentary is uneven with the sulcus dentalis bearing the acrodont teeth visible near the dorsomedial edge of the element. The Meckelian canal is open medially and extends from the anterior tip of the dentary towards and onto the medial surface of the posteroventral process. The dorsal and ventral margins of the canal is hardly noticeable anteriorly, but become more prominent posteriorly. The dorsal margin extends downwards towards the middle portion of the canal overhanging it slightly. An anteriorly directed canal is visible below the overhanging dorsal margin, directly above the Meckelian canal. The posterior portion of the ventral margin is depressed for the attachment of the long anteriorly directed lower process of the angular.

B. **Chamaeleo**

The lateral surface is even and smooth with four well separated mental foramina ialong the ventrolateral edge of the element. A fifth mental foramen is present directly behind the fourth. The Meckelian canal extends from the ventrolateral edge of the anterior tip of the dentary, along its ventral margin and curves inwards to continue posteriorly along the ventromedial surface of the element to the medial surface of the smaller, posteroventral process. An anteriorly directed foramen is present in the dorsal margin of the Meckelian canal near the midline of the element. The foramen is visible in ventral view only.

A shallow groove on the anteromedial surface of the dentary lies directly above the Meckelian canal. The anterior tip of the dentary extends upwards and slightly anteromedially to reach its counterpart at the symphysis where they are syndesmotically attached to each other. The dorsal edge, which bears acrodont teeth, extends backwards and upwards to end as a large posterodorsal process. The ventral edge of this process is blade-like and extends downwards to reach a narrow notch separating it from the smaller posteroventral process. The ventral margin of this smaller process is also blade-like and it tapers inwards.

The dorsolateral edge of dentary bears grooves between consecutive teeth which indicates that the teeth of the upper jaw overlap that of the lower jaw. No conical teeth are present. The question that arises is whether the chameleons are more advanced than the agamids with a loss of conical teeth or is it the other way round. If not, it may confirm the statement of Camp (1923) that ..." chameleons are offshoots of agamid stock" (p.417). According to Frost and Etheridge (1989) the Agamidae and the Chamaeleonidae form a monophyletic group.

A large anteriorly directed foramen is present in the posteroventral tip of the bigger posterodorsal process.

C. **Cordylus**

In a dorsal view the tip of the element shows no inward curvature in an anteromedial direction, while the lateral ascending edge of the sulcus dentalis appear as a straight line. The lateral surface is smooth and even with a row of eight foramina in the midline of the element.

The anterior tip of the dentary curves inwards with the eight mental foramina visible in an anterior view. The element widens posteriorly with the dorsal edge diverging upwards to form a short posterodorsal process. The ventral edge of the latter curves downwards towards a wide notch which seperates the posterodorsal process from a larger posteroventral process.

The Meckelian canal is visible in the middle of the medial surface becoming less prominent as it curves anteriorly towards the ventromedial edge of the dentary. The dorsal edge of the Meckelian canal forms a ledge, the sulcus dentalis (Leonard, 1973) which suports the pleurodont teeth. The medial edge of the sulcus curves upwards to form a groove extending anteriorly to reach the tip of the dentary. The teeth are pleurodont and occur in the lateral portion of the groove, whilst the medial portion of the groove remains open.

An anteriorly directed foramen is present directly below the posterior section of the sulcus dentalis. A thin blade-like ridge, present in the ventral surface of the posterodorsal process, extends anteriorly towards the foramen mentioned.

D. **Pachydactylus**

In dorsal view the anterior tip of the dentary curves markedly inwards to the symphysis. The element widens posteriorly. The lateral ascending edge of the sulcus dentalis curves inwards towards the middle of the dentary and reaches the posterodorsal process. The lateral surface of the ascending edge extends ventrolaterally in the posterior portion of the element. Midway along the dentary a small foramen is present in the floor of the sulcus dentalis.

In lateral view the lateral ascending edge of the sulcus dentalis extends upwards towards the back. The lateral surface of the element is smooth except for a pitted area on the ventrolateral margin of the dentary extending posteriorly to reach the posteroventral process. A small notch is present in the larger, posterodorsal process. The posterodorsal process is separated from the posteroventral process by a larger notch. Six mental foramina, of which the hindmost is the largest, are present anterolaterally on the element.

In medial view the prominent sulcus dentalis bears the pleurodont teeth. The shelf of the sulcus, formed by the ascending squame (Skinner,1968) extends backwards to terminate as a small, posteromedially directed process. The latter is also visible in dorsal view. The

Meckelian canal is partially closed with a small V-shaped uncovered posterior section. This uncovered section is closed by the splenial. A depression surrounding the open section indicates the position of the splenial.

In posterior view the large Meckelian canal extends anteriorly. The canal branches into a dorsolateral and a ventromedial canal in the anterior half of the element. A small inconspicuous ridge is present in the roof of the Meckelian canal. Anteriorly it becomes confluent with the roof.

E. **Meroles**

In dorsal view the anterior tip curves slightly anteromedially. The lateral ascending edge of the sulcus dentalis runs parallel to the lateral border of the element, but curves inwards posteriorly towards the midline. The medially extending floor or ascending squame of the Meckelian canal is narrow and bears pleurodont teeth on its dorsal surface. No foramen is present in this floor portion of the sulcus dentalis.

In lateral view the element is smoothly convexed. Six mental foramina are present in the anterior half of the element. The third foramen from the front lies slightly lower than the rest. The ventral margin curves slightly towards the back, whilst the dorsal margin of the laterally ascending edge curves upwards posteriorly. These margins terminate in the posterodorsal and posteroventral processes respectively.

In medial view the small, inconspicuous floor of the sulcus dentalis (=ascending squame of the sulcus dentalis) is visible. The Meckelian canal is open with the anterior portion of the descending squame (ventral edge of the Meckelian canal) curving dorsolaterally. The result is that the anterior section of the Meckelian canal is visible in ventral view. A small, anteriorly directed foramen is present in the roof of the Meckelian canal.

F. **Mabuya**

In dorsal view the anterior tip of the bone curves slightly anteromedially. The ascending squame of the sulcus dentalis is very prominent and forms the posterior section of the symphysis. The squame extends posteromedially, then curves dorsolaterally and becomes confluent with the posterodorsal process. No foramina are present in the floor of the sulcus dentalis. The dorsal margin of the laterally ascending edge of the sulcus dentalis extends posteromedially in the posterior half of the element. It terminates as the dorsal edge of the posterodorsal process.

In lateral view the element is convex. Nine mental foramina are present along its anterior half. The spacing of the foramina is irregular with the anteriormost foramen virtuallly part of the symphysis. This foramen appears to be the anterior opening of the Meckelian canal. The ninth foramen is the largest. The dorsal margin of the lateral ascending edge curves posterodorsally causing the element to appear wider towards the back. A wide notch separates the posterodorsal and posteroventral processes. A clearly marked ridge surrounds the notch where some of the jaw muscles attach.

In medial view the anterior two thirds of the margin of the ascending squame curves downwards and forms the ventral margin of the dentary. The anterior half of the Meckelian canal is closed due to the fusion of the ascending and the descending squames. The posterior half of the canal is closed by the splenial. The descending squame extends posteriorly, but as mentioned before, the ascending squame extends posterolaterally causing the posterior section of the Meckelian canal to divert.

In posterior view the Meckelian canal is visible in a ventral position with a foramen lying dorsolateral to the canal.

G. **Varanus**

In dorsal view the dentary has a consistent thickness from back to front. The anterior tip curvies slightly anteromedially at the symphysis. The pleurodont teeth have broad flaring bases ankylosed to the dorsomedially sloping sulcus dentalis.

Viewed laterally, the dorsal margin of the lateral ascending edge of the sulcus dentalis curves posterodorsally towards the posterodorsal process. The ventral margin of the dentary is convex ventrally, with the posterior section terminating as the posteroventral process. The lateral surface is smooth with a line of six mental foramina lying parallel to the dorsal margin of the lateral ascending edge. The hindmost foramen is the largest and lies close to the posterior margin of the posterodorsal process. The area between the posterodorsal and the posteroventral processes slopes gradually to form a C-shaped posterior edge. The anteromedial margin of the anterior tip possesses a small notch dividing the former in a dorsal and a ventral section. The notch curves posteromedially and becomes confluent with the anterior portion of the enclosed Meckelian canal.

In medial view the Meckelian canal is open with a wide Y-shaped posterior extremity which narrows towards the front. The descending squame runs along the ventral edge of the dentary, extending from the ventral posterior process towards the front where it curves anterodorsally. The ascending squame extends downwards from the posterodorsal process towards the descending squame. The former then extends parallel to the descending squame in an anterior direction where it curves anterodorsally. The middle portion of the Meckelian canal is deeper than its anterior and posterior portions. The result is a prominent sulcus dentalis with a very wide middle section. The floor of the sulcus slopes downwards from the dorsolateral edge towards the ventromedial margin.

In posterior view the lateral and medial edges of the posterodorsal process enclose a large anteriorly directed foramen. The ventral margin of the medial edge of the posterodorsal process is deeply notched. A small, posteriorly directed process is present directly below the notch. The large hindmost mental foramen can be seen through the notch referred to above. Signs of osteoclastic activity are visible on the sloping sulcus dentalis floor during which teeth are loosened to eventually be replaced.

2. Splenial (Figs. 103 - 106)

This element normally lies on the medial surface of the dentary below the anteroventral process of the coronoid. It is also closely related to the closing of the Meckelian canal. Jollie (1960) states that even within genera the splenial may be present or absent. Camp (1923) notes that owing to the absence of the splenial in some families, the dentary is enlarged to take its place. "The splenial is small or absent in Agamidae and absent in Chamaeleontidae; being well-developed in other families" (Camp, 1923, p. 375). Jollie (1960) notes that the splenial in geckos is rather peculiar because it occupies in part the position of the angular. He further states that the splenial and angular are lacking in some geckos. Webb (1951) found that the angular is fused to the compound bone, which consists of the articular, prearticular and surangular. Jollie (1960) mentions that in lizards the splenial is initially reduced and the angular lost subsequently. In geckos, however, it appears that the angular is lost before the splenial (Jollie, 1960).

A. **Agama**

The splenial absent in the specimens used in this study. Jollie (1960) noted its loss in many agamids. Camp (1923) states that the splenial may be absent or small in the agamids.

B. **Chamaeleo**

The element is absent in the Chamaeleonidae. (Camp, 1923; Engelbrecht, 1951; Jollie, 1960).

C. **Cordylus**

The splenial consists of a bar of bone with a wing-shaped ascending ledge. The posterodorsal margin of the ledge is firmly applied to the anteroventrally extending section of the coronoid. The ventral edge of the element forms part of the ventral border of the lower jaw. The medial surface of the splenial is smooth with a laterally directed foramen in the anterior half, just above the ventral edge. The anterior tip is bifurcated directly above the ventral edge. A small splint-like process forms the dorsal margin of the notch. The dorsal edge slopes posterodorsally towards the coronoid process and posterior to the coronoid process, is excavated towards the ventral edge. The posterior tip of the splenial thus terminates in an enlongated posteriorly directed process.

In lateral view a groove runs parallel to the ventral margin of the element. This groove forms the medial extremity of the Meckelian canal and is bordered by a short blade-like ridge dorsally and a long blade-like ridge ventrally. The ventral ridge of the groove extends along the length of the element. The posterior third of the ventral ridge extends into an upper and lower ridge. A foramen is present in the anterior half of the element directly above the ventral ridge.

The surface behind the groove widens posteriorly and appears uneven to enhance contact with the coronoid and the fused compound element. The surface above the dorsal, blade-like ridge is slightly excavated for attachment to the posterior section of the dorsal squame on the dentary.

D. **Pachydactylus**

The shape of the splenial, in medial view, resembles that of *Cordylus*, except that it is fairly short and the ascending ledge wider. The anterior tip of the element slopes posteroventrally and it is bisected by a deep, but narrow notch with a foramen near the ventral tip directly below the notch. The ascending ledge slopes posterodorsally to reach a thin blade-like edge which curves downward in staggered fashion to reach the long posteriorly directed ventral process. The anteroventral surface directly below the foramen is grooved for firm attachment to the dentary. The anterior edge of the element is syndesmotically applied to the posterior edge of the closed Meckelian canal. The medially directed area near the base of the ascending ledge is slightly excavated towards the back. The laterally directed surface of the ascending ledge is jagged for application to the posterodorsal process of the dentary and the anteroventral process of the coronoid. A narrow groove runs parallel to the ventral edge of the element. The groove is bordered ventrally by a small ridge with a foramen present in the anterior tip of the ridge. The groove is bordered dorsally by a small ridge formed by the middle third of the ascending ledge. The lower half of the groove is present on the long posteroventral process.

E. **Meroles**

The splenial is a splint-like structure with a wide posterior margin. The medial surface of the anterior half contains a shallow groove extending towards the slightly bifurcated anterior tip. A large foramen lies in the middle of the bone, near the ascending dorsal margin. A smaller secondary foramen is present directly below the large one. A thin strip of bone seperates the two foramina. The posterodorsal tip of the wingshaped posterior half curves slightly dorsolaterally and is syndesmotically applied to the coronoid and the fused compound element. The ventral margin of the element is confluent with the ventral margin of the lower jaw.

In lateral view the splenial shows an irregular surface with grooves and small excavations for firm attachment to the surrounding elements. The posteroventral tip of the wing-shaped section possesses a small ridge.

F. **Mabuya**

In medial view the ventral margin is rodlike with a small ascending ledge in the middle third of the bone. The anterior part of the ascending ledge extends anteroventrally to reach a thin horizontal, blade-like anterodorsal process. The anterior tip of the element possesses a deep posteriorly directed notch. The area behind the notch forms a narrow posteriorly directed groove parallel to the ventral edge of the element. This groove terminates on the posteroventral process. A small foramen lies directly behind the notch and in line with the descending anterior part of the small ascending ledge. The posterior section of the ascending ledge extends posterolaterally to meet the anterior descending portion of the coronoid. The ventral edge of the element extends backwards as a narrow posteroventral process. The dorsal edge of the posteroventral process is confluent with the posterior section of the ascending ledge. The anterior half of the ventral edge of the splenial is syndesmotically applied to the dorsal surface of the posteroventral process of the dentary.

In lateral view a thin, anterodorsal process extends posterodorsally as a thin blade-like ridge on the lateral surface of the ascending ledge.

G. **Varanus**

The structure of the splenial resembles an axe. The ventral margin is rods-haped as in the other genera, with an enormous and unusual ascending ledge.

In medial view a needle-like anteroventral process covers the Meckelian canal. The ventral edge of the element forms the ventral margin of the lower jaw, while the dorsal edge extends posterodorsally. A large foramen is present in this dorsal edge. The middle section of the anterodorsal border of this foramen is partly missing, but is formed by the posteroventral edge of the ascending squame of the sulcus dentalis on the dentary. The dorsal edge extends onwards above the foramen to an inconspicuous, dorsally directed process. This section of the dorsal edge forms the posteroventral border around the base of the hindmost tooth on the dentary. The dorsal edge, posterior to the small, dorsally directed process, continues posteriorly and terminates as the posterodorsal process of the splenial. The posterior border of the ascending ledge possesses a deep, wide anteriorly directed notch extending from the ventral surface of the posterodorsal process towards the posteroventral process. The latter is continuous with the ventral border of the splenial and the needle-like antero-ventral process. The posteroventral process is bifurcated by a narrow, anteriorly directed slit dividing the former in a short superior process and a long, inferior process with a sharp tip. A large foramen lies above the ventral border of the splenial, directly below a large foramen on the dorsal margin.

In lateral view the needle-like anteroventral process extends backwards and becomes confluent with the lateral surface of the element. A narrow groove occurs above the ventral margin of the splenial, but disappears as it reaches the inferior posterior process. A prominent ridge forms the dorsal border of this groove. A second groove, above this ridge, becomes confluent with the lateral surface of the large ascending ledge. The foramen dorsal to the ventral edge on the medial surface of the splenial opens in the middle of this ridge. A short anteriorly directed process extends from the posterior border of the foramen and partly covers the latter to form a dorsal and a ventral entrance towards the foramen. The posterior tip of the ridge terminates as a posteriorly directed process with a sharp tip.

3. Coronoid (Figs. 107 - 109)

Romer (1956) mentions that a number of coronoids were present in primitive tetrapods, but two of these eventually disappeared to give the single element present in most reptiles. Skinner (1968) and Leonard (1973) describe the coronoid as an irregular triradiate bone consisting of a dorsal radius (=dorsal process), an anterior radius (=anterior process) and a posterior radius (=posterior process). The anterior and posterior processes as well as the base of the dorsal process are firmly anchored to the remaining bones of the mandible, except the angular (Skinner, 1968). Leonard (1973), however, states that the base of the coronoid rests on a dorsally expanded anterior portion of the angular. The former gives rise to a small anteroventrally directed outer process and two inner processes of which one is posteriorly and the other anteriorly directed. Skinner (1968) finds the anterior process to be wedged between the dentary and the splenial medially, and the dentary, the surangular and the prearticular laterally. The posterior process contributes to the inner surface of the jaw and is in syndesmosis with the surangular and the prearticular laterally. The base of the dorsal process rests on an elevated portion of the surangular. According to Jollie (1960) the coronoid is well developed with a large dorsal process. The bone straddles the dorsal margin of the lower jaw with a single outer flange and two internal processes. The outer process shows marked variations as discussed by Jollie (1960,p.45).

A. **Agama**

In medial view the coronoid is cross-shaped with a prominent dorsal process. The tip of the latter bends backwards and slightly towards the middle. A ventrally directed ridge on the medial surface extends from the posterior edge of the dorsal process towards the tip of the ventral process. The ridge becomes more prominent ventrally to end as a tuberosity at the tip of the ventral process. The latter overlaps the anteromedial surface of the compound bone mentioned in the introduction of the lower jaw. A small recessed area is present in the middle of the element, anterior to the mentioned ridge. The surface anterior to the recessed area tapers towards the front to form a blade-like anteriorly directed process. This process is syndesmotically applied to the posteromedial surface of the dentary, directly above the posterior portion of the Meckelian canal. The dorsal edge of the anteriorly directed process is thicker than the blade-like ventral edge. The posterior section of the former bends upwards to become confluent with the anterior surface of the prominent dorsal process. The thin blade-like ventral edge of the anterior process is in syndesmosis with the middle part of the dorsomedial edge of the angular.

The posterior edges of the dorsal process and the ventrally directed process curve backwards to form a tapered posteriorly directed process. The latter is syndesmotically applied to the dorsomedial surface of the posterodorsal process of the dentary and the dorsomedial surface of the compound bone respectively.

A small anteriorly directed foramen is present near the middle of the posterior surface of the ridge extending between the dorsal and the ventral processes respectively.
The lateral surface of the element is smooth and shows the distinctive cross-shaped structure.

B. **Chamaeleo**

In medial view the coronoid shows a short dorsal process with a posteriorly slanting tip. A prominent ridge extends from the tip of the dorsal process and recedes towards the tip of the ventral process. A dorsolaterally extending foramen is present in the middle of the posterior surface of the above-mentioned ridge. A recessed area above this foramen extends towards the tip of the dorsal process. The edge of this posterior surface is serrated and extends vertically upwards to the ventral margin of the posterior process of the compound bone. The tip of the ventral process is small and bends backwards. The ventral edge of the tip extends anterodorsally to form the ventral rim of a large surface present anteriorly to the dorsoventrally directed ridge. An anteriorly directed notch is present in the middle of the ventral rim of the large surface mentioned. The portion of the ventral rim above the notch becomes confluent with the tip of the anteroventrally directed anterior process. The dorsal edge of the anterior process thickens posteriorly and becomes confluent with the anterior edge of the dorsal process. The posterior surface of the dorsal process slants downwards and curves posteriorly to form the broad dorsal margin of the posterior process. The posterior tip of the latter is uneven and slightly bifurcated with the inner tip extending further backwards than the outer tip.

In dorsal view the medial edge of the posterior process curves posterolaterally from the tip of the dorsal process and the lateral edge curves posterolaterally form the lateral surface of the dorsal process. The anterodorsal surface of the dorsal process is rugose to facilitate the insertion of the adductor musculature.

In lateral view the coronoid shows a large, prominent surface extending ventromedially. This surface has interlocking rugosities and a medially directed foramen near the base of the dorsal process, below the laterally extended wing-shaped lateral edge of the posterior process.

The middle section of the ventral surface of the posterior process possesses an anteroposteriorly directed excavation with a thin blade-like flange in the middle of the excavation, dividing it into two narrow grooves.

C. **Cordylus**

In medial view the element has two inner processes with a large notch between them. The large surface referred to in *Agama* and *Chamaeleo* is reduced by this notch. The dorsal process is short and stubby. The tip is slightly contorted posteromedial. The posteromedial edge of the process forms a broad ridge which extends ventromedially towards the tip of the rounded and ventrally directed posterior process. The latter is syndesmotically applied to the compound bone, but no contact with the angular can be seen. The anterior edge of the posterior process forms the posterior border of the large notch. The former extends upwards towards the dorsal process and becomes recessed laterally, forming the ventral edge of a recessed surface below the tip of the dorsal process. The ventral edge of the recessed surface continues anteroventrally and slightly towards the middle to form the posterior edge of the rather big anteroventrally directed anterior process. The posterior edge forms the anterior border of the large notch. The anterior edge of the dorsal process extends anteroventrally to reach a small tubercle-like projection, but continues forwards from below the tubercle to the pointed tip of the anterior process. The tip of the anterior process below the tubercle is rugose and it is overlapped by the ascending squame of the dentary with which it is in syndesmosis.

In lateral view the posterolateral edge of the dorsal process extends anteroventrally to the tip of the small stubby, wing-like process. (The outer process referred to is the ventral process mentioned in *Agama* and *Chamaeleo*.) The anterior edge of the outer process extends medially and then curves anteroventrally to form a ridge-like structure in the middle of the lateral surface of the anterior process. The surface dorsal and ventral to this ridge is uneven to ensure firm syndesmotic contact with the dentary. The lateral surface of the somewhat vertical posterior process is also rugose for syndesmotic attachment to the compound bone.

In ventral view a small, dorsally directed groove is seen forming a bridge between the tip of the outer process and the middle section of the base of the dorsal process. This middle section forms the dorsal rim of the large notch.

D. **Pachydactylus**

In medial view the bone is triangular with a prominent dorsal process forming the apex, which curves posterodorsally. A thin, wing-like flange extends from the posteromedial tip of the dorsal process in a posteroventral direction towards the tip of the posterior process (= inner posterior process). The latter is syndesmotically applied to the compound bone, but not to the angular. The anterior edge of the dorsal process slants anteroventrally and slightly outwards. Midway between the dorsal process and the anterior process the edge curves slightly upwards, but continues anteroventrally to the tip of the broad anterior process. The dorsal edge of the anterior process ends as an anteriorly directed spike. The anterior edge below the spike slants posteroventrally to reach the ventral edge of the anterior process. The ventral edge of the anterior process extends posteriorly, but at the base of the dorsal process it curves medially to form the ventral edge of the posterior process. The result is a laterally extended C-shaped ventral edge where the coronoid is in syndesmosis with the compound bone.

In posterior view the element has a ventromedially directed flange with an anterolaterally directed recess towards the base of the dorsal process. Two small anteroventrally directed foramina occur in the dorsal margin of the recess near the edge. The edge extends from the dorsolateral side of the dorsal process in a ventrolateral direction towards the outer process (=ventral process). The posteroventral edge of the flange curves posteroventrally to form a ridge, syndesmotically applied to the dorsal margin of the compound bone.

In lateral view the dorsal process extends ventrally, close to the outer process. The surface curves anteroventrally towards the tip of the anterior process. The middle portion of the lateral surface of the anterior process is excavated to form a groove, overlapped by the dorsal part of the posteroventral process of the dentary. The posterolateral edge of the dorsal process extends anteroventrally to form a wide, short outer process. The latter is in syndesmosis with the compound bone posteriorly and the ventral part of the posterodorsal process of the dentary anteriorly.

Ventrally, a groove is present between the outer process (=ventral process) and the ventromedial edge of the anterior process.

E. **Meroles**

In medial view the dorsal process is directed posterodorsally. Its posteromedial edge extends posteroventrally towards the rounded tip of the inner posterior process (=posterior process). The anteroventral margin of the posterior process extends laterally, turns anteriorly at the base of the dorsal process and then bends medially to form the posteroventral edge of the anterior process which in turn forms a large notch shaped like an inverted U between the anterior and the posterior processes. The anterior edge of the dorsal process extends downwards, but halfway down it bends slightly upwards and continues anteriorly. Close to the bend, the anterior edge forks to form the anterior process medially and the anterior portion of a rather broad, but short outer process (=ventral process) laterally. The dorsal edge of the anterior process forms a sharp tip. The anterior edge below the tip slants posteroventrally to meet the short ventromedial edge of the anterior process.

In posterior view the posterior margin edge of the rounded tip of the posterior process forms a flange with a small notch midway up the edge. The notch forms part of the anterior border of the fossa prearticularis. The flange-like edge continues dorsolaterally to reach the posterior portion of the outer process. The posterior surface below the dorsal process is excavated and forms a groove which recedes towards the posterior edge of the posterior process.

In lateral view, the middle portion of the lateral edge of the broad, short outer process extends slightly further downwards. The posterolateral edge of the dorsal process forms a small flange-like ridge extending anteroventrally to become confluent with the rounded middle section of the lateral edge discussed above. A small, anteromedially directed foramen is present in the lateral surface of the dorsal process below the flange-like ridge referred to above. The anterior tip of the outer process extends further backwards than the tip of the anterior process.

In ventral view a deep groove extends anteroposteriorly from the notch between the tip of the anterior process and the anterior tip of the outer process towards the posterior tip of the outer process. The inverted U -shaped notch is clearly visible.

F. **Mabuya**

In medial view the dorsal process, with its rounded tip, extends posterodorsally. A minute dorsally directed projection is present dorsomedially on the tip of the dorsal process. A thin, wing-like flange extends posteroventrally from the posteromedial edge of the small projection to the ventrally directed posterior process. The anteroventral edge of the latter extends dorsolaterally, curves anteriorly at the base of the dorsal process and continues anteroventrally to form the posteroventral edge of the anterior process. The same inverted U-shaped notch is present as in *Meroles*. Anteromedially the posteroventral edge of the anterior process has a small, anteriorly directed notch.. The ventromedial edge of this notch forms a posteriorly directed projection in line with the sharp, anteriorly directed tip of the anterior process. The broad anterior edge of the dorsal process slants anteroventrally, curves medially and ends as a small, anteromedially directed projection near the tip of the anterior process. The anterior surface below this small projection is notched and continues anteriorly to the tip of the anterior process. The lateral and medial margins of the anterior process extend ventrolaterally and ventromedially respectively. The medial edge is overlapped by the dorsal part of the splenial and the lateral edge is overlapped by the ventral surface of the posterodorsal tip of the dentary.

In lateral view the lateral edge of the dorsal process extends anteroventrally towards the base of the dorsal process. Near the base, the edge curves anteromedially towards the tip of the anterior process. An anteromedially directed groove is present in the middle of the anteromedial edge. The groove reaches the small notch below the small anteromedially directed projection. The groove is overlapped by the posterodorsolateral tip of the dentary.

In posterior view the posterolateral edge of the dorsal process extends anteroventrally to a small, ventrally directed ridge. The anterior section of this ridge forms the ventrolateral margin of the anterior process of which the posterior section may be a vestige of the ventral process. The surface medial to the posterolateral edge of the dorsal process possesses a fan-shaped excavation extending dorsomedially. A small, anteriorly directed foramen is present in the narrow ventral section of the fan-shaped recess. The thin, blade-like ventromedial edge of the posterior process forms the edge of the fan-shaped recess.

G. **Varanus**

In medial view the tip of the dorsal process extends posteromedially. The posteromedial edge of the dorsal process extends posteroventrally to the tip of the posterior process. The anteroventral edge of the posterior process extends dorsolaterally to reach the base of the dorsal process. It then curves anteriorly to form the dorsal rim of an inverted U-shaped recess found between the anterior and the posterior processes. The ventral margin of the anterior process extends anteromedially. Midway towards the tip of the anterior process the ventral edge has a ventrally directed flange ending in a small anteromedially directed process. A small notch lies dorsal to the small process mentioned. The dorsal edge of the notch extends anteriorly to form the ventral border of a long anteriorly directed spicular process. The anterodorsal edge of the dorsal process extends anteroventrally, but halfway downwards the edge curves slightly upwards and continues anteriorly. The anterior tip of the anterodorsal edge widens anteriorly and is bifurcated by a deep posteriorly directed notch, forming the anterior process medially and the anterodorsal portion of the ventral process laterally. The notch is clearly visible in dorsal view. A shallow groove extends posterodorsally from the notch along the anterodorsal edge of the dorsal process. The anterior surface of the edge below the tip of the anterior process extends anteriorly to form the dorsal edge of the long splint-like process referred to above. The ventromedial edge of the anterior process possesses a medially directed ridge with a thin blade-like flange extending anteroventrally. The thin, blade-like flange is overlapped by the dorsolateral surface of the splenial. The latter reaches up to the medially directed ridge mentioned above. A small ventrally directed foramen is present in the dorsomedial surface below the tip of the dorsal process.

In lateral view a lateraly directed protuberance is present in the middle of the anterolateral edge of the dorsal process. A small foramen lies on the posterolateral surface, below the tip of the dorsal process, directly posterior to the above protuberance. A second small foramen is present in the ventrolateral surface below the anterior portion of the protuberance. The anteroventral edge of the ventrolateral surface possesses interlocking rugosities where the coronoid is in syndesmosis with the dorsal portion of the posterodorsal process of the dentary. The ventral edge of the ventrolateral surface is blade-like and extends posteriorly as the ventral edge of the posterolateral surface below the tip of the dorsal process. The ventral edge can be seen as the vestige of the ventral process referred to in the coronoid in the genera discussed previously. The posterior portion of the ventral edge curves upwards and slightly to the back to form a laterally directed flange which becomes the posterior edge of the posterolateral surface below the tip of the dorsal process. The posterior tip of the posterior edge forms a small posterolaterally directed process which forms part of the anterior border of the fossa praearticularis (= adductor fossa; = mandibular fossa; fossa Meckelii) (Fuchs, 1931; Romer, 1956; Jollie, 1960; Skinner, 1968). The posteroventral surface of the posterior process is clearly visible in lateral view.

In ventral view a large, well defined groove extends from the anteriorly directed notch towards the small posterolaterally directed process forming the posterodorsal portion of the ventral process. The ventral margin of the ventral process extends as a blade-like flange from the anterior process towards the posterior process. The blade-like flange forms the lateral border of the large groove. The medial edge of the large groove is formed by the ventral rim of the inverted U-shaped recess between the anterior and the posterior processes. A small anteroposteriorly directed ridge forms the border between the posterior portion of the large groove and the posterolateral surface of the posterior process. The anterior section of the posterolateral surface is perforated by 6 to 8 foramina. Four small foramina, arranged in a square, are present in the posterior section of the large groove anterolateral to the small anteroposteriorly directed ridge. Two larger foramina lie in the groove at the base of the dorsal process. The anterior section of the groove is perforated by 20 to 25 foramina of variable size.

4. Angular (Figs. 110 - 112)

Generally the bone is splint-like and variations occur. Cope (1892) states that in the Gekkonidae the angular is fused with the articular (=articular and prearticular). Jollie (1960) describes the element as a ventral bone of the mandibular ramus. Its posterior end is wrapped up onto the lateral side of the mandible where it overlaps the surangular and the prearticular. The anterior end lies along the inner ventral margin of the lower jaw where it is overlapped by the ventral posterior process of the dentary. Barry (1953) finds that in *Agama hispida* the element occurs in the middle portion of the lower jaw partially covering the Meckelian canal medially. It extends upwards to reach the prearticular (=gonial) and then slants posteroventrally as part of the ventral border of the fossa praearticularis. According to De Beer (1937) the angular arises on the ventral side of the middle part of Meckel's cartilage anterior to the prearticular. Romer (1956) describes the element as a large posteroventral element of the lower jaw. It frequently forms part of the lateral surface where it occurs behind the splenial, posteroventral to the dentary and ventral to the surangular. The element is exposed on the inner surface below the prearticular, where it takes part in forming the infra-Meckelian foramen (=fossa). Towards the back the element covers the ventral and lateral surfaces of the articular respectively. Anteriorly the angular is pierced by the angular foramen.

A. **Agama**

The bone is splint-like and forms part of the ventral margin of the middle section of the lower jaw.

Viewed dorsally, a deep anteroposteriorly directed groove is present on the dorsal surface of the element. The posterior third of the dorsal surface tilts upwards and slightly inwards with the posterior portion of the dorsal groove facing inwards. Ascending blade-like edges form both the inner and outer margins of the groove. The anterior third of the inner margin is recessed and becomes confluent with the lower surface of the anterior portion of the groove. The anterior end of the outer margin is also slightly recessed and it continues anteriorly to terminate in a spicular anterior tip. A small, ventrally directed foramen is present in the centre of the middle section of the groove.

In ventral view a narrow blade-like ridge in the anterior half of the element is confluent with the spicular anterior tip. The blade-like ridge extends posteriorly and slightly outwards forming a wide posteroventral surface in the posterior half of the angular. The wide posteroventral surface is continuous with the anteromedial surface of the element. The anterolateral surface continues anteriorly towards the spicular anterior tip. It is slightly rugose to ensure firm syndesmotic attachment to the ventromedial surface of the ventral border of the open Meckelian canal (=sulcus cartilaginis Meckelii). The angular closes this canal towards the back. The rugose surface is clearly visible if the element is viewed laterally. The middle third of the inner ascending margin of the dorsal groove is raised, but it slants anteroventrally and posteroventrally respectively. Anteriorly it slants towards the spicular anterior tip and posteriorly towards a slightly raised posterior tip. A small, laterally extending foramen is present near the dorsal edge of the raised inner ascending margin and it becomes confluent with the small ventrally directed foramen mentioned previously.

Viewed medially, the element is boat-shaped with a slightly raised posterior tip and a spicular anterior tip. The raised inner ascending margin forms the middle section of the boat shape.

B. **Chamaeleo**

The long slender splint-like element forms the ventral border of the middle section of the mandible.

In ventral view the anterior half of the angular is syndesmotically attached to the ventral border of the open Meckelian canal. The element is not associated with the dorsal border of the Meckelian canal, nor the closing of it. The canal remains open along the length of the dentary. The posterior half is syndesmotically applied to the compound bone. The latter is discussed later. The anterior tip is spicular whilst the slightly wider posterior tip is bifurcated. The latter divides the posterior tip in a larger lateral, spicular tip and a smaller medial, spicular tip.

In dorsal view the wide posterior tip curves dorsomedially. The lateral edge of the posterior tip is confluent with the smaller spicular tip and curves upwards to form a small groove. The posterior end of the groove originates between the larger and the smaller spicular tips and extends anteroventrally. The lateral rim of the groove is formed by a ridge which extends anteriorly from the larger spicular tip and ends in a very thin, ascending blade-like ridge in the anterior portion of the element. The lateral surface of the ascending ridge is rugose to assist a syndesmotic attachment to the medial surface of the dorsal border of the Meckelian canal. A very small foramen lies in the middle of the dorsally directed ridge. The latter ends anteriorly as the blade-like ascending ridge. The anterior section of the ascending ridge is excavated in an anteroventral direction and becomes confluent with the dorsal surface of the spicular anterior tip. The dorsomedial surface of the ascending ridge is slightly excavated in a posterior direction. This indicates the surface where the angular is applied to the anterior extremities of the compound bone, directly below the ventral edge of the coronoid.

C. **Cordylus**

The element forms the ventral margin of the posterior half of the lower jaw. Only the wider posterior half of the element is visible in the lower jaw.

The small, spint-like element, if viewed ventrally, shows the lateral edge of the anterior half of the element tapering anteromedially to form a spicular anterior tip. The posterior half of the element is rectangular, with the posterior edge showing marked variations such as being bifurcated in one animal and pointed in another of the same species. The medial edge of the element extends from the spicular anterior tip towards the posterior margin. A small recess in the lateral margin of the element indicates the border between the posterior half and the anterior half. The lateral edge of the posterior half of the element forms a laterally extending ledge syndesmotically applied to the ventral edge of the surangular portion of the fused compound bone. The ventrolateral surface of the anterior half of the element is slightly recessed towards the anterior spicular tip. A small, shallow, anteriorly directed groove lies near the medial edge of the recessed surface. This surface is rugose for firm syndesmotic attachment to the dorsomedial surface of the ventral posterior process of the dentary. A distinctive <-shaped border indicates where the dentary overlaps the anterior half of the angular.

In dorsal view the surface of the element is even with the border between the anterior half and the posterior half clearly visible. A small anteromedially directed foramen is present in the middle of the posterior half of the element. The medial edge of the posterior half of the bone extends dorsomedially, forming a small dorsomedially directed ledge. The latter is applied to the ventrolateral edge of the prearticular element of the compound bone.

In medial view the thin, blade-like anterior half of the element is visible. The posterior half of the element appears wider due to the dorsomedially directed ledge mentioned above. A small posterolaterally directed foramen is present in the middle of the dorsomedially directed ledge. This foramen exits on the medial surface of the bone.

D. **Pachydactylus**

Jollie (1960) states that the angular is presumed to be absent or fused to the prearticular and surangular in most geckos. He further notes that the trend in lizards is to reduce the splenial first and then loose the angular later. In geckos the angular is lost (as the result of fusion or reduction) before the splenial. The element is not seen in disarticulated skulls of the Gekkonidae (Cope, 1892), but is fused with the articular (=articular + gonial; = prearticular). Although the medial margin of the element is visible, the remaining border is indistinct because of fusion with the compound bone. The spicular anterior tip of the element is characteristic and clearly visible in the fused element (=compound bone). The ventrolateral surface of the element is pitted and uneven. The description of the element will be included as part of the fused compound bone.

E. **Meroles**

The anterior half of the bone forms the ventral margin of the lower jaw, whilst the posterior half forms the ventrolateral margin.

In ventral view the anterior half is splint-like with the posterior half slightly thicker. A small posterodorsally directed foramen is present in the middle of the ventral edge of the angular.

In lateral view the posterior half of the element is expanded. The dorsal ledge is syndesmotically applied to the ventral margin of the surangular, while the ventromedial edge is applied to the dorsolateral edge of the prearticular element of the compound bone. The anterior half of the element forms the spicular anterior tip. The lateral surface of the spicular tip is recessed and rugose for firm attachment to the overlapping dorsomedial surface of the ventral posterior process of the dentary. The <-shaped border is also visible.

In medial view the deeply recessed posterior half of the angular is visible. The dorsal border of the recessed area extends upwards as an ascending ledge which is applied to the ventral edge of the surangular. The ventral edge of the recess extends medially to form a flange which is applied to the dorsolateral edge of the prearticular.

F. **Mabuya**

The bone is present as a mere splinter. The anterior half forms part of the ventral margin of the lower jaw. The posterior half forms a narrow strip on the ventrolateral surface of the lower jaw. In lateral view the element is thin and blade-like.

In ventral view the narrower anterior half extends forwards to form the spicular anterior tip. The posterior half is slightly wider than the anterior half. The lateral edge of the posterior half forms a dorsolaterally extending ledge where it is applied to the ventral edge of the surangular. A small dorsomedially directed foramen is present in the middle of the posterior half of the angular. The anterior two thirds of the element is recessed towards the spicular anterior tip. The surface of the recessed area is rugose for attachment to the overlapping dorsomedial surface of the ventral posterior process of the dentary. The border between the elements coincides with the foramen referred to above.

In dorsal view a wide anteroposteriorly extending groove is present on the dorsal surface of the element. The spicular anterior tip and the truncated posterior border is also clearly visible in dorsal view. A small, ventrally directed foramen lies in the middle of the posterior half of the element. The medial edge of the angular extends dorsally to form a slightly thicker flange which is firmly applied to the ventral edge of the prearticular. The thin, blade-like, dorsolaterally extending ledge mentioned above, slants from the middle of the element in an anterolateral direction towards the spicular anterior tip.

G. **Varanus**

The anterior half of the element, overlapped by the ventral posterior process of the dentary, forms the ventral border of the lower jaw. The posterior half of the bone extends posterodorsally to form a thin, blade-like ledge terminating in a posterior spicular tip. The dorsal surface of this ledge is syndesmotically applied to the middle portion of the ventral edge of the surangular and the middle section of the ventral edge of the prearticular respectively. These midventral edges meet in a suture line between the prearticular and the surangular respectively. The area on both the surangular and prearticular, covered by the dorsal surface of the blade-like ledge, is recessed with the posterior spicular tip firmly wedged in the posterior extremity of the recessed area.

In ventral view the posterior half of the element resembles the blade of a knife with the sharp edge (the thin blade-like edge mentioned above) extending dorsolaterally. It tapers posteromedially towards the posterior spicular tip. The sharp edge is recessed near the middle of the element and becomes confluent with a small but prominent anterolaterally extending ridge which leads to the spicular anterior process. A small, laterally directed cusp-like process lies at the border between the sharp, recessed edge posteriorly and the anterolaterally extending ridge anteriorly. The ridge slants dorsolaterally to form an ascending ledge. The latter abuts against the inner ventral surface of the surangular. The medial edge of the anterior half of the element extends ventrally to form a prominent descending ridge. Both ridges on the anterior half of the angular are covered by the ventral posterior process of the dentary. The anterior half of the descending ridge extends dorsally to a small, anteriorly directed tip (=lesser spicular anterior tip) situated on the inside of the spicular anterior tip. The area between the anterolaterally directed ridge and the descending ridge is recessed. The anterior edge of the recess is jagged.

The dorsal surface of the blade-like posterior half of the element is rugose. A shallow tortuous groove lies in the dorsal surface from the spiky posterior tip to the incline formed by the dorsolaterally slanting ascending ledge seen in ventral view. The margin of the ascending ledge extends anteriorly towards the spiky anterior tip. The dorsal surface of the anterior half of the element has a wide groove which extends from the jagged anterior edge backwards towards the middle of the element. The medial margin of the wide groove is present as a raised ridge extending from the lesser spicular anterior tip towards the middle of the element. From the middle, the raised ridge flattens and becomes confluent with the dorsal surface of the posterior half of the angular, thus completing the medial margin of the element. A short, narrow groove is present in the middle of the element lateral to the wide groove. A large medially directed foramen lies in the middle of the short, narrow groove. A small foramen passes through the ridge which separates the wide and narrow grooves and enters the large foramen.

In medial view the posterior extremity of the element slants upwards towards the posterior spicular tip. The bone is laterally compressed and deepest at its middle portion. Anteriorly it tapers to a spicular tip. A large foramen, confluent with the foramen seen in dorsal view, lies in the posteriorly on the middle portion. The portion of the bone anterior to the large foramen is slightly recessed, indicating the area covered by the inner surface of the ventral posterior process of the dentary.

In lateral view the anteroventrally slanting blade-like edge of the posterior half of the element and the dorsolaterally extending edge of the anterior half is visble. A short, anteroposteriorly directed groove in the middle of the element seperates these two edges. The ventrally extending ventral edge of the wide medial surface in the anterior half of the element, is also visible in ventral view.

5. Fused surangular + articular + prearticular (Figs. 113 - 115)

Camp (1923) mentions that the articular and the prearticular(=gonial) are fused in all the adult lizards he has studied. It implies that the articular must be seen as part of the fused, composite element and not as a seperate bone. Du Plessis (1944) states that the gonial (=prearticular) and the surangular are fused to the articular, but not to each other. Jollie (1960) also notes that fusion of the surangular, prearticular and articular occurs. The articular extends from the articular surface in a posterior direction to form the retroarticular process except in the chameleons (Engelbrecht, 1951; Jollie (1960) where it is absent. Camp (1923) and Van Pletzen (1946) indicate that the retroarticular process is formed by the fused articular and prearticular. The prearticular possesses a medial process (=processus subarticularis of Siebenrock, 1895;

angular process of Oelrich, 1956) below the articulatory surface. The process may be large and winglike as in *Agama* or poorly developed or even absent in other lizards (Jollie, 1960). The general structure of this compound bone consists of the surangular laterally, the articular posteriorly and the prearticular medially, except for most geckos, where the angular is presumed absent or fused to the surangular and prearticular. The mandibular fossa (=prearticular fossa; adductor fossa, Romer, 1956), found in the composite bone, is bordered laterally by the surangular; posteriorly by the articular surface and medially by the prearticular. The ventral border/floor of the fossa is formed by the surangular and the prearticular. The suture line between these two elements is overlapped by the posterior half of the splint-like angular. The anterior border is formed by the posterior process of the inverted V-shaped coronoid. Due to fusion, the composite bone will be discussed as a unit.

A. **Agama**

In ventral view the retroarticular process is fairly long with a truncated tip. The medial edge of the process extends anteriorly and near the middle of the element it slants anteromedially to form the posterior margin of the wing-like medial process discussed above. The anterior edge of the medial process extends posterolaterally but curves anteriorly to continue as the medial edge of the prearticular towards a thin blade-like anterior tip. The lateral edge of the prearticular forms a ridge and extends from the anterior tip posteriorly along the suture line between the prearticular and surangular. The ventral surface of the prearticular portion has a posterolaterally extended recessed area for the attachment of the posterior half of the angular. The dorsal surface of the recessed area forms the base/ floor of the mandibular fossa. The medial border of the recessed area slants posterolaterally towards a tapered tip in line with the tip of the medial process. The lateral border of the recess is formed by the narrow ventral edge of the surangular. The latter is present as a narrow, blade-like element extending posteriorly from an anterior tip along the lateral border of the compound bone to a laterally extended protuberance that indicates the lateral border of the articular surface. The posterior margin of the protuberance extends medially towards the body of compound bone and then curves posteriorly to form the lateral edge of the retroarticular process.

In dorsal view the prominent retroarticular process extends dorsally. The anterior border of the process diverts to form the posterior edge of the articulatory surface. A small medial and a lateral excavation is present on the posterior border of the articular surface. A small anteriorly directed foramen lies in the anterior border of the small medial excavation. The articular surface has a medial and a lateral depression, with a wide ridge-like structure bisecting the surface. The mandibular condyle of the quadrate articulates with the articular surface. The mandibular fossa is present as a narrow, elongated vacuity bordered posteriorly by the dorsolaterally extending anterior rim of the articular surface. The prominent medial process and the laterally extending protuberance can be seen on the medial and lateral sides of the articular surface respectively. The dorsal edge of the prearticular extends anteriorly from the anterior rim of the articular surface towards the anterior tip. The ventral margin of the prearticular slants medially forming a curved surface in the anterior two thirds of the element. The dorsal edge of the surangular is wider than that of the prearticular and it extends anteriorly from the dorsolateral extremity of the articular surface towards the anterior tip. The dorsal edge of the surangular has a recessed, rugose area where the posterior process of the coronoid is syndesmotically applied. The ventral portion of the coronoid extends downwards from this recess as the ventral process crossing over the anterior extremity of the prearticular to form the anterior border of the mandibular fossa.

Viewed medially, the element is boat-shaped with the distinctive, elongated retroarticular process. The dorsal edge of the process curves anterodorsally towards the posterior margin of the articular surface. The medial tip of the posterior margin of the articular surface is tubercle-like. Anterior to the tubercle the dorsal surface curves gradually towards the truncated anterior tip of the prearticular. A feint, anteroventrally directed ridge extends from the medial edge of the tubercle towards the tip of the medial process. The ventral edge of the retroarticular process curves downwards and slightly medially to become confluent with the tip of the medial process. The surface behind the feint, anteroventrally directed ridge is slightly excavated. The excavation extends posteriorly becoming narrower dorsoventrally and slightly more shallow. Anterior to the medial process the ventral margin curves upwards to reach the truncated anterior tip of the prearticular. The surface anterior to the medial process is deeply recessed, forming a wide groove towards the truncated anterior tip. The dorsal margin of the surangular rises anterodorsally to protrude above the dorsal margin of the prearticular. The recessed area for attachment of the posterior half of the angular on the ventral surface of the prearticular is also visblein medial view.

In lateral view the retroarticular process extends posterodorsally. The dorsal surface of the process curves anteroventrally towards the articular surface. The dorsal margin of the surangular slants anterodorsally to the dorsal aspect of the anterior edge of the element. The ventral margin of the retroarticular process curves anteroventrally up the ventral extremity of the articular surface and then continues anterodorsally towards the truncated anterior tip of the prearticular. The lateral surface of the retroarticular process extends anteriorly and then curves laterally to form the laterally extending protuberance which forms the lateral border of the articular surface. The dorsal and ventral edges of the surangular converge posteriorly to form a spicular posterior tip. The feint sutural lines of this spicular posterior tip is present on the lateral surface of the laterally extending protuberance. The lateral surface of the surangular broadens from the spicular posterior tip anteriorly. A small, medially extending foramen is present in the middle of the spicular posterior tip. A deep <-shaped recess is present in the dorsal extremity of the lateral surface for the syndesmotic attachment of the dorsal posterior process of the dentary. A shallow <-shaped recess is present in the ventral extremity of the lateral surface for the attachment of the ventral posterior process of the dentary. A C-shaped vacuity occurs between the two <-shaped recessed areas on the lateral surface. The vacuity forms the posterior part of a large medially directed foramen. The anterior border of this foramen is formed by the posterior margin situated between the dorsal and ventral posterior processes on the lateral surface of the dentary. The lateral surface of the anterior portion of the prearticular protrudes beyond the anterior tip of the surangular.

B. **Chamaeleo**

In ventral view the ventral margin of the prearticular extends from a spicular anterior tip towards a tubercle-like posterior tip. A narrow, posteriorly directed recessed area is present on the anterior half of the ventral margin for the syndesmotic attachment of the angular. The ventral margin of the prearticular continues posteriorly towards the tubercle-like posterior tip. The articular surface lies on the dorsal surface of the tubercle-like posterior tip. A retroarticular process is absent. The lateral and medial surfaces of the tubercle are indented with a small circular excavation on either side. Both the medial process and the lateral extending protuberance are absent.

In dorsal view the articular is recessed both medially and laterally with prominent posterior and anterior rims. The anterior rim is raised and extends anteriorly to form the dorsal margin of the surangular. This margin is bisected and the medial portion extends anteriorly. The lateral portion slants anteroventrally towards a large, inverted C-shaped notch which represents the posterior extremity of a large, laterally situated foramen. The anteroventrally extending margin curves posteriorly below the inverted C-shaped notch to form the ventral margin of the surangular. A small, ventromedially directed recess is present on the dorsal surface of the anteriorly extended medial section of the surangular. The posterior process of the coronoid is syndesmotically applied to this recess. The ventrolateral edge of the posterior process of the coronoid is applied to the dorsal edge of the dorsal posterior process of the dentary. Ventral to the surangular, the rodlike prearticular extends anteriorly towards a spicular anterior tip. A deep, narrow anteroposteriorly directed groove is present on the dorsal surface of the prearticular. The groove continues backwards and forms a posteriorly directed foramen underneath the articular surface. The groove forms part of the ventral border of the mandibular fossa.

In lateral view the surangular is short and sturdy compared to the long, narrow, ventrally situated prearticular. The articular surface is directed posterodorsally and notched. The anterolateral surface of the anteroventrally extending lateral margin, directly above the inverted C-shaped notch, is slightly recessed where the posterodorsal process of the dentary is applied. The longer ventral border of the notch extends anteriorly to form a spiky anterior tip. The ventral side of the tip extends posteriorly as the dorsal edge of a large excavation covered by the posteroventral process of the dentary. The ventromedial border of the large excavation is formed by a thin membrane-like ventromedial surface of the surangular. A suture line is present between the ventral edge of the membrane-like surface and the dorsal edge of the posterior half of the prearticular. The suture line extends towards the anteroventrolateral tip of the articulatory surface where it fades. A small, medially directed foramen lies above the posterior margin of the large excavation and directly in line with the lateral margin of the articular surface. The surface of the anteriorly directed medial portion of the dorsal edge of the surangular, which is visible above the anteroventrally extending lateral edge, extends ventrally to become confluent with the thin membrane-like ventromedial surface of the large excavation. The prearticular extends anteriorly from the tubercle-like posterior tip of the articular surface as a rod-like element towards the spicular anterior tip. The dorsomedial edge of the prearticular groove, discussed above, rises slightly above its dorsolateral edge.

In medial view the posterodorsally directed articular surface is visible. The medial edge of the articular surface has a medially directed tubercle which forms the dorsal margin of the circular excavation present on the medial surface of the tubercle-like posterior tip of the prearticular. A small anterolaterally directed foramen occurs in the middle of the circular excavation. A small medially directed tubercle completes the anterior margin of the circular excavation. The prearticular extends anteriorly from this small tubercle towards the spicular anterior tip on the dorsomedial edge of the prearticular where the ventral process of the coronoid is attached. The anterior extremity of the recess on the ventral surface of the prearticular, for attachment of the posterior portion of the angular, is visible in medial view. The anterior rim of the articular surface curves anterolaterally and becomes confluent with the anteriorly directed medial section of the dorsal edge of the surangular. The anterior rim of the articular surface is formed by the surangular as the suture line between the surangular and the articular is clearly distinguishable. A small, posteriorly directed foramen lies in the middle of the curvature in the posterior extremity of the surangular directly below the anterior rim of the articular surface. The ventrally directed membrane-like surface of the surangular forms the lateral wall of the mandibular fossa. The overlapping, ventrally directed ventral process of the coronoid completes the anterior border of the mandibular fossa and covers the truncated anterior tip of the surangular.

C. **Cordylus**

In ventral view the slender, ventromedially situated prearticular extends from a spicular anterior tip, widening slightly outwards towards a laterally compressed retroarticular process, which curves posteromedially. A small laterally directed tubercle lies on the posteroventral tip of the retroarticular process. The surangular extends anteriorly from the retroarticular process, curving along the lateral margin of the posterior half of the lower jaw. Ventrolaterally the surangular forms an anteriorly extending suture with the narrow, blade-like margin of the prearticular. Both the ventrolateral surface of the dorsolaterally extending edge of the prearticular and the ventrolateral surface of the ventrolaterallly extending edge of the surangular are recessed and rugose for the syndesmotic attachment of the posterior half of the angular. A small foramen is present on the lateral surface of the posterior half of the surangular.

In dorsal view the retroarticular process is laterally compressed. The ventral margin of the articular surface is ridge-like and possesses a small, medially directed tubercle. The posterior edge of this small tubercle extends posteriorly as a small ridge on the medial surface of the retroarticular process. The ridge-like anterodorsal rim of the articular surface extends laterally and curves posteriorly to become confluent with the dorsolateral edge of the surangular. The anterodorsal rim extends medially towards a large dorsomedially directed tubercle. The large tubercle is confluent with the ventrolateral ridge present on the articular surface. The surface is slightly excavated anterior to the anterodorsal rim. Two small, ventrally directed foramina, one in the posteromedial and one in the posterolateral edge of the excavation, are present. A small, dorsally directed tubercle lies on the dorsolateral edge of the surangular and forms the lateral border of the small posterolaterally situated foramen. Anterior to this tubercle the lateral edge of the anterior third of the element curves anteromedially and slightly ventrally. It then slants anteroventrally towards the spiky anterior tip. Anterior to the large dorsomedially directed tubercle the medial edge of the surangular curves anterolaterally towards a large dorsomedially directed and blade-like tubercle. The latter is bordered anteromedially by the upper extremity of the posterior process of the coronoid. Anterior to the anterodorsal rim of the articular surface, the wide dorsal surface of the surangular extends anteriorly towards the middle of the element. The surface then slants ventrolaterally and becomes confluent with the lateral edge of the surangular. Anterior to the large, dorsomedially directed and blade-like tubercle the medial edge slants anteroventrally towards the spiky anterior tip. A posteriorly directed foramen lies on the ventrolateral surface, below the tip of the large blade-like tubercle. The posterodorsal extremity of the outer ventral process of the coronoid is applied to the anterior edge of the blade-like tubercle. The anterodorsal surface of the anteroventrally slanting anterior third of the surangular is slightly recessed and uneven for the firm attachment to the inner surface of the dorsal posterior process of the dentary. A small, blade-like ridge is present on the slanting surface referred to above. A small, narrow anteroventrally directed groove lies medial to the ridge.

In lateral view the retroarticular process is sturdy and laterally compressed. Its posterodorsal margin extends anterodorsally from the small, laterally extending tubercle to a dome-shaped tubercle representing the lateral border of the articular surface. The anterior margin of the dome-shaped tubercle slants anteroventrally and continues anteriorly as the dorsolateral edge of the ventrolaterally slanting dorsal surface of the surangular. The anterior edge of the retroarticlar process extends slightly anteriorly to form a small tubercle. The dorsal edge of the small tubercle is slightly excavated towards the back. It then curves anterodorsally and becomes confluent with the ventromedial margin of the surangular. This margin extends anteriorly to the rugose ventrolateral margin where the dorsal surface of the posterior half of the angular is syndesmotically applied. A small, medially directed foramen lies on the smooth, lateral surface of the surangular, in line with the anterior edge of the dorsally directed dome-shaped tubercle.

In medial view the prearticular is rod-like medially and the surangular, which rises above the prearticular, is broad. The dorsal edge of the spicular anterior tip slants posterodorsally to form a small dorsally directed tubercle. The posterior edge of this tubercle slants posteroventrally but then rises again to form a larger, dorsally directed tubercle. The dorsolateral surface of this second tubercle is syndesmotically applied to a narrow ventromedially directed flange of the surangular to form the anterior border of the mandibular fossa. The ventromedially directed posterior process of the coronoid extends over the syndesmosis of the surangular and the prearticular and is syndesmotically applied to a small recessed area on the medial surface of the second tubercle of the prearticular. This completes the anterior border of the mandibular fossa. The posterodorsal edge of the second tubercle slants ventrally and continues posteriorly as the dorsal edge of the prearticular forming the ventromedial border of the mandibular fossa. The dorsal edge of the prearticular reaches the base of the large dorsomedially directed tubercle at the medial tip of the anterior rim of the articular surface. The medial edge of the tubercle extends ventrally and becomes confluent with the dorsal edge of the prearticular. The dorsal edge continues backwards as a posteroventrally directed ridge on the dorsal surface of the retroarticular process. A small anterolaterally directed foramen lies in the middle of the medial surface of this posteroventrally directed ridge. The ventral margin of the retroarticular process curves medially. The blade-like, ventral margin of the surangular passes below the ventral margin of the prearticular, but is concealed by the latter in the vicinity of the second tubercle. The dorsal margin of the spicular anterior tip of the surangular slants posterodorsally and rises above the dorsal edge of the prearticular reaching the anterior margin of the blade-like tubercle mentioned above. The dorsal margin of the surangular extends posteriorly from the anterior tip of the bladelike tubercle towards the anterior edge of the large tubercle on the medial side of the anterior rim of the articular surface. The medial surface of the surangular possesses a longitudinal excavation extending from the anteromedial edge of the articular surface towards the spicular anterior tip of the bone. A narrow, ventromedially directed flange situated posteroventral to the blade-like tubercle, divides the longitudinal excavation in an anterior portion and a posterior portion.

D. **Pachydactylus**

The angular could not be disarticulated during preparation. It is assumed that the element is either absent or fused with the surangular and prearticular. The surangular and prearticular are not fused to each other but both are probably fused with the articular. A suture between the surangular and prearticular demonstrates this fact. The angular is associated with both these elements by means of syndesmosis. What seems to be a fused area between the surangular and the prearticular, may in fact be the angular. If the suture between the surangular and prearticular is complete, it can be presumed that the angular is absent. Embryonic studies may solve this problem.

In ventral view the surangular dominates the prearticular in that only a small splint-like prearticular is visible medial to the surangular. The lateral edge of the prominent surangular curves posterolaterally from the spicular anterior tip to the anterior edge of an anteromedially directed and dorsoventrally flattened retroarticular process. The lateral margin of the surangular extends from the anterior edge of the anteromedially directed notch in an anterolateral direction. Near the middle of the element, the lateral edge slants anteromedially to the spicular anterior tip. The posterior half of the ventrolateral surface is therefore wide whilst the narrower anterior half tapers anteriorly. A pitted surface lies midway along the ventrolateral edge. A small, anteromedially directed foramen is present next to the posterolateral edge of the ventral surface of the surangular, directly anterior to the anteromedially directed notch. A second small, posterodorsally directed foramen lies directly anteromedially to the first. The anteromedial edge of the dorsoventrally flattened retroarticular process slants anterolaterally and continues anteriorly as the medial edge of the thin, splint-like prearticular. An anterodorsally directed ridge originates on the anteromedial edge of the retroarticular process, diagonally opposite the anteromedially directed notch, forming the medial rim of the articular surface when viewed dorsally. A feint ridge, confluent with the medial edge of the prearticular, extends ventrally midway along the ventrolateral surface of the retroarticular process.

In dorsal view the articular surface slants posteromedially to the proximal portion of the retroarticular process. A dorsoventrally directed ridge bisects the articular surface and extends from the middle of the dorsal rim of the articular surface towards the anterior edge which forms the posterior border of the anteromedially directed notch. A prominent dorsoventrally directed groove lies between this ridge and the lateral rim of the articular surface. The ventral border of the groove is formed by the anteromedially directed groove. A second dorsoventrally directed groove, parallel to the first, lies between the dorsoventrally directed ridge and the medial rim of the articular surface. The second groove curves posteriorly and continues on the dorsolateral surface of the retroarticular process. A small anterolaterally directed groove is present at the base of the medial rim of the articular surface.

A dorsally directed tubercle forms the tip of the dorsoventrally directed ridge, bisecting the articular surface. The mandibular fossa extends posteriorly as a large foramen in the anterior surface, directly below the dorsally directed tubercle. The anterior surface of the medial rim of the articular surface curves anterolaterally to continue anteriorly as the medial edge of the prearticular. The middle portion of the prearticular forms the medial border of the mandibular fossa. A triangular, dorsolaterally directed flange is present on the dorsal edge in the anterior half of the prearticular. The upper half of the tip of the triangle is syndesmotically applied to a slight depression on the medial surface on the anterior half of the surangular. The anterior margin of the triangle slants anteromedially to the spicular anterior tip, whilst the posterior margin slants posteromedially and becomes confluent with the dorsal edge of the prearticular. The posteromedially slanting edge forms the anteromedial border of the mandibular fossa. The medial surface of the upper-half of the triangle is depressed and confluent with the depression on the surangular. The depression of the triangle on the prearticular is bordered anteriorly by the posterior surface of the anterior process of the coronoid, dorsally by the ventral surface of the dorsal process of the coronoid and posteriorly by the anterior surface of the ventral process of the coronoid. The lateral rim of the articular surface continues anterolaterally as the lateral edge of the surangular. The anterior half of the lateral edge extends anteromedially to the spicualr anterior tip of the surangular. A portion of the Meckelian canal is visible ventromedially on the surangular. The medial walll of the anterior half of the canal is formed by three elements: ventrally by the inner surface of the ventral posteroventral process of the dentary, medially by the posterior half of the splenial and dorsally by the anterior process of the coronoid. The spicular anterior tip of the prearticular and the lower half of the lateral surface of the triangle complete the posterior half of the medial wall of the canal. Directly above the canal the medial surface of the spicular anterior tip of the surangular is rugose for the attachment of the ventral surface of the posterior process and the body of the coronoid. Behind the rugosities the medial surface is recessed for the upper half of the triangle of the prearticular. The anterior half of the dorsal edge of the surangular above the recess is rugose for the attachment of the posterior process of the coronoid. The posterior half of the dorsal edge of the surangular continues backwards and becomes confluent with the anterolateral edge of the tip of the dorsally directed tubercle. The former forms the dorsolateral rim of the mandibular fossa. The medial surface below the posterior half of the dorsal edge of the surangular forms the lateral wall of the mandibular fossa. It also forms the medial wall of a posteriorly directed canal which indicates a bifurcation in the Meckelian canal posteriorly. Medially it leads to the mandibular fossa and laterally it continues as the Meckelian canal. A small, posterodorsally directed foramen is present in the posterolateral wall of the mandibular fossa.

In lateral view the posteriorly extending portion of the dorsoventrally flattened retroarticular process is visible. The anteromedially directed notch forms the anterior border of the retroarticular process. The anterolateral edge of the notch extends anterodorsally to form the lateral rim of the articular surface. The anterodorsal tip of the lateral rim rises medially to reach the dorsally directed tubercle of the bisecting dorsoventral ridge. The anterior edge of the tubercle slants anteroventrally to form the dorsal surface of the surangular. Near the middle of the element the dorsal edge curves anterodorsally and then slants anteroventrally towards the spicular anterior tip. The ventral margin of the surangular extends anteriorly from the tip of the anterolateral edge of the anteromedially directed notch towards the spicular anterior tip of the bone. The dorsolateral surface of the posterior half of the surangular slants ventrolaterally towards the ventral edge. A small, posteriorly directed foramen is present in the anterior portion of the dorsolateral surface. Ventral to the foramen the anterior margin of the pitted lateral surface is L-shaped. The surface between the L-shaped margin and the spicualar anterior tip, is recessed and rugose for the attachment of the inner surfaces of the dorsal and ventral posterior processes of the dentary. A small, posteriorly directed foramen, in line with the foramen on the anterior portion of the dorsolateral surface, lies in the upper portion of the depression.

Viewed medially, the dorsal surface of the dorsoventrally flattened retroarticular process slants anterodorsally to the dorsally directed tubercle on the anterior rim of the articular surface. The medial edge of the anterodorsally slanting surface forms the medial rim of the articular surface. The dorsal margin of the surangular extends anteriorly from the anterolateral surface of the dorsally directed tubercle to form the dorsal aspect of the lateral wall of the mandibular fossa. The dorsal edge of the fossa extends anterodorsally before it slants anteroventrally towards the spicular anterior tip. The recess in the medial surface of the surangular lies in line with the triangle of the prearticular. Anteriorly the Meckelian canal traverses the ventromedial portion of the surangular. The ventral margin of the groove extends posteriorly from the spicular anterior tip along the suture between the prearticular and the surangular. This ventral edge becomes confluent with the ventral edge of the prearticular directly below the ventral border of the mandibular fossa. The dorsal tip of the medial rim of the articular surface slants anteroventrally and becomes confluent with the anteromedially slanting surface of the dorsally directed tubercle to form the dorsal surface of the prearticular. The latter forms the dorsal surface of the medial wall of the mandibular fossa. This dorsal surface slants anterodorsally as the posterior edge of the triangle, before it slants anteroventrally to the spicular anterior tip of the prearticular.

E. **Meroles**

In ventral view the prearticular is rod-like posteriorly and blade-like anteriorly. The retroarticular process is directed posterolaterally. A small, wing-like flange is present on the lateral and medial sides of the retroarticular process. The medial flange extends anterodorsally towards a small, laterally directed notch before it joins the ventral margin of a medially directed tubercle. The ventral margin of the prearticular extends anteriorly from the retroarticular process towards the spicular anterior tip of the element. A thin, recessed flange lies on the ventrolateral edge of the prearticular. It is bordered medially by a small, posterolaterally extending diagonal groove. Anteromedially the prearticular is slightly excavated and is confluent with the depression bordered by the anterior and posterior processes of the coronoid. An anterolaterally directed suture line on the anteroventral edge of the anterodorsal rim of the articulatory surface lateral to the medially directed tubercle mentioned above indicate the fusion between the surangular and the articular.

In dorsal view a depression is present in the dorsal surface of the retroarticular process. It is bordered medially by an anterodorsally directed ridge which extends from the tip of the retroarticular process towards the ventral tip of the medial rim of the articular surface. The lateral border of the depression is formed by an anterodorsally directed ridge which extends from the tip of the retroarticular process towards the ventral tip of the lateral rim of the articular surface. Anteriorly the depression is bordered by the posteroventral rim of the articular surface. The lateral rim of the articular surface curves dorsomedially, becomes confluent with the anterodorsal rim and extends medially to the medially directed tubercle. The latter marks the dorsomedial border of the articular surface. A wide ventromedially directed ridge extends from the medially directed tubercle in the dorsomedial rim of the articular surface to the ventrolateral tip of the lateral rim of the articular surface and becomes confluent with the lateral edge of the posteroventral rim. The anteromedial edge of the medially directed tubercle extends anterolaterally to form the medial edge of the surangular. The middle portion of the medial edge rises slightly in an anteromedial direction to form a small protuberance for the syndesmotic attachment of the ventral edge of the dorsal process of the coronoid. The anterior edge of the protuberance slants anteroventrally and continues anteriorly towards the spicular anterior tip of the bone. The latter is overlapped by the dorsal and ventral posterior processes of the dentary. The anterior margin of the anterolateral tip of the lateral rim of the articular surface extends anteriorly to form the lateral edge of the surangular and reaches the lateral extremity of the spicular anterior tip.

In lateral view the ventral margin of the retroarticular process extends anteriorly to form the ventral margin of the prearticular. The dorsal margin of the prearticular slants anteroventrally along the suture line between the surangular and the prearticular and then turns dorsolaterally so that the dorsal surface of the element becomes confluent with the ventral edge of the element. The ventral edge continues anteriorly to the spicular anterior tip. The ventral margin of the surangular follows the suture line between the surangular and the prearticular to the spicular anterior tip of the surangular. The dorsal margin of the spicular anterior tip slants posterodorsally to the protuberance mentioned above. The dorsal margin continues posteriorly from the protuberance to the anterior margin of the dorsal rim of the articular surface. The latter slants posteroventrally to the posterior tip of the retroarticular process. The lateral surface of the surangular bulges outwards from the dorsal margin towards the suture line. Anterolaterally the surangular is recessed for the syndesmotic attachment of the dorsal and ventral posterior processes of the dentary. The lateral surface of the protuberance is recessed for the syndesmotic attachment of the ventral surface of the dorsal process of the coronoid. The ventral margin of this depression is clearly marked on the anterodorsal extremity of the lateral surface of the surangular, directly above the attachment for the dentary. A recessed area, which overlaps the suture line between the surangular and the prearticular, is present on the ventrolateral surface of the compound bone. The posterior half of the angular is syndesmotically applied to this recessed area. The dorsal two thirds of the recess occurs above the ventral edge of the surangular and the ventral third below the dorsal edge of the prearticular. The dorsal and ventral margins of the recess extends posteriorly to converge at a point below the dorsal rim of the articular surface. A small, posteromedially directed foramen is present in the posterodorsal corner of the lateral surface, directly anterior to the anterodorsal tip of the lateral rim of the articular surface. A small depression lies on the ventrolateral surface below the posteroventrally slanting ridge extending from the lateral rim of the articular surface and the tip of the retroarticular process.

In medial view the prominent medially directed tubercle of the anterodorsal rim of the articular surface is visible. The ventral margin of the tubercle extends posteroventrally to form the medial rim of the articular surface. The medial rim continues posteroventrally towards the tip of the retroarticular process forming the medial edge of the recess in the dorsal surface of this process. The ventral margin of the prearticular extends anteriorly from the tip of the retroarticular process towards the spicular anterior tip. The dorsal edge of the spicular anterior tip extends posterodorsally to form a triangular protuberance syndesmotically applied to a slight recessed area in the medial surface of the protuberance on the dorsal margin of the surangular. This syndesmotic contact is overlapped by the posterior process of the coronoid. The posterior edge of the triangle slants posteroventrally and continues posteriorly as the dorsal edge of the prearticular to the anterior surface below the medially directed tubercle. The anteromedial edge of the tubercle slants anterolaterally and continues anteriorly as the dorsal edge of the surangular to the dorsally directed protuberance before it slants anteroventrally towards the spicular anterior tip. The ventral edge of the surangular extends from the spicular anterior tip posteriorly to the anterior surface below the medially directed tubercle. The medial surface of the surangular, which extends anteriorly from the dorsally directed protuberance towards the spicular anterior tip, is rugose for the attachment of the anterior process of the coronoid and the dorsal posterior process of the dentary respectively. The tip of the triangle of the prearticular is syndesmotically attached to the ventral edge of the rugose medial surface of the protuberance of the surangular. The anteroventral surface of the triangle of the prearticular is recessed for the attachment of the posteromedially directed process of the coronoid. The mandibular fossa is bordered anteriorly by the posterior edge of the triangle, ventrally by the dorsal surface of the posterior half of the prearticular, dorsally by the ventral surface of the posterior half of the surangular and posteriorly by the anterior surface below the anterodorsal rim of the articular surface. The ventral edge of the posterior half of the surangular extends ventrolaterally to form the lateral wall of the mandibular fossa. The anterior part of a wide posteriorly directed groove, bordered dorsally by the ventral surface of the dorsal edge of the surangular, laterally by the lateral surface of the surangular, anterolaterally by the anterior part of the angular, ventrally by the ventral posterior process of the dentary and medially by the inner surface of the spicular anterior tip of the prearticular, extends backwards to become confluent with the anterior part of the mandibular fossa.

F. **Mabuya**

In ventral view the narrow blade-like ventral margin of the prearticular extends anteriorly from the ventral tip of the retroarticular process towards the slightly medially directed spicular anterior tip. A recessed area extends from the ventromedial surface of the spicular anterior tip, along the anterior half of the ventral edge of the prearticular and continues posterolaterally onto the lateral surface of the surangular. An anteromedially directed ridge extends from the medial edge of the tip of the retroarticular process towards a prominent anteromedially directed tubercle on the medial edge of the anterodorsal rim of the articular surface. A small, medially directed protuberance lies on the ridge midway between the tip of the retroarticular process and the anteromedially directed tubercle. The spicular anterior tip of the prearticular extends anteromedially while the spicular anterior tip of the surangular continues anteriorly. The result is that the surangular is longer than the prearticular and the suture line between these two elements widens anteriorly. The ventral surface of the surangular has a posteriorly directed groove which disappears below the shorter tip of the prearticular.

In dorsal view the posteromedially directed articular surface is bisected by a wide but inconspicuous posterolaterally directed ridge. This ridge extends from the anteromedially directed tubercle on the medial tip of the anterodorsal rim and becomes confluent with the dorsal margin of the retroarticular process. The anterodorsally directed lateral rim of the articular surface is continuous with the dorsal margin of the retroarticular process. A small, posterodorsally directed tubercle is present where the anterodorsal rim and the dorsal tip of the anterodorsally directed lateral rim of the articular surface meet. A large excavated area lies on the medial surface of the retroarticular process, bordered anteriorly by the articular surface, dorsally and ventrally by the dorsal and ventral margins of the retroarticular process respectively, and posteriorly by a truncated tip. The ventral margin of the retroarticular process extends anterodorsally along the medial rim of the articular surface to the anteromedially directed tubercle on the medial tip of the anterodorsal rim of the articular surface. A lesser, medially directed tubercle lies midway along the ridge formed by the anterodorsally directed ventral edge of the retroarticular process. This edge extends from the larger anteromedially directed tubercle towards the posteroventral extremity of the truncated posterior tip. Anterior to the anterodorsal rim of the articular surface the dorsal surface of the surangular extends anteriorly and tapers anteromedially towards the spicular anterior tip. The anterior margin of the anteromedially directed tubercle curves anteriorly to form the medial border of the dorsal surface of the surangular. A small, ventrally directed foramen lies in a small recess in the dorsal surface of the surangular, anterior to the anterodorsal rim of the articular surface and near the tip of the anteromedially directed tubercle. The thin, blade-like, dorsally directed dorsal margin of the prearticular slants posterodorsally to form a dome-shaped elevation. The posterior margin of the dome slants posteroventrally and becomes confluent with the dorsal edge of the posterior half of the prearticular bordering the mandibular fossa anteriorly and ventromedially.

In lateral view the retroarticular process extends ventromedially and the posterior margin is truncated. The dorsal tip of the truncated edge possesses a small, dorsolaterally directed tubercle which forms the posterior extremity of the dorsal edge of the retroarticular process. This dorsal edge extends anteriorly, then curves dorsally and forms the lateral perpendicular rim of the articular surface. The dorsal tip of the lateral rim slants anterodorsally along the dorsal edge of the surangular to a raised, triangular tuberosity before sloping anteroventrally towards the spicular anterior tip. The dorsal area of the triangular tuberosity is rugose for the attachment of the ventral surface of the dorsal process of the coronoid. The ventral margin of the surangular extends posteroventrally in the anterior half of the element then curves posterodorsally towards the back along the suture line between the surangular and the prearticular. A recessed area on both sides of the suture line indicates the attachment of the angular to the surangular and the prearticular. The prearticular is visible below the surangular in line with the triangular elevation, widens posteriorly along the ventral edge of the compound element and becomes confluent with the ventral margin of the retroarticular process. A small, ventromedially directed foramen lies on the lateral surface of the surangular above the posterior margin of the recessed area for the angular. A small, posteromedially directed foramen is present on the lateral surface near the apex of the triangular elevation.

In medial view a laterally directed excavation in the medial surface of the retroarticular process is bordered posteriorly by the truncated posterior tip. The ventral margin of the excavation slants anterodorsally to the lesser, medially directed tubercle, continues anterodorsally and eventually reaches the larger anteromedially directed tubercle refered to in dorsal view. A small, anteriorly directed foramen lies in the posterior wall of the lesser, medially directed tubercle. The ventral surface of the ventral margin of the excavation slants ventrolaterally and becomes confluent with the ventral margin of the retroarticular process. This ventral surface also extends anterodorsally to become confluent with the ventral surface of the larger anteromedially directed tubercle. The ventral surface of the larger tubercle extends laterally, then curves ventrally and continues anteriorly as the medial surface of the prearticular. The dorsal margin of the medial surface of the prearticular slants anteroventrally from the anteroventral extremity of the larger anteromedially directed tubercle and continues anteriorly to form the ventromedial border of the mandibular fossa. The ventral margin of the medial surface of the prearticular extends anteriorly from the ventral extremity of the truncated posterior tip of the retroarticular process to the spicular anterior tip. The dorsal margin of the spicular anterior tip slants posterodorsally to a small dome-shaped elevation which is syndesmotically applied to the middle of the medial surface of the surangular, posteroventral to the triangular elevation on the surangular. The posterior margin of the dome slants ventrally forming the anterior border of the mandibular fossa and curves posteriorly as the dorsal margin of the prearticular. The dorsal margin of the spicular anterior tip of the surangular slants posterodorsally to the triangular elevation discussed above and then continues posteriorly as the dorsal margin of the surangular. The latter then slants ventrally to form the perpendicular, lateral rim of the articular surface and curves posteriorly as the dorsal margin of the retroarticular process. The medial surface of the surangular is confluent with the anterior margin of the larger anteromedially directed tubercle and extends anteriorly to the spicular anterior tip. The ventrolateral margin of the medial surface of the posterior half of the surangular forms the lateral wall of the mandibular fossa. A small, dorsolaterally directed foramen lies in the posterior extremity of the lateral wall of the mandibular fossa. The ventral surface of the spicular anterior tip of the surangular has a posteriorly directed groove which, together with the posteriorly directed groove in the dorsal surface of the spicular anterior tip of the prearticular, form the Meckelian canal. The canal continues backwards to the prominent mandibular fossa. A small anterior portion of the canal remains open as the spicular anterior tips of the surangular and the prearticular are not in syndesmosis. A recessed area on the ventral margin of the prearticular, into which the angular is syndesmotically applied, is clearly distinguishable.

G. **Varanus**

The compound bone, compared to that of other genera discussed, is rather large.

In ventral view the retroarticular process is stout and posteriorly truncated. The ventromedial margin of the retroarticular process extends anteromedially to a large anteromedially directed tubercle situated on the medial extremity of the anterodorsal rim of the articular surface. The anterior margin of this tubercle slants anterolaterally, curves anteriorly along the medial edge of the prearticular to the laterally directed excavation and continues anteriorly towards the spicular anterior tip. The posterior margin of the excavation is formed by an anterodorsally directed ridge and becomes confluent with the syndesmotically applied ventral process of the coronoid. The lateral margin of the retroarticular process extends anterodorsally towards a laterally directed elevation which represents the lateral rim of the articular surface.

The anterior margin of the elevation extends anteriorly and curves anteromedially in the anterior half of the compound bone towards the spicular anterior tip of the surangular. A rugose, recessed area is present on the lateral surface of the spicular anterior tip, indicating the attachment between the surangular and the posterior processes of the dentary. A prominent suture line between the surangular and the prearticular originates in the lateral edge of the retroarticular process midway between the laterally directed elevation and the truncated posterior tip of the retroarticular process. This suture line extends anteromedially along the ventral edge of the compound bone terminating in a vacuity formed by the spicular anterior tips of the surangular and the prearticular. A small, anteriorly directed groove lies in the ventral margin of the anterior half of the prearticular. This groove terminates in the posterior extremity of the vacuity. A recessed area in the anterior half of the compound bone overlaps the suture line. This recessed area extends anteromedially from the lateral margin of the surangular towards the vacuity. The anterior half of the angular is syndesmotically attached to the recessed area and closes the vacuity as part of the Meckelian canal. The ventrolateral edge of the spicular anterior tip of the prearticular has a small, posteriorly directed tube-like recess. The inner edge of this recess is perforated by 12 - 16 foramina.

In dorsal view the retroarticular process is bordered posteriorly by a truncated tip. The lateral margin of the process extends anterolaterally and becomes confluent with the lateral rim of the articular surface. The anterior portion of the lateral rim is raised anterodorsally and becomes confluent with the lateral portion of the anterodorsal rim of the articular surface. A small, blade-like, dorsolaterally directed ridge extends anteromedially from the posterolateral side of the truncated posterior tip towards the anterolateral extremity of the posterior rim of the articular surface. The posterior rim extens posteromedially, curves anteromedially and becomes confluent with the posterior portion of the anteriorly directed medial rim of the articular surface. The medial margin of the retroarticular process extends anteriorly and becomes confluent with the medial rim. A small, medially directed tubercle lies midway on the medial edge of the retroarticular process. The dorsal surface of the retroarticular process has a wide recessed area bordered medially and laterally by the medial and lateral edges of the retroarticular process, posteriorly by the truncated tip and anteriorly by the posterior rim of the articular surface. A large, anteriorly directed foramen lies on the base of the anterior surface of the posterior rim. The anterodorsal rim extends dorsomedially towards the medial rim near the anteromedially directed tubercle. The anteromedial margin of the tubercle extends anterolaterally along a suture line. This line terminates in a small, oval, anteriorly directed mandibular fossa. A broad, anteriorly directed ridge lies midway along the anterior surface of the anterodorsal rim of the articular surface and forms the border between the rim and the anterolateral extending surface of the surangular. A small foramen, lateral to the broad, anteriorly directed ridge, lies on the anterior edge of the anterodorsal rim. The anteromedial surface of the surangular extends anteroventrally, then curves anterolaterally and forms the lateral wall of the mandibular fossa. The anteromedial surface of the surangular is bordered by a broad, anteriorly directed ridge laterally, the anterior edge of the anterodorsal rim posteriorly and the suture line medially. A large, posterolaterally directed foramen lies midway between the broad, anteriorly directed ridge and the anteromedial surface of the surangular. A smaller, posterolaterally directed foramen lies anteroventrally to the larger foramen. The dorsal edge of the surangular extends anteriorly from the lateral tip of the anterodorsal rim towards a small, anterolaterally directed flange. This flange extends across the broad, dorsal edge of the surangular and becomes confluent with a small ridge on the lateral margin of the surangular. The area anterior to this ridge is recessed for the syndesmotic attachment to the ventrolateral margin of the coronoid. The recessed area anterior to the small flange extends anteriorly towards a small, anterolaterally directed groove. The lateral portion of the groove extends anteroventrally on the dorsomedial margin of the surangular towards the anteriorly directed protuberance on the dorsal margin of the spicular anterior tip. The medial portion of the groove extends posteromedially towards the suture line between the medial surface of the surangular and dorsal edge of the prearticular. The contact between these two elements forms the anterodorsal border of the mandibular fossa. A small, anteriorly directed flange is present on the lateral margin of the protuberance and the spiky, anteromedially directed spicular process on the medial edge of the surangular. The dorsoventrally directed groove, between the small flange and the anteriorly directed protuberance, is perforated by 9 - 12 small foramina. Numerous foramina lies on the medial surface of the protuberance. The dorsal margin of the spicular anterior tip of the prearticular extends posterodorsally forming a blade-like dorsally directed ridge. This ridge is in syndesmosis with the medial surface of the surangular. The syndesmotic contact extends from the posterior portion of the anteriorly directed spicular process towards the anterior border of the mandibular fossa. The suture line between the surangular and the prearticular extends posteromedially from the mandibular fossa towards the anteromedial tip of the large anteromedially directed tubercle. The dorsal edge of the prearticular extends ventrally from the tip of the anteromedially directed tubercle towards the dorsomedial edge of the surangular. The dorsal edge of the prearticular forms the medial border of the mandibular fossa.

In lateral view the retroarticular process has a deep, annular groove anterior to the truncated posterior tip. A small, medially directed foramen lies inside the groove midway on the retroarticular process. The dorsal margin of the retroarticular process extends anterodorsally towards the posterior rim of the articular surface. The dorsolateral surface of the retroarticular process extends anterodorsally and becomes confluent with the lateral rim of the articular surface. The dorsal margin of the surangular extends antroventrally from the anterodorsal rim, then curves anterodorsally and reaches the small anterolaterally directed flange. The dorsal margin extends from this flange towards a triangular protuberance in the anterior half of the surangular. The anterior margin of the surangular extends ventrally from the ventral edge of the anteriorly directed protuberance towards the spicular anterior tip. A small, posteriorly directed foramen lies ventrolaterally on the tip of the anteriorly directed protuberance. The ventral margin of the spicular anterior tip extends posteriorly and then posterodorsally towards the triangular protuberance on the dorsal edge of the surangular. The ventral margin of the surangular continues posterodorsally along the suture line towards the lateral surface of the retroarticular process. A recessed area in the ventral margin of the middle third of the surangular is bordered ventromedially by a recessed area on the prearticular. The posterior half of the angular is in syndesmosis with this recessed area. The lateral surface of the retroarticular process extends anteriorly and becomes confluent with the lateral surface of the prearticular. A small, medially directed foramen lies on the lateral surface of the surangular anterior to the rim of the articular surface. A small, anteroventrally directed ridge, confluent with the flange on the dorsal margin of the surangular, forms the ventral border of a recess at the base of the triangular protuberance. The ventrolateral margin of the coronoid is in syndesmosis with this recessed area. A large, posteriorly directed foramen lies on the lateral surface of the surangular, below the middle portion of the small, anteroventrally directed ridge. The recessed area, dorsal to the small, anteroventrally directed ridge, is bordered anteriorly by the small, anteriorly directed flange. This flange is on the lateral surface of the protuberance on the dorsal margin of the spicular anterior tip. The ventral margin of the small, anteriorly directed flange extends posteroventrally as a rugosed ridge on the lateral surface of the surangular and fades at the ventral edge of the element. The area anterior to this flange is recessed. The dorsal and ventral posterior processes of the dentary are in syndesmosis with the recessed area.

In medial view the ventrally directed recess in the dorsal surface of the retroarticular process is visible. The recess is bordered anteriorly by the posterior rim of the articular surface, posteriorly by the truncated posterior tip, laterally by the small, blade-like, dorsally directed ridge and medially by the medial edge of the retroarticular process. The medial edge of the retroarticular process extends anteriorly and becomes confluent with the medial rim. A lateromedially extending excavation lies in the posterior half of the articular surface. The anterior half of the articular surface is bordered by the anterodorsal rim anteriorly which terminates medially in the anteromedially directed tubercle. The suture line extends anterolaterally from the anteromedially directed tubercle and terminates in the mandibular fossa. The dorsal edge of the surangular extends anteriorly towards the small, anterolaterally directed flange and continues anterodorsally towards the dorsally directed triangular protuberance. The anterior margin of the triangular protuberance extends anteroventrally and curves upwards. It then extends ventrally towards the anteriorly directed protuberance on the dorsal edge of the spicular anterior tip. The ventral edge of the protuberance extends ventrally towards the spicular anterior tip forming the anterior edge of the surangular. The dorsolateral surface of the surangular extends anteriorly from the anterior edge of the anterodorsal rim. Midway between the rim and the small flange it tilts medially and becomes confluent with the dorsal edge of the surangular laterally and the anterior portion of the anteriorly directed ridge medially. A large, posterolaterally directed foramen lies in the posterior portion of lateral wall of the mandibular fossa below the posterior portion of the broad, anteriorly directed ridge. A smaller, posterolaterally directed foramen lies anteroventrally to the larger foramen. The lateral wall of the mandibular fossa fades behind the anterolaterally extending dorsal edge of the prearticular. The broad, anteriorly directed ridge continues anterodorsally and terminates in the posteroventral portion of the small, anterolaterally directed groove. A posterolaterally directed recess, perforated by numerous posteriorly directed foramina, is present below the anteroventral margin of the small, anterolaterally directed groove. The recess extends anteriorly and becomes confluent with the medial surface of the anterior potion of the surangular. The recess is bordered ventrally by the suture line and the dorsal edge of the anterior portion of the prearticular. The anteroventral part of the anteriorly directed medial surface of the surangular extends ventromedially to form the anteromedially directed spicular process. A small, posterolaterally directed foramen lies midway between the tip of the anteromedially directed spicular process and the posterior wall of the posterolaterally directed recess above the suture line. The anterodorsal portion of the anteriorly directed medial surface continues anteriorly towards the tip of the anteriorly directed protuberance. A large, posteriorly directed foramen lies on the medial surface of the protuberance. Numerous small foramina lie above and below this large foramen. A posteriorly directed groove lies in the middle of the medial surface of the surangular ventral to the protuberance. The spicular anterior tip of the surangular, anteroventrally to the posteriorly directed groove, is obscured by the spicular anterior tip of the prearticular. A deep, posteriorly directed notch lies between the ventral margin of the anteromedially directed spicular process and the dorsal margin of the spicular anterior tip of the prearticular. The ventral margin of the retroarticular process curves anterodorsally towards the anterior border of the mandibular fossa and continues anteriorly towards the spicular anterior tip of the prearticular. The dorsal margin of the spicular anterior tip of the surangular rises posterodorsally along the suture line to a large posteriorly directed foramen in the anterior tip of the dorsal margin of the prearticular. The foramen opens in the anterodorsal extremity of the mandibular fossa. The dorsal margin of the prearticular extends anteriorly from the tip of the anteromedially directed tubercle of the anterodorsal rim towards the suture line. The dorsal margin of the prearticular extends anterolaterally towards the posteroventral tip of the small, anterolaterally directed groove on the dorsal margin of the surangular and forms the medial border of the mandibular fossa. The prearticular is recessed anteromedially for the syndesmotic attachment of the posteroventral process of the coronoid. The narrow, anteromedial surface of the anterolaterally extending dorsal margin of the prearticular curves anteriorly along the smooth medial surface of the prearticular towards the spicular anterior tip.

C. **Dentition** (Figs. 116 - 122)

A concise explanation of dental terminology is required before describing the lacertilian dentition. Mesial, distal, labial and lingual are terms preferred rather than orientations such as anterior, posterior, lateral and medial respectively. The change in terminology is brought about by the curvature of the dental arcade. The tip or apex of the tooth is referred to as the crown or the occlusal surface whist the part in contact with the jaw bone is called the base. The crown may be biconodont, triconodont or tritubercular. Biconodont and triconodont refer to teeth with two or three cusps arranged in a straight mesiodistal row, while tritubercular refers to three cusps arranged in a triangular pattern on the occlusal surface of the tooth. Teeth occur in a marginal row on the maxilla, premaxilla and dentary, but may also occur on the pterygoid and palatine in single or subparallel rows.

Reptilian teeth are constantly being replaced throughout the life of the animal, a condition referred to as polyphyodonty. According to Edmund (1969 p. 120) the teeth are not replaced as "sets", but many teeth in different parts of the mouth undergo replacement at any one time. Polyphyodonty is essential to reptiles, as the jaws are relatively small when hatched and must increase in size many times before reaching maturity. Also, because of the simple structure of the reptilian teeth, replacement is necessary to ensure proper crown shape and sharpness as the young must be ready to feed and defend themselves soon after hatching. Tooth replacement may be partially or completely suppressed in some species after a certain age. The condition, referred to as oligophyodonty, is demonstrated in the acrodont lizard species (Edmund, 1960).

Edmund (1969) mentions that the replacement rhythm may or may not be synchronous on both sides of the mouth. If synchrony is present, it is usually manifest only on the premaxilla. He further notes that quite commonly a midline tooth, possibly a successor to the egg tooth, is present and that it is flanked by two or three symmetrically arranged teeth.

The shape of the reptilian teeth correlate with their carnivorous or herbivorous habits. The cheek teeth of the adult molluscivorous Nile Monitor, *Varanus niloticus*, are broad and biscuit-shaped (Edmund, 1969). In the most primitive reptiles all the teeth are of approximately the same size and form, a condition termed homodonty. Where different modes of feeding occur, the teeth in different areas of the jaw have become specialized so that they are of different sizes or shapes, a condition called heterodonty.

Edmund(1969) mentions that the three classical types of tooth implantation, viz. acrodont, pleurodont and thecodont, found in most modern reptiles, are derived from a fourth type, called subthecodont or protothecodont. The latter is not found in any living reptile. In a subthecodont dentition, the base of each tooth is ankylosed in a deep socket. These sockets are arranged in a row in a dental groove bordered by a labial and a lingual wall or ridge.

Acrodonty occurs where both the lingual and the labial walls of the dental groove are absent, leaving the teeth ankylosed to the crest of the tooth-bearing bone. Acrodont teeth are rarely replaced once a certain stage of growth is reached (Edmund, 1969).

Pleurodonty, a common mode of implantation in lizards, is attained by the loss of the lingual wall, leaving the teeth ankylosed to the inner side of the labial wall. The degree of affiction of individual teeth varies greatly, even along the length of a single jaw (Edmund, 1969).

Thecodonty, where each tooth possesses a long cylindrical base, set in a deep bony socket, is restricted to the Crocodilia.

The dentine of the teeth is ankylosed to the dentary by "bone of attachment", which seems to be essentially the same as cementum. The bone of attachment is formed and resorbed as each tooth completes its life cycle. The bone of attachment is more cellular, the lacunae are larger and the collagen fibres in the matrix are coarser, more prominent and less orderly arranged than that of the bones of the jaw (Edmund, 1969).

The number of teeth in the different taxa used in this study vary remarkably, but Edmund (1969) warns against the use of tooth counts as absolute taxonomic criteria in any group, especially for single individuals of unknown age. Dental histology, dental development, detailed study of tooth replacement or dental ontogeny are beyond the scope of this study and will not be discussed.

A. Agama

The dentition is predominantly acrodont, but a number of pleurodont teeth are present in the anterior regions of the upper and lower jaw. Both acrodont and pleurodont teeth vary in size in different areas of the mouth which imply specialization. Only the pleurodont teeth are actively replaced, while new acrodont teeth are added to the posterior end of each tooth row. The lower dentition mirrors that of the maxilla.

A single, small conical pleurodont tooth is present in the midline of the premaxilla and is flanked by one small and two large conical pleurodont teeth on the anterior tip of each maxilla. A small conical pleurodont tooth is present on the mesial side of a larger conical tooth at the symphysis mandibularis of the lower jaw. The small conical teeth of the upper and the lower jaws are sharp-tipped and incisiform, while the larger conical teeth are caniniform. The constant replacement of the pleurodont teeth may sometimes result in having only one large conical tooth in the right upper or left upper jaw instead of two. The tip of the larger conical tooth of the dentary curves anterolaterally to fit snugly in a vacuity between the outer incisor and the first of the larger caniniform teeth of the maxilla. The labial surface of the larger conical teeth is convex and the lingual surface is slightly flattened and excavated. The tips of the caniniform teeth are sharp and recurved in order to firmly grip prey items.

The acrodont teeth have broad bases, crescentic-tips and are laterally compressed giving each tooth a distinctive, triangular profile. The bases of consecutive teeth follow directly onto that of the antecedent tooth without any mentionable gaps between any two adjoining teeth. The teeth in the anterior half of the upper and lower jaw are small, become larger towards the middle of the posterior half and end off with two to three slightly smaller teeth. The teeth mentioned serve as crushing cheek teeth and can be regarded as molars. The heterodont teeth of *Agama* are therefor incisiform, caniniform and molariform..

The occlusal surfaces of the maxillary and dentary teeth do not make contact when the mouth is closed, but do interdigitate.. The lingual surfaces of the maxillary teeth shear against the labial sides of the dentary teeth. This shearing action is abrasive on the two mentioned surfaces and consequently they become triangular. The tips of the maxillary teeth lean slightly ventromedially and as the abrasive action of the maxillary teeth extends beyond the dentary teeth, they eventually cut vertical V-shaped grooves into the dorsolateral edge of the labial wall of the dentary. The opposite surfaces of the dentary and the maxillary teeth, not taking part in the shearing action, remain convex.

The fact that the maxillary teeth shear against the teeth of the dentary might be an explanation why the grooves are V-shaped. Vestiges of single accessory mesial and distal cusps are present on the cutting edges of each of the larger acrodont teeth to make them triconodont. The cutting edges of all the acrodont teeth are faintly crenulated.

B. Chamaeleo

The dentition is entirely acrodont with small teeth in the anterior third of the maxilla and the dentary. The teeth gradually increase in size towards the back of both the upper and the lower jaw. Each tooth is laterally compressed with a broad-base and a distinctive triangular profile. The last tooth in the lower jaw is flanked medially by the coronoid. The teeth in the posterior half of the lower jaw are recurved whilst that of the upper jaw slant ventromedially. Vestiges of mesial and distal accessory cusps are present on the mesial and distal shoulders of the teeth in the posterior half of the lower jaw. Accessory mesial and distal cusps are present on the cheek teeth of the upper jaw to make them undoubtedly triconodont.

The teeth of the upper and the lower jaw do not follow each other consecutively as in *Agama*, but alternate with distinctive gaps to allow the teeth of the upper jaw to interlock with the teeth of the lower jaw. The result is the loss of the abrasive action, as seen in *Agama*, between the lingual and labial surfaces of respectively, the maxillary and mandibular teeth. The ventromedially slanting tips of the teeth of the upper jaw cut shallow anteroventrally directed U-shaped grooves in the dorsolateral edge of the labial wall of the dentary. The grooves coincide with gaps between the teeth of the lower jaw and therefore indicate an interdigital overlap. The maxillary teeth do not shear against the dentary teeth, but carve directly onto the dentary which might explain why the carved grooves are U-shaped.

Two small acrodont teeth are present in the reduced premaxilla. Their size and general shape indicate that these teeth are incisiform.

Although no caniniform teeth are present, the remaining teeth can be regarded as molariform. The dentition is therefore heterodont.

C. Cordylus

The pleurodont teeth are homodont, more or less cylindrical in shape and their bases are mesiodistally compressed. The tips of the teeth are crescent-shaped with sharp incurved cutting edges. Vestiges of single accessory mesial and distal cusps occur on the cutting edges of some of the teeth in the middle portion of both upper and lower jaws. The teeth of the lower jaw are attached to the dentary in a vertical position, but those of the upper jaw are recurved. This condition plays a role when the animal seizes its prey. The occlusal surfaces of the teeth of the upper and lower jaws interdigitate, resulting in the tapered cutting edges described above. .The lingual surface of each tooth tapers inward from the cutting edge towards the mesiodistally compressed base giving each tooth a triangular profile with an inward flaring base when viewed medially. The bases of the teeth of the upper jaw are not lingually directed as the teeth of the lower jaw, but are slightly turned to face distolingually.

Replacement teeth in resorption pits lie in the compressed bases of their predecessors. The bone of attachment, present at the base of each ankylosed tooth, is being resorbed as the new replacement tooth becomes visible. When the replacement tooth is still small, its predecessor is shed, leaving a large area for the new developing tooth.

D. Pachydactylus

The numerous pleurodont teeth are small, bluntly pointed and closely set. They are cylindrical in shape and occur on the marginal bones only. The replacement teeth are numerous and lie in resorption pits at the bases of their respective predecessors.

Two teeth at the tip of each dentary, flanking the symphysis mandibularis, are small and incisiform. The teeth in the anterior third of the dentary jaw are elongated, incurved and caniniform. The teeth in the middle third are slightly shorter and less incurved, and those in the last section of the dentary are very short, not incurved and molariform. The occlusal surfaces of the molariform teeth are triangular due to the contact with the teeth of the upper jaw.

The teeth in the anterior half of the upper jaw are slightly elongated, incurved and caniniform. Those in the posterior half are much shorter, not incurved and molariform. Although the dentition is homodont, these variations make them heterodont.

Cusps are absent, but the cutting edges of some of the teeth are slightly crenulated.

E. Meroles

The pleurodont teeth are cylindrical, but in the posterior half of both the upper and lower jaw the teeth are mesiodistally compressed with flared bases. The lingual wall of the bases of the teeth bulge inwards and the tips of the teeth is curve lingualy. Although small structural differences are apparent, the dentitiion is homodont.

The teeth are bicuspid with the smaller cusp on the mesial side of the cutting edge. The cusps are prominent on the teeth in the posterior half of the mouth. Only a few replacement teeth are present in the resorption pits. Four ,small conical teeth are present on the posteromedial extremity of the palatine process of the pterygoid. An open space medial to the row of palatine teeth indicate the replacement of worn teeth.

F. Mabuya

The pleurodont teeth are long and cylindrical with mesiodistally compressed bases. Replacement teeth are present in resorption pits on the lingual side of the flared bases. Lingually the tooth bases bulge inwards and the tips of the teeth are curved lingually. The cutting edges of the teeth are blunt, the slightly incurved tips dome-shaped and cusps are absent. Although confined to the marginal bones, two small conical teeth lie on the posteromedial extremity of the short palatine process of the pterygoid. As in *Meroles*, an open space indicate the replacement of palatine teeth. The right premaxilla bears five teeth compared to four in the left premaxilla. As if to compensate the left maxilla possesses an extra tooth. The dentition is definitely homodont.

G. Varanus

The dentition is pleurodont and confined to the marginal bones. Open depressions occur at various sites which indicate active tooth replacement. Rieppel (1979) notes that a discontinuity of functional teeth occurs at any given site in the jaw of *Varanus* because a tooth must first be shed before it can be replaced. According to Edmund (1969) the old teeth are loosened by osteoclastic activity in the bone of attachment and that a new tooth is not ankylosed until the broad tooth base is formed. Research by Edmund (1969) shows that a regular wave-like replacement cycle is present in *Varanus*.

The shape of individual teeth vary considerably both between species and during growth (Edmund, 1969). In some species like *Varanus* the teeth change form due to age and dietary adaptations. The anterior teeth are long, cylindrical, pointed and recurved while the posterior teeth are short and bulbous with strong, flaring, striated bases. The long cylindrical recurved anterior teeth are critical for seizing and handling of large prey. In juveniles the cheek teeth are sharp-pointed but later become barrel-shaped with blunt tips as the result of a molluscivorous diet (Edmund, 1969). Rieppel (1979) mentions that recurvature in varanid dentitions developes shortly before the tooth moves into its functional site. He also notes that the recurvature increases towards the rear of the tooth row in both of the upper and lower jaw.

The teeth of the specimen used in this discussion increase in size toward the rear of the jaws. The seven teeth on the premaxilla and the anterior two teeth on the dentary are cyindrical, laterally compressed, recurved and incisiform. The anterior five teeth on the maxilla and the four teeth, succeeding the anterior two incisiform teeth on the dentary, are pointed, recurved and caniniform. The remaining three teeth at the rear of the tooth row of both the dentary and the maxilla are broad, conical, barrel-shaped and molariform. Based on the above the dentition of *Varanus* can be regarded as heterodont.

The bases of all the teeth (excluding the incisiform teeth) are broad, flaring and overgrown with bone. Striations are present on the bases of the all teeth, but are more prominent on the caniniform and the molariform teeth. The lingual wall of the tooth base of each caniniform tooth bulges lingually and the tip is recurved in lingually.

DISCUSSION AND CONCLUSIONS

Because of the generally delicate nature of fossilized lizard skulls, most specimens are fragmented or disarticulated. This severely limits the possibility of correctly identifying small specimens as is shown by the Early Pliocene material from the west coast of Southern Africa.

This preliminary but extensive osteological description of individual skull bones in seven lizard genera clearly shows that definite structural differences can be identified on single bones or bone fragments. These differences should now be tested on a larger sample of representative taxa in order to determine their applicability as parameters for identifying skull fragments in fossil assemblages.

Whether these differences are also representative of entire families should be investigated further. Anomalies such as sexual dimorphism, proportional changes in elements as well as the absence, presence or fusion of elements within genera and even species should also be addresed. However, in spite of the uncertainties mentioned above, it is clear that structural differences do exist and can be utilized as diagnostic features.

Consequently, as the result of this investigation the following groupings of features are presented as a preliminary attempt to solve this vexing problem

A. **Agama**

1. The dorsoventrally flattened, triangular skull with large close-set orbits.
2. The large pineal foramen flanked by a large supratemporal fenestra.
3. The reduced premaxilla with a single conical caniniform tooth.
4. The bifurcated ascending ledge of the maxilla and the two prominent conical teeth at the anterior tip of the bone. Five maxillary foramina are present.
5. The cleft anterior margin of the frontal with a short process lateral to the cleft.
6. The X-shaped parietal with the posterior 2/3 of the parietal foramen on the anterior margin of the bone.
7. The triangular postorbital.
8. The postfrontal is absent.
9. The jugal is L-shaped with a vestige of a posterior process.

10. The posterior extremity of the C-shaped squamosal possesses a small T-shaped process. This process may be a vestige of the supratemporal.
11. The quadrate has a well-defined cephalic condyle, bisected by a large lateral flange in an anterior and a posterior "head".
12. A vomeropalatine is present.
13. The quadrate ramus of the pterygoid is laterally compressed and its posterior half is excavated. A vertical transverse process is present.
14. The posterodorsal and the anteroventral projections of the maxillary process of the transversum are both small, but the posteroventral projection is large. A deep, wide notch is present between the maxillary and the pterygoid processes.
15. The basisphenoid is rectangular, with a small ventrolaterally directed wing-like basipterygoid process on each side.
16. The basioccipital is rectangular with a broad condylar process of the tripartite occipital condyle.
17. The tip of the short processus anterior tecti on the rectangular supraoccipital is not excavated anteriorly.
18. The lateral surface of the dentary is smooth with five mental foramina.
19. The coronoid is cross-shaped with a prominent dorsal process.
20. The long posteriorly extending retroarticular process of the fused composite bone ends in a truncated posterior tip.
21. The teeth are acrodont with conical pleurodont teeth in the anterior regions of the upper and lower jaw.

B. **Chamaeleo**

1. The skull is elongated with a large parietal crest or casque (Rieppel, 1981). The fairly large laterally.placed orbits are covered by a medially depressed shield-formed-by the aired and syndesmotically bounded frontals.
2. Ornamentation is present on the elements of the dorsal and lateral surfaces of the skull.
3. Extensive sutural interdigitations between most neibouring bones of the skull.
4. A reduced premaxilla with two small, acrodont.teeth.

5. The bifurcated ascending ledge of the maxilla and the prominent acrodont teeth. A single maxillary foramen is present.
6. The shield-shaped frontal has a central crest of protuberances.
7. The parietal is T-shaped with a long posterior process joining the squamosals to form the casque.
8. The postorbital is absent.
9. The postorbitofrontal is present in *Chamaeleo* only.
10. An L-shape jugal with rugose ornamentation on the lateral margin is present.
11. An inverted Y-shaped squamosal forms part of the crest.
12. The rod-shaped quadrate possesses a small cephalic condyle with a dorsomedially directed process. Vestiges of the lateral and.medial flanges are present.
13. The winglike laterally compressed quadrate ramus of the pterygoid is confluent with the winglike posterior margin of the transverse process.
14. The epipterygoid is absent.
15. The posterodorsal and the anteroventral projections of the maxillary process of The transversum are long, but the posteroventral projection is small and short. A shallow, wide notch is present between the maxillary and the pterygoid processes.
16. The "fused braincase" possesses distinctive suture lines with Numerous interdigitations. The paroccipital processes are short.
17. The lateral surface of the dentary is smooth with four widely spread mental foramina and a fifth foramen directly posterior to the fourth.
18. The coronoid possesses a very short posterior slanting dorsal process.
19. The retroarticular process of the fused composite bone is absent.
20. The teeth are acrodont.

C. **Cordylus**

1. The posterior half of the skull, behind the fairly large orbits, is square and the anterior half is triangular and dorsoventrally flattened.
2. The proc. internasalis of the premaxilla is wedge-shaped.

3. The maxilla is wedge-shaped. Eight maxillary foramen are present.
4. The single semi-lunate excavation on the anterior margin of the frontal indicates the extent of the overlap by the nasal elements.
5. The triangular dent, vestige of the parietal foramen, lies in a diamond-shaped area on the dorsal surface of the square parietal.
6. The narrow blade-like postorbital, with its rugose dorsal surface, possesses a posteriorly directed and tapered tip attached to the squamosal.
7. A small rectangular postfrontal is present. The anterior edge is tapered and its dorsal surface is rugose.
8. An inverse T-shaped jugal with a well developed posterior ramus is present.
9. A C-shaped squamosal is present with an inward extending flange in the middle third of the element.
10. The cephalic condyle of the quadrate appears laarger because of the the dorsal extremity of the lateral flange, but it is less prominent than the bisected mandibular condyle.
11. The ventral edge of the elongated quadrate ramus is blade-like and its medial surface is grooved. The transverse process possesses an anterodorsally directed process.
12. The pterygoid process of the transversum is bifurcated. The anteromedial projection of the maxillary process is long, the posteroventral projection is small and short and the posterodorsal projection is absent.
13. The "fused braincase" possesses no suture lines. The ventrolaterally extending basipterygoid processes are slender with small wing-like extremities. The short paroccipital processes extend posterolaterally.
14. The lateral surface of the dentary is smooth with eight mental foramina.
15. The dorsal process of the coronoid is short and stubby.
16. The retroarticular process of the fused composite bone is laterally compressed.
17. The homodont teeth are pleurodont with crescent-shaped tips.

D. **Pachydactylus**

1. The pitted dorsal surface of the slightly dome-shaped skull with two large wide-set orbits. The rectangular roof of the braincase is bisected by a groove to form a right and a left dome. The posteroventral rim of the orbits are incomplete.
2. The large posteriorly expanded lateral flanges with a short pointed proc. internasalis of the premaxilla.
3. The anterior tip of the ascending ledge of the wedge-shaped maxilla is notched. Nine maxilary foramina are present.
4. The two semi-lunar depressions on the anterior edge of the frontal, with its pitted dorsal surface, indicate the overlap by the two adjoining nasal elements.
5. The pitted dorsal surface of the square parietal, with its descending parietal processes, shows two small neighbouring domes.
6. The postorbital is absent.
7. A triangular postfrontal is present.
8. The jugal is present as a rodlike bar of bone.
9. The sqamosal is absent.
10. The cephalic condyle of the quadrate is smaller than the bisected mandibular condyle. The lateral flange is exceptionally large with only a vestige of the medial flange present.
11. The rodlike quadrate ramus of the pterygoid is long. The transverse process terminates in a sharp spiky tip.
12. The anteroventral projection of the maxillary process is long. Both the posteroventral and the posterodorsal projections are absent.
13. The "fused braincase" shows no suture lines. The long, laterally extending paroccipital processes are slender and ends in a wide flattened tip.
14. The lateral surface of the dentary is smooth, except for a pitted area on the ventrolateral edge. Six mental foramina are present with the sixth the largest.
15. The coronoid is triangular with a prominent posterodorsally curving dorsal process.
16. The ventromedially directed retroarticular process of the fused composite bone is dorsoventrally flattened.

17. The numerous pleurodont teeth are small, bluntly pointed and closely set.

E. **Merolus**

1. The small rectangular "braincase" in the posterior third of the skull is bordered anteriorly by two large close-set orbits in the middle third of the skull. The narrow, funnel-shaped and sharp-tipped anterior third of the skull borders the orbits anteriorly.
2. Distally the proc. Internasalis has a round tip.
3. The maxilla is wedge-shaped. Six maxillary foramina are present.
4. The two U-shaped depressions on the round-tipped anterior edge of the frontal indicate the attachment to the nasal elements. Dermal ornamentation, not as prominent as in *Chamaeleo*, is visible on both sides of a short longitudinal groove.
5. The longitudinal groove on the dorsal surface of the parietal forms an anterior diamond-shaped structure with the small parietal foramen.
6. The postorbital is absent.
7. A rectangular postfrontal with a rounded anterior edge is present.
8. A L-shaped jugal is present with a vestige of the posterior ramus at the posterior tip of the maxillary process. The maxillary process possesses a ventral flange.
9. The tapered anterior extremity of the squamosal is grooved and is not attached to the jugal.
10. The dorsal extremity of the narrow medial flange of the quadrate is confluent with the cephalic condyle, whilst the ventral tip of the medial flange forms a wing-like process on the mandibular condyle.
11. A groove is present in the medial surface of the slender splint-like quadrate ramus. The transverse process is short and pointed. Four prominent pterygoid teeth are present in the middle of the anteriorly directed palatine process.
12. The maxillary process is present as an elongated, anteroventral projection with vestiges of the posteroventral and posterodorsal projections.
13. The "fused braincase" possesses suture lines, but is difficult to disarticulate. The basipterygoid processes are short and stub-like. The laterally extending paroccipital processes are very short. Although the lateral margin of the basipterygoid process extends

backwards, it slants towards the prootic and not towards the spheno-occipital tubercle as in the other genera

14. The lateral surface of the dentary is smooth with six mental foramina. The foramen third from the front is slightly lower than the rest.
15. The dorsal process of the coronoid curves posterodorsally.
16. The retroarticular process of the fused composite bone extends ventrolaterally. A small wing-like flange is present on both the lateral and medial edges of the retroarticular process.
17. The pleurodont teeth are cylindrical, but in the posterior half of both the upper and lower jaw the teeth are laterally compressed with flared bases.

F. **Mabuya**

1. The small square "braincase" in the posterior half of the skull borders the large and slightly close-set orbits posteriorly. The slightly close-set orbits lie in the anterior half of the skull.
2. A pair of unfused premaxillaries are present.
3. The wingl-ike ascending process of the maxilla. Seven maxillary foramina are present.
4. The double W-shaped anterior edge of the frontal indicate attachment to the nasal elements.
5. The anteriorly directed convex coronal suture indicate firm contact with the frontal. The parietal foramen occurs in a V-shaped depression on the dorsal surface of the parietal.
6. The postorbital is present as a small splint of bone.
7. A rectangular postfrontal is present. The tips of the anterior edge form small, sharp dorsal and ventral processes. A depression in the ventral process accomodates the small postorbital.
8. The jugal is L-shaped with an exceptional long temporal process. The maxillary process is short and splint-like.
9. The squamosal is C-shaped with a vestige of the medial flange on the posterodorsal edge.
10. A shallow notch is present between the dorsal end of the medial flange of the quadrate and the cephalic condyle. The flange also possesses a small ventrally extended foramen.

11. The medial surface of the long slender quadrate ramus is grooved. A small ventral flange is present on the posterior edge of the thin anterolateral transverse process. The posteroventral part of the palatine process bears 1 - 2 pterygoid teeth.
12. The anteriorly extending maxillary process of the transversum is very small. The medial process(=pterygoid process) is bifurcated.
13. The basisphenoid is rectangular with a broad and flat ventrolaterally directed wing-like basipterygoid process on each side.
14. The basioccipital is rectangular with a narrow condylar process of the tripartite occipial condyle.
15. The anterior surface of the tip of the short processus anterior tecti on the rectangular supraoccipital is excavated.
16. The lateral surface of the dentary is smooth with nine mental foramina spaced irregularly.
17. The dorsal process of the coronoid curves posteromedially.
18. The retroarticular process of the fused composite bone extends ventromedially.
19. The pleurodont teeth are long and cylindrical with mesio-distally compressed bases.

G. **Varanus**

1. The large supratemporal fenestra bordered laterally by the rod-like, anteriorly directed squamosal and the wide-set, laterally and slightly dorsally directed orbits. The prominent, anteroposteriorly extended paired prefrontal fontanelles bisected by the very long proc. internasalis of the premaxillary
2. The long prominent proc. internasalis of the premaxilla.
3. The ascending ledge is situated posteriorly and is confluent with the posterior process of the maxilla. Ten maxillary foramina are present.
4. Paired, unfused frontals are present.
5. The anterior edge of the parietal possesses sutural interdigitations for firm contact with the frontal along the coronal suture. The small parietal foramen is oval in shape.
6. The postorbital is absent.
7. A triangular postfrontal with an elongated posterior process is present. The dorsal surface is smooth with a few small ridges and a small foramen.

8. The jugal is L-shaped with a short temporal process and a well defined maxillary process.
9. A short and shallow dorsomedial groove is present in the medial surface of the C-shaped jugal.
10. A narrow lateral flange extends ventrally from the anterior aspect of the cephalic condyle towards the mandibular condyle. A prominent foramen is present in the recessed area between the lateral flange and the curved body.
11. The quadrate ramus of the pterygoid is long and rod-like. The palatine process is bifurcated. A small dorsal process is present on the posterior edge of the well developed transverse process.
12. The maxillary process consists mainly of a long, bifurcated anteroventral projection. Vestiges of the of the posteroventral and posterodorsal projections are present. The pterygoid process is bifurcated.
13. The basisphenoid is square with a fairly large ventrolaterally directed wing-like basipterygoid process on each side.
14. The basioccipital is triangular with a broad condylar process of the tripartite occipial condyle.
15. The anterior surface of the tip of the very short processus anterior tecti on the elongated supraoccipital is wide and excavated with a small sharp-tipped anteriorly directed process on both sides of the excavation.
16. The lateral surface of the dentary is smooth with six mental foramina. The hindmost foramen is large and close to the posterior edge of the dorsal posterior process.
17. The dorsal process of the coronoid curves posteromedially.
18. The stout posteroventromedially directed retroarticular process of the fused composite bone is bordered posteriorly by a truncated tip.
19. The pleurodont teeth curve backward and are sharped-tipped.

LIST OF ABBREVIATIONS

a	Angular
bo	Basioccipital
bs	Basisphenoid
c	Coronoid
d	Dentary
e	Epipterygoid (=alisphenoid)
ext.nos	External nostril
f	Frontal
f.mag	Foramen magnum
f.par	Parietal foramen
fus.sap	Fused surangular + articular + prearticular
interpt.vac	Interpterygoid vacuity
int.nos	Internal nostril
inf.tem.fen	Infratemporal fenestra
it	Intertemporal
j	Jugal
l	Lacrimal
m	Maxilla
n	Nasal
occ.con	Occipital condyle
orb	Orbit
ot	Otoccipital
p	Parietal
p.ant.tec	Processus anterior tecti
p.par	Parietal process
p.parocc	Paroccipital process
parasph.r	Rostrum of the parasphenoid
pf	Postfrontal
pm	Premaxilla
po	Postorbital
pof	Postorbitofrontal
pos.tem.fen	Posttemporal fenestra
pp	Postparietal
pr	Prootic
prf	Prefrontal
pt	Pterygoid
q	Quadrate

qra	Quadrate ramus (=quadrate process)
s	Stapes (=columella auris)
sm	Septomaxilla
so	Supraorbital
soc	Supraoccipital
sp	Splenial
sq	Sqamosal
st	Supratemporal
sub.orb.fen	Suborbital fenestra
sup.tem.fen	Supratemporal fenestra
t	Tabular
tr	Transversum (=ectopterygoid)
vpl	Vomeropalatine

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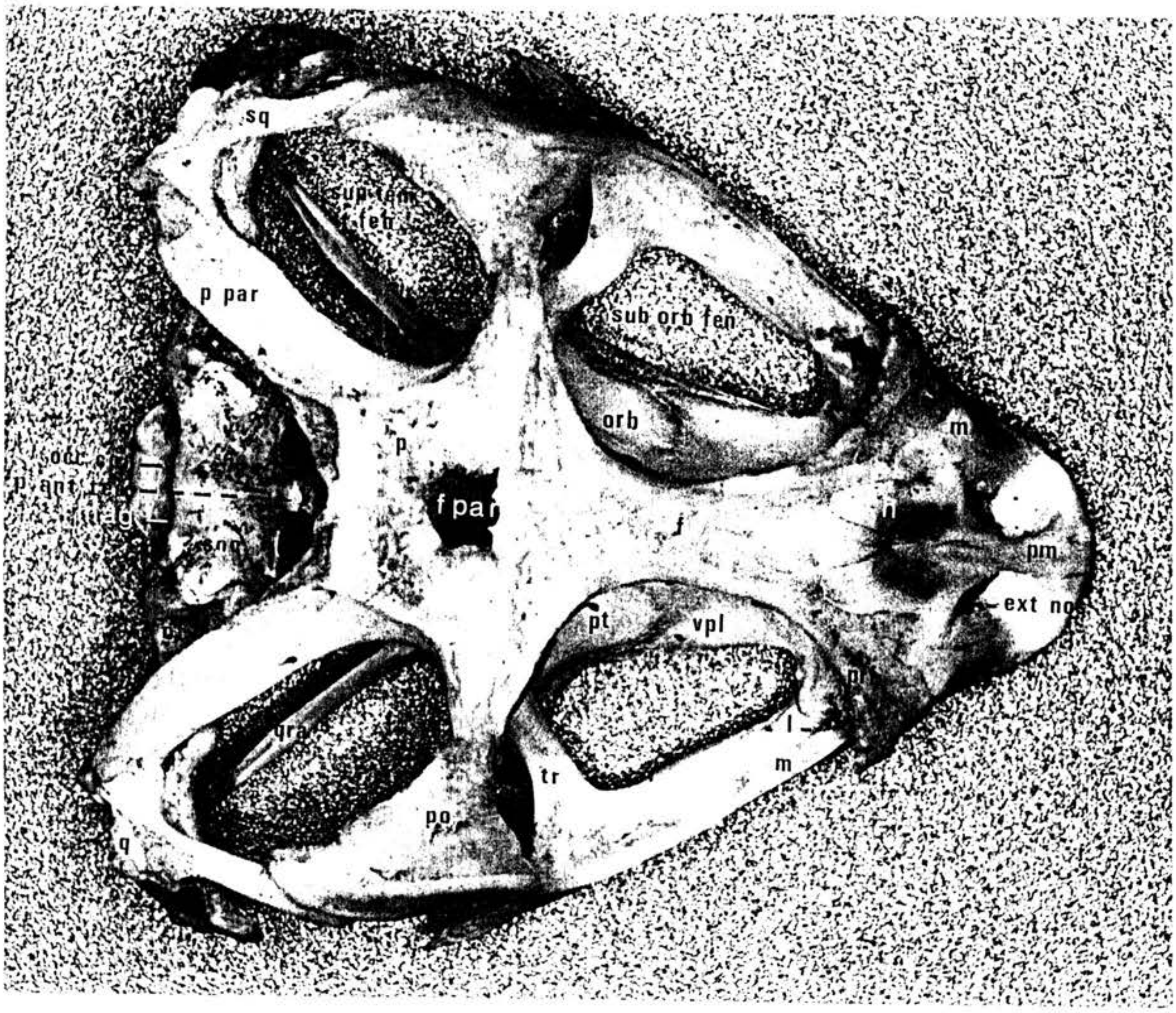

Figure 1 The skull of *Agama atra atra* - Dorsal view (x 6)

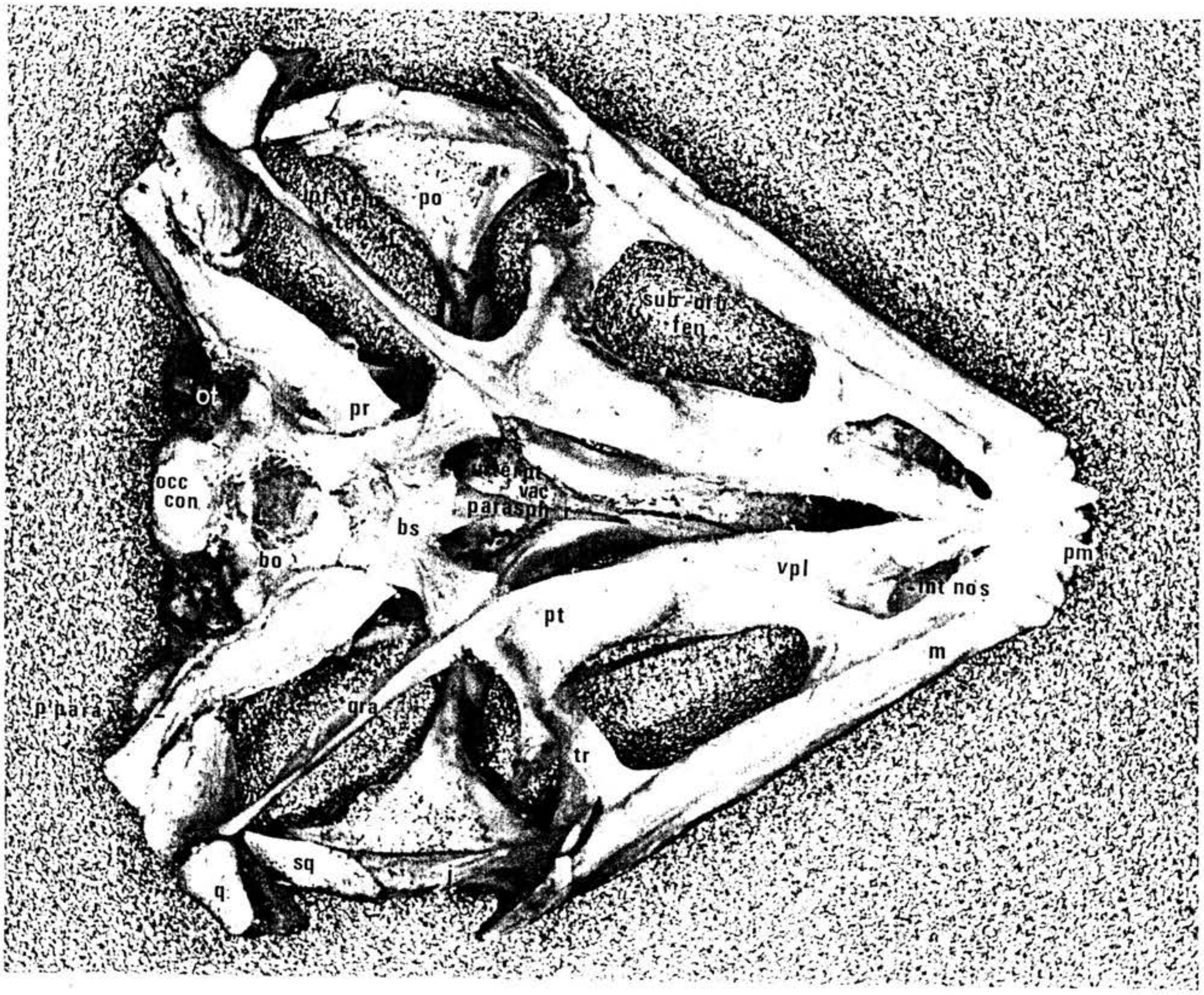

Figure 2   The skull of *Agama atra atra* - Ventral view (x 6)

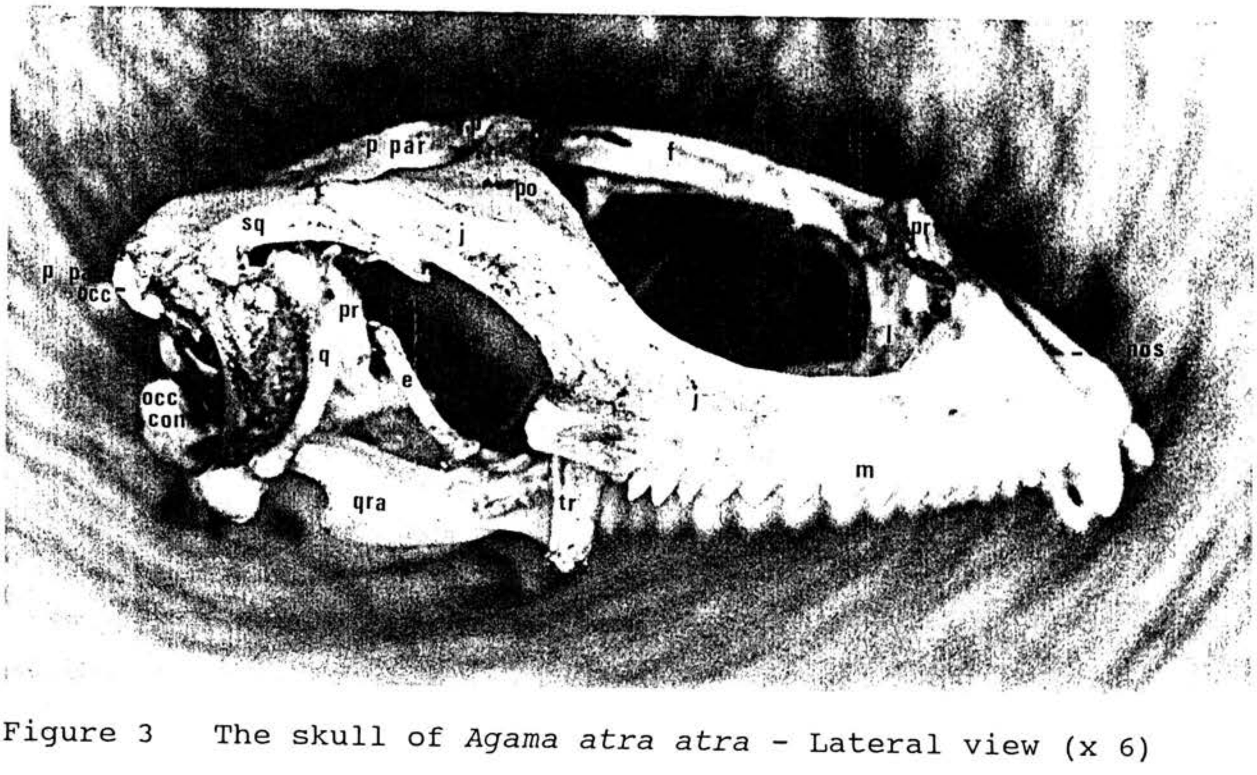

Figure 3 The skull of *Agama atra atra* - Lateral view (x 6)

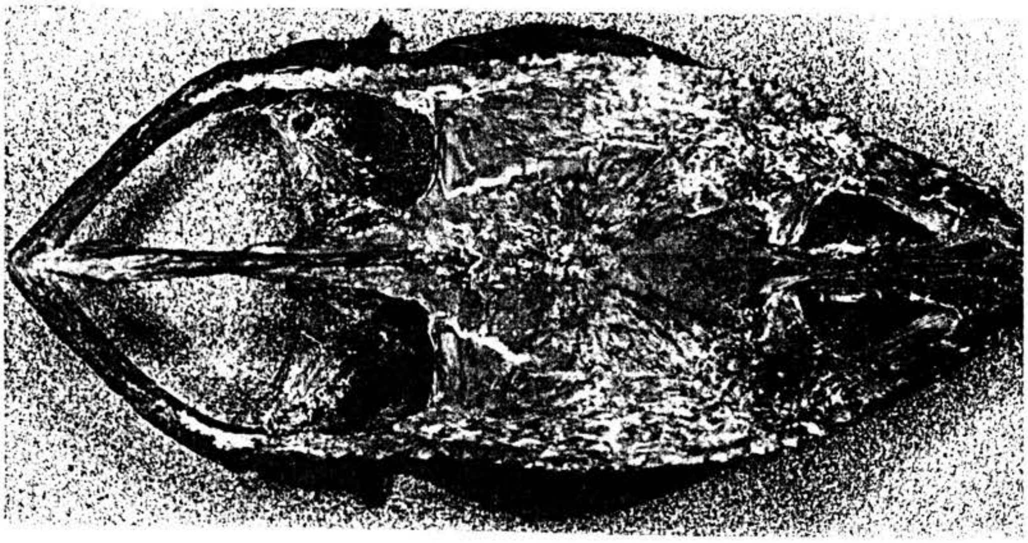

Figure 4 The skull of *Chamaeleo dilepis* - Dorsal view (x 4)

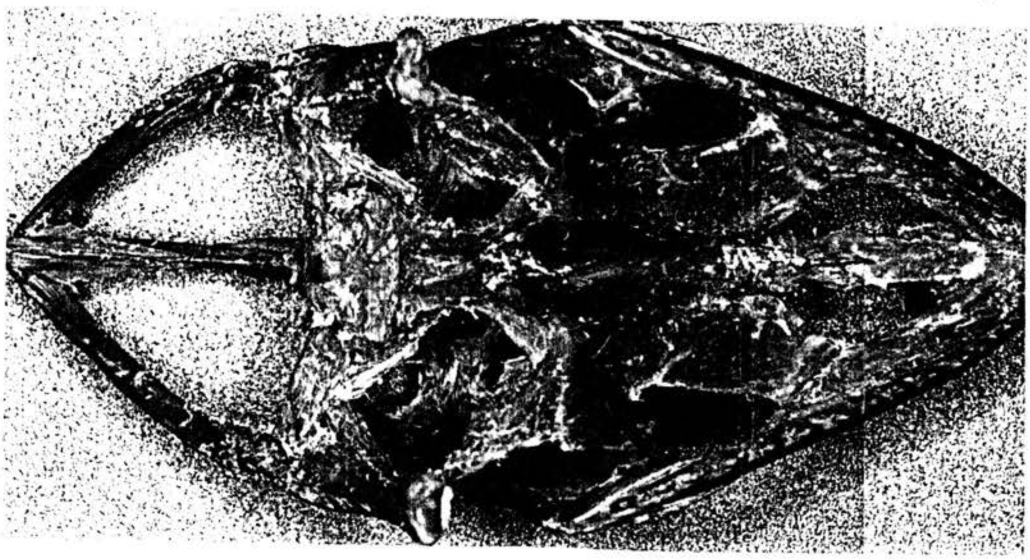

Figure 5 The skull of *Chamaeleo dilepis* - Ventral view (x 4)

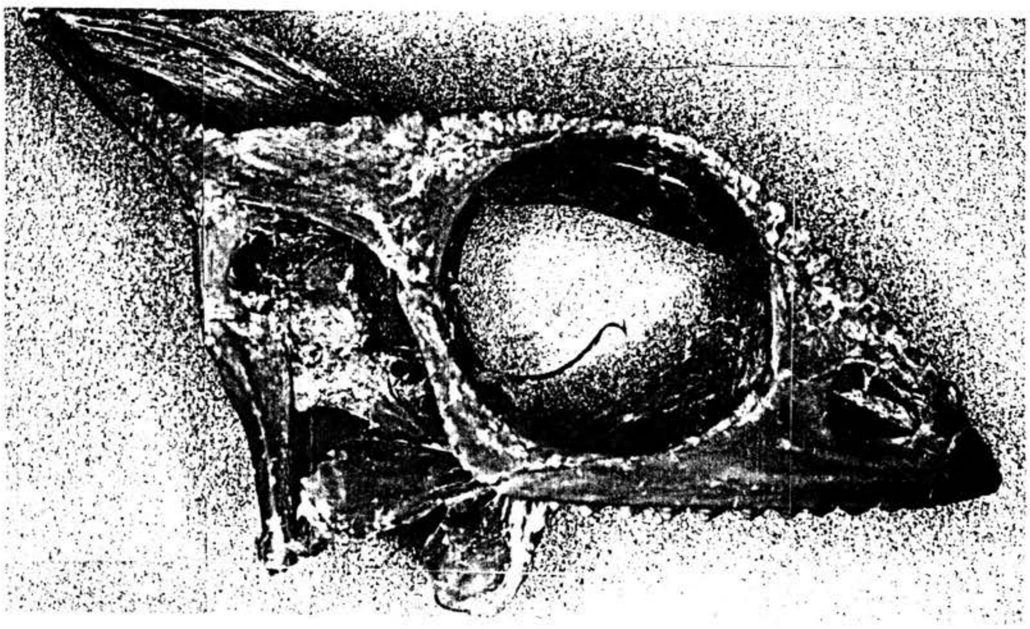

Figure 6 The skull of *Chamaeleo dilepis* - Lateral view (x 4)

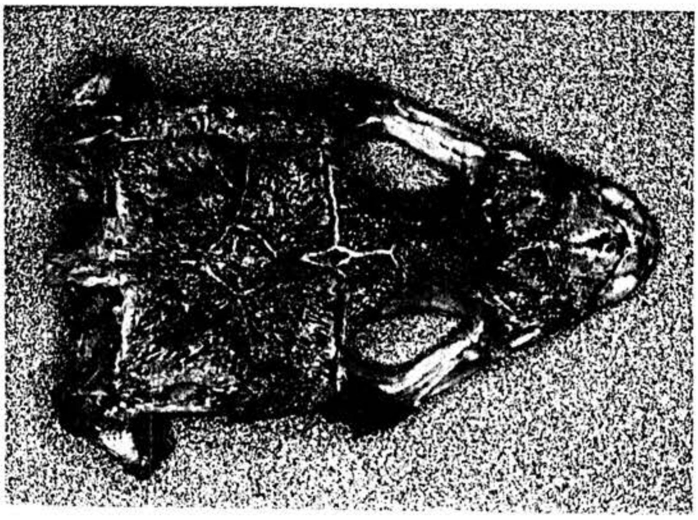

Figure 7 The skull of *Cordylus cordylus cordylus* - Dorsal view (x 4)

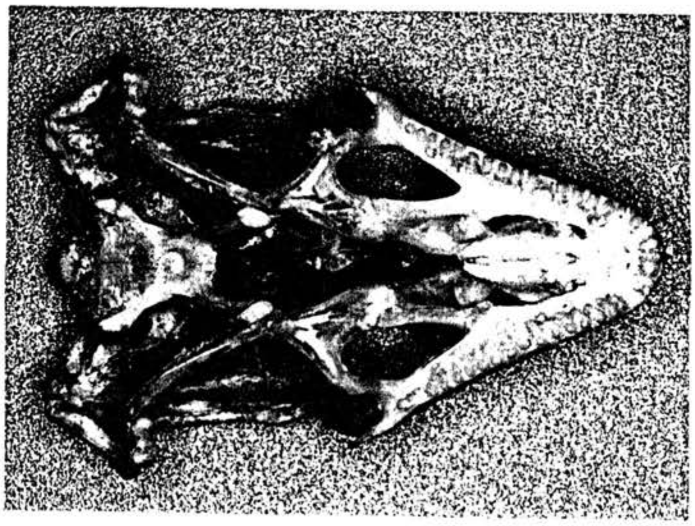

Figure 8 The skull of *Cordylus cordylus cordylus* - Ventral view (x 4)

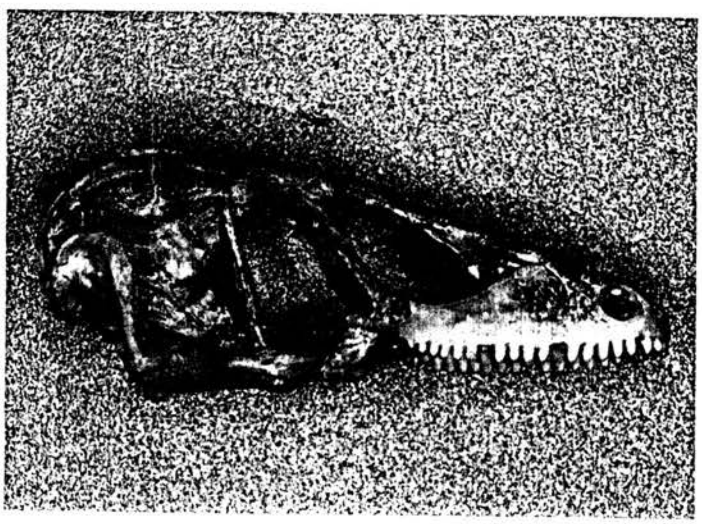

Figure 9 The skull of *Cordylus cordylus cordylus* - Lateral view (x 4)

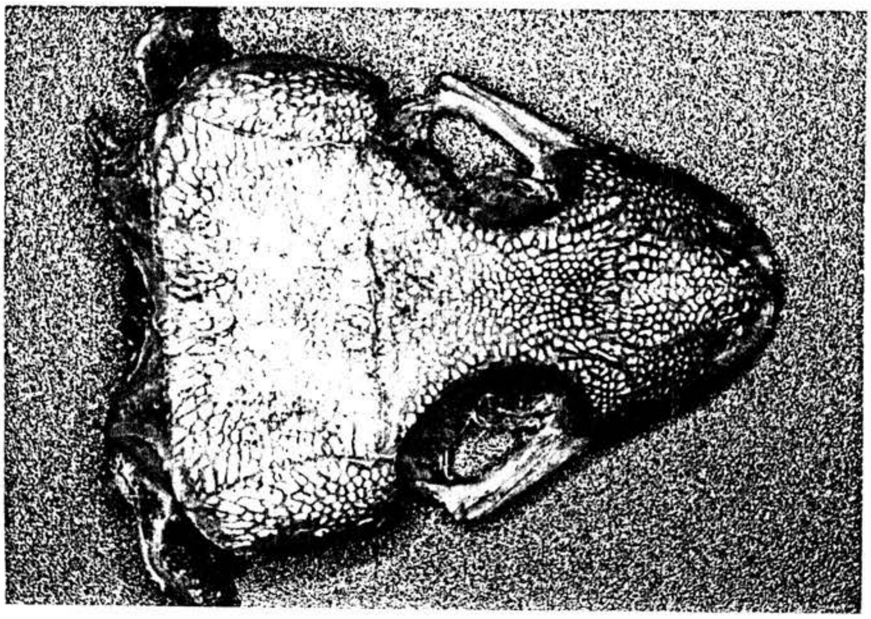

Figure 10 The skull of *Pachydactylus bibronii* - Dorsal view (x 4)

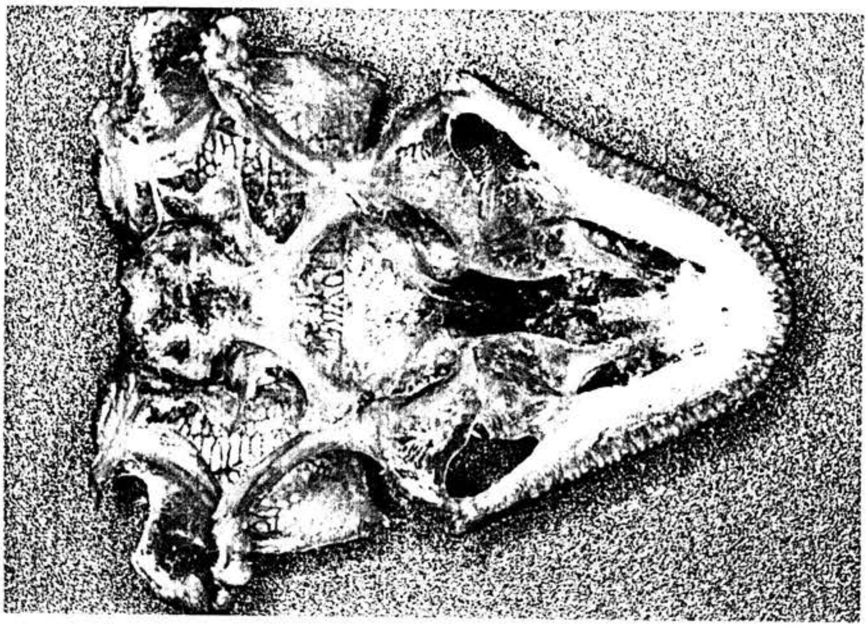

Figure 11 The skull of *Pachydactylus bibronii* - Ventral view (x 4)

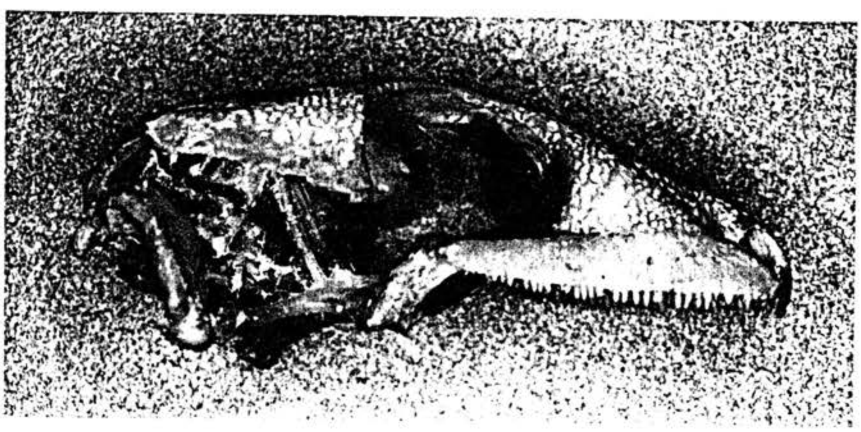

Figure 12 The skull of *Pachydactylus bibronii* - Lateral view (x 4)

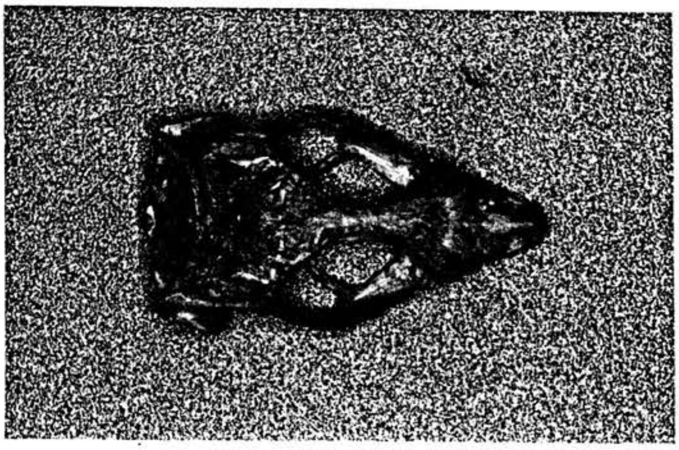

Figure 13 The skull of *Merolus knoxii* - Dorsal view (x 3)

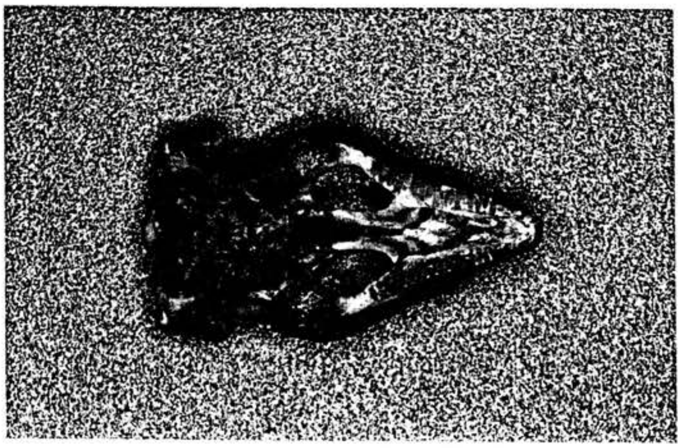

Figure 14 The skull of *Merolus knoxii* - Ventral view (x 3)

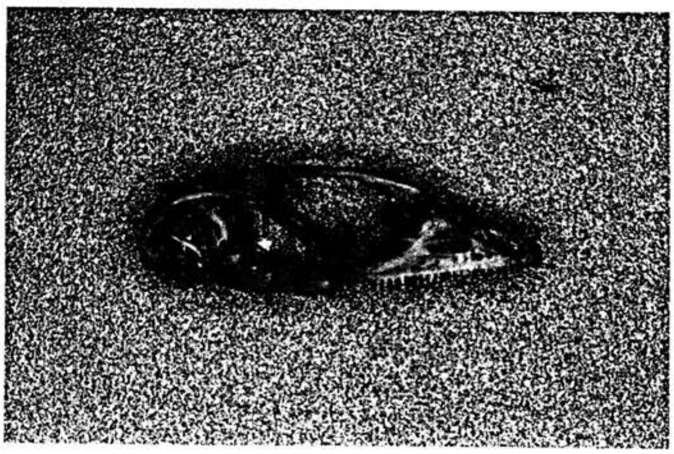

Figure 15 The skull of *Merolus knoxii* - Lateral view (x 3)

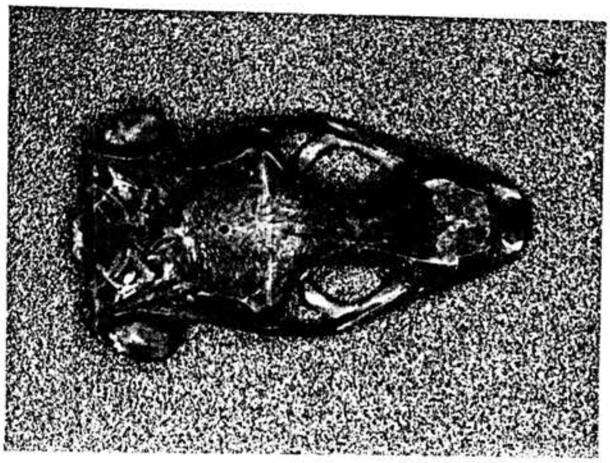

Figure 16 The skull of *Mabuya capensis* - Dorsal view (x 4)

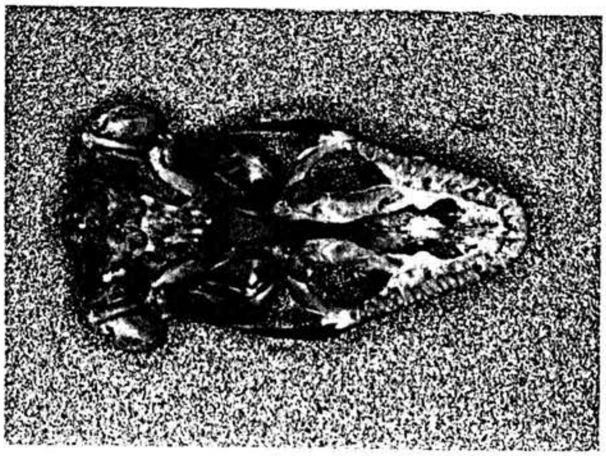

Figure 17 The skull of *Mabuya capensis* - Ventral view (x 4)

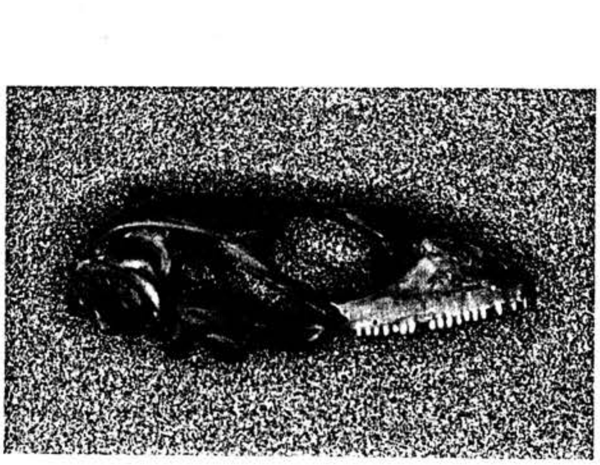

Figure 18 The skull of *Mabuya capensis* - Lateral view (x 4)

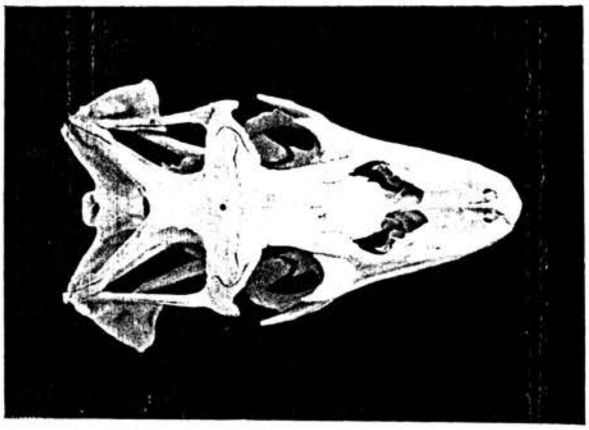

Figure 19 The skull of *Varanus niloticus* - Dorsal view (x 1)

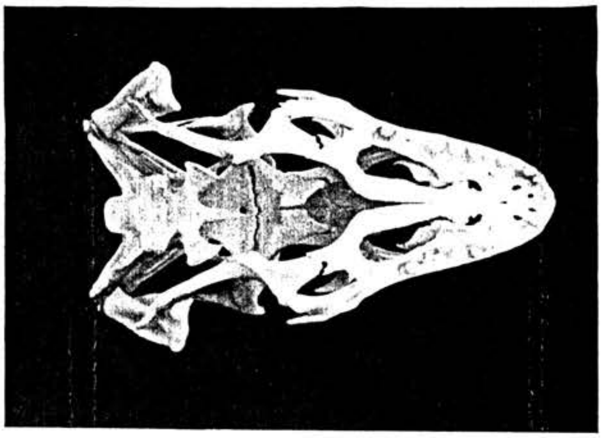

Figure 20 The skull of *Varanus niloticus* - Ventral view (x 1)

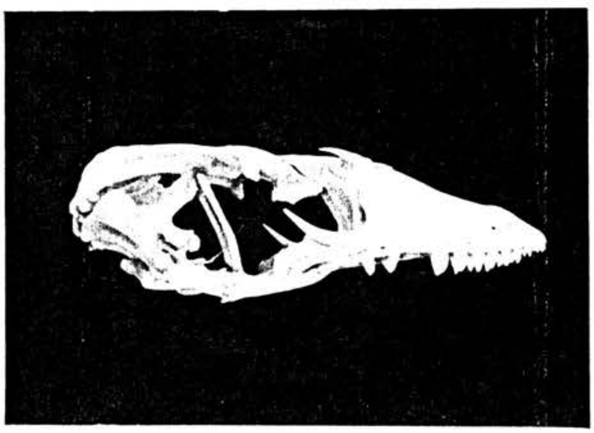

Figure 21 The skull of *Varanus niloticus* - Lateral view (x 1)

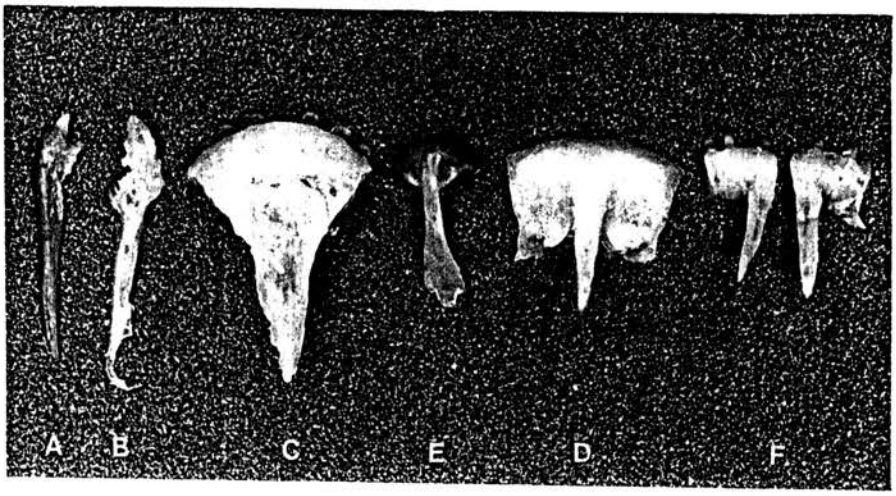

Figure 22 The premaxilla - A, B, C, D, E, F - Dorsal view (x 7)

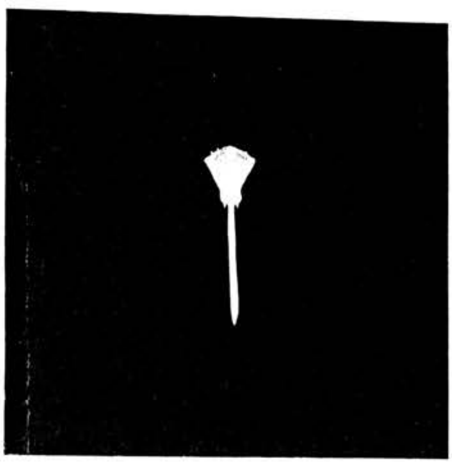

Figure 23 The premaxilla - G - Dorsal view (x 0,6)

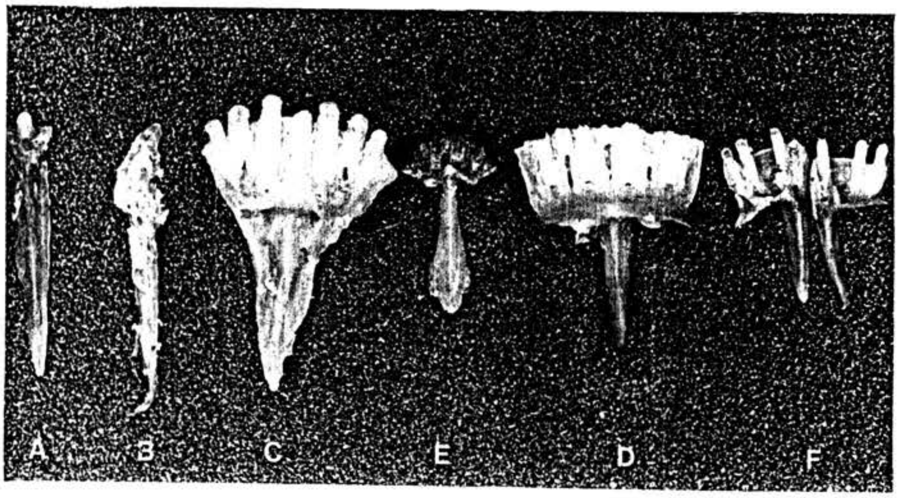

Figure 24 The premaxilla - A, B, C, D, E, F - Ventral view (x 7)

Figure 25 The premaxilla - G - Ventral view (x 0,6)

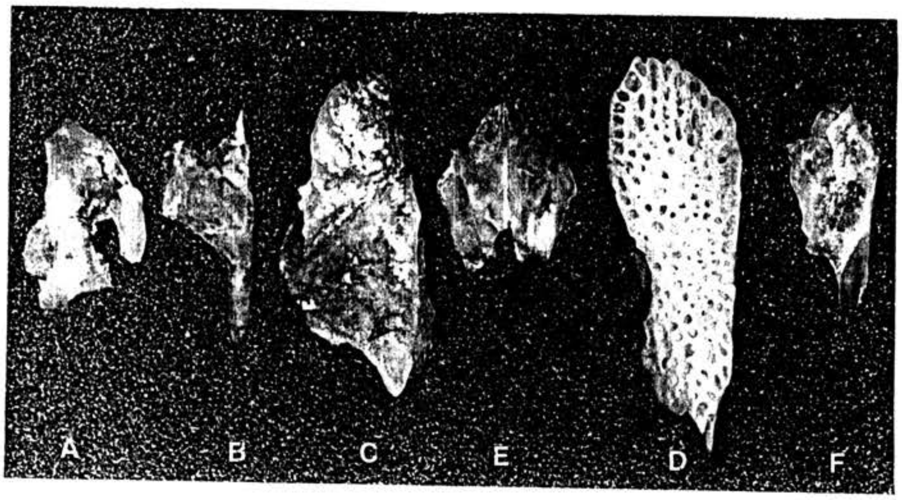

Figure 26 The nasal - A, B, C, D, E, F - Dorsal view (x 9)

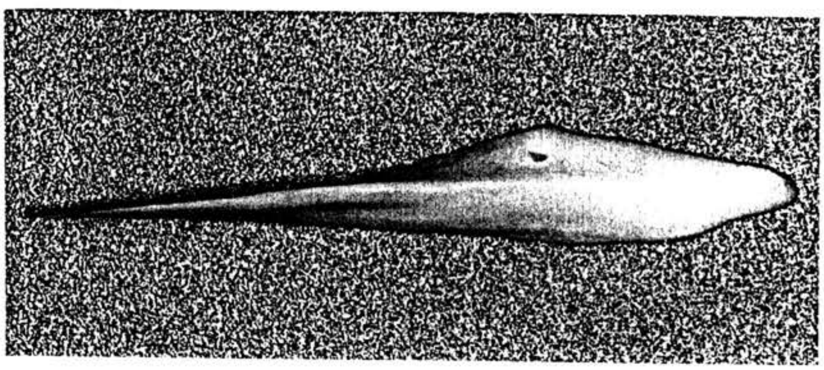

Figure 27 The nasal - G - Dorsal view (x 6)

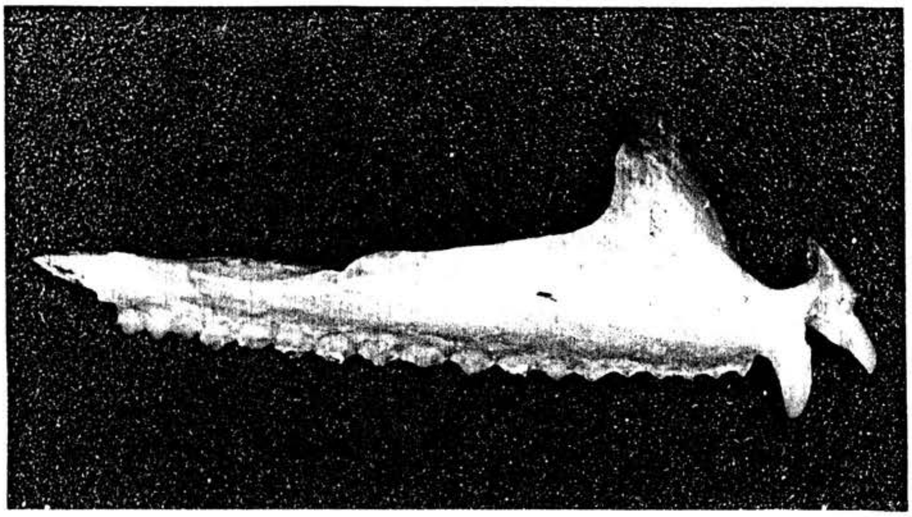

Figure 28 The maxilla - A - Lateral view (x 7)

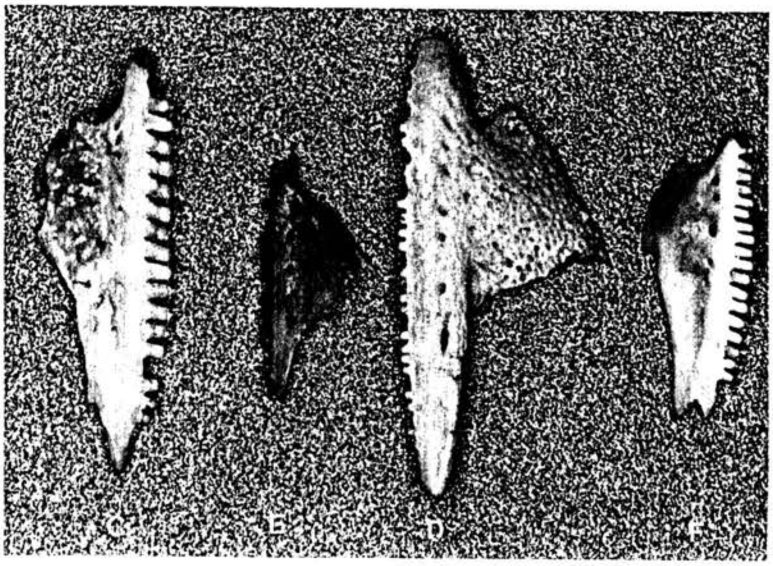

Figure 29 The maxilla - C, D, E, F - Lateral view (x 5)

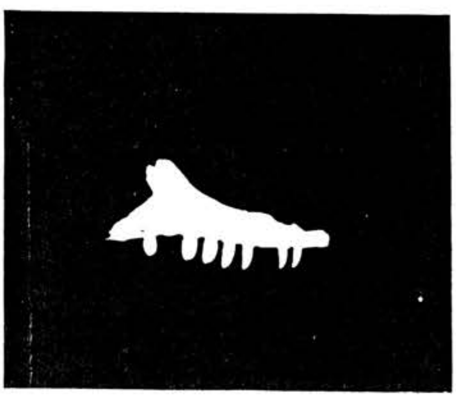

Figure 30 The maxilla - G - Lateral view (x 0,7)

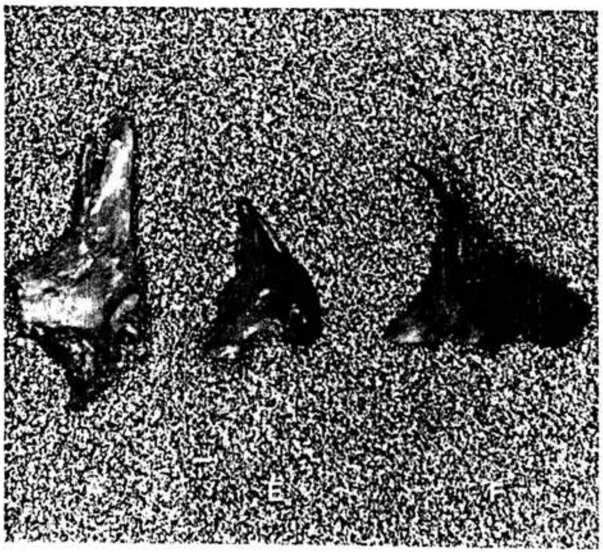

Figure 31 The prefrontal - A, E, F - Posterolateral view (x 7)

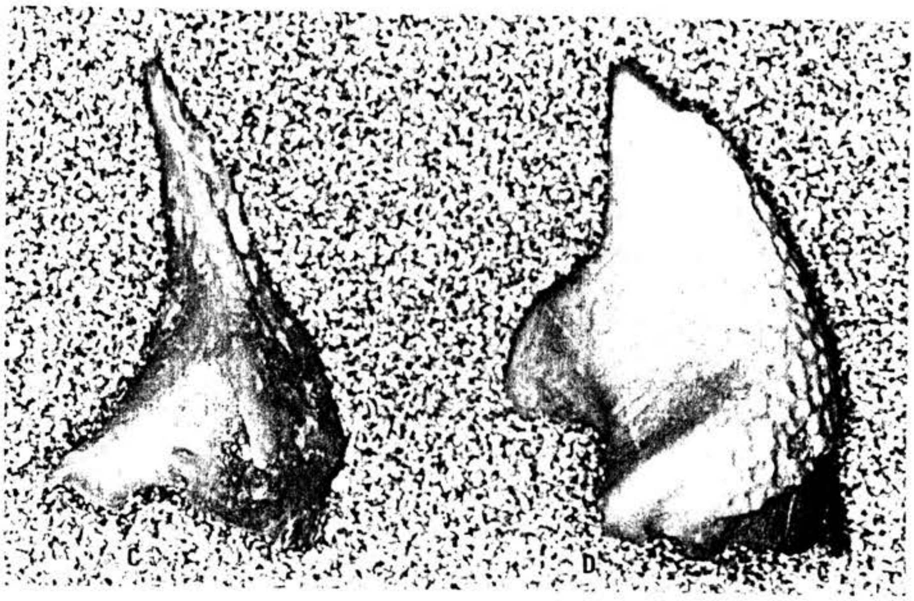

Figure 32 The prefrontal - C, D - Posterolateral view (x 11)

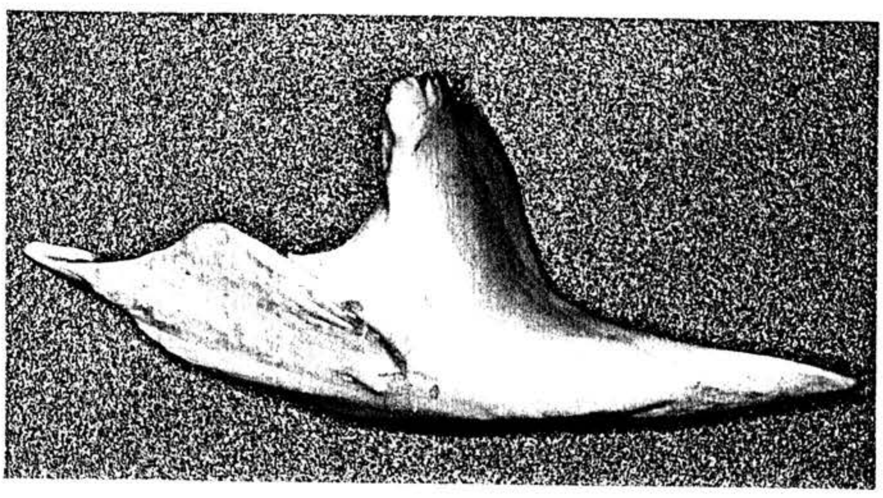

Figure 33 The prefrontal - G - Posterolateral view (x 4)

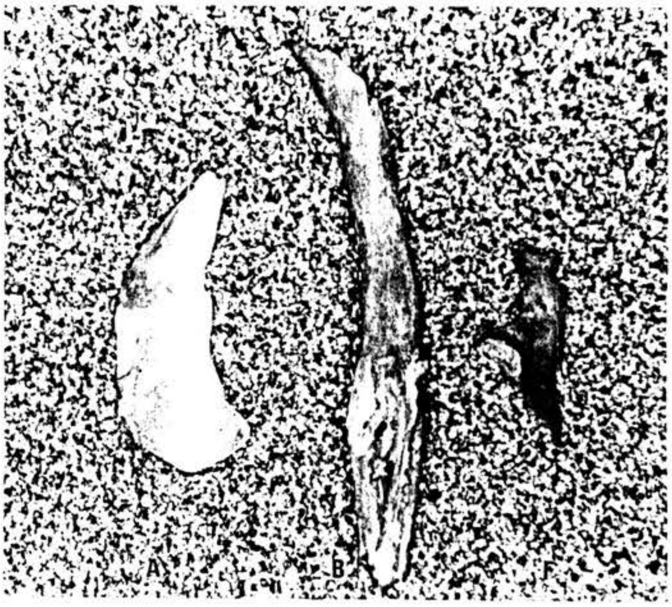

Figure 34 The lacrimal - A, B, F - Posterior view (x 17)

Figure 35 The lacrimal - G - Posterior view (x 6)

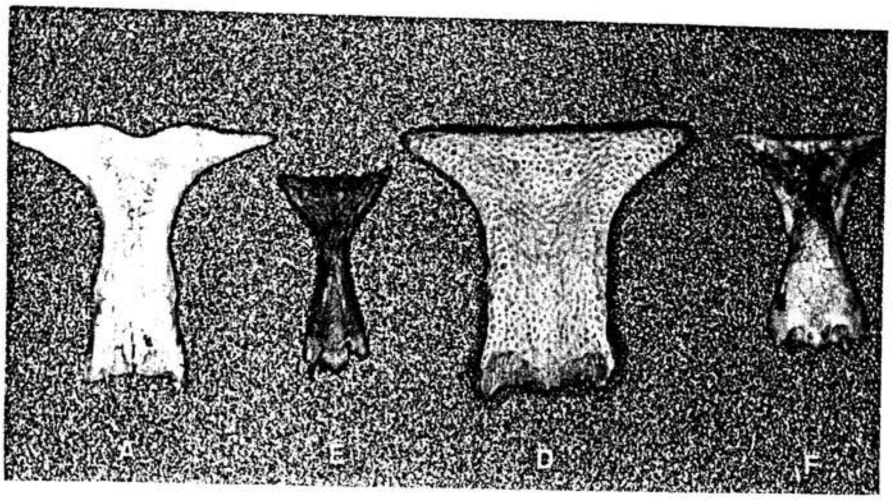

Figure 36 The frontal - A, D, E, F - Dorsal view (x 4)


Figure 37 The frontal - G - Dorsal view (x 0,6)

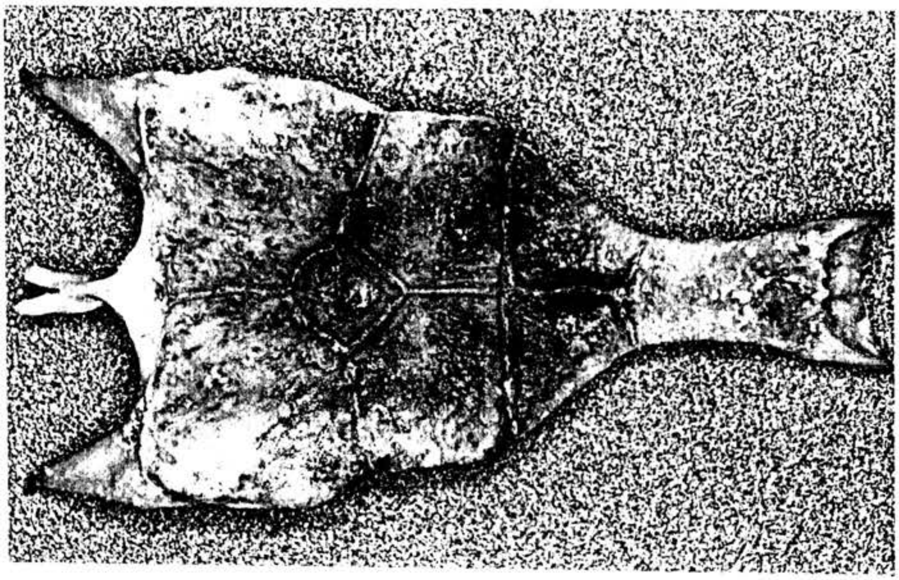

Figure 38 The frontal and parietal in syndesmosis - C - Dorsal view (x 6)

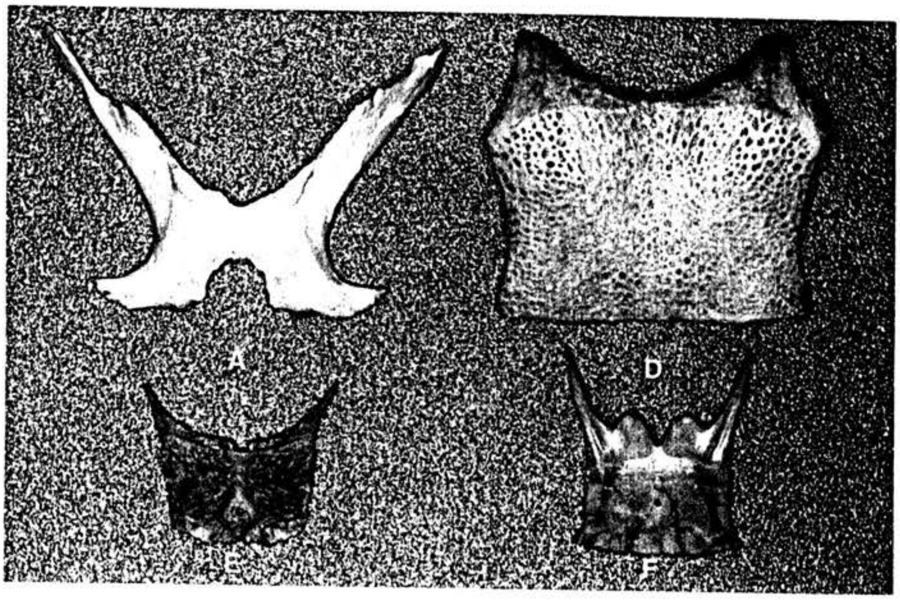

Figure 39 The parietal - A, D, E, F - Dorsal view (x 4)

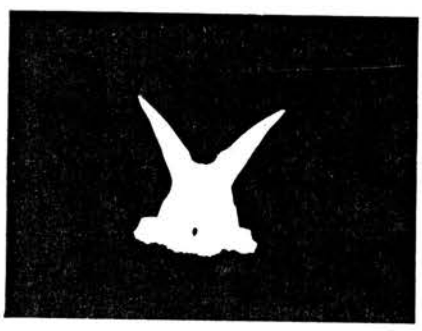

Figure 40 The parietal - G - Dorsal view (x 0,6)

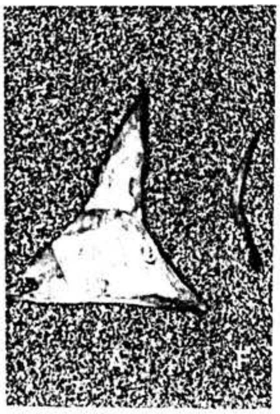

Figure 41 The postorbital - A, F - Dorsal view (x 6)

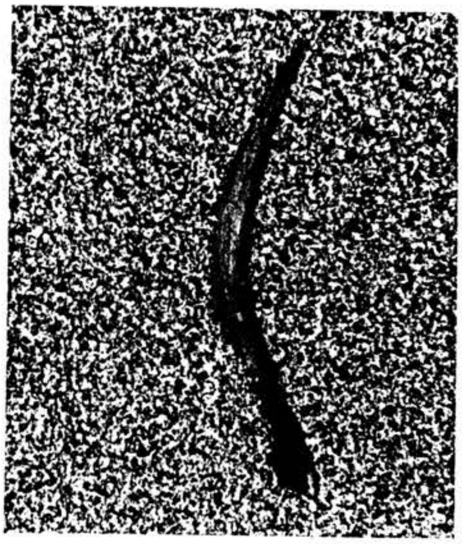

Figure 42 The postorbital - F - Dorsal view (x 19)

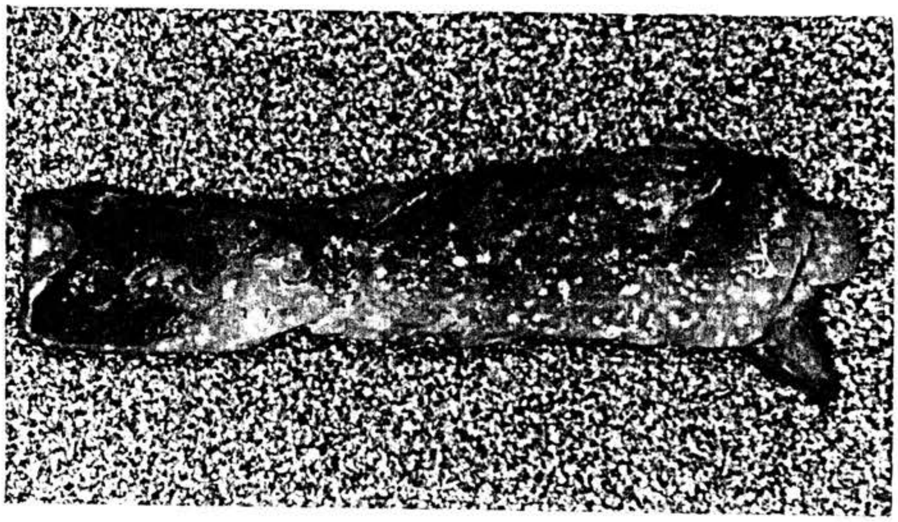

Figure 43 The postfrontal and postorbital in syndesmosis - C - Dorsal view (x 12)

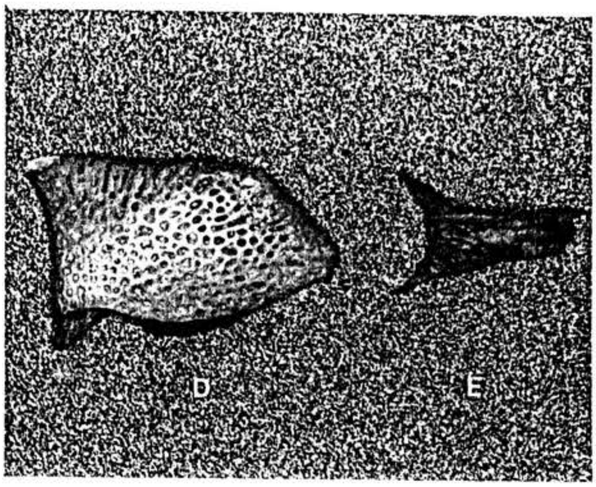

Figure 44 The postfrontal - D, E - Dorsal view (x 6)

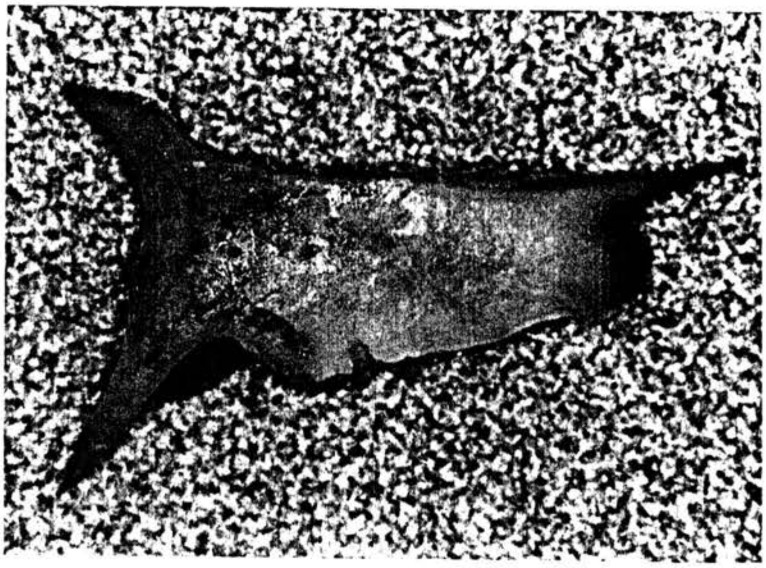

Figure 45 The postfrontal - F - Dorsal view (x 20)

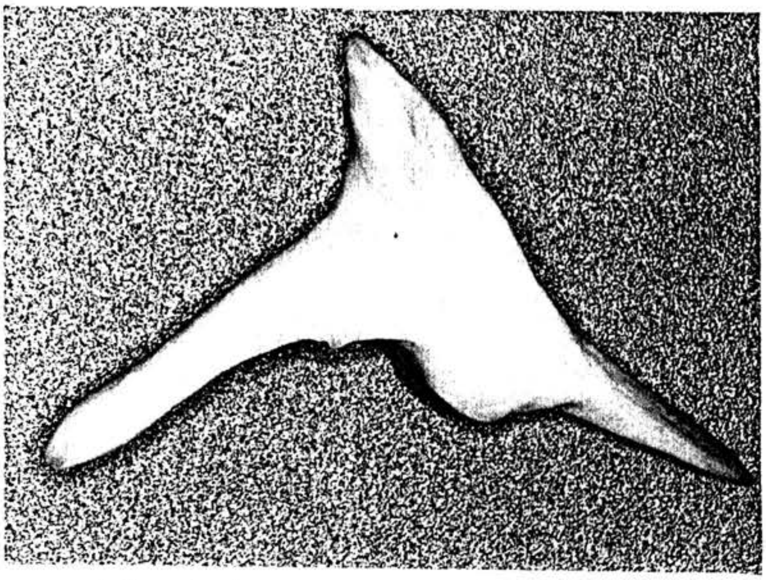

Figure 46 The postfrontal - G - Dorsal view (x 6)

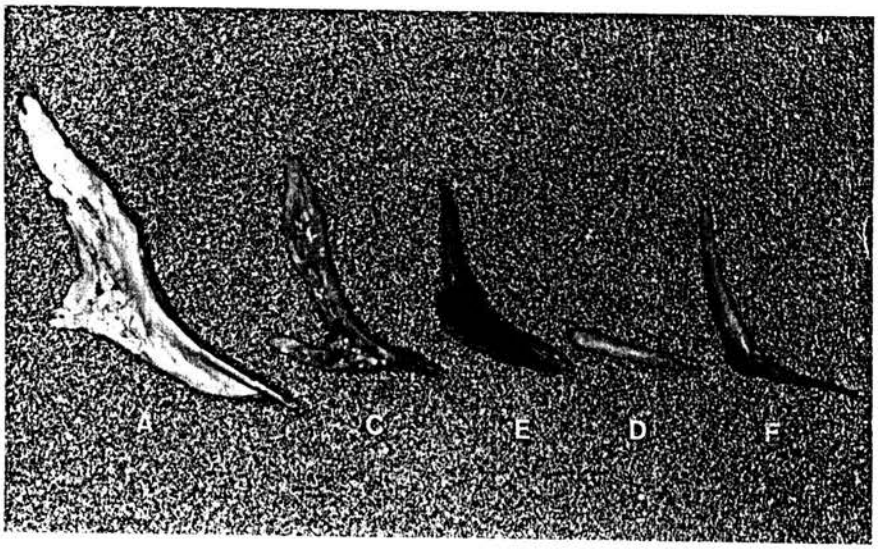

Figure 47 The jugal - A, C, D, E, F - Lateral view (x 5)

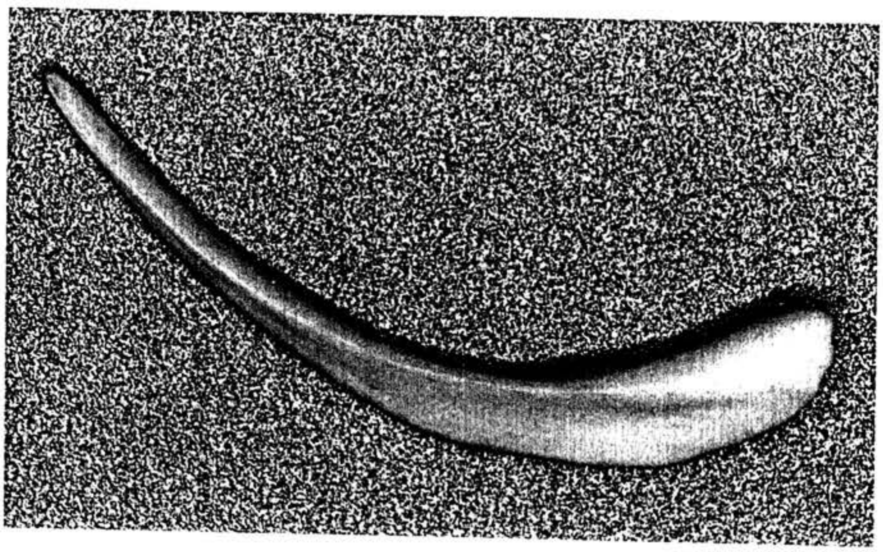

Figure 48 The jugal - G - Lateral view (x 6)

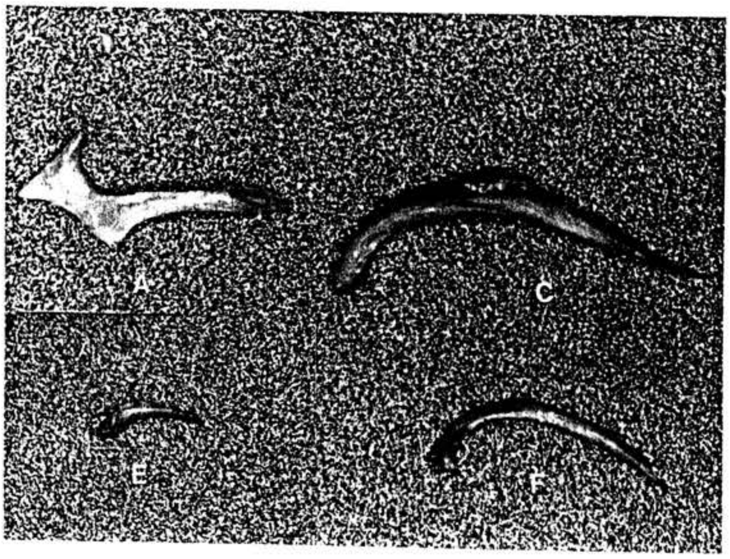

Figure 49 The squamosal - A, C, E, F - Lateral view (x 6)

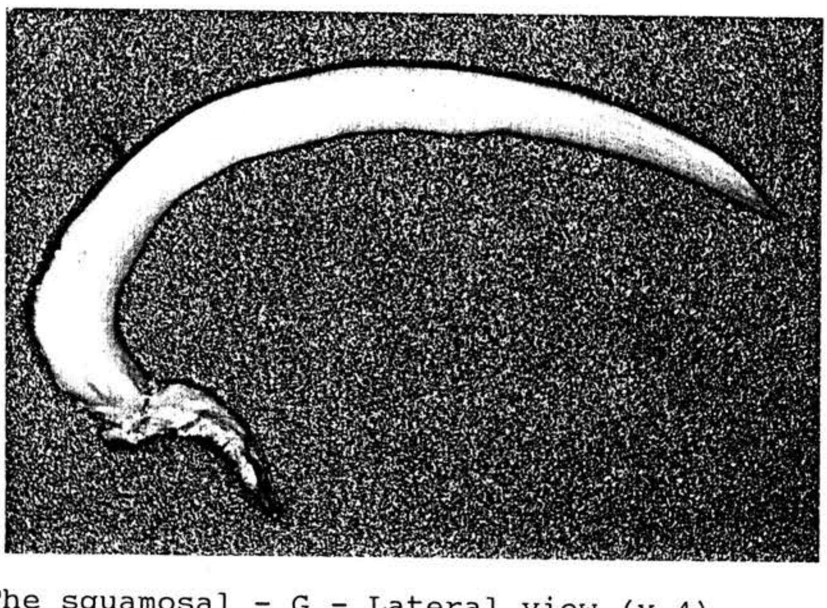

Figure 50 The squamosal - G - Lateral view (x 4)

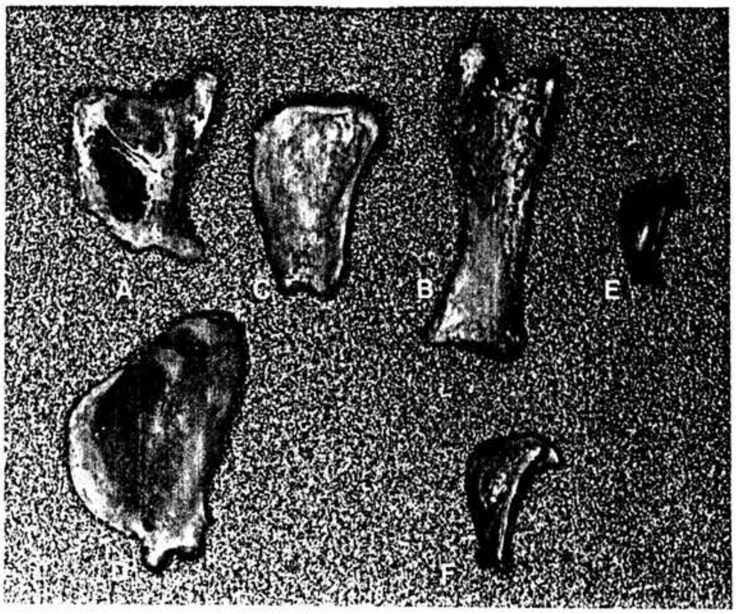

Figure 51 The quadrate - A, B, C, D, E, F - Anterior view (x 5)

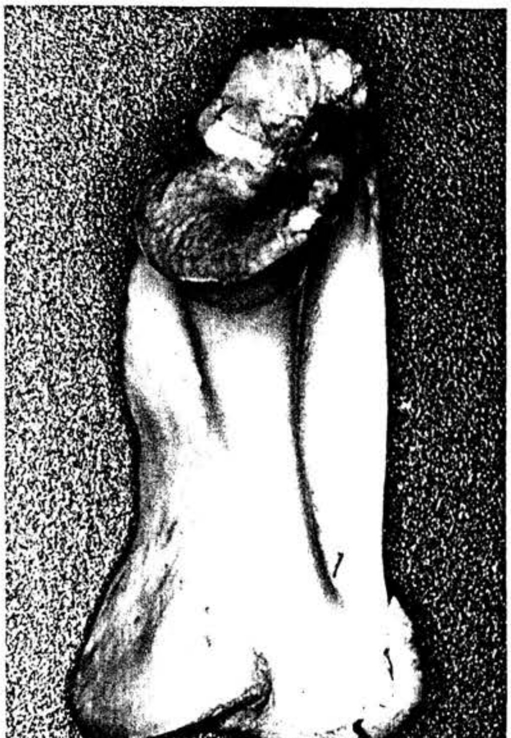

Figure 52 The quadrate - G - Posterior view (x 5)

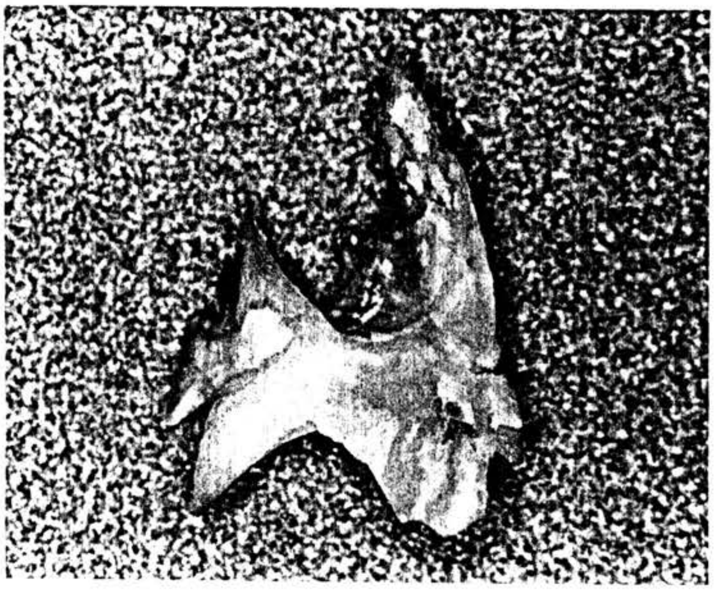

Figure 53 The vomeropalatine - A - Ventral view (x 13)

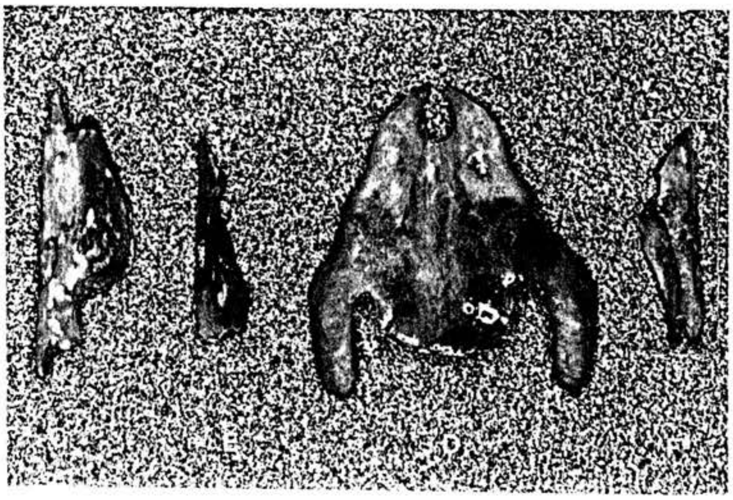

Figure 54 The vomer - C, D, E, F - Ventral view (x 8)

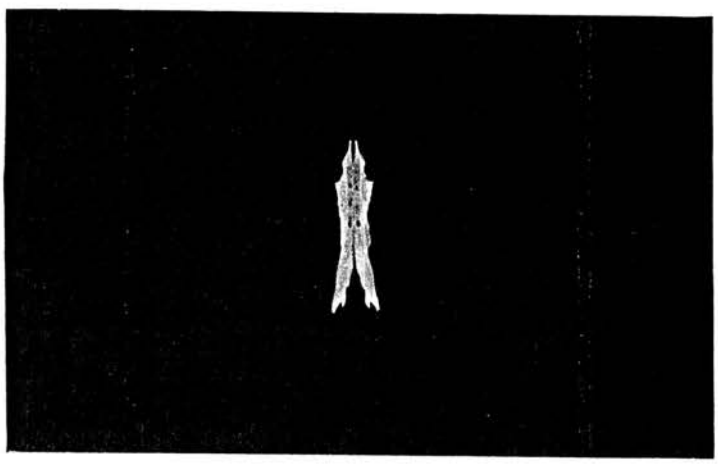

Figure 55 The vomer - G - Ventral view (x 0,6)

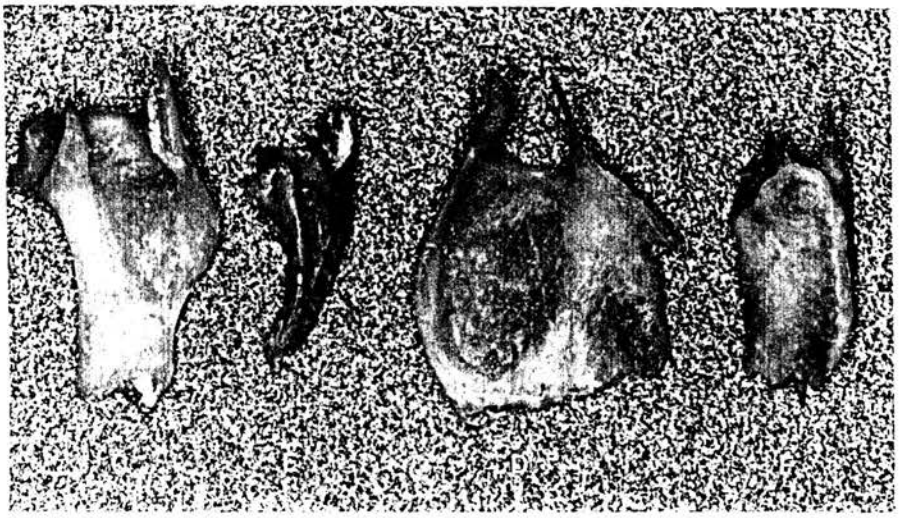

Figure 56 The palatine - C, D, E, F - Ventral view (x 9)
(Anterior to the top)

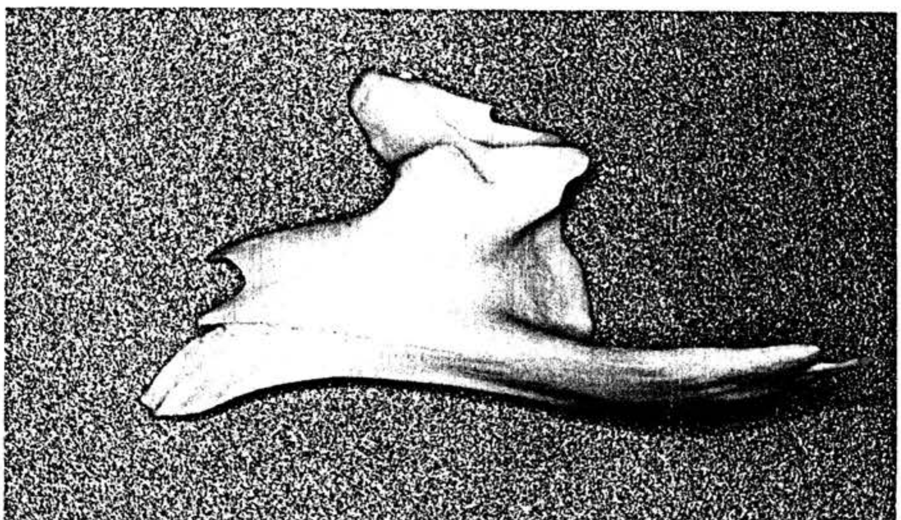

Figure 57 The palatine - G - Ventral view (x 4)
(Anterior to the right)

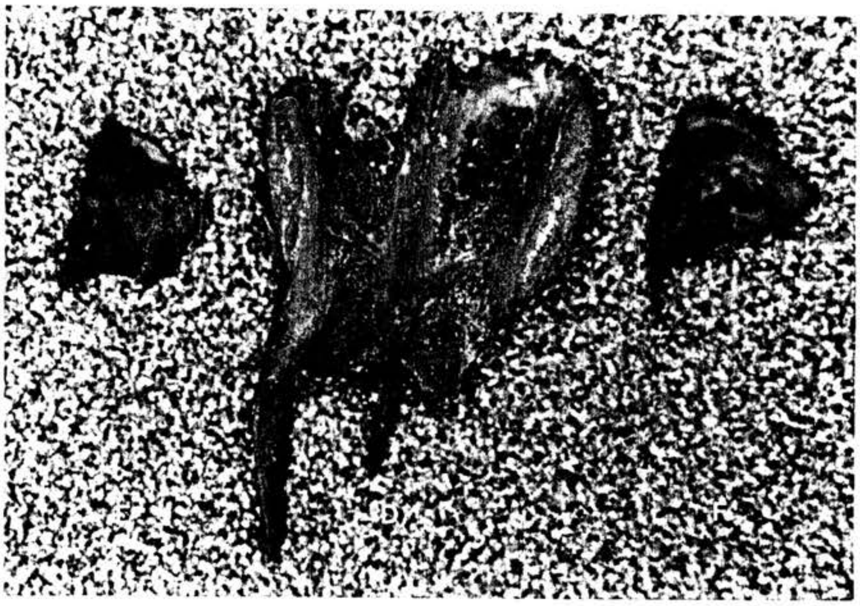

Figure 58   The septomaxilla - D, E, F - Ventral view (x 17)

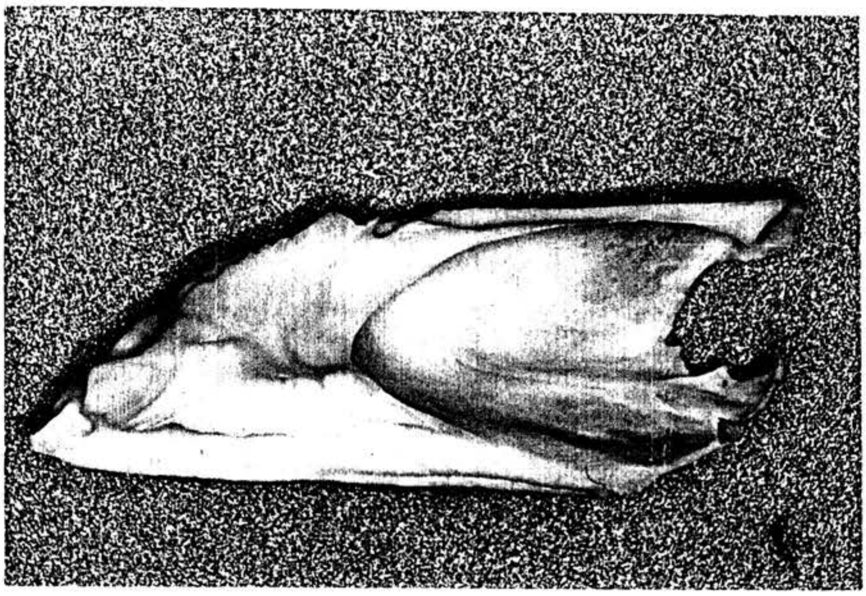

Figure 59   The septomaxilla - G - Ventral view (x 5)

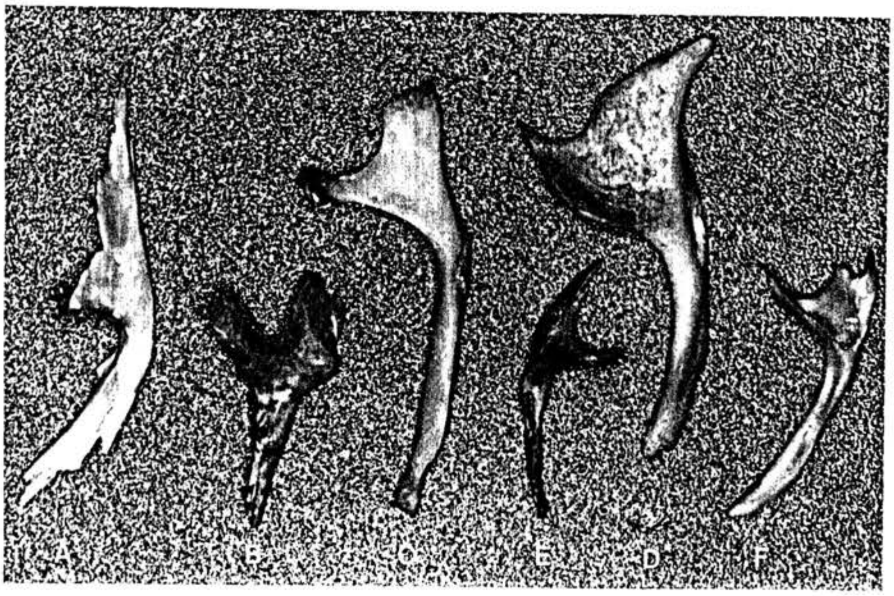

Figure 60 The pterygoid - A, B, C, D, E, F - Ventral view (x 5)
(Elements of right side of skull; E of left side)
(Anterior to the top)

Figure 61 The pterygoid - G - Ventral view (x 0,6)
(Element of left side of skull; anterior to the top)

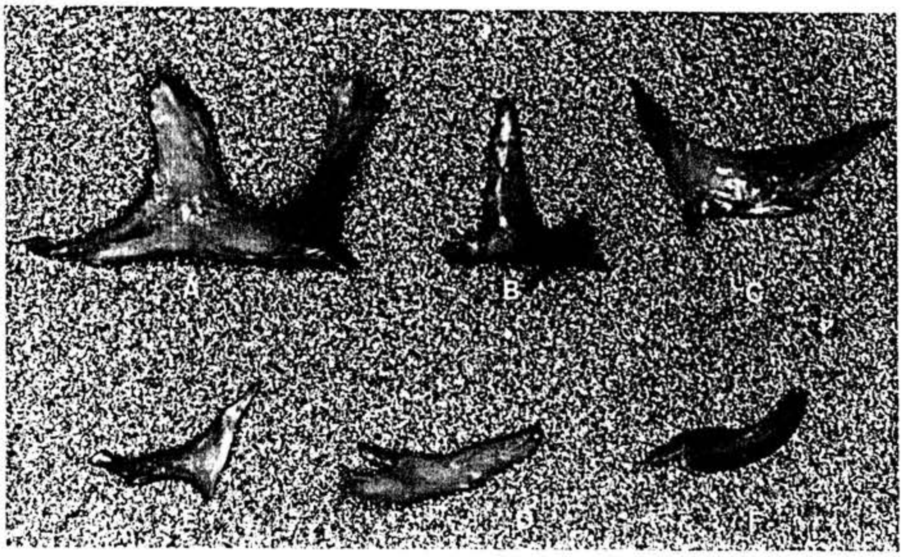

Figure 62 The right transversum - A, B, C, D, E, F - Dorsal view (x 8) (Anterior to the right)

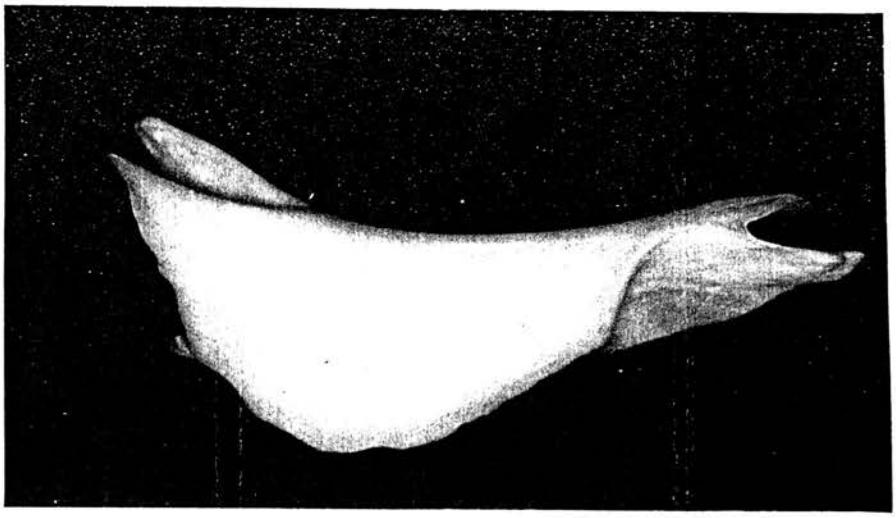

Figure 63 The left transversum - G - Ventral view (x 6) (Anterior to the right)

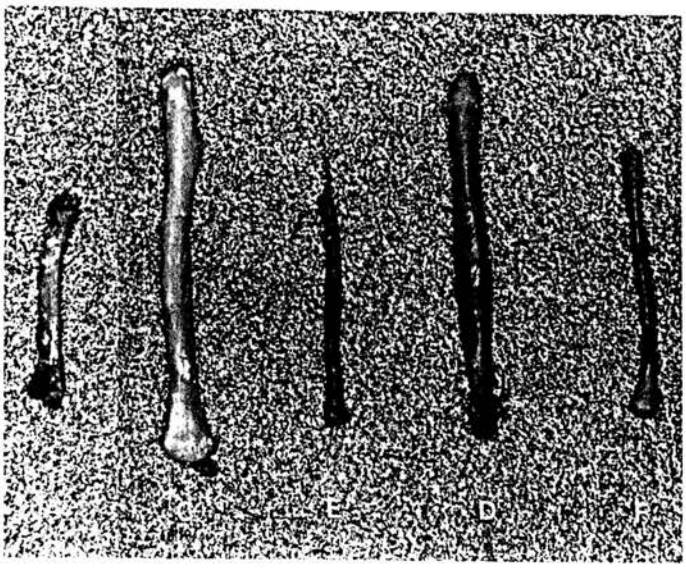

Figure 64 The epipterygoid - A, C, D, E, F - (x 8)

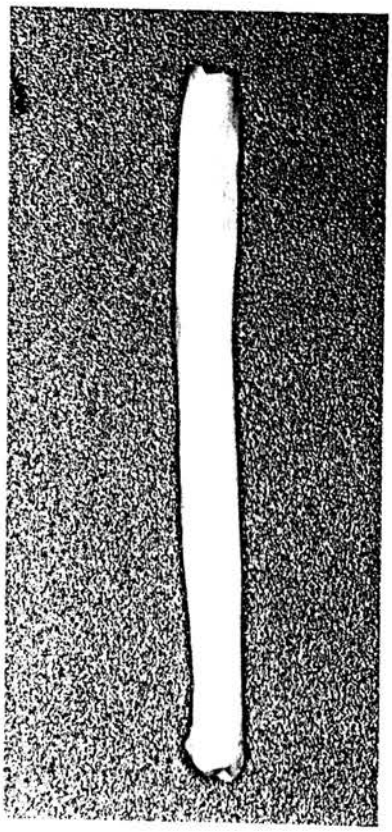

Figure 65 The epipterygoid - G - (x 5)

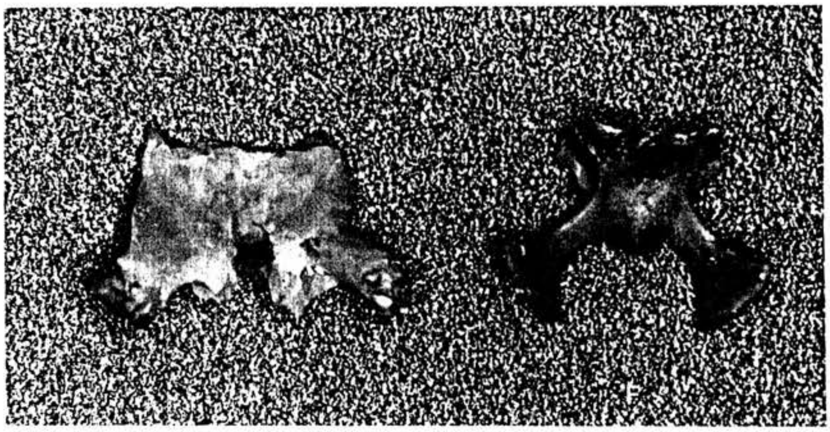

Figure 66 The basisphenoid - A, F - Ventral view (x 9)
(Anterior to the bottom)

Figure 67 The fused braincase - B - Ventral view (x 6)
(Posterior to the top)

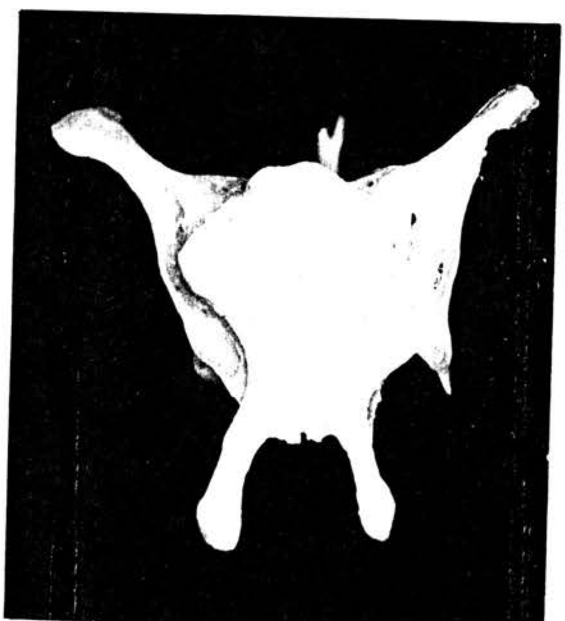

Figure 68 The fused braincase - C - Ventral view (x 6)
(Posterior to the top)

Figure 69 The fused braincase - D - Ventral view (x 6)
(Posterior to the top)

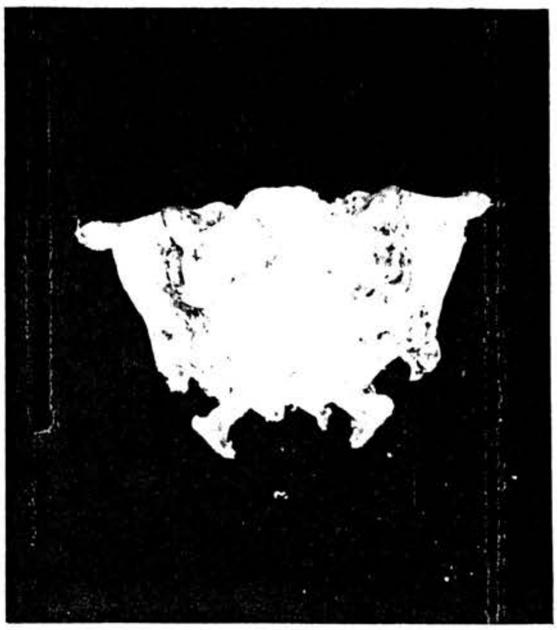

Figure 70 The fused braincase - E - Ventral view (x 8)
(Posterior to the top)

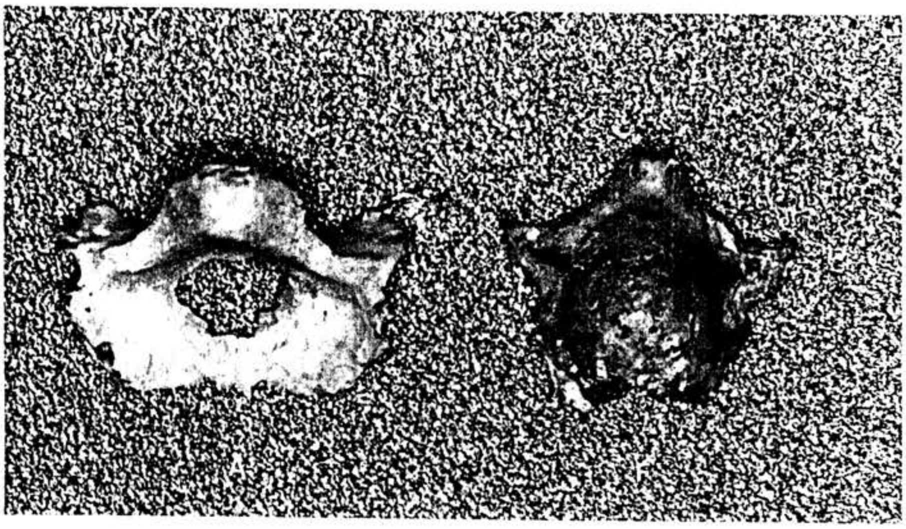

Figure 71 The basioccipital - A, F - Dorsal view (x 10)
(Posterior to the top)

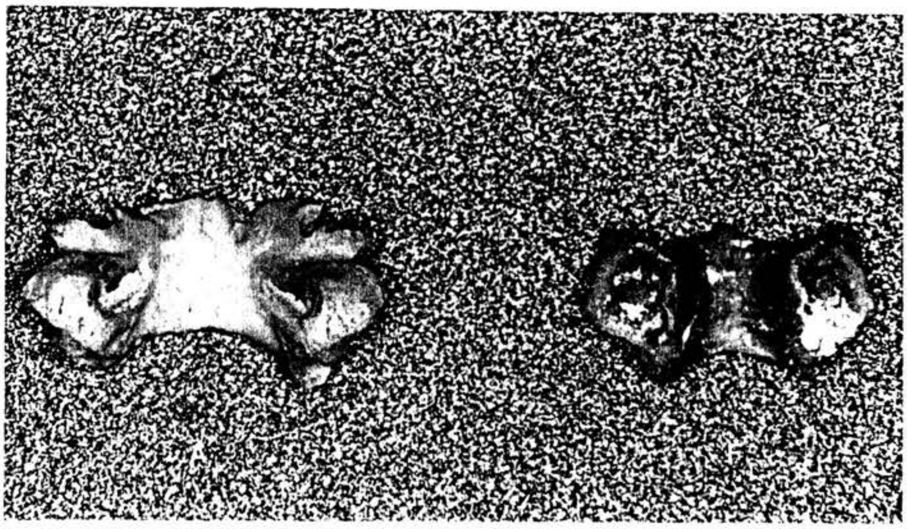

Figure 72 The supraoccipital - A, F - Ventral view (x 10)
(Posterior to the top)

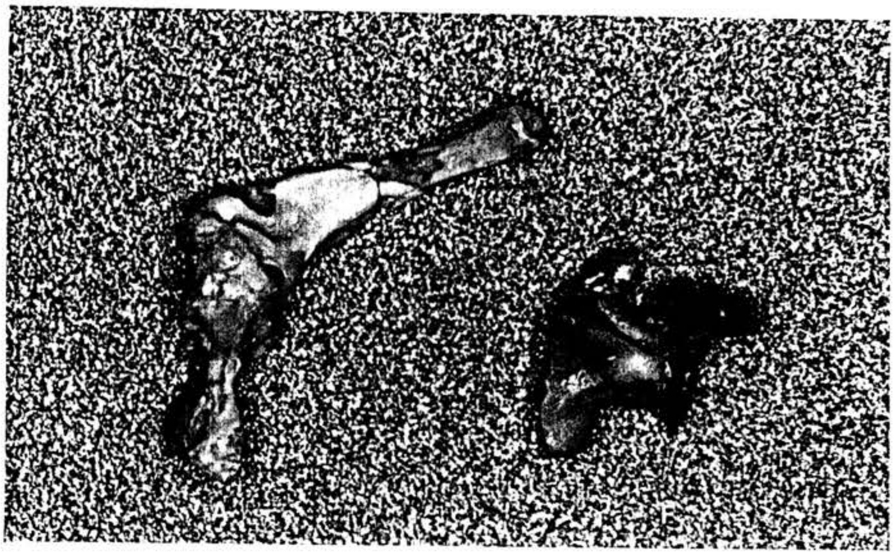

Figure 73 The otoccipital - A, F - Ventral view (x 10)
(Paroccipital process to the right)

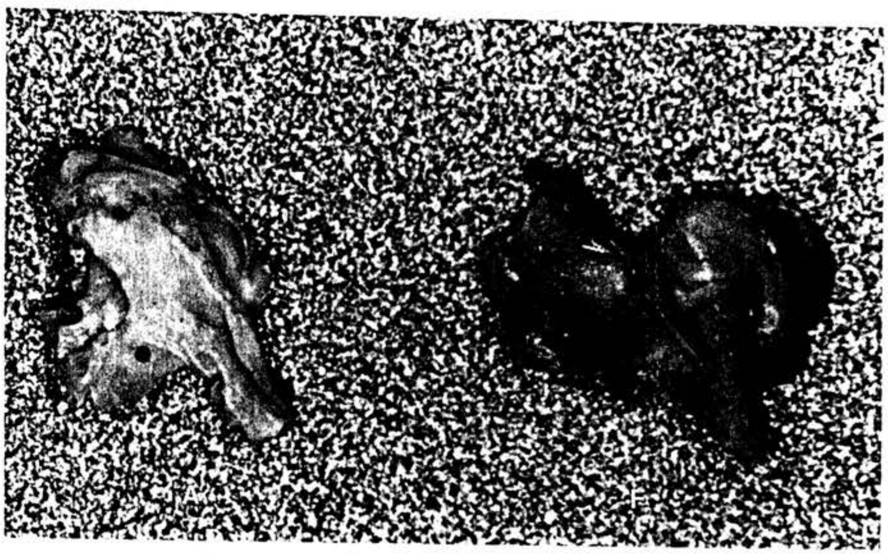

Figure 74 The Prootic - A, F - Ventrolateral view (x 10)
(Anterior to the top)

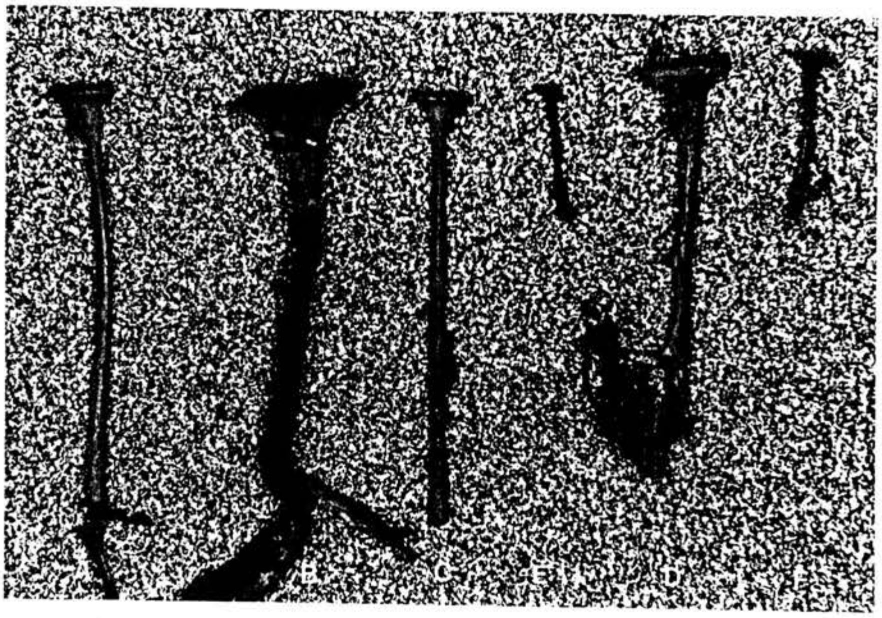

Figure 75 The stapes - A, B, C, D, E, F - (x 13)

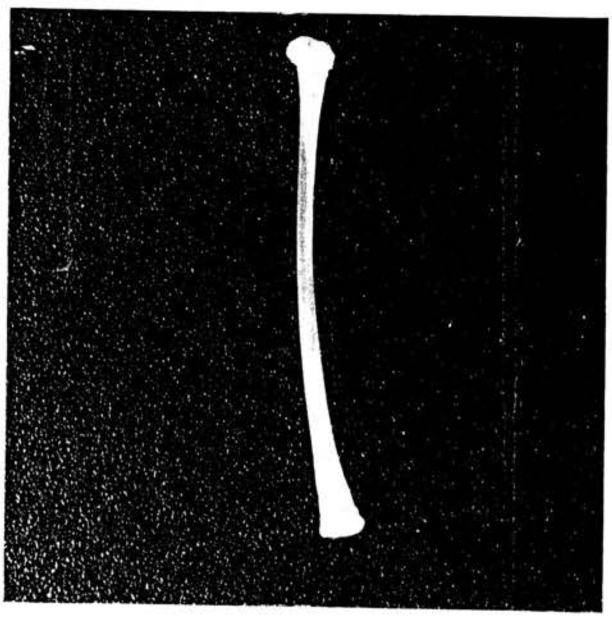

Figure 76 The stapes - G - (x 6)

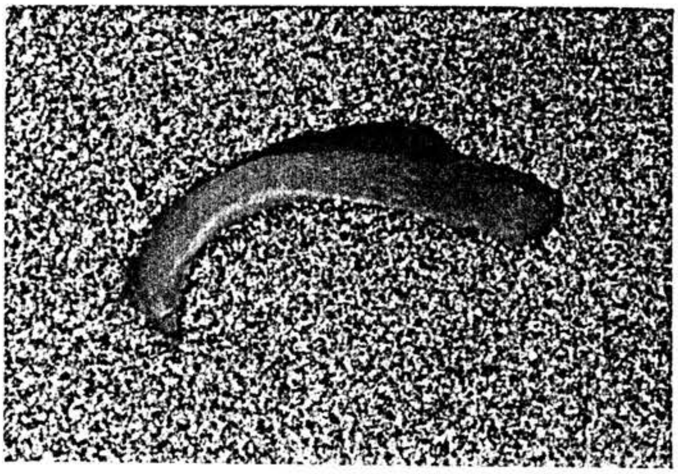

Figure 77 The supratemporal - D - Dorsolateral view (x 12)
(Anterior to the right)

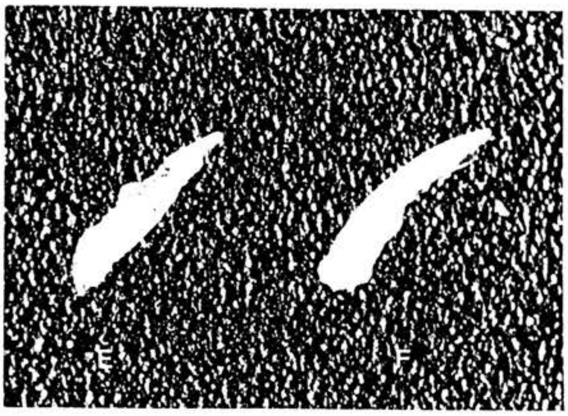

Figure 78 The supratemporal - E, F - Lateral view (x 17)
(Anterior to the right)

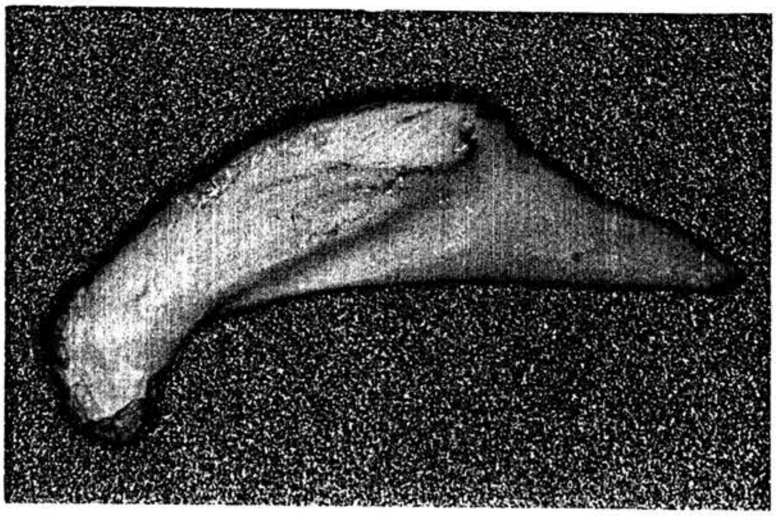

Figure 79 The supratemporal - G - Lateral view (x 5)
(Anterior to the right)

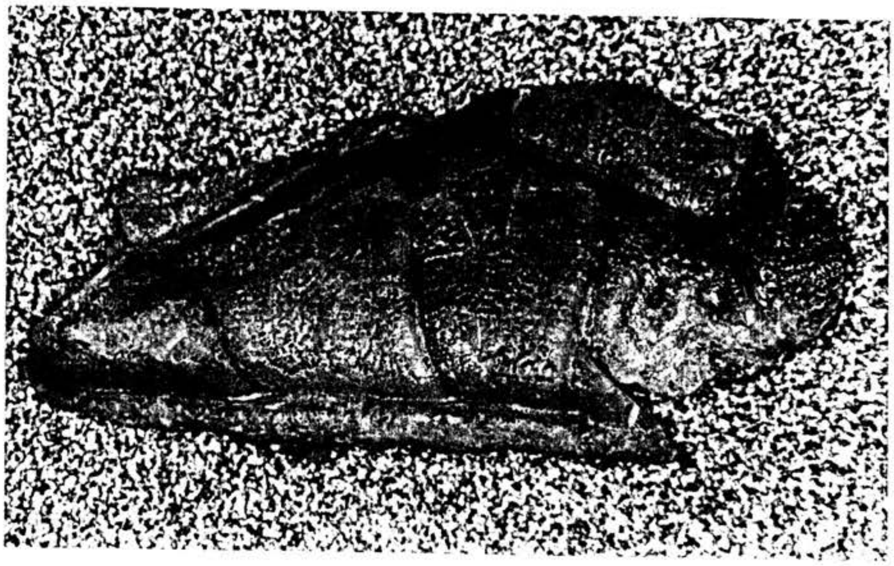

Figure 80 The supraorbital - F - Dorsal view (x 15)

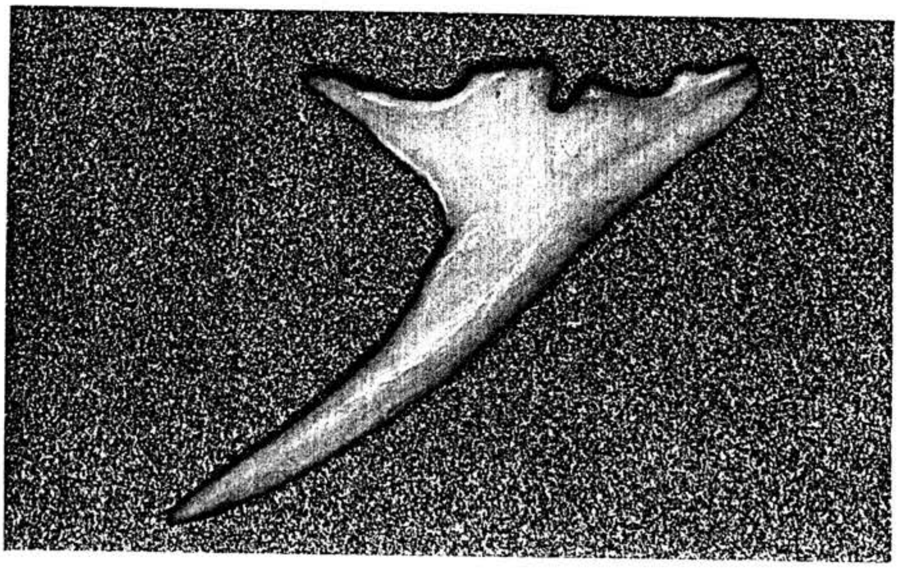

Figure 81 The supraorbital - G - Dorsal view (x 5)

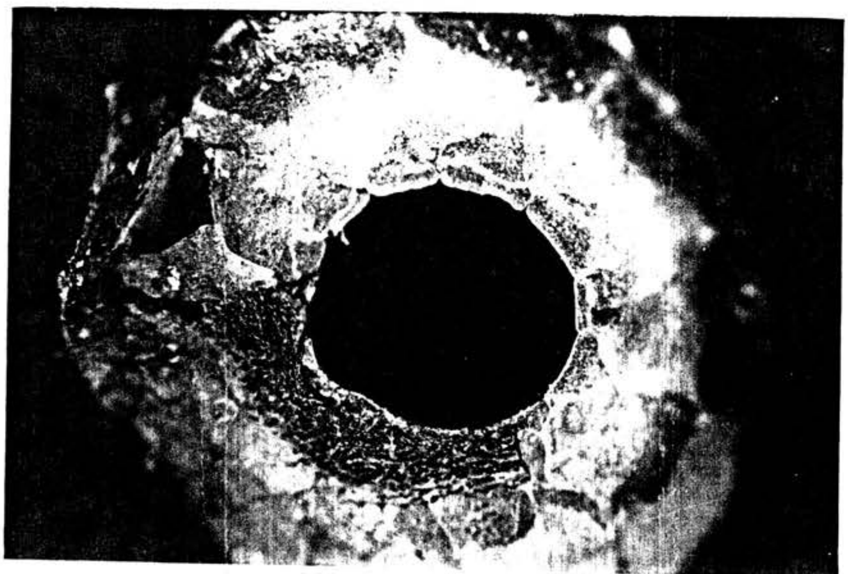

Figure 82 The sclerotic ossicles - A - (x 15)

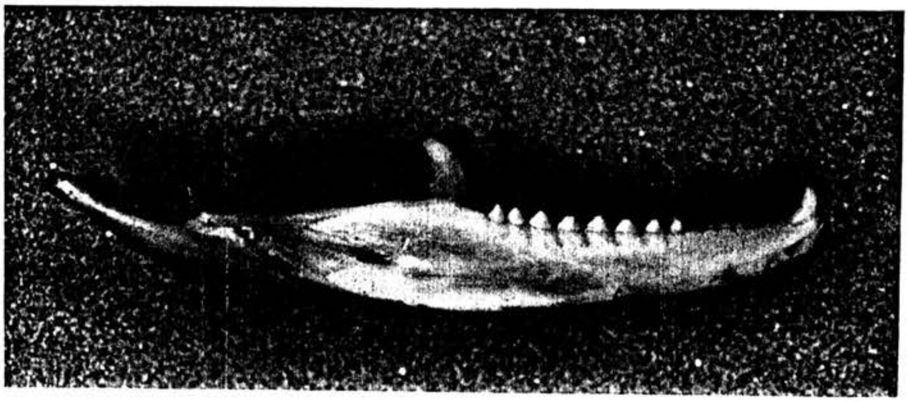

Figure 83 The mandible - A - Lateral view (x 4)

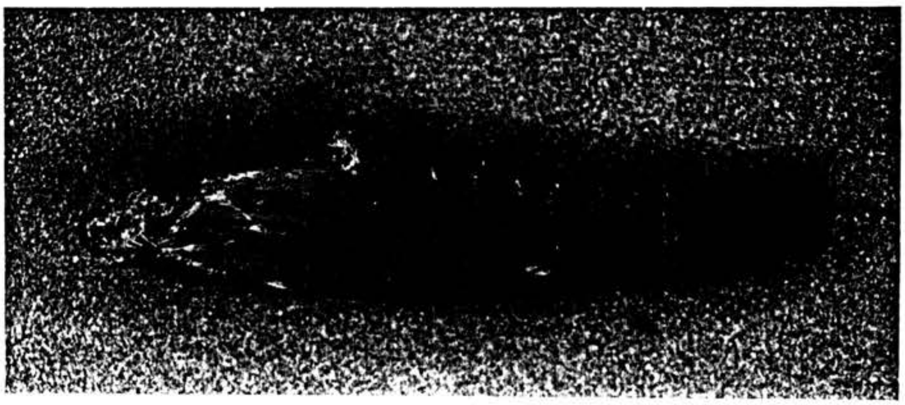

Figure 84 The mandible - B - Lateral view (x 4)

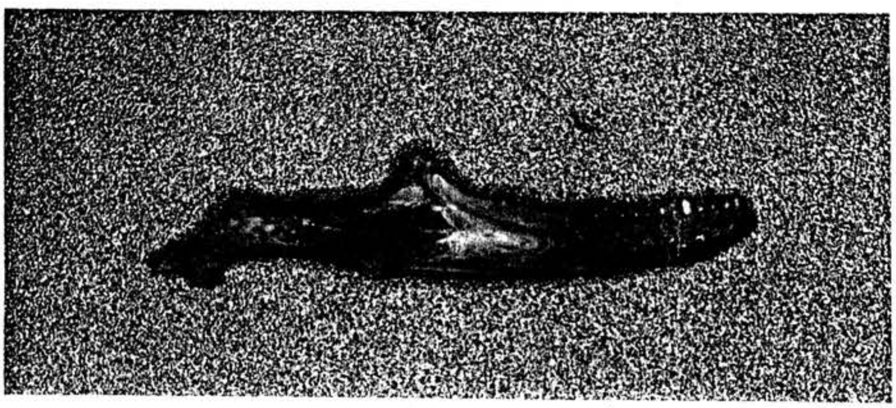

Figure 85 The mandible - C - Lateral view (x 4)

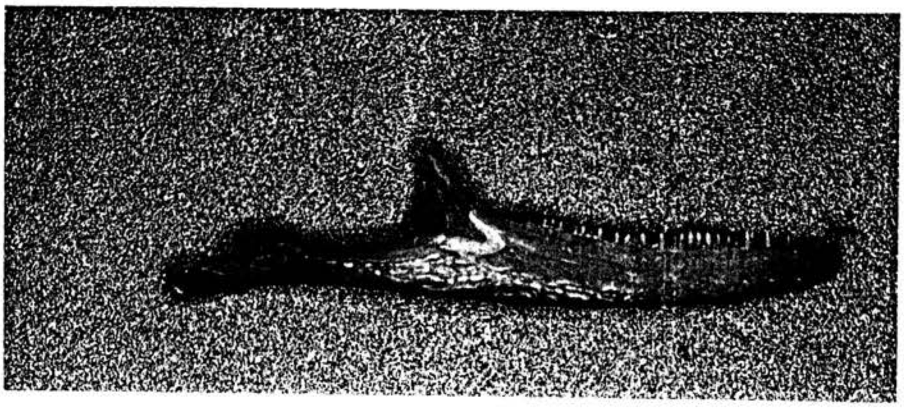

Figure 86 The mandible - D - Lateral view (x 4)

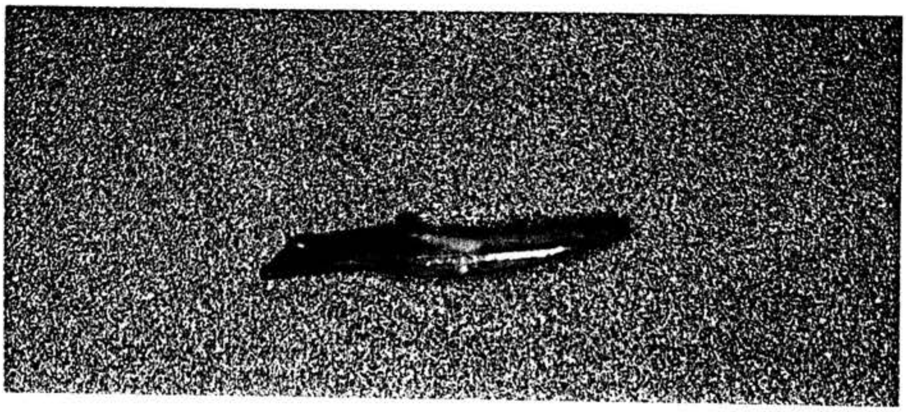

Figure 87 The mandible - E - Lateral view (x 4)

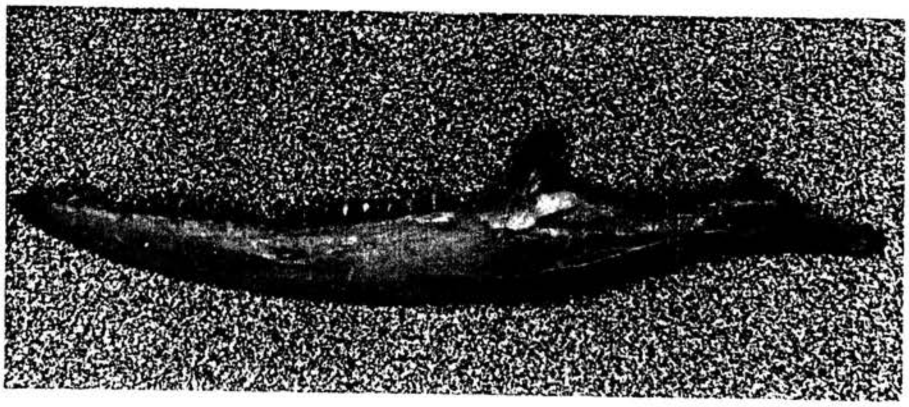

Figure 88 The mandible - F - Lateral view (x 7)

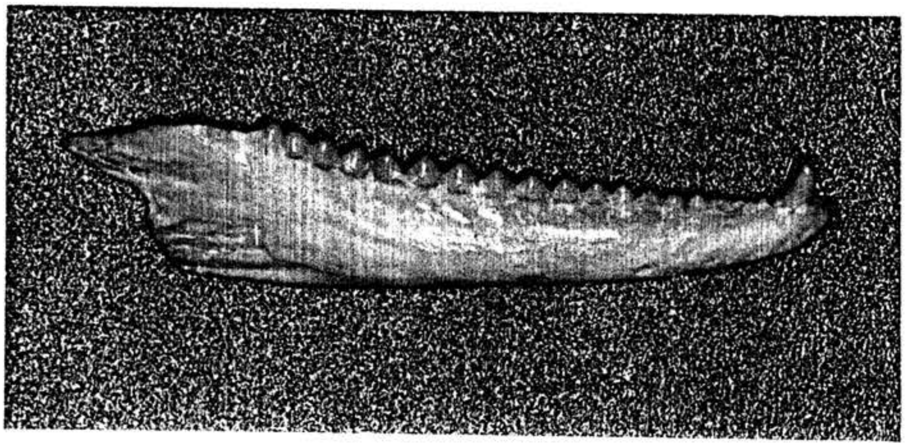

Figure 89 The dentary - A - Lateral view (x 6)

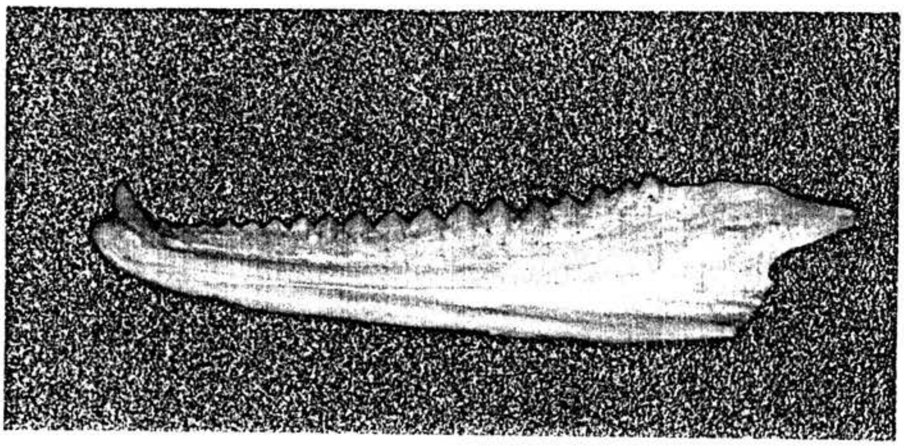

Figure 90 The dentary - A - Medial view (x 6)

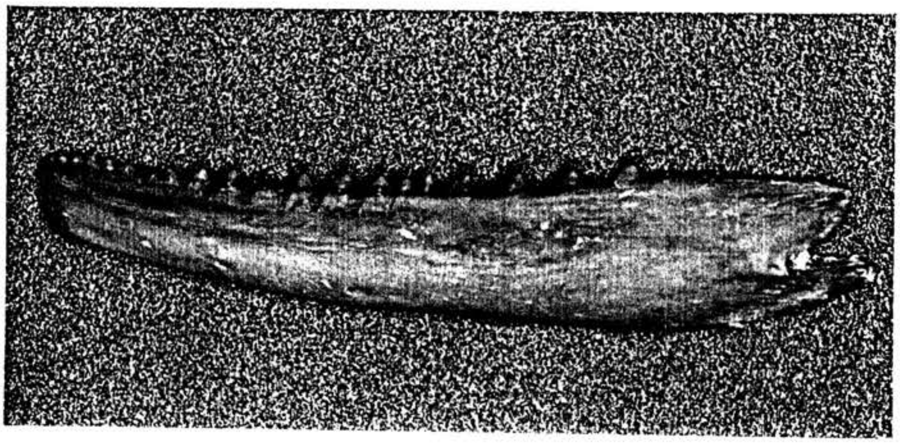

Figure 91 The dentary - B - Lateral view (x 5)

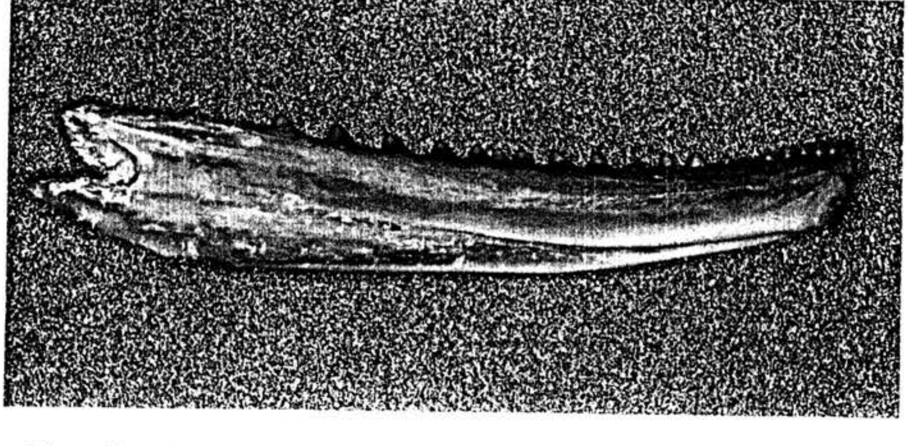

Figure 92 The dentary - B - Medial view (x 5)

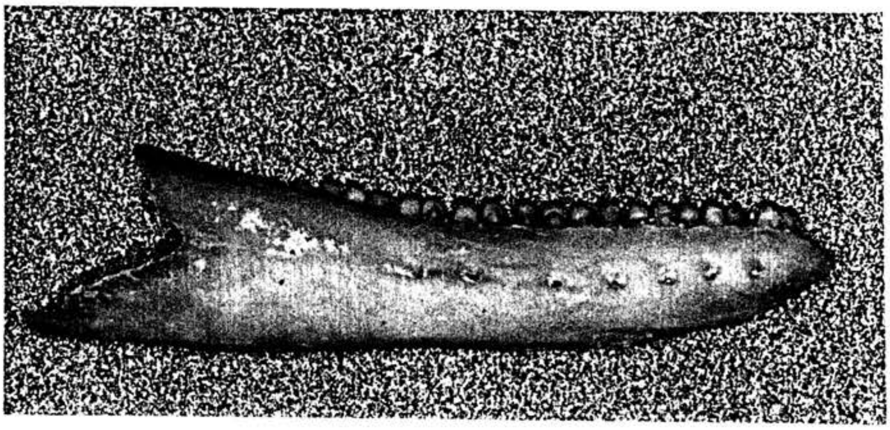

Figure 93 The dentary - C - Lateral view (x 8)

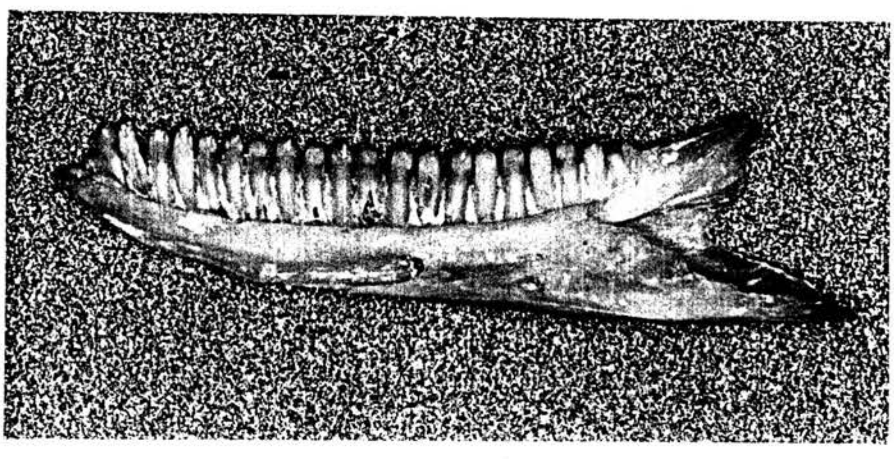

Figure 94 The dentary - C - Medial view (x 8)

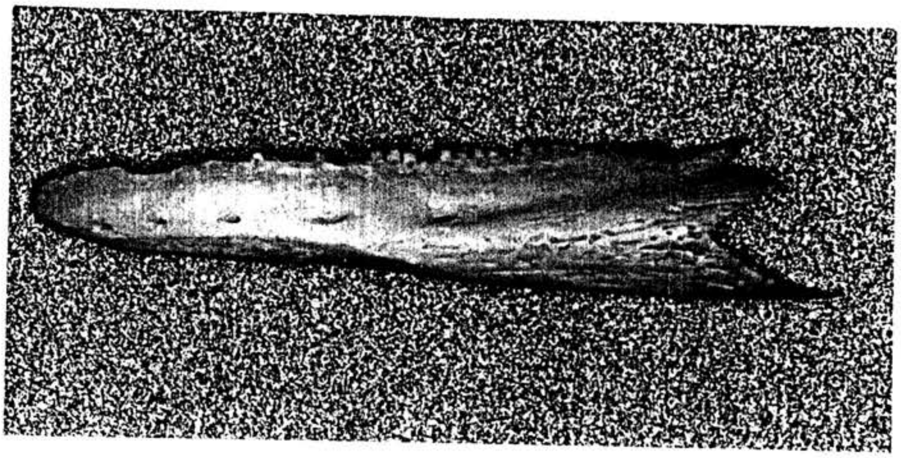

Figure 95 The dentary - D - Lateral view (x 8)

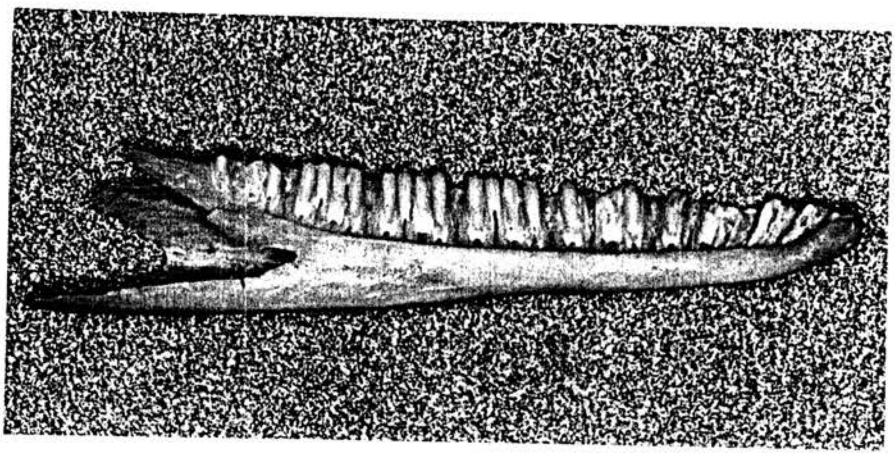

Figure 96 The dentary - D - Medial view (x 8)

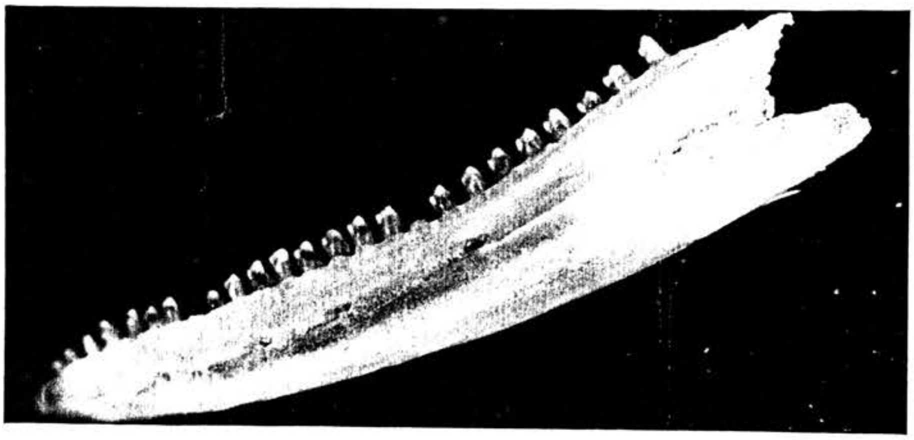

Figure 97 The dentary - E - Lateral view (x 14)

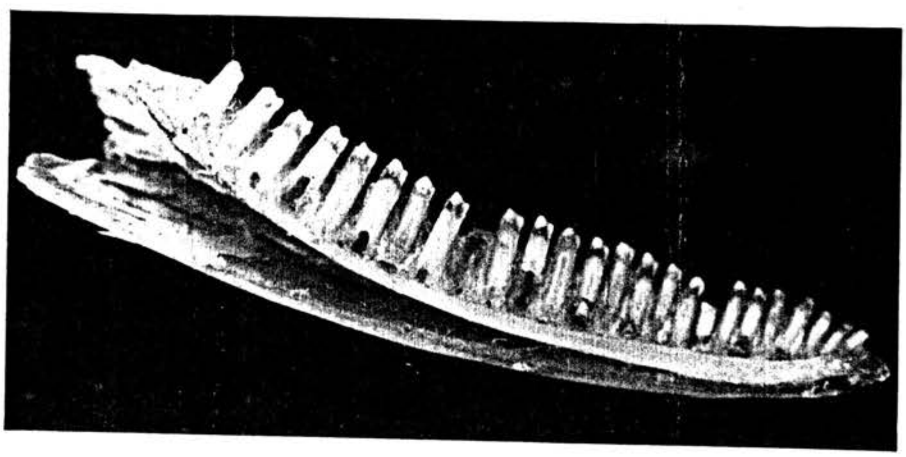

Figure 98 The dentary - E - Medial view (x 14)

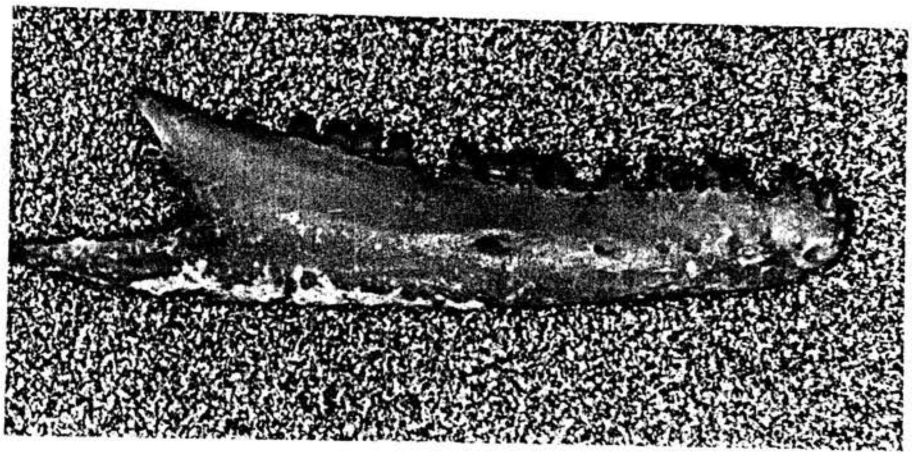

Figure 99 The dentary - F - Lateral view (x 13)

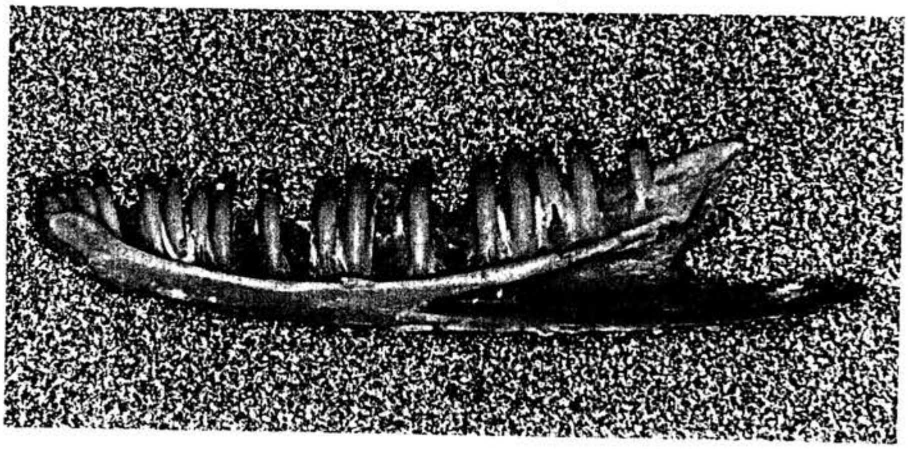

Figure 100 The dentary - F - Medial view (x 13)

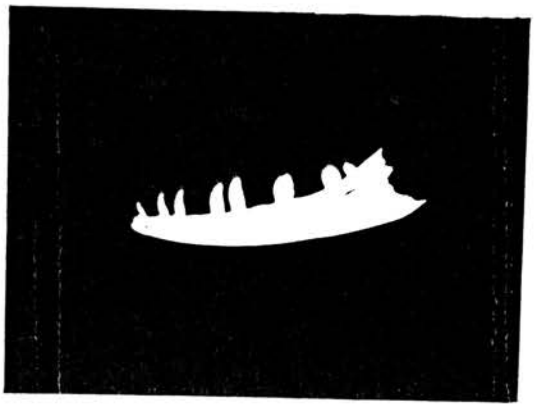

Figure 101 The dentary - G - Lateral view (x 0,7)

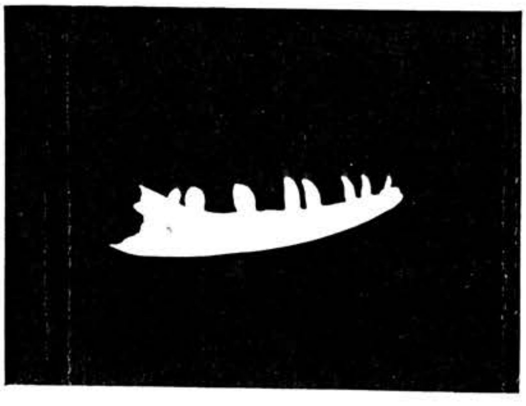

Figure 102 The dentary - G - Medial view (x 0,7)

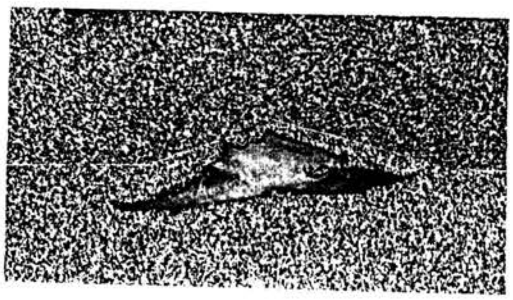

Figure 103 The splenial - D - Medial view (x 8)

Figure 104 The splenial - E - Medial view (x 15)

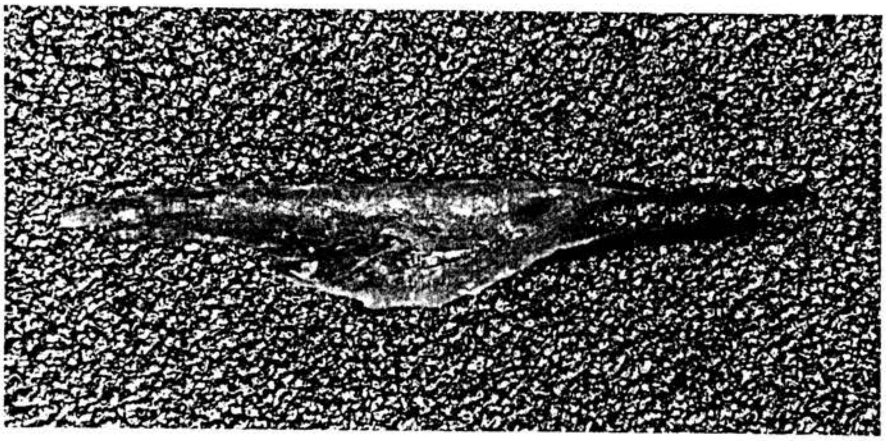

Figure 105 The splenial - F - Medial view (x 19)

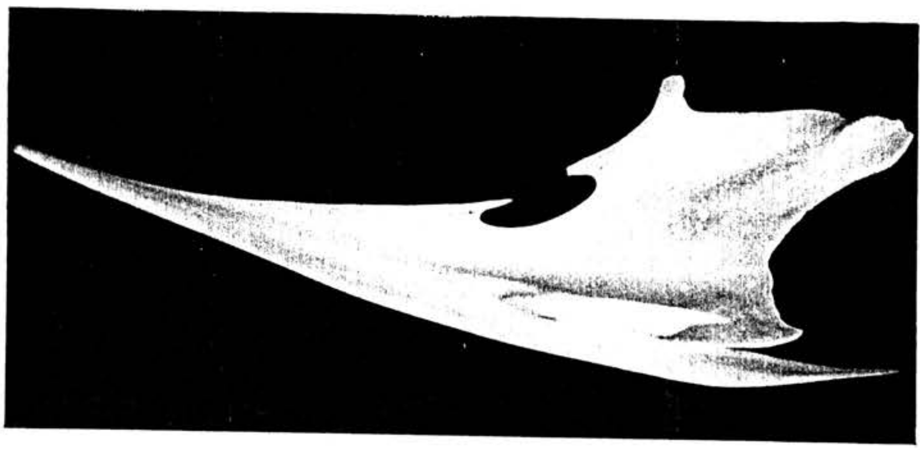

Figure 106 The splenial - G - Medial view (x 3,4)

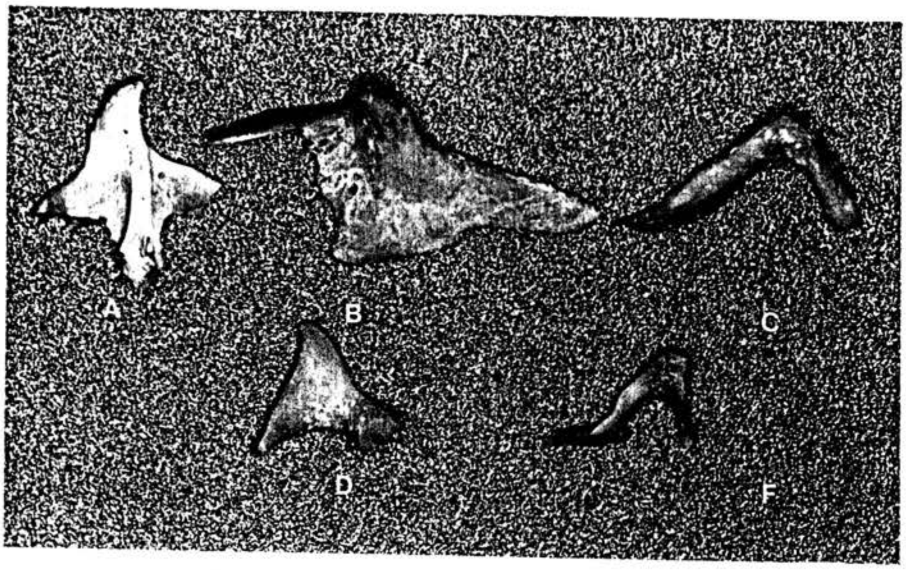

Figure 107 The coronoid - A, B, C, D, F - Medial view (x 5)

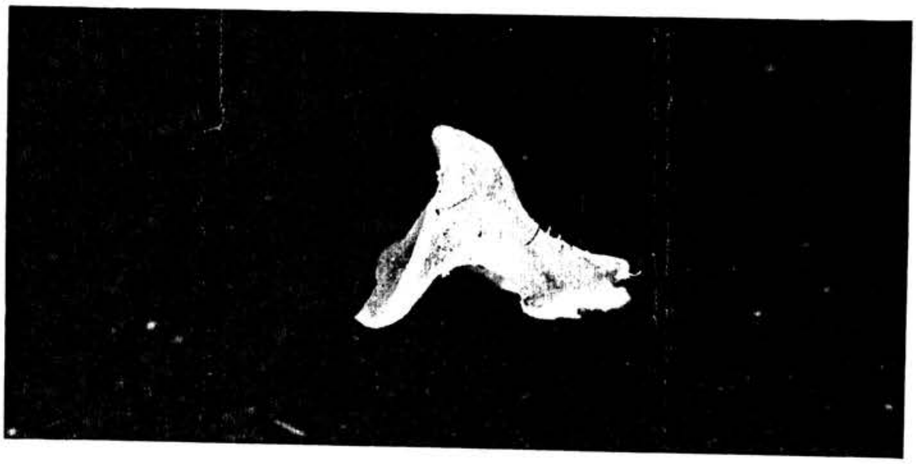

Figure 108 The coronoid - E - Medial view (x 14)

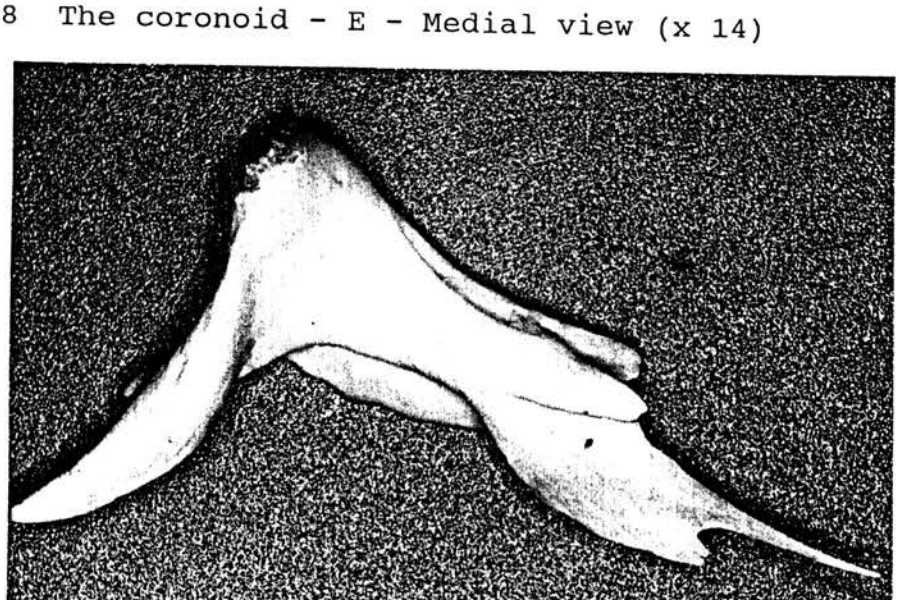

Figure 109 The coronoid - G - Medial view (x 4)

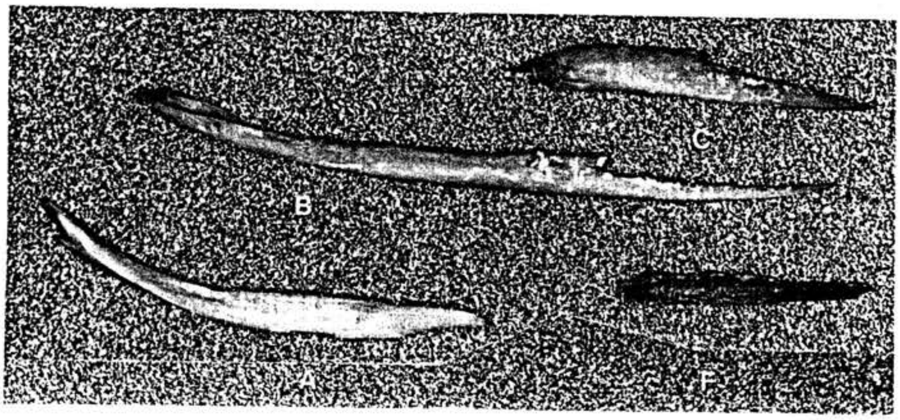

Figure 110 The angular - A, B, C, F - Lateral view (x 6)

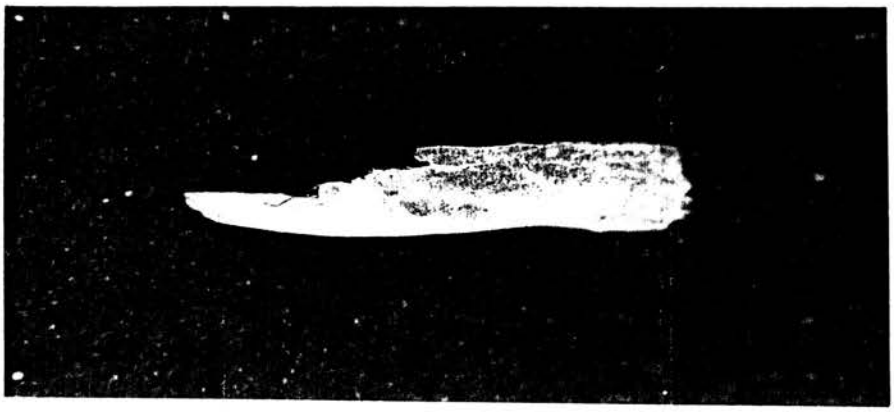

Figure 111 The angular - E - Lateral view (x 15)

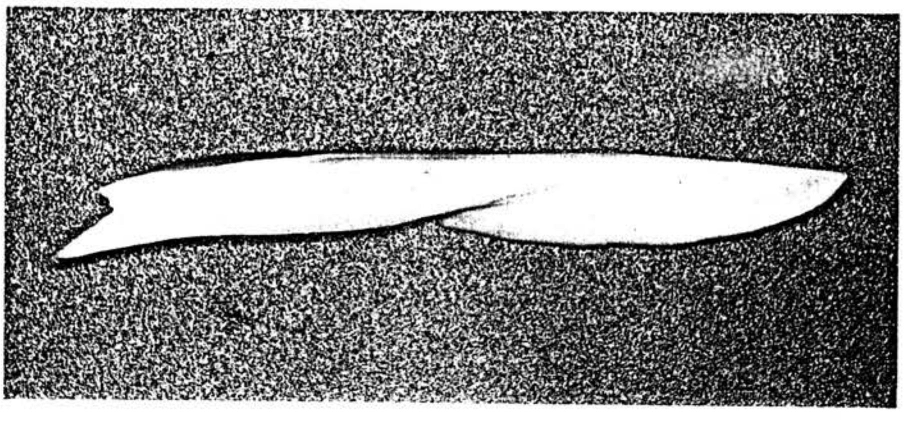

Figure 112 The angular - G - Medial view (x 4)

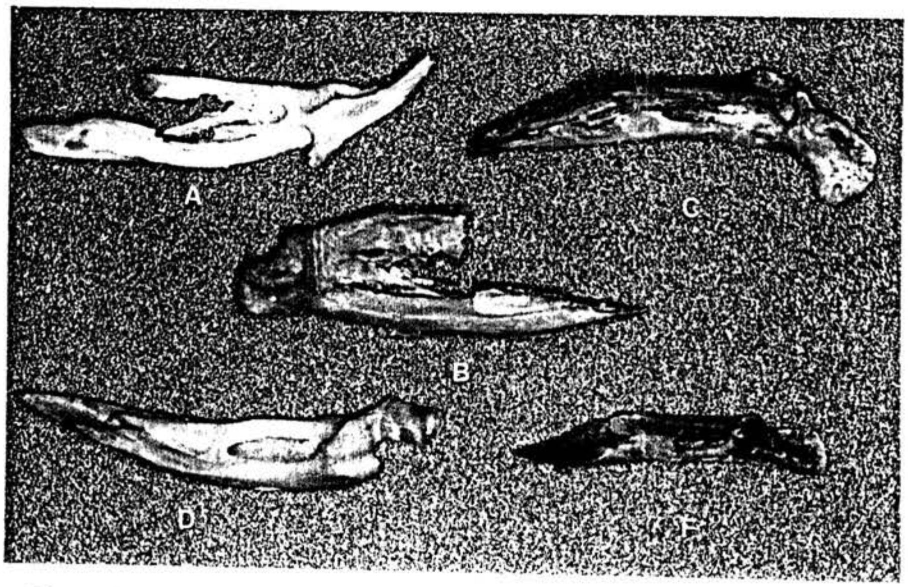

Figure 113 The fused surangular, prearticular and articular - A, B, C, D, F - Dorsomedial view (x 4)

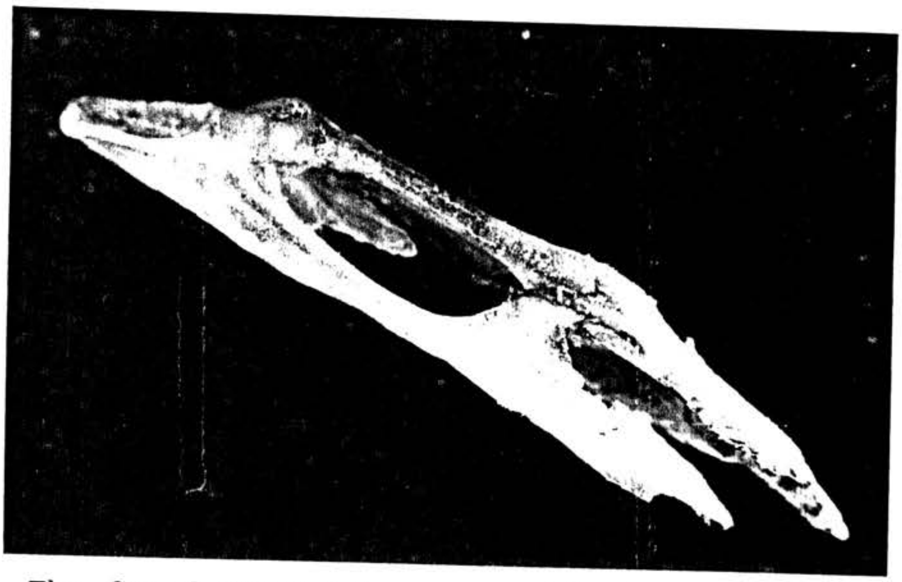

Figure 114 The fused surangular, prearticular and articular - E - Dorsomedial view (x 16)

Figure 115 The fused surangular, prearticular and articular - G - Dorsomedial view (x 0,8)

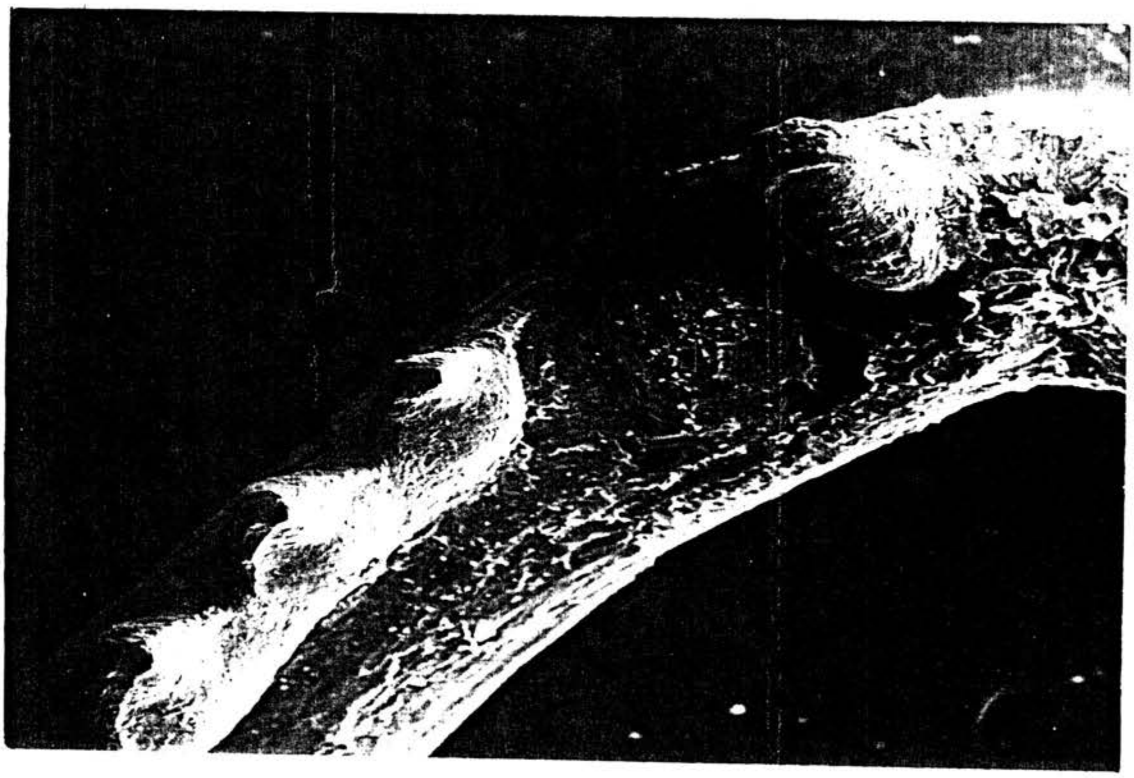

Figure 116 The dentition of *Agama atra atra* - (x 70)

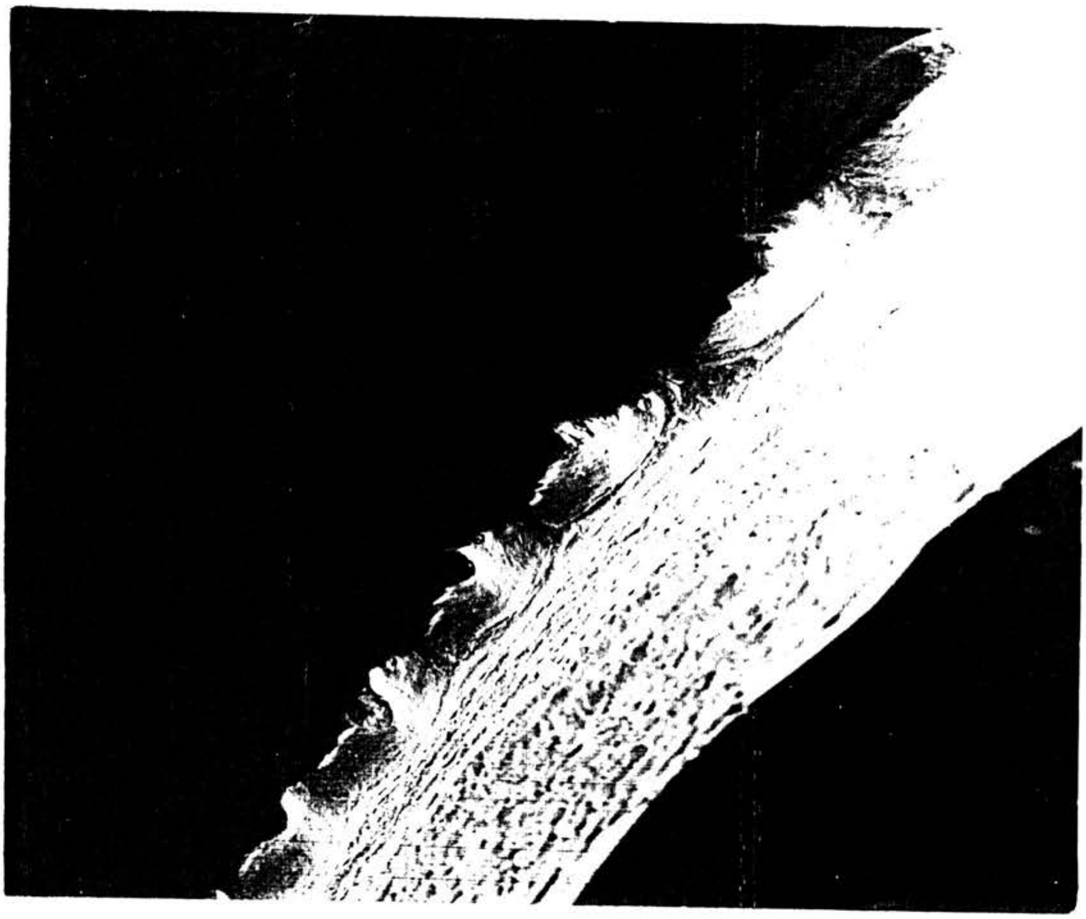

Figure 117 The dentition of *Chamaeleo dilepis* - (x 45)

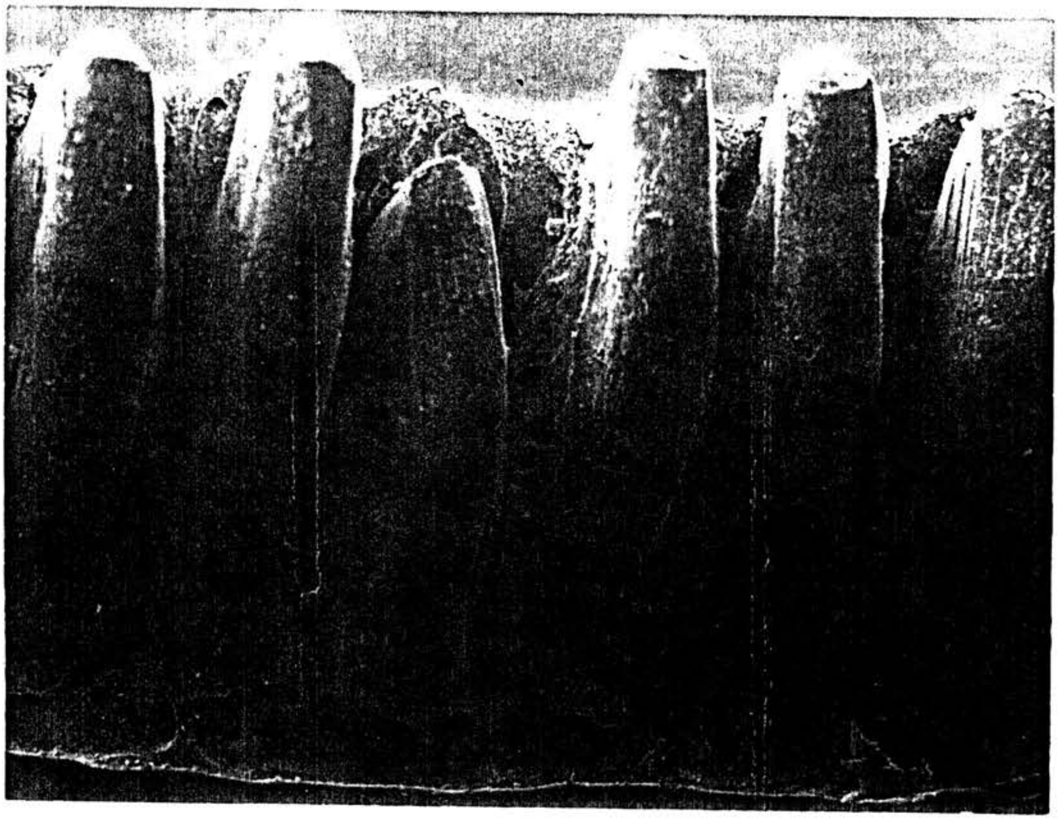

Figure 118 The dentition of *Cordylus cordylus cordylus* - (x 33)

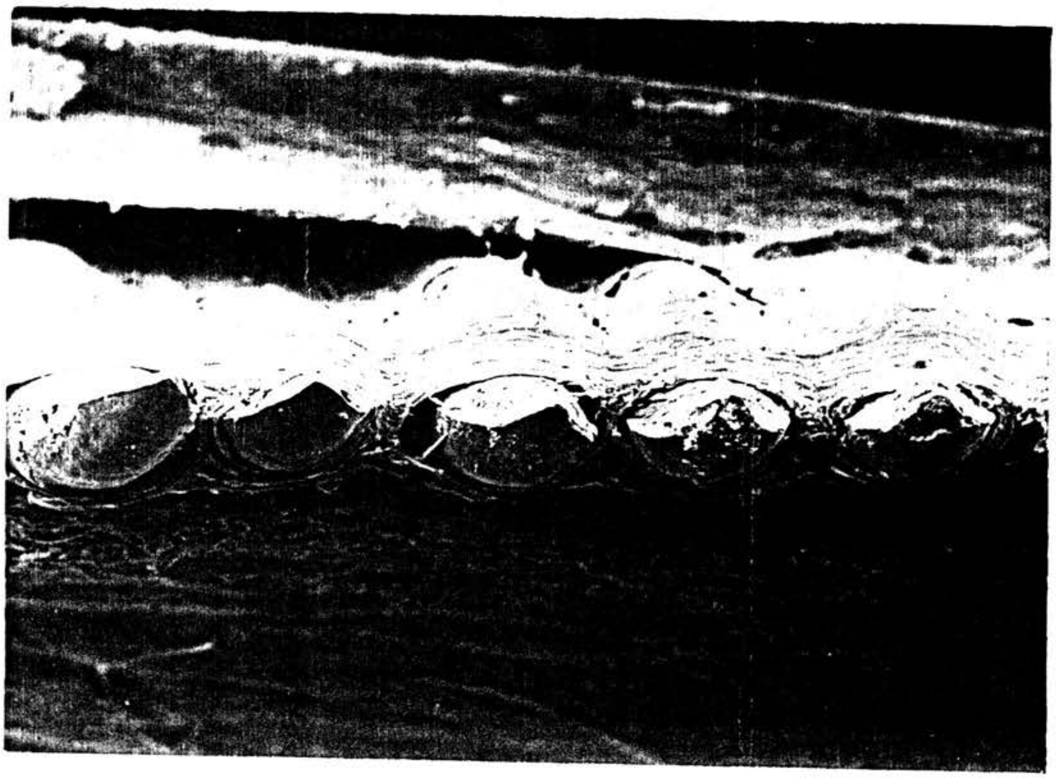

Figure 119 The dentition *of Pachydactylus bibronii* - (x 75)

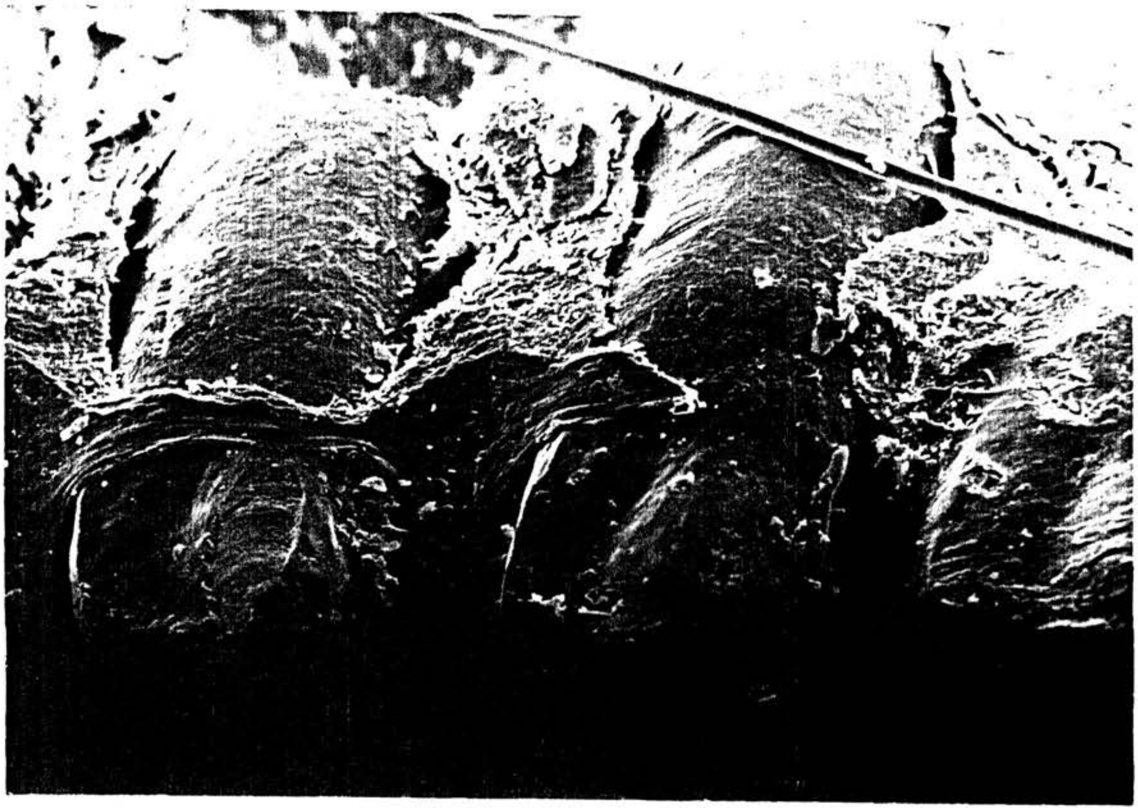

Figure 120 The dentition of *Merolus knoxii* - (x 180)

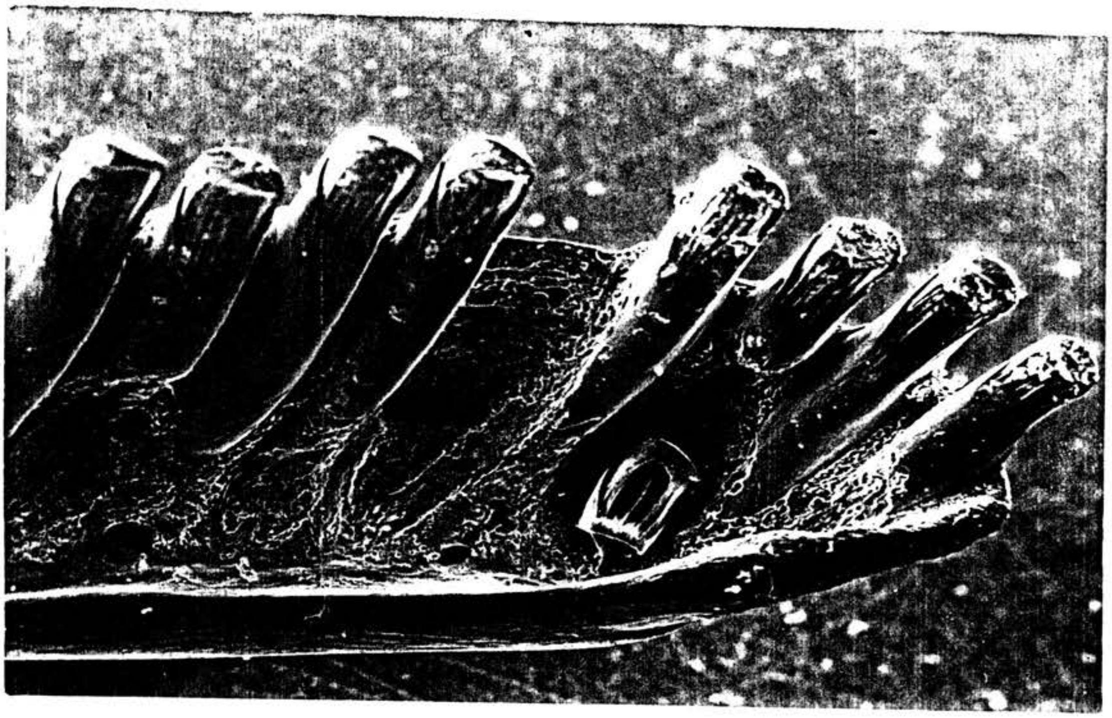

Figure 121 The dentition of *Mabuya capensis* - (x 54)

Figure 122 The dentition of *Varanus niloticus* - (x 15)