

Contributions to the comparative anatomy of the
nasal capsule and the organ of
Jacobson of the Lacertilia.

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Introduction

The present investigation is an attempt to give as complete an account as possible of the morphology of the nasal organ and the ductus nasolacrimalis of lizards, and to determine the extent to which the comparative anatomy of these organs illuminates the existing taxonomic "systems" of the order.

Unfortunately representatives of the smaller families: the Uroplatidae, Feyliniidae, Dibamidae, Pygopodidae, Helodermatidae and Xenosauridae were not available. Since these are all, however, highly specialized forms, their omission does not seriously affect the general conclusions drawn.

For the American material I am especially indebted to Mr. A.Loveridge of the Museum of Comparative Zoology, Harvard College, who kindly sent me a number of youthful specimens admirably suited for microtomy. I also wish to thank Dr. S.R.Atsatt of the University of California at Los Angeles for a specimen of Xantusia vigilis. Serial sections of a great number of lizards and snakes kindly donated to this department by Dr. G.T.Brock have proved to be of inestimable value. My thanks are also due to Dr. V.F.Fitzsimons of the Transvaal Museum and to Dr. R.Lawrence of the Natal Museum for specimens of an adult Typhlosaurus and of Varanus embryos respectively.

The present investigation has been carried out under the supervision of Prof. C.G.S. de Villiers, whom I wish to thank

most sincerely for his constant assistance and advice.

Historical Introduction.

This introduction is intended to serve as a short summary of the constitution of the nasal organ and palate of *Lacerta*, as well as a résumé of the terminology adopted. An adequate account of the existing literature on the subject matter is discussed in connexion with each family as it is being treated of. For a most comprehensive discussion of the extant literature on the vertebrate nasal capsule the reader is referred to the work of Hafferl (1921).

The outermost part of the nasal cavities consists of a fairly extensive vestibule lined by cavernous (erectile) elastic muscular tissue (Lapage, 1926) leading from the external naris to open anteriorly into the true nasal cavity dorsal to the middle of the organ of Jacobson. The true or olfactory part of the nasal cavity is subdivided into a main portion situated next to the septum and an extraconchal recess, communicating with the former cavity above and behind the concha nasalis; it lies between the outer side-wall of the concha and the side-wall of the capsule itself. Behind the choana and the concha, a posterior blind cavity (the antorbital chamber), lined with respiratory epithelium, is formed.

The "inner choana" (Göppert, 1903) connects the true nasal cavity with the respiratory choanal passage ("Choanengang", Fuchs 1908), and this in turn communicates with the oral cavity by means of the slit-like "outer choana." The development of

3.

a "secondary palate" in the upper level of the choanal passage transforms its anterior end into a choanal groove ("Choanenrinne", Fuchs, 1908). Into the anterior end of the latter the organ of Jacobson (lined by sensory epithelium) opens from the medial side. The ductus nasolacrimalis opens into the anterior end of the functional choana and the secretion of the Harderian and lacrimal glands is carried to the organ of Jacobson along an open gutter in the choanal groove (the "Winkeltasche" of Beecker, 1903).

The nasal capsule may be divided into three regions of approximately equal size: (a) an anterior one, comprising the cupola anterior (protecting the vestibule) and the cartilago alaris superior and c.a.inferior associated with the fenestra narina, (b) the conchal region, the only one possessing a floor (lamina transversalis anterior) completing the zona annularis ventrally, (c) and a posterior region consisting chiefly of the lamina antorbitalis the roof being very incomplete owing to the presence of a large foramen olfactorium. In the cupolar region the tectum is interrupted by a fenestra superior nasi, and in the conchal region the side wall covering the extraconchal recess is incomplete owing to the presence of a fenestra lateralis nasi.

The glandula nasalis lateralis is located in the extra-capsular cavum conchale encased by the conchal cartilage, and opening through an anteriorly facing aditus conchae. The duct of the lateral nasal gland issues from the aditus and enters the nasal capsule through a posterior bay in the fenestra narina behind the cartilago alaris superior, to open into the nasal cavity

on the border between the vestibule and the true nasal cavity.

The ramus ethmoidalis of $\bar{V}a$ enters the nasal capsule through the fissura orbitonasalis underneath the sphenethmoid commissure connecting the nasal capsule with the planum supra-septale. Inside the capsule it divides into its two components: the ramus lateralis issuing through the foramen epiphaniale immediately above the aditus conchae to innervate the glandula nasalis lateralis, while the ramus medialis runs alongside the septum to issue through the foramen apicale in the cupola anterior.

The skeletal capsule of the organ of Jacobson is described on page 105. For an account of the function of the organ the reader is referred to the work of Broman (1920). Two cartilages project from the lamina transversalis anterior: the paraseptal fusing with the planum antorbitale, and the ecto-choanal supporting the lateral edge of the choana and ending freely.

The descriptive part of the investigation is based mainly on taxonomic data as set forth in the well-known work of Camp (1923); Broom (1935) has also testified to the excellence of Camp's system. In a few cases only was it found necessary to deviate from Camp's arrangement, as in the case of the Geckonidae, which are placed at the end of the Ascalabota, since they represent a natural transition to the Autarchoglossa, as far as the nasal region is concerned.

The Rhynchocephalian nasal capsule is described fairly

fully since it forms a convenient introduction and a morphological link with that of the primitive Iguanidae.

Discussion of homologies and affinities and comparison with conditions obtaining in other Vertebrate groups have been confined as far as possible to the résumé at the end of the work in order to avoid repetition.

List of forms investigated.

(length signifies distance from tip of snout to tip of tail)

Iguanidae:	<u>Sceloporus undulatus</u>	Latreille	(young adult, 5 c.m.)
	<u>Uta stansburiana</u>		(adult)
	<u>Phrynosoma douglassii</u>		(adult)
	<u>Iguana iguana iguana</u>	Shaw	(young adult)
	<u>Anolis sagrae</u>	Duméril & Bibron	(young adult, 4.8c.m.)
Agamidae:	<u>Agama atra</u>	Daud.	(adult)
	<u>Agama hispida</u>		(embryo, 2.7 c.m.)
	" "		(" , 3.2 c.m.)
	" "		(" , 3.5 c.m.)
	" "		(" , 3.9 c.m.)
Chamaeleontidae:	<u>Chamaeleon bitaeniatus höhnelii</u>	Steindachner	
			(adult)
	<u>Microsaura (= Lophosaura) pumila pumila</u>	Daud.	
	" "	" "	(adult)
	" "	" "	(embryo, .9 c.m.)
	" "	" "	(embryo, 1.5 c.m.)
	" "	" "	(embryo, 1.9 c.m.)
	" "	" "	(embryo, 2.4 c.m.)
	" "	" "	(embryo, 2.5 c.m.)
	" "	" "	(embryo, 3.1 c.m.)
	" "	" "	(embryo, 3.7 c.m.)
	" "	" "	(embryo, 4 c.m.)
	" "	" "	(embryo, 5 c.m.)
	" "	" "	(embryo, 5.4 c.m.)

Geckonidae:	<u>Pachydactylus weberi gariesensis</u> Hwt.	(adult)
	<u>Pachydactylus ocellatus</u> Cuv.	(adult)
	<u>Pachydactylus</u> sp.	(embryos, various stages)
	<u>Lygodactylus capensis</u>	(" , " ")
Xantusiidae:	<u>Xantusia vigilis</u>	(adult)
Scincoidea:	<u>Mabuia capensis</u> Gray	(adult)
	" " "	(embryo, 1.2 c.m.)
	" " "	(embryo, 1.8 c.m.)
	" " "	(embryo, 2.7 c.m.)
	" " "	(embryo, 3.9 c.m.)
	" " "	(embryo, 4.5 c.m.)
	" " "	(embryo, 5.8 c.m.)
	<u>Scelotes bipes</u>	(adult)
	<u>Ablepharus wahlbergii</u> (A.Smith)	(adult)
	<u>Acontias meleagris meleagris</u> (Linn.)	(adult)
	" " "	" (embryos, various stages)
	<u>Typhlosaurus vernis</u> Boul.	(adult)
Teiidae:	<u>Teius teyo teyo</u> Daud.	(young adult)
	<u>Ameiva undulatus</u> Wiegmann	(adult)
	<u>Cnemidophorus sexlineatus</u>	(adult)
Amphisbaenidae:	<u>Monopeltis capensis</u>	(adult)
	<u>Rhineura floridana</u>	(adult)
Varanidae:	<u>Varanus niloticus</u> (Linn.)	(embryo, 23 c.m.)
Anguidae:	<u>Celestus pleii</u> Duméril & Bibron	(adult, 12.6 c.m.)
	<u>Ophisaurus ventralis</u> Linn.	(adult, 15 c.m.)

8.

Anniellidae: Anniella pulchra Gray (adult)

Cordylidae: Cordylus cordylus (young adult)

(=Zonuridae) Cordylus sp. (embryo, hatched)

Platysaurus capensis A.Smith (adult, 10 c.m.)

Chamaesaura anguina (Linn.) (adult)

RHYNCHOCEPHALIA.

The classical work on the development of the chondrocranium of *Sphenodon* is that of Howes and Swinnerton (1901) and Schauinsland (1900 and 1903). In 1906 Broom published a work on the organ of Jacobson in *Sphenodon* in which he stresses the mammalian characteristics of the organ and its capsule. Fuchs (1908) figures a very complete series of sections through the nasal region of a fairly old embryo of *Sphenodon* in his comprehensive account of the palatal structures of Vertebrates, and in a work of 1911 he compares the septomaxillary and its relations to the cartilaginous capsule of Jacobson's organ in *Sphenodon* with that of a mammal (*Dasypus*). Both Göppert (1903) and Lakjer (1927) mention *Sphenodon* in their studies on the external topography and the bones of the palate respectively. Unfortunately the recent work of Hoppe (1934) on the nasal organ of *Sphenodon* was not available beyond the short summary by Matthes (1934). Also Schauinsland's investigations were not available, so that one was obliged to depend on quotations from other authors.

The following account of the cartilaginous and bony capsule of the nasal cavities is based chiefly on the abovementioned sources, and the figures are based on illustrations from the publications of Fuchs (1908 and 1911) and Broom (1906).

Although the cartilaginous nasal capsule shows such remarkable similarity with that of *Lacertilia*, that, judged on the nasal region alone, *Sphenodon* would certainly be classified as a primitive lizard, it yet provides in several instances the morphological

link which connects the primitive Lacertilian capsule with that of the primitive Mammalia and the Amphibia.

The roof and side wall of the adult capsule are very incomplete because of the exceptionally large size of the fenestra narina, and the presence of both the fenestra lateralis nasi and the fenestra superior nasi (figs. 1-3) (Howes and Swinnerton, 1901).

In addition to the lateral nasal gland homologous with the single gland of Lacertilia, a second, ventrally situated gland is present, which also opens into the posterior end of the vestibule and is probably homologous with the ventral nasal gland of Chelonia (Hoppe, 1934). The lateral nasal gland is situated in the typical Lacertilian position, but is not lodged in a cavum conchale (Howes and Swinnerton, 1901), although there is a concha on the inner surface of the cartilaginous wall in a corresponding position. Hoppe (1934) regards this as undoubtedly homologous with the concha of Lacertilia. This homology is substantiated by the position of the foramen epiphaniale. In Lacerta this foramen is situated immediately anterior to the fenestra lateralis and indicates the line of fusion between the parietotectal and paranasal cartilages (de Beer, 1937). In Sphenodon it is found near the anterior, upper border of the fenestra lateralis (Howes and Swinnerton, 1901) apparently in the immediate neighbourhood of the concha. Judging by all available figures the glandula nasalis lateralis is situated in a shallow groove on the side wall, from the floor of which the anterior part of the concha projects into the nasal cavity.

The duct runs forwards and enters the posterior end of the vestibule through the upper hind corner of the fenestra narina as it also does in *Lacerta*.

According to Fuchs (1911) the anterior end of the concha is closely associated with the posterior end of the septomaxillary and the opening of the ductus nasolacrimalis (cf. *Geckonidae*).

De Beer (1937) states that all reptiles possess a concha except *Sphenodon* and the *Chelonia*. Presumably a cavum conchale lodging the lateral nasal gland is implied, since *Sphenodon* undoubtedly possesses a concha (fig. 4) corresponding to that of *Lacertilia*. No structure comparable with it occurs in the *Chelonia* (Peter, 1906). From the invariable presence of a cavum conchale in the living Diapsidan reptiles it may be argued that this structure has been secondarily lost in *Sphenodon*, so that its absence constitutes no evidence in favour of Chelonian or mammalian affinity. The absence of a cavum conchale in the *Chamaeleontidae*, the *Agamidae* and in many of the *Iguanidae* does not necessarily point to affinity with *Sphenodon* either, since it is clear that its absence in these families is the result of parallel evolution: it has been obliterated by a shortening of the nasal region and an extreme backward elongation of the vestibule and its associated skeletal elements.

In addition to the "hintere Muschel" which Hoppe homologises with that of *Lacertilia*, he describes a second anterior concha which has disappeared in *Lacertilia* and is represented only by "jene Lippe am Choanengang, die zwischen der Winkeltasche und dem

horizontalen Schenkel des Choanengangs liegt" (Matthes, 1934). Fuchs (1911) has already called attention to the presence of a concha in *Sphenodon* (fig. 4), but without having seen the work of Hoppe in the original it is impossible to decide whether this corresponds to Hoppe's posterior concha or not.

The posterior part of the roof, the sphenethmoid commissure, the planum antorbitale and the processus maxillaris posterior are identical with those of *Lacerta*.

The floor of the nasal capsule shows the same degree of incompleteness as that of *Lacerta*, a zona annularis being completed for a short distance only, in front of the organ of Jacobson by the lamina transversalis anterior.

The anterior ventral edge of the septum nasi is produced into a short rostral process (prenasal process of Howes and Swinnerton, 1901), directed downward and forward between the two premaxillaries (Broca, 1906). Broca compares the rostrum with a similar process in *Echidna*, and since he finds it to be absent in snakes, lizards, and tortoises regards it as a mammalian characteristic retained by *Sphenodon*. An anterior rostral prolongation of the nasal septum into the internasal cavity between the two cupolar cartilages is, however, present throughout the *Iguanidae* (figs. 8, 15 and 18). The prenasal process of *Crocodyles* also is undoubtedly homologous with that of *Sphenodon* (de Beer, 1937 and Meek, 1911), although the anterior part of the nasal capsule shows adaptational specialization caused by the dorsal position of the external nares. The presence of a prenasal

process would thus tend to confirm the relationship of *Sphenodon* with the other diapsid reptiles and especially the *Lacertilia*, rather than point to mammalian affinities through resemblance to *Echidna*, the snout region of which shows a very high degree of specialization.

On the ventral edge of the nasal septum in the region immediately in front of the organs of Jacobson, there occurs a short, median, backwardly directed process, forming a cartilaginous support for the papilla palatina (Broom, 1906). According to Broom's figures and description it lies ventral to the anterior tips of the vomers, which would appear to be largely instrumental in its formation (fig. 1). They penetrate the ventral edge of the nasal septum, which is greatly enlarged at this point to accommodate the anterior parts of the organs of Jacobson.

Broom takes the presence of this "papillary cartilage" as proof of the mammalian affinities of *Sphenodon*, since a structure which he regards as homologous with it, is widespread through the primitive *Mammalia*, while it is absent from reptiles other than *Sphenodon*. It occurs in *Echidna* as "a short and isolated cartilaginous rod forming the skeletal basis of the papilla palatina" (Wilson, 1901). Judging from one of Wilson's figures the relation of this structure is essentially the same as in *Sphenodon*, except that it is detached from the septum.

A papillary cartilage is further present in most *Marsupials* and also in *Macroscelides* and *Miniopterus* among higher forms

(Broom, 1896 and 1906). In the Marsupials it appears to consist of an isolated horizontal cartilaginous plate invariably situated ventral to the palatine process of the premaxillaries and between the nasopalatine ducts. It serves as a support for their median walls (Broom, 1896).

According to Broom (1906) a papillary cartilage is present in the crocodile, but I was unable to find any homologous element in a 7.5 cm. embryo of Alligator mississippiensis, and it is not featured or mentioned by Meek for Crocodylus porosus (1911), or by de Beer for Crocodylus bitorquatus (1937).

Sphenodon is therefore the only reptile possessing a papillary cartilage, but since the homologies of the various cartilaginous elements occurring in the vicinity of the nasopalatine canal and the papilla palatina of mammals are by no means clear, it seems wiser not to stress this similarity between Sphenodon and the primitive Mammalia.

In addition to the paraseptal and ectochoanal cartilages projecting backwards from the lamina transversalis anterior in Lacerta, a third cartilaginous process, which forms a roof over the organ of Jacobson, is present in Sphenodon (Broom 1906) (figs. 2 and 3). The septomaxillary, instead of roofing the organ as it does in Lacertilia and Ophidia, is entirely limited to the postero-ventral edge of the fenestra nasina, thus forming part of the bony side wall of the nasal capsule (Fuchs 1911). An anterior, horizontally inclined process rests upon the upper, outer corner of Jacobson's capsule, where this forms part of the

border of the fenestra narinā (fig.1). Beyond this indirect relation to the organ of Jacobson, the bone is solely concerned with the support of the floor and lateral wall of the vestibule (figs. 1 and 2). According to Fuchs (1911) the same relations obtain in *Dasypus*. The posterior end of the septomaxillary comes into close contact with the anterior part of the concha (cf. *Geckonidae*) and with the ductus nasolacrimalis (Fuchs, 1911).

According to Hoppe (1934) the vestibule differs from that of the *Lacertilia* in that it enters the nasal cavity laterally at an angle of 90° (fig. 1) instead of lying in the same longitudinal plane with it. This may merely be due to the fact that it is extremely short, as in *Ophidia*, and would thus represent the lateral outer sac of the *Lacertilian* vestibule only. The septomaxillary appears to be a bone primarily investing the vestibular wall, and, in the *Lacertilia*, secondarily acquiring connection with the organ of Jacobson as a result of the backward elongation of the vestibule (cf. Lapage, 1928 and Solger, 1876); conditions obtaining in the *Iguanidae* support this view.

A small anterior part of the organ of Jacobson is encased in a complete cartilaginous cupola (fig. 1). Further back, at about the same vertical niveau as the duct, the roof, side wall and floor become detached from the septum (the median wall), and from one another, to form three independent cartilaginous elements (fig. 3). The side wall is continued as the ectochoanal cartilage (fig. 2). This cartilage supports the anterior wall of the duct of Jacobson's organ, the lateral wall of the choana,

and the ventral wall of the ductus nasolacrimalis which enters the choana laterally and immediately opposite the duct of Jacobson's organ whose orifice is situated medially.

The roofing cartilage is also continued backwards as an independent element, but does not quite reach the hind end of the organ, whose posterior wall, judging from all available descriptions and figures, is completely unprotected by cartilage or bone. After describing the three elements mentioned above de Beer (1937) says: "Jacobson's organ eventually becomes almost completely enclosed in a cartilaginous capsule of its own". I was however, unable to find any confirmatory description of a stage older than those described by Howes and Swinnerton, Broom and Fuchs. Except for two rather confusing statements by Born (1879) and Fleischer (1877), quoted by Born p.75, a roofing cartilage for the organ of Jacobson has not to my knowledge been described for any other reptile. Broom (1906) considers its presence in *Sphenodon* as peculiar to this order and indicative of its mammalian affinities. As will, however, be explained below, the organ of Jacobson in the *Iguanidae* is completely roofed by cartilage; additional evidence of the close relationship of *Sphenodon* to the *Lacertilia*.

The paraseptal forms a trough-like support for the floor of the organ of Jacobson (fig. 2), instead of supporting part of the median wall as in *Lacerta* (fig. 44). This median position of the paraseptal in the *Lacertilia* is apparently due to rotation of the organ through 90° on its longitudinal axis, thus resulting

in an alteration of the position of the duct from a lateral one, in which it opens into the medial wall of the choana, to a ventral one in which it opens directly into the oral cavity (Beecker, 1903). The absence of a concha of Jacobson's organ in *Sphenodon* proves that this cartilaginous development (on the zona annularis), pushing into the lumen of the organ from the lateral side, was largely responsible for the rotation of the organ. This morphogenetic explanation would account for the ventral position of the duct and the medial position of the paraseptal in *Lacertilia*. This theory is moreover substantiated by ontogenetic evidence derived from the development of *Lacerta* (Born, 1879).

Although, therefore, the relations of the paraseptal of *Sphenodon* are singularly mammal-like as was stressed by Broom, this circumstance does not necessarily imply non-relationship of *Sphenodon* with lizards.

LACERTILIA.Iguanidae.

To the best of my knowledge no detailed work on the nasal region of the Iguanidae has appeared, with the exception of that of Born (1879) on the ductus nasolacrimalis, in which a description of the nasal capsule, the organ of Jacobson and the ductus nasolacrimalis of the following Iguanid genera is given:

Liolaemus pictus, Leiosaurus bellii and Sceloporus undulatus.

Of these I was able to examine only the last. Born called attention to the very primitive relations of the ductus nasolacrimalis and Jacobson's duct to the choana: a condition approximating to that of the Rhynchocephalia in which these ducts open into the extreme anterior end of the choana directly opposite each other (Fuchs, 1908).

The more recent work of Lakjer (1927) includes an account of the bony palate of a number of Iguanidae. He stresses the primitive position which this family occupies with respect to the degree of development of the choanal opening in the bony skull. His "Palaeochoanata", comprising the Iguanidae and the Agamidae, come very close to the primitive Sphenodon type.

Stebbins (1943) describes the adaptation of the nasal passages for sand-burrowing in the genus *Uma*, giving an interpretation of the muscular mechanism of the external nares.

In the following account it will be attempted to show that, regarding the nasal region, this family occupies a unique position

among the Lacertilia, since in spite of the unusual type of vestibule, it shows in a number of points quite a remarkable resemblance to *Sphenodon*, proving that the isolated order to which the latter belongs is even more closely related to the Lacertilia than has hitherto been maintained.

I was fortunate in having been able to investigate a fairly large number of representative forms belonging to the Iguanidae. I am particularly indebted to Mr. A. Loveridge of the Museum of Comparative Zoology, Harvard, who very kindly sent me a number of specimens belonging to this and other American families. It is to be regretted that neither of the Madagascar genera was available for study, since an investigation of Jacobson's capsule might finally have established their affinities.

The following forms were investigated: *Sceloporus undulatus*, *Uta stansburiana*, *Phrynosoma douglassii*, *Iguana iguana iguana*, *Anolis sagrae*.

The Iguanidae are a large family showing several well-defined trends of development in the nasal region. *Iguana* itself is primitive in the retention of a typical Lacertilian concha. *Sceloporus*, *Uta* and *Phrynosoma* appear to constitute a closely related group, while *Liolaemus* and *Leiosaurus* (Born, 1879) show a common type of specialization in the position of the vestibule. The genus *Anolis* is aberrant as indicated by the reduction of cartilage in the nasal region.

Sceloporus undulatus was selected for detailed description, since it appears to be primitive in as much as it retains an

extraordinarily large amount of cartilage in the nasal region. It further represents a convenient morphological starting-point for the derivation of the Agamidae and the Chamaeleontidae.

Born (1879) gave a description of the nasal cavities of the "Eunota" of Duméril and Bibron, including the Old World Agamidae and the New World Iguanidae; these two families constitute the "Iguania" of Camp (1926). In most of the representatives of this group the vestibule, instead of entering the olfactory cavity in the usual Lacertilian manner, runs above it for practically its whole length, and enters it dorsally through a wide orifice occupying its posterior third. In *Sceloporus* it actually opens behind the choana into the *cavum antorbitale* (fig. 7). Solger (1876) has already pointed out that in *Chamaeleo*, and to a smaller extent in the *Leguan*, an anterior blind sac of the olfactory cavity is situated underneath the vestibule. In the *Varanidae*, however, the latter opens into the antero-dorsal part of the olfactory cavity. The backward extension of the vestibule in *Iguanidae* is explained by Born as having been caused by a shortening and thickening of the snout region relative to the rest of the skull. This tendency is present to a greater or lesser degree throughout the *Ascalabota* of Camp (i.e. the *Geckonidae*, the *Iguania* and the *Chamaeleontidae*).

In *Sceloporus* the true olfactory cavity has been pushed forward underneath the vestibule, and outward by the organ of Jacobson, so that its extreme anterior end is situated lateral to this organ (fig. 9). The posterior limit of the vestibule together with its associated structures have undergone a dorsal

and backward displacement(fig. 7).

These peculiarities in the nasal cavities are associated with equivalent differences in the cartilaginous nasal capsule (figs. 5, 6 and 8). In *Sceloporus* the anterior half of the septum nasi is complete, but its posterior half is divided by a posterior incisura into a ventral cylindrical bar and a dorsal lamina (fig. 10). The latter forms a dividing wall between the left and right vestibules and rapidly loses height when it passes backward to disappear immediately in front of the planum antorbitale. As will be clear from fig. 10, the dorsal part represents the fused median walls of the nasal capsules themselves, and the ventral bar only is of trabecular origin. The lower anterior edge of the septum is continued forward and downward as a short prenasal process or rostrum (fig. 8); it projects into a shallow cavum internasale between the cupolar cartilages, and is identical with the rostrum of *Sphenodon* (cf. fig.8, pl. III in Howes and Swinnerton 1901). Among lizards a rostrum occurs also in the *Teiidae*, the *Varanidae* and the *Chamaesaurinae*, where, however, a cavum internasale is absent, and the process projects beyond the rest of the nasal capsule (cf. du Plessis, 1945). It is absent in the *Cordylinae*, the other subfamily of the *Cordylidae* (= "*Zonuridae*" auctorum). De Beer (1937) records its presence in *Crocodilus biporcatus*; and I have observed it in sections of a 7.5 c.m. embryo of *Alligator mississippiensis*.

The tectum and paries nasi are complete, there being no indication of the fenestrae so typical of *Sphenodon* and most

Lacertilians.

The vestibule is roofed over by a curved dome continuous with the dorsal edge of the septum (ontogenetically the "parietotectal" of De Beer, 1930). The cupola anterior and the processus alaris inferior and p.a. superior are normal (figs. 5 and 8).

A more lateral dome-like structure forms the roof and side-wall of the lateral half of the olfactory cavity projecting from underneath the vestibule (ontogenetically the "paranasal" of de Beer, 1930) (fig. 6). The anterior end of this dome is fused to the postero-lateral corner of the capsule of Jacobson's organ (fig. 8). Where the two domes meet each other on either side, a longitudinal groove is formed, the trough of which is filled with the glandula nasalis lateralis which is not lodged in a cavum conchale. The outer edge of the septomaxillary projects into the slit-like opening between these two cartilages on the floor of the groove, so that they remain separate along practically the whole length of the nasal capsule (figs. 9 and 10). A similar though less pronounced structure in the Gecko has been termed the fissura lateralis nasi by Hafferl (1921), and I have adopted this nomenclature for the "Iguania" as well.

At the postero-dorsal corner of the nasal capsule the fissura widens out to allow for the entrance of the duct of the glandula nasalis lateralis into the nasal capsule (fig. 8). The actual point of entrance indicates externally the posterior boundary of the vestibule (fig. 7). Behind the duct the two

cartilages fuse and the tectum nasi becomes continuous for a very short distance in front of the foramen olfactorium (fig.6).

In *Lacerta* the duct of the glandula nasalis lateralis runs forward from the cavum conchale and enters the nasal capsule through the postero-dorsal corner of the fenestra narina and behind the processus alaris superior. Essentially the same conditions obtain in *Sceloporus*, except that the duct has migrated backward with the posterior border of the vestibule, and it has consequently carried the upper hind corner of the fenestra narina with it. The fissura lateralis nasi, therefore, merely represents a backward, slit-like continuation of the fenestra narina (fig. 8). In adult *Lacertidae*, older than the stage described by Gaupp (1900), that part of the fenestra narina allowing the entrance of the duct of the glandula nasalis lateralis is also partly closed off from the fenestra itself by an approximation of the outer edge of the tectum nasi to the upper outer edge of the capsule of Jacobson. The fissura lateralis may therefore be regarded as a normal *Lacertilian* structure which has been greatly exaggerated in the "*Ascalabota*" by the elongation of the vestibule.

Once the homology of the fissura lateralis nasi is established the interpretation of the rest of the tectum nasi is easy. In *Lacerta* the aditus conchae is situated immediately behind the fenestra narina, but the region lying behind the vestibule in *Sceloporus* has been telescoped to such an extent, that the concha has entirely disappeared. The loss of olfactory epithelium thereby entailed is adequately compensated for by the large size

of the organ of Jacobson (cf. Snakes). The *glandula nasalis lateralis*, normally lodged in the *cavum conchale*, has shifted forward, filled up the cavity of the lateral groove, and come to lie in front of its duct, which now runs backward along the groove, before entering the nasal capsule.

The course of the *ramus ethmoidalis* of $\bar{V}a$ and its branches, and the position of the *foramen epiphaniale* are of the utmost importance in establishing the homologies of the various structures in the posterior half of the nasal capsule of *Sceloporus*. In *Lacerta* the *ramus ethmoidalis* enters the nasal capsule through the *fissura orbitonasalis* which is separated from the *foramen olfactorium* by the *cartilago sphenethmoidalis* (Gaupp, 1900). The lateral branch of the ethmoid issues from the nasal capsule through the *foramen epiphaniale*, situated immediately above the *aditus conchae* and indicating the line of demarcation between the paranasal and the parietotectal cartilages (de Beer, 1930).

In *Sceloporus* two small foramina occur practically next to each other on the upper hind edge of the nasal capsule (fig. 6). The lateral one is slightly larger and represents the *fissura orbitonasalis* and part of the *foramen olfactorium*. The ^{true} nasal fibres of the *nervus olfactorius* and the *ramus ethmoidalis* of $\bar{V}a$ enter through it, and are separated by the *sphenethmoid cartilage* (fig. 6). The branch of the *nervus olfactorius* which innervates the organ of Jacobson (*nervus vomero-nasale*) enters the capsule separately. After branching off from the *nervus olfactorius* it passes directly downward on either side

of the septum and enters the nasal capsule through a slitlike incisura between the septum and the lamina antorbitalis (fig. 8, FNV). It then runs parallel with the septum to the organ of Jacobson. Dorsally this incisura is separated from the foramen already described by a strip of tectal cartilage which has no homologon in *Lacerta* where both the rami of the olfactorius enters through the large communal fenestra olfactoria (cf. fig. 14).

In the small size of the foramen olfactorium the *Iguania* resemble the *Chelonia* and *Crocodylia*; but the condition is probably a secondary one in the *Iguania*, since the foramen olfactorium of *Sphenodon* is large like that of *Lacerta* and both the olfactory branches enter through it (Howes and Swinnerton, 1901). In the *Chelonia* and *Crocodylia* the nervus vomeronasale is of course absent. Inside the capsular wall the ramus ethmoidalis gives off its lateral branch which almost immediately issues from the medial foramen; this therefore represents the foramen epiphaniale. The short continuous tectal zone separating it from the incisura for the duct of the glandula nasalis lateralis is homologous with the entire conchal region (fig. 6).

In *Sceloporus* there is no indication of a concha, but in *Uta* and *Phrynosoma* a feebly developed concha occurs on the inside of the capsular wall of this region, although no cavum conchale exists. That the cavum conchale has been secondarily lost in the *Iguanidae* is proved by its presence in the genus *Iguana* itself. Its loss in *Sphenodon* must therefore have occurred independently.

Neither the paries nasi nor the planum antorbitale shows any peculiarities. The posterior part of the ventral edge of

the paries bends upward and outward to form a gutter-like process maxillaris anterior in which the ductus nasolacrimalis lies (fig. 8). This trough is converted into a complete skeletal duct by the prefrontal. A well-developed processus maxillaris posterior is also represented.

The solum nasi is more complete than in any other Lacertilian examined and shows a number of peculiarities found in this family only. A lamina transversalis anterior is present and forms, as in *Lacerta*, the ventral completion of a zona annularis. The presence of a zona annularis is not immediately apparent from transverse sections, since the cartilaginous ring slopes back at an angle of 45° (fig. 8). Its dorsal rim has presumably been carried back by the fissura lateralis. This gives some indication of the degree of relative displacement which has taken place between the dorsal and the ventral parts of the capsule as a whole.

From the lamina transversalis anterior the ectochoanal and the paraseptal cartilages project back in the normal Lacertilian manner (fig. 5). The paraseptal is uninterrupted and its posterior end fuses with the inner ventral corner of the lamina ant-orbitalis. The ectochoanal is a small structure jutting outward and backward and supports the anterior end of the ductus nasolacrimalis.

In addition to these two longitudinal structures the lateral wall and roof of the capsule of Jacobson's organ are conjointly continued backward as a third cartilaginous bar lying parallel

to the paraseptal and also medial to the choanal opening (fig. 5). About halfway along its length, and behind the choana, its lateral edge turns sharply outward towards the paries nasi and fuses with it and with the lamina antorbitalis. The wide gap between the paraseptal and this second bar is closed over by the vomer and the palatine. A considerable portion of the true olfactory part of the nasal cavity is provided in this way with a cartilaginous solum. Born (1879) regards both these cartilages as homologous with the paraseptal, since they are both situated medial to the choana. I propose to call the second bar the lateral paraseptal although this is not intended to imply that the two structures are regarded as having arisen by a longitudinal division of the original paraseptal. The objection to this latter interpretation is the fact that the anterior end of the lateral paraseptal lies lateral to the duct of Jacobson's organ and therefore lateral also to the primitive choana (Fuchs, 1908). It thus bridges the primitive choana, and forms a cartilaginous support for the "secondary palate" (Fuchs, 1908). If this interpretation is correct, the choana of Iguanidae cannot be regarded as primitive. This apparent contradiction is cleared up if Beecker's (1903) theory respecting the lateral rotation of the organ of Jacobson in the ancestral lizard is accepted. A similar cartilaginous secondary palate is moreover formed in a number of other Lacertilians by the fusion (behind the duct of Jacobson's organ) of the paraseptal itself with the side wall of Jacobson's capsule and in some instances with the ectochoanal. (See pages 34 and 40, and fig. 44)

In the other Iguanid genera investigated the lateral parasseptal is interrupted behind the organ of Jacobson for some distance (fig. 16). The specimen of *Sceloporus* was, however, quite small (approximately 2 inches from snout to tip of tail) and may not have been adult.

Isolated nodules of cartilage occur in the same position as the lateral parasseptal immediately behind the organ of Jacobson in several Lacertilian genera eg. *Teius* and *Agama*.

The capsule of the organ of Jacobson is more complete than in any non-Iguanid lizard, since it possesses a cartilaginous roof in addition to the bony covering provided by the septomaxillary (figs. 6 and 9). With the sole exception of *Sphenodon*, I do not know of any other reptile for which a cartilaginous roof for the organ of Jacobson has been described. Broom (1906) states explicitly: "In the Squamata the organ of Jacobson is never roofed by cartilage as in *Sphenodon*, and the septomaxillary bone is highly developed to protect the very large organ". Born (1879) does not fully describe the nasal capsule of *Sceloporus* but merely compares it with that of *Liolaemus* and *Draco*. About the organ of Jacobson he states: "Nur ist das knorpelskelett des Jacobson'sches Organs viel entwickelter" (i.e. than that of *Draco*), without going into any details or mentioning a roofing cartilage. For *Liolaemus*, however, he records the existence of a cartilaginous roof; but the nasal organ of this genus is apparently very atypical and the roof is clearly not homologous with that of *Sceloporus*. It would seem that the anterior half

of the organ of Jacobson, instead of being situated beneath the vestibule, lies medial to it, and is consequently roofed over by the tectum nasi. The septomaxillary supports the lateral wall, and lies between the organ and the vestibule. The true roofing cartilage which should have been situated medial to the bone is apparently absent or partly incorporated in the cupola anterior (See p.56). *Leiolepis* shows a similar development, but since the organ of Jacobson is not quite so large as it is in *Liolaemus*, only its medial half is roofed by the tectum (Born, 1879). The occurrence of two distinct morphological types of cartilaginous roofing to Jacobson's organ in the same family is most remarkable. Strange that Born should have failed to record its presence in *Sceloporus*!

The cartilaginous roof in *Sceloporus* is interrupted by a fairly extensive fontanelle covered over by the septomaxillary (fig. 8). In *Uta* exactly similar conditions obtain, but in *Phrynosoma* and *Iguana* the roof is complete.

The septomaxillary is closely applied to the upper surface of the cartilaginous roof, but apart from this bears the same relations to the organ as it does in *Lacerta*. The bone is, however, not limited by the posterior end of the organ, but is continued very far back and reaches up to the posterior border of the vestibule, thus acting as a support for its floor. This serves to strengthen the hypothesis that the septomaxillary in the *Squamata* as well as in the *Rhynchocephalia* and mammals is primarily an investing bone of the (ectodermal) vestibular wall,

and its association with the organ of Jacobson is merely incidental, and due to the topographical relations of these two structures. It, moreover, serves as a bony roof to the medial part of the olfactory nasal cavity, behind the organ of Jacobson (fig. 10); but equally incidentally!

Anteriorly the organ of Jacobson is protected by a cartilaginous cupola. As always in *Lacertilia* the medial wall of the capsule is formed by the septum nasi. The roofing cartilage is continuous with the latter about halfway along its height (fig. 9). As already stated an anterior prolongation of the domelike cartilage roofing the olfactory cavity is fused to the upper postero-lateral corner of the capsule (fig. 8). The anterior end of the ductus nasolacrimalis opens into the "Choanenrinne" immediately beneath this bridging cartilage (cf. figs. 7 and 8). The lateral paraseptal is continuous with the capsule at its lower postero-lateral corner. A pronounced concha projects into the organ of Jacobson from the side wall of the capsule.

The presence of the roofing cartilage of the organ of Jacobson in the *Iguanidae* allows of two interpretations: it may, of course, represent a secondary backward growth of the upper edge of the anterior cupola, and thus be part of the general backward elongation of the dorsal half of the nasal capsule. The bulk of the evidence, however, is in favour of a second interpretation: that the primitive condition of the *Lacertilian* capsule, as typified by that of *Sphenodon* has been retained in the *Iguanidae*. A cartilaginous ledge along the septum nasi,

supporting the inner edge of the septomaxillary has been described for several lizards belonging to the Scincidae and Lacertidae. This presumably represents a medial rudiment of a once existing roof. Born (1879) quotes Fleischer (1877) as having noted the presence in an adult specimen of *Lacerta* (species not mentioned) of a thin cartilaginous lamella beneath the Os conchae (= septomaxillary). Born, however, denies the presence of any such element in the developmental stages investigated by him. Neither did the two specimens of *Lacerta agilis* at my disposal, one adult and one newly hatched, exhibit this.

In *Teius*, however, thin, isolated strips of cartilage appear underneath the septomaxillary (fig. 46). Moreover, the extreme posterior end of the organ is surrounded by a complete ring of cartilage, through which the vomeronasal branch of the olfactory nerve enters (fig. 47). This ring is also present in all three Lacertids investigated. If the ring mentioned above were greatly enlarged to accommodate the entire posterior half of the organ, it would correspond to the *Sceloporus* capsule, except that *Sceloporus* would exhibit a ventral discontinuity; the ring is complete in *Phrynosoma* and *Iguana*.

We may therefore conclude that a roofed capsule is the primitive condition in the Squamata, and that the Iguanidae have retained it unchanged except for a secondary fenestration present in some genera. In the Teiidae and Lacertidae this process of fenestration has gone much further; in the other lizard families practically all traces of a roofing cartilage have been lost.

Uta stansburiana.

According to Smith Hobart (1939): "Uta is perhaps directly allied to Sceloporus and presumably derived from one of its branches". Conditions in the nasal region of *Uta stansburiana* support this view, since the nasal capsule corresponds in all important aspects with that of *Sceloporus*.

The vestibule reaches so far back that it is doubled on itself and opens into the true nasal cavity from a postero-dorsal direction. It thus extends back beyond the nasal cavity, and the *cavum antorbitale* is lined almost entirely by the characteristic vestibular epithelium. Consequently the upper corner of the *fenestra narina* accompanies the duct of the *glandula nasalis lateralis* right into the *cavum antorbitale*. The lateral groove harbouring the gland is deep and broad.

The dome-like tectum roofing the vestibule shows signs of incipient fenestration, corresponding to a *fenestra superior*. The most anterior portion of the nasal capsule exhibits slight deviations from the *Sceloporus* type. A *cupola anterior* is practically non-existent, since the external nares are situated dorsally on the very tip of the snout. This position of the nostrils also occurs in *Phrynosoma* and in many other sandburrowing forms eg. *Uma* (Stebbins 1943). The apical foramina lie far back on the tectum over the anterior portions of the organs of Jacobson. The prenasal process, instead of being cylindrical, consists of a thin vertical lamina partly separating the otherwise fused premaxillaries. This laminar rostrum is interrupted

by a fairly extensive fenestra.

The capsule of Jacobson's organ is identical with that of *Sceloporus*, but the lateral paraseptal is interrupted behind the organ for a relatively long distance. As in many lizards the paraseptal itself is also incomplete in the region of the organ of Jacobson.

Phrynosoma douglassii.

In *Phrynosoma* the *Sceloporus* type of nasal capsule reoccurs, although it shows a greater degree of deviation than that of *Uta*.

The cartilaginous dome roofing the vestibule is interrupted by a very large fenestra superior nasi commencing immediately behind the external naris and extending over the entire tectum right up to the posterior border of the vestibule, which is situated very far back as in *Uta*. Wherever this fenestra is present, its extent would seem to be determined by the size of the vestibule. Similarly the lateral edge of the medial dome is greatly reduced, with the result that the fissura lateralis is very wide. Since the fenestra superior reaches right up to the septum, the only vestige of the medial dome consists of a thin bar of cartilage between the fenestra superior and the fissure lateralis (fig. 11).

In both *Uta* and *Phrynosoma* the organ of Jacobson lies very far forward, its duct opening into the choanal groove beneath the hind end of the external nares, a condition possibly correlated with the extreme backward elongation of the vestibule in these genera. Such a position of the organ of Jacobson shows an

approach to the Chamaeleon type of nasal capsule in which the organ has been displaced so far forward as to be completely obliterated in most species. As a result of its position the anterior portion of the organ is not covered by the septomaxillary. This is a further proof that the relation of the septomaxillary to the organ of Jacobson is purely incidental.

The cartilaginous roof of Jacobson's organ is not fenestrated in this genus (fig. 11). Behind the duct of the organ the paraseptal is fused to its side wall for a short distance, and encloses the nervus vomeronasalis in a cartilaginous ring, complete except for the interruption between the paraseptal and the base of the septum (cf. figs. 12 and 47). It has already been pointed out that such a connection must be regarded as a cartilaginous "secondary palate" (Fuchs, 1908), since it bridges the primitive choana. The paraseptal itself is uninterrupted, but the anterior end of the lateral paraseptal is incomplete.

With respect to the nasal region the three genera treated above apparently form a closely related group exhibiting only unimportant variations which in some instances form definite links in a morphological series.

Iguana iguana iguana Shaw.

Iguana exhibits the typical backward displacement of the tectal half of the nasal organ relative to its ventral half, but differs from all other Iguanidae investigated by Born (1879) and the author, in that it possesses a cavum conchale. The nasal capsule of Iguana, therefore, represents a morphological link

between the Agamid-Iguanid type and the normal Lacertid type. Since the possession of a concha must be regarded as a primary condition in Lacertilia, Iguana occupies a primitive position among the Iguanidae.

The nasal cavities, in contrast to those of the above genera, are extremely complicated. The vestibule enters the true nasal cavity some considerable distance behind the organ of Jacobson, but, as a result of the presence of the concha it does not attain to the extreme degree of backward elongation found in the Sceloporus group.

The extreme anterior portion of an extensive blind sac of the true nasal cavity has intruded between the posterior half of the organ of Jacobson and the vestibule, the septomaxillary being excavated to receive the anterior part of this sac. Further back the bone becomes divided into two horizontal squames, the upper lying between the vestibule and the blind sac, and the lower between the latter and the organ of Jacobson (fig. 12, left side). This lower squame has thus become independent of the vestibular wall and serves solely as a covering for the posterior half of Jacobson's organ, where the cartilaginous roof is incomplete. A somewhat similar condition obtains in *Agama atra*.

Behind the organ of Jacobson the sac increases in height and occupies the position of the vestibule next to the septum nasi, the latter cavity being displaced laterally so that it lies on the side of the true nasal cavity, from which direction it effects its opening (fig. 12). Similar conditions have been

recorded for *Varanus* (Born, 1879), and for *Microsaura* (Brock, 1941).

From Born's description it appears that the anterior parts of the nasal cavities of *Liolaemus* and *Leiosaurus* are very similar to those of *Iguana* except that, as a result of the enormous size of the organ of Jacobson, especially in the former genus, the vestibule is situated lateral to this organ as well as to the blind sac. Consequently the organ of Jacobson is roofed over by the tectum nasi (Born, 1879). In *Liolaemus* Born describes synchondrotic continuity of the cartilage roofing the vestibule, with the cartilage forming the capsule of Jacobson's organ and the roof of the anterior part of the true nasal cavity (= ontogenetically the "paranasal" of de Beer 1930). Obviously Born considers the former cartilage as representing the ordinary roofing cartilage of the vestibule (= ontogenetically the "parietotectal" of de Beer): "*Liolaemus pictus* zeichnet sich in sehr eigenthümlicher Weise dadurch aus, dass das vordere Ende des Jacobsons'schen Organs nicht unter, sondern neben dem Vorhofe gelegen ist. Es besitzt dasselbe in Folge dessen ein Knorpeliges Dach, das aus dem oberen Rande des Septums hervorgeht;

In no other Lacertilian, however, does the anterior part of the parietotectal cartilage (i.e. the cupola anterior) fuse with either the capsule of Jacobson's organ or with the paranasal in this region. It is evident, therefore, that the cartilage roofing both the organ of Jacobson and the vestibule represents the common product of the roofing cartilage of Jacobson's organ and the cupola anterior. This apparent fusion would seem to

be a result of the extreme anterior position of the organ and to its large size. The organ of Jacobson with its capsule has been pushed so far forward that it has reached the anterior edge of the septum, and simulates the true cupola anterior which has been laterally displaced. A glance at fig. 15 of Iguana, where the organ of Jacobson is situated very far forward and the cupola is much reduced will support this deduction (cf. also Brock's work on *Microsaura*, 1941).

Both *Liolaemus* and *Leiosaurus* lack a *cavum conchale*, but the lateral groove containing the *glandula nasalis lateralis* is continued backward beyond the posterior end of the *fissura lateralis*, and an extensive cartilaginous process formed by the confluent edges of the parietotectal and the paranasal cartilages projects into the nasal cavity in the region where the concha containing the *cavum conchale* is normally situated (Born, 1879: Taf. VIII, fig. 18). A similar "concha" is noted by Born for the Agamid, *Draco volans*, which also lacks a *cavum conchale*.

In Iguana the structure of the true nasal cavity is further complicated by the presence of a typical Lacertilian *concha nasalis*. A *cavum extraconchale* is present between the outer conchal wall and the outer capsular wall. In *Lacerta* only a very small anterior portion of the *cavum* forms a blind recess, since the concha becomes detached from the *tectum nasi* almost immediately behind the *aditus conchae*. Resulting from the posterior displacement of the *tectum nasi* in Iguana, the point of detachment has shifted so far back that the *cavum extraconchale*

remains blind for more than half its length and has no communication with the nasal cavity itself except by a roundabout way through the *cavum antorbitale*. The concha loses its connection with the *paries nasi* some distance in front of the posterior end of the choana, (and in front of the point where the dorsal connection is lost), so that the *cavum extraconchale* communicates directly with the oral cavity (via the "Choanengang") (fig. 13). In spite of the fact that the direct respiratory air current apparently does not pass through this recessus, it is lined with typical olfactory epithelium.

These peculiar conditions can only be accounted for on the assumption for *Iguana* of a relative backward displacement of the tectal half of the nasal capsule, similar to but less advanced than in the *Sceloporus* group which lack a concha. Additional evidence for this hypothesis is provided by the structure of the *aditus conchas* which is prolonged backward into a long fissure-like opening leading down into the *cavum conchale* (fig. 14).

A well-developed *processus praenasalis* is present between the two *cupolae anteriores*, which are somewhat reduced in size, since the external nares open on the extreme tip of the snout as in *Uta* and *Phrynosoma*. With the removal of the skin, preparatory to sectioning, the region around the external nares was unfortunately slightly damaged, so that it was not possible to determine whether a *processus alaris inferior* is present or not. The *alaris superior* consists of a mere knob of cartilage as in all *Iguanidae*.

The contiguous edges of the cartilages roofing the vestibule and the anterior blind sac of the true nasal cavity have been sunk into the interior of the nasal organ, as a result of the inward migration of the true nasal cavity. Consequently the anterior part of the fissura lateralis lies at the bottom of a deep, narrow cleft (fig. 12) which widens out posteriorly to accommodate the anterior part of the glandula nasalis lateralis and then leads into the cavum conchale. Inside the cavum conchale the edges of the fissura lateralis effect synchondrotic continuity; so that an independent foramen is established in the posterior confines of the fissura. Through this foramen the duct of the glandula nasalis lateralis enters the nasal cavity (cf. Young, 1942 for *Xantusia*).

As in *Sceloporus* the fenestra olfactoria is divided into two separate foramina. The ramus ethmoidalis of $\bar{V}a$ and the nervus olfactorius enter through the dorsally situated one, and the olfactory branch innervating the organ of Jacobson (nervus vomeronasalis) enters through the medial, vertically situated foramen (fig. 14). The foramen epiphaniale lies relatively far forward above the recessus extraconchalis.

The maxillary processes are represented by a large laminar structure strongly reminiscent of the detached plate found in *Microsaura* (= *Lophosaura auctorum*).

The lamina transversalis anterior completes a zona annularis which slopes back at the same angle (approximately 45°) as in *Sceloporus*. The degree of relative movement inferred to have

taken place between the tectum and solum nasi thus appears to be the same as in the other Iguanidae but the posterior part of the nasal capsule has not been shortened to the same extent as in the forms lacking a concha.

The roofing cartilage of the organ of Jacobson is not as extensive as in the other Iguanid genera investigated, only the anterior half of the organ lying in front of the duct being completely covered (figs. 15 and 16). The posterior half of the organ is roofed over by the lower horizontal squame of the septo-maxillary. The ectochoanal is extremely reduced, being represented by a mere knob of cartilage supporting the lateral wall of the anterior tip of the ductus nasolacrimalis. The paraseptal, on the other hand, is a well-developed, broad, horizontal structure except for a portion opposite the duct of Jacobson's organ which is vertically placed, and forms the greater part of the median wall of the organ (fig. 16). Behind the duct the paraseptal is connected with that part of the lamina transversalis anterior from which the ectochoanal and the lateral paraseptal project backward. Jacobson's duct, therefore, appears to issue through a large foramen in the lamina transversalis anterior (fig. 16). It has already been pointed out that this connection must represent a cartilaginous "secondary palate", since the organ of Jacobson opened primitively into the anterior part of the choana (Fuchs, 1908). The lateral paraseptal is incomplete, but strongly developed anterior and posterior rudiments indicate a secondary reduction.

Anolis sagrae.

The nasal region of this genus is very different from that of the other genera investigated; and if it were not for the presence of one or two typical Iguanid characteristics (e.g. the rostrum), it would not be recognizable as belonging to a member of this family.

The nasal cavities themselves are of very simple structure. The vestibule, in contrast to that of the other Iguanidae, has undergone but a slight degree of elongation and the duct of the glandula nasalis lateralis enters its posterior border not far behind the organ of Jacobson. It lies, moreover, in front of the true nasal cavity and enters it in the normal Lacertilian manner. The nasal cavity itself is a simple sac, oval in cross-section with the breadth measuring about twice, and the length three times the height (fig. 19). The median two-thirds of the surface is lined with respiratory epithelium. There is no indication of a cavum conchale; the glandula nasalis lateralis being extremely reduced in size and scarcely reaching back beyond its duct.

The choana, in direct contrast to that of all the other Iguanidae investigated, opens into the posterior third of the nasal cavity (cf. figs. 19 and 7). As in the Chamaeleontidae virtually no cavum conchale exists.

Born (1879) distinguishes between an "inner" and an "outer" choana. The inner represents the opening between the nasal cavity itself and the "Choanengang" (of Fuchs, 1908), and the

outer the opening of the latter into the oral cavity. According to Fuchs (1908) a "secondary palate" may be formed behind the organ of Jacobson by a fusion of the sides of the "Choanen-gang" at either of the two levels corresponding to Born's inner and outer choanae.

The extensive "secondary palate" of *Anolis* is very peculiar in that both these closures are present, thus transforming the "Choanengang" into a duct leading from the opening of the organ of Jacobson to the choana (fig. 17). The ductus nasolacrimalis runs parallel to this duct and opens opposite the duct of Jacobson's organ into its anterior end, which in turn leads into the oral cavity (figs. 17 and 19).

The upper of the two "secondary palates" is not supported by any skeletal element and is homologous both with respect to topography and structure with the "secondary palate" occurring in Lacertidae and Scincidae etc. (Fuchs, 1908). The lower closure on the other hand is supported by the enormously enlarged ectochoanal which covers quite an extensive area of the vomer ventrally (figs. 17 and 18). In the Geckonidae and the Xantusiidae (Young, 1942) the ectochoanal also shows an enlargement, but here it serves as^a support for the sides of a "ductus nasopharyngeus". In the families Teiidae, Anguidae, Anniellidae, Amphisbaenidae, Varanidae and in snakes, the "Choanenrinne" (choanal groove), present in *Lacerta* between the opening of Jacobson's organ and the choana (Fuchs, 1908), is also obliterated externally by the development of a "secondary palate" (figs. 47, 52 and 55). In these forms a single duct runs above the secondary palate,

and it is clear that the condition has been arrived at independently in *Anolis*, being derived from a normal Iguanid type. The homology of the single duct is discussed elsewhere.

The cartilage of the nasal capsule, especially that of the solar region shows an extreme degree of reduction. A relatively long prenasal process juts out between the two cupolar cartilages as in all Iguanidae. The superior alar process is rudimentary. The parietotectal cartilage is uninterrupted throughout, since a fenestra superior nasi is absent. The paranasal cartilage, forming the side wall and part of the posterior roof has been greatly reduced, besides having been interrupted by a large fenestra lateralis behind the glandula nasalis lateralis (fig. 18).

Beyond a brief anterior cupola, the capsule of the organ of Jacobson consists solely of a rod-like side wall, bearing, however, a concha which juts into the lumen of the organ dorso-laterally. There is no indication of a paraseptal or a roofing cartilage, the place of the latter being taken by the septomaxillary as in all non-Iguanid lizards. A small ledge near the lower edge of the septum supports the septomaxillary medially. The septum does not reach down between the right and left organs of Jacobson, and the medial walls are formed by vertical squames of the vomer (cf. Chamaeleontidae). Behind the organ the side wall is continuous with the anterior part of the paranasal. The shortness of the fissura lateralis nasi may be correlated with the fact that the vestibule does not reach back much beyond the organ of Jacobson.

The lamina transversalis anterior is very narrow, and both the paraseptal itself and the lateral paraseptal are absent (fig.18).

The ectochoanal, on the other hand, is a broad, flat structure reaching back to the anterior edge of the choana; it is situated dorsal to the maxillary, but its median edge overlaps the vomer, to which it is closely applied (figs. 17 and 18).

The course of the lateral branch of the ramus ethmoidalis of $\bar{V}a$ also indicates that the nasal capsule of *Anolis* must be derived from an ordinary Iguanid type, in spite of the wide divergence exhibited by the vestibule and the position of the choanal opening. The ramus ethmoidalis divides into its two branches immediately in front of its entry into the nasal capsule. The ramus lateralis, however, instead of entering together with the ramus medialis, remains outside the capsule (cf. *Crocodylus*). It crosses immediately in front of the point of attachment of the cartilago sphenethmoidalis on its way to the glandula nasalis lateralis. This total absence of a foramen epiphaniale is explained by a comparison with the condition found in *Sceloporus* (fig. 6); for if the thin strip of cartilage separating the foramen epiphaniale from the fissura orbitonasalis were to disappear, a condition similar to that of *Anolis* would be arrived at. As a result of the reduction of the lamina orbitonasalis the two branches of each olfactory nerve do not enter separately as in the other Iguanidae. In *Anolis* itself there is no apparent morphological reason for the extreme posterior migration and consequent loss of the foramen epiphaniale, unless a course of events similar to that culminating in the usual Iguanid condition is accepted. A subsequent lengthening of the nasal region must, therefore, account for the position and relative shortness of

the vestibule.

The cartilago sphenethmoidalis is about .4mm. long and is not continuous with the planum supraseptale. The musculus obliquus inferius is attached to its free end.

Agamidae.

The Agamidae and the Iguanidae are regarded as so closely related that they are placed in the same group, Eumota, by, Duméril and Bibron (1834 - 1854), while Camp stresses their affinity by creating a separate section, Iguania, for them. Investigation of the nasal capsule points to a derivation of the Agamidae from an Iguanid ancestor, which must have resembled Sceloporus, Uta and Phrynosoma in the absence of a concha. The Agamidae, however, lack the primitive Rhynchocephalian characters e.g. the prenasal process and the roofing cartilage of the organ of Jacobson, which are so typical of the Iguanidae. The only work done on the nasal capsule of the Agamidae is that of Born (1879), who investigated Draco volans L. and Grammatophora barbata Kaup.

Of this family I have investigated an adult specimen of Agama atra and four embryological stages of Agama hispida. The results agree in all important points with Born's description of Draco and Grammatophora, so that the Agamidae appear to constitute a much more compact family than the Iguanidae, whose nasal capsule shows an astonishing amount of divergence.

The configuration of the nasal cavities corresponds with that of Sceloporus in all particulars except for differences in

46.

the relative size of the various parts. The outermost horizontal sac of the vestibule is very large, as is also the anterior part of the nasolacrimal duct. The latter opens into a very extensive "Choanengang". The true nasal cavity appears relatively very small, and the surface lined by sensory epithelium much reduced (fig. 21). The organ of Jacobson, on the other hand, is well-developed thus amply compensating for the reduced function of the nasal cavity (cf. Ophidia). As in *Seeloporus* the vestibule reaches very far back and opens into the antorbital cavity from above. The anterior portion of the true nasal cavity resembles that of *Iguana* in that it has intruded between the vestibule and the posterior half of the organ of Jacobson.

The most notable feature of the nasal capsule of *Agama* is the very large size of the cupola anterior and the alar processes (figs. 22 and 24). The superior alar process is unique in projecting laterally beyond the widest margin of the paries nasi. An extensive internasal cavity is formed between the two cupolae, but there is no indication of a prenasal rostral process of the septum. Dorsally the cupola anterior shows a wide, shallow depression occupied by the body of a large narial muscle. This muscle has three heads: a long outer one originating on the outer surface of the maxillary, and a short median one arising from the under surface of the nasal inside the anterior part of the canal formed between the bony and the cartilaginous nasal capsules harbouring the lateral nasal gland, and a third head consisting of a small strand of fibres attaching to the processus

alaris inferior (fig. 62). The bulk of the fibres run forward to insert on the superior alar process and the anterior part of the cupola itself. The occurrence of an apparently most effective opening and closing mechanism in the external nares of a genus with habits not dissimilar from many other lizards is extremely puzzling. The muscle itself is present in all lizards investigated by me but does not exhibit this excessive development in any other form. Its homologies are discussed on page 108.

The fissura lateralis nasi and the position of the ductus glandulae nasalis lateralis are similar to those of *Sceloporus* (figs. 21 and 23). The lateral nasal groove harbouring the lateral nasal gland is prolonged backward up to the fissura orbitonasalis. As in *Iguana* the inner edge of the paranasal accompanies the true nasal cavity deep into the interior of the nasal organ and forms a cartilaginous support for the lateral part of the vestibular floor (fig. 21), the medial half of which is supported by the septomaxillary. A cavum conchale is absent, but behind the fissura lateralis nasi a small cartilaginous ledge projects into the nasal cavity from the floor of the lateral nasal groove (cf. Born, 1879).

In *Agama* it is evident that the dorsal part of the septum, in the posterior part of the capsule at any rate, is of capsular origin since it is formed by the fusion of the laminae antorbitales along practically the entire height of the capsule. The true trabecular septum is represented by a cylindrical rod lying

between the paraseptals (fig.23). As a result of these conditions it appears as if the planum antorbitale were fused to the septum.

The nerve foramina have been greatly altered and displaced by the backward movement of the dorsal part of the capsule relative to the ventral. The olfactory nerve enters the nasal capsule through a number (three or four) of foramina in the planum antorbitale (fig. 24). The nervus vomeronasalis enters through a separate foramen as in the Iguanidae, but owing to the fusion of the antorbital plates this foramen is situated so low down on the posterior face of the capsule as to be almost ventral in position. The left and right vomeronasals run downward alongside each other behind the fused antorbitals, and each enters its own half of the capsule immediately in front of the point of fusion of the paraseptal and the planum antorbitale. The nerve then passes forward along the dorsal surface of the paraseptal and enters the organ of Jacobson in the usual manner. As in *Anolis* the foramen epiphaniale is absent, since the lateral branch of the ramus ethmoidalis of $\overline{V}a$ does not enter the capsule at all, but separates from the medial branch outside the fissura orbitonasalis to pass directly to the lateral nasal gland, whose posterior end lies immediately anterior to the fissura (fig. 22). Contrary to what may be expected the medial branch does not enter through the large slit-like foramen situated underneath the sphenethmoid commissure, but through a small more medianly situated foramen (fig. 22). A part of the olfactory enters through the former.

The solum nasi and the capsule of Jacobson's organ are most incomplete and do not resemble the Iguana condition at all. There is no indication of the roofing cartilage to the organ of Jacobson, the septomaxillary alone covering the organ as it does in all lizards except the Iguanidae. To a lesser extent than in Iguana the medial migration of the anterior part of the true nasal cavity is responsible for the bisquamous nature of the septomaxillary; a horizontal squame separates the vestibule from the organ of Jacobson and a vertical one supports the partition between the vestibule and the true nasal cavity. As a result of the position of the anterior part of the true nasal cavity, the anterior end of the dome-like cartilage covering it (i.e. ontogenetically the paranasal) is fused to the middle of the side wall of Jacobson's capsule instead of to its posterior end (fig. 23). From the lower edge of the side wall a pronounced concha juts into the lumen of the organ of Jacobson.

The short ectochoanal cartilage projects backward from the lamina transversalis anterior and partly covers the side wall cartilage of Jacobson's organ which reaches back some distance beyond the organ and the ectochoanal (fig. 22). The paraseptal is interrupted over the length of the organ of Jacobson and consequently does not reach the lamina transversalis anterior. According to Born (1879) the paraseptal is absent in Draco volans. In a young embryo of Agama hispida, however, the paraseptal is continuous throughout. In Agama atra a number of small, isolated cartilage nodules of points to a former connexion between the side wall of the organ of Jacobson and the free anterior end of the para-

-septal. The posterior continuation of the side wall cartilage would moreover seem to represent the rudiment of the lateral paraseptal present in Iguanidae. There is, however, no posterior rudiment.

The maxillary processes are totally absent as in most snakes.

Chamaeleontidae

This family differs from all other lizards in several fundamental points, and older systematists seem to have found difficulty in determining their taxonomic position. They were placed in a separate suborder by Cope (1900), Fürbringer (1900) and Gadow (1901). Cope was the first to suggest their derivation from the "Pachyglossa" (= Agamidae and Iguanidae), and although their affinities are still somewhat obscure, Camp (1923), Broom (1935) and Brock (1941) incline to the view that they are an offshoot from a pro-agamid ancestor. Camp (1923) gives the section Rhiptoglossa (= Chamaeleontidae) equal taxonomic value with the sections Iguania and Gekkota under the principal sub-division Ascalabota, all the remaining families being placed under the Autarchoglossa. The present investigation on the nasal capsule fully supports the view that the Chamaeleontidae have diverged from the pro-agamid-iguanid stock.

Both Solger (1876) and Born (1879) have described the nasal cavities of a number of lizards belonging to the genus Chamaeleo. Parker (1881) in his monograph on the Chamaeleon skull has given a brief description of the nasal capsule. More recently Haas (1937) published a paper on the structure of the nasal cavities

in Ch. chamaeleon. Brock (1941) in a study of the skull of Microsaura (= Lophosaura) ventralis has given a very convincing interpretation of the nasal capsule, which disagrees somewhat with Haas's view, especially with respect to the anterior solar elements.

For the present investigation I had at my disposal sections of adult specimens of Microsaura pumila (Daud.) and Chamaeleo bitaeniatus höhnelii Steindachner, and a very complete set of embryological stages of M.pumila collected by Dr. C.A.du Toit.

Brock (1941) is of the opinion that the peculiarities of the nasal organ are wholly due to the enormous development of the eye which has caused the telescoping of the ethmoid region and especially the posterior part of the nasal capsule; this shortening being compensated for by the enlargement of the anterior nasal region to accommodate the nasal organ. A comparison with the Iguanidae and Agamidae shows, however, that, although a telescoping of the ethmoid region has undoubtedly caused the fusion of the planum supraseptale to the planum antorbitale, squashing the sphenethmoid commissure out of existence, the type of the nasal capsule itself is directly derivable from the Iguanid condition as described by Born for Liolaemus and Leiosaurus. In reality the explanation of the peculiarities of the nasal capsule (i.e. the absence of the concha and the position of the organ of Jacobson) is the shortening of the nasal region relative to the total length of the skull; this had already taken place in the ancestral Iguanid-Agamid type, but has been further complicated in the Chamaeleontidae by the enlargement of the eye and the tongue.

Microsaura pumila pumila (Daud.) is selected for detailed description, since like many South African animals it appears to have retained a more primitive structure than the Northern members of the family. The retention and position of a fairly well-developed organ of Jacobson (Brock 1941) is especially instructive since in the other representatives of the family it is either rudimentary, as in Ch. chamaeleon (Haas 1937), or entirely absent as in Ch. bitaeniatus höhnelii.

Except for the extreme anterior position of the organ of Jacobson the nasal cavities of Microsaura are practically identical with those of a generalized Iguanid. Liolaemus even approaches the chamaeleon condition with respect to the position of the organ of Jacobson. The nasal cavities of Microsaura are chiefly characterized by the high degree of reduction of olfactory epithelium. The vestibule is very large, and since the organ of Jacobson is isolated in front of the external nares (fig. 25), it is for some considerable distance the only part of the nasal cavity to appear in transverse sections. A small anterior blind portion of the true nasal cavity lies medial to the vestibule; the latter opening into the nasal cavity laterally in the niveau of the anterior end of the choana. The opening of the vestibule is very large, so that the vestibular epithelium is continued very far back and the foramen for the duct of the lateral nasal gland lies nearly in the same plane as the small foramen olfactorium (figs. 26, 28 and 29). The olfactory

chamber is very small and the olfactory epithelium so reduced, that, since the epithelium of the organ of Jacobson also shows signs of degeneration, the nasal organ has apparently completely lost its sensory function.

In Ch.chamaeleon the posterior end of the vestibule is transformed into a blind "lateral respiratory cavity" (Haas, 1937). In Microsaura this is not the case, but the opening of the vestibule into the reduced olfactory chamber is prolonged backward as an extensive groove. Since the vestibular opening is situated directly above the choana, the respiratory air current can pass directly through the nasal cavities instead of having to follow the tortuous course Haas describes for Ch.chamaeleon. As in Anolis there is no definite *cavum antorbitale*, so that both the vestibular and olfactory epithelia merge gradually into the epithelium of the oral cavity in the orbitonasal groove.

As has been described for Agama atra a smooth muscle associated with the external naris is present in addition to the elastic muscular tissue lining the vestibule. In Microsaura this muscle originates on the postero-ventral edge of the fenestra narina and divides into two heads behind the narial opening. (H 1, 2 and 3 in fig. 61). The upper of these lies above the narial opening and inserts on the dorsal edge of the fenestra narina in the position of the *processus alaris superior*. The lower one inserts on the *processus alaris inferior* beneath the narial opening. The relations of the narial muscle to the skeletal elements point to an homology with the *musculus constrict-*

-or naris of Urodeles (See p108). A similar though considerably larger muscle is found in Ch. bitaeniatus höhnelii.

The organ of Jacobson in Microsaura is situated exceptionally far forward, in front of the narial opening (fig. 25). It opens directly into the oral cavity because it is cut off from the choana and the ductus nasolacrimalis by an extensive "secondary palate" (Fuchs, 1908). Among lizards this separation of the ductus nasolacrimalis from the organ of Jacobson is unique and is undoubtedly correlated with the specialisation of the tongue and the feeding habits. In all other members of the family investigated the organ of Jacobson is absent or extremely reduced. In Microsaura it is lined by typical olfactory epithelium which, however, shows a certain amount of degeneration such as may also be observed in the olfactory nasal chamber itself.

The development of Microsaura pusilla proves that the separation of the organ of Jacobson and the nasolacrimal duct arose through secondary specialisation of the normal Lacertilian condition. In the youngest embryo at my disposal (.9 c.m. total length) the primitive nasal groove is still open along its whole length and the anlage of the ductus nasolacrimalis has not yet made its appearance. In the next stage (1.5 c.m.) Fuch's primitive palate has separated the external narial opening from the primitive choana. The organ of Jacobson opens into the medial wall of the anterior end of the primitive choanal groove, and opposite it in the unthickened epithelium of the lateral wall a deep pocket has now appeared (fig.31). In the same section a

groove lined with thickened epithelium and representing the anlage of the nasolacrimal duct is situated in front of the eye. A solid epithelial cord originating from this groove is already growing towards the lateral pocket in the choanal groove. Unfortunately the 1.9 c.m. stage shows no advance on the previous one, so that the actual fusion of the two rudiments could not be observed. In the next stage (2.4 c.m.) the outlines of the fused trabeculae and the parietotectal cartilages are indicated by dense blastematos tissue, and the relations of the nasal cavities has already become altered to some extent. The external narial opening is still situated in front of the organ of Jacobson, but the opening of the latter has become independent of the rest of the choanal groove through the development of a "secondary palate" (Fuchs, 1908). The anlage of the ductus nasolacrimalis, however, still ends near the posterior portion of Jacobson's organ and some considerable distance in front of the choana. This is best illustrated by reference to fig. 32 of the 2.5 c.m. stage in which the relations of the nasal cavities are the same as in the previous one, but the nasal capsule has reached the procartilaginous stage and the maxillary and pterygoid have made their appearance. In the 3.1 c.m. specimen which is considerably older than the previous stages, adult relations obtain: the organ of Jacobson is situated in front of the external nares and the opening of the nasolacrimal duct has migrated backward to open into the anterior end of the choana.

The structure of the cartilaginous nasal capsule reflects

the reduction of the olfactory area in the nasal cavities (figs. 26, 27 and 29): the anterior cupola harbouring the vestibule appears greatly enlarged in comparison with the rest of the capsule.

The septum nasi is peculiar in that it sharply loses height in passing forward and eventually dwindles away in the anterior third of the capsule (figs. 25 and 29). The left and right organs of Jacobson are separated by a bony septum formed by the anterior fused tips of the vomers (fig. 5). As Brock (1941) has pointed out, it appears as if the organ of Jacobson has been "pushed out" in front of the septum (cf. fig. 28).

In a 2.5 c.m. stage of Microsaura pumila the anterior tip of the fused trabeculae still reaches a point between the anterior ends of the organs of Jacobson.

As in Liolaemus (Born, 1879) the vestibule lies lateral to the organ of Jacobson, but is separated from it by a cartilaginous wall (fig. 25) instead of by the septomaxillary. There is no sign of this bone in Microsaura, and the anterior part of the organ is roofed over by cartilage apparently forming part of the tectum nasi (fig. 25). But as already pointed out in connexion with Liolaemus this cartilaginous roof cannot represent the tectum, as was suggested by Born (1879), but must be homologised with the anterior cupola of Jacobson's organ, which has come to lie on the dorsal surface of the nasal capsule owing to the lateral displacement of the vestibule and its cupola anterior normally covering the organ of Jacobson (fig. 25). The position

of the foramen apicale on the roof of the nasal capsule behind the organ of Jacobson (fig.26) supports this view. The cartilage separating the vestibule from the organ of Jacobson undoubtedly represents the laterally displaced roofing cartilage of the organ and it serves to emphasize the close relationship of the Chamaeleontidae with the Iguanidae, the only other Lacertilian family in which a complete cartilaginous roof is present. The position of the septomaxillary in *Liolaemus* (cf. p.28) establishes the homology of the cartilage.

It would seem that the peculiarities of the anterior part of the nasal organ of *Microsaura* is a result rather of the large size of the tongue than of the forward bulging of the eye: The anterior buccal roof is dome-shaped to accommodate the tongue, the nasal organ has been compressed dorso-ventrally so that the septum is diminished in height, the vestibule has been laterally displaced and the organ of Jacobson forwards (fig.25).

The cupola anterior bears a well-developed processus alaris inferior (fig.23). The processus alaris superior is absent but its position is indicated by the attachment of the dorsal head of the smooth nasal muscle (fig.61). The transverse part of the lamina transversalis anterior is situated vertically in front of the organ of Jacobson and thus forms part of the anterior wall of the nasal capsule (fig.29). In a 3.1 c.m. embryo the cupolar part of the parietotectal cartilage has not yet fused with the cartilaginous capsule of Jacobson's organ in front of the apical foramen (fig.28), although it is continuous

with the backwardly directed part of the lamina transversalis anterior. In the same developmental stage it appears that the most anterior tip of the fused trabeculae is incorporated into the anterior vertical part of the lamina transversalis so that although the organ of Jacobson lies so very far forward it is not situated in front of the septum as Brock (1941) maintained.

The paraseptal cartilage is absent in the adult Microsaura pumila, and according to Brock (1941) it is not recapitulated in the ontogeny of Microsaura ventralis. In a 5.4 c.m. embryo of Microsaura pumila a paraseptal does occur as a small unattached nodule of procartilage on the medial side of each organ of Jacobson (fig.30). In older embryos it has disappeared. This proves conclusively that the anterior part of the cartilage called by Haas (1937) the "paraseptal" must represent a longitudinally directed part of the lamina transversalis anterior (fig.29) (cf. Brock, 1941). This view is supported by the presence of a rudimentary concha of Jacobson's organ projecting from this cartilage (fig. 30). The ectochoanal is bifurcated into an outer, broad, laterally directed process supporting the anterior end of the ductus nasolacrimalis, and an inner, slender, palatal process supporting the lateral edge of the choana for some distance (fig.29).

A foramen in Microsaura ventralis called by Brock the "fenestra superior" would appear to be the foramen for the duct of the lateral nasal gland, since both the nasal fenestrae are absent as in most Ascalabota (cf. text fig. 3 in Brock, 1941 with

figs. 26 and 28). The lateral nasal gland in Microsaura pumila is restricted to a small area behind its duct on the postero-lateral corner of the nasal capsule and fills the small groove which marks the transition between the nasal capsule proper and the planum supraseptale (figs. 26 and 27). The foramen must have acquired its independence from the fenestra narina by the loss of the septomaxillary which in the Iguania and Geckonidae projects into the fissura lateralis nasi and prevents the fusion of its sides (p.22). In a 3.1 c.m. embryo the fissura lateralis has already been obliterated (fig. 28), although most of the nasal capsule is still procartilaginous. Morphologically the zona annularis passes behind the foramen for the duct of the lateral nasal gland since it represents part of the fenestra narina. In spite of the virtual distortion of the lamina transversalis anterior (fig. 27) the angle of backward inclination of the zona annularis is practically the same as in the Iguanidae i.e. 45° . A secondary zona annularis is formed in Microsaura by a fusion of the lamina transversalis anterior with the paries nasi in front of the nasolacrimal duct (fig. 27).

The peculiar orbitonasal canal formed by the fusion of the supraseptal plate to the nasal capsule has been described by both Haas (1937) and Brock (1941). The ramus ethmoidalis of V enters the canal ventrally (fig. 29), divides into its two constituents inside the canal and emerges separately on the dorsal surface of the capsule (fig. 26). The ramus medialis enters the capsule again through a small foramen situated immediately

anterior to the canal (fig. 26). This foramen, therefore, represents the fissura orbitonasalis of the normal lizard type. In Microsaura ventralis (Brock, 1941) this foramen is incorporated into the canal with the result that the ramus medialis does not appear on the dorsal surface of the capsule at all. In both Microsaura ventralis and M. pumila the foramen epiphaniale is incorporated into the canal and the ramus lateralis never enters the nasal capsule at all but passes directly to the lateral nasal gland (fig. 26). Because of the degeneration of sensory epithelium and the reduction of the olfactory nerves the olfactory foramina are very small (figs. 26, 28 and 29).

It is difficult to trace the extent of the paranasal cartilage in the Lacertilian nasal capsule since it does not chondrify independently as in the mammal, but Brock's identification of Haas' "pseudoconcha" with its anterior end seems to be correct. Posteriorly it extends over a small area of the paries nasi lying between the three outer foramina (fig. 26).

As in Iguana the processus maxillares are very large, but in the adult Microsaura it consists of a completely detached plate of cartilage lying on the maxillary and palatine. A long, slender, vertical process indicates its previous fusion with the greatly reduced paries nasi (fig. 27). In embryos up to the 3.7 c.m. stage this fusion is still complete (fig. 28), but in the next stage (4 c.m.) the connexion has been lost.

It is impossible to determine the existence of a separate planum antorbitale in any of the embryological stages of Microsaura pumila. In a

3.1 c.m. specimen the vertical bar of the maxillary process is clearly attached to the cartilage homologised by Brock (1941) with the "planum antorbitale". Since this element cannot be the paranasal alone, being attached to the septum medially, it would appear that no matter whether a planum antorbitale is incorporated in the adult nasal capsule or not, it is not recapitulated as a separate centre of chondrification.

Geckonidae.

Most authors regard the Geckonidae as either very primitive (e.g. Fürbringer, 1900) or as having diverged from the primitive Lacertilian stock early in the phylogeny of the group. The latter view, elaborated chiefly by Hafferl (1921), serves to explain the presence in the anatomy of both primitive and highly specialized features. Camp (1926) stresses their central position within the order by placing them among the primitive Ascalabota, which in addition contains the Iguania and the Chamaeleontidae, while also indicating that they are related to the Autarchoglossa through the Xantusiidae.

The nasal cavities and nasolacrimal duct of Hemidactylus ovalensis, Platydictylus lugubris and Pl. muralis were investigated by Born (1879). He emphasizes the primitive position of the opening of the ductus nasolacrimalis near the duct of Jacobson's organ. Fuchs (1908) in an investigation into the structure of the palate and choana of Phyllodactylus europaeus and other Geckonid genera states that the nasal capsule closely resembles

that of *Lacerta*, but that the primitive *Sphenodon* condition has been retained in the type of ductus nasolacrimalis. The work of Hafferl (1921) on the development of *Platydictylus annularis* includes an excellent and detailed account of the nasal capsule. The present account is restricted to some remarks of a comparative nature, intended to elucidate the possible affinities of the Geckonidae with previously mentioned families.

The account and the figures apply to *Pachydictylus weberi gariesensis* Hwt. An adult *P. ocellatus* Cuv. was also examined, and I was fortunate in having at my disposal Dr. Brock's sections of a number of embryological stages of *Lygodactylus capensis* and *Pachydictylus* sp..

As far as the general structure of the nasal capsule is concerned, the Geckonidae appear to be more closely related to the Autarchoglossa (and especially to the Xantusiidae) than to the rest of the Ascalabota. The large size of the fenestra olfactoria (fig. 33) and the absence of a roofing cartilage of Jacobson's organ are typical Autarchoglossid characters. They have in common with the Ascalabota the possession of a fissura lateralis nasi (fig. 34), and the absence of the lateral and superior nasal fenestrae. These contradictory features together with the very simple structure of the concha nasalis would seem to indicate that the Geckonidae are closely related to an early, unspecialized group of lizards which gave rise to both the principal subdivisions into which the living families are grouped by Camp (1923).

The structure of the nasal cavities also support the hypothesis of the intermediate nature of the group. The vestibule reaches further back than in a typical Autarchoglossid such as *Lacerta*, but does not show nearly the same degree of elongation as that of the *Ascalabota*. As in *Sceloporus*, the backward migration of the duct of the lateral nasal gland has resulted in the formation of a *fissura lateralis nasi* (fig. 34), so called by Hafferl (1921). The vestibule opens simultaneously into the small recessus extraconchalis and the anterior blind sac of the true nasal cavity where these two latter communicate with each other immediately above the posterior portion of the organ of Jacobson. In *Lacerta* the vestibule passes into the true nasal cavity over the middle of the organ, while the recessus extraconchalis communicates with it some considerable distance behind the organ. The relative displacement of the various cavities, which, in the other *Ascalabota* has resulted in the curious condition typified in *Sceloporus*, is therefore present in the *Geckonidae* though to a less degree.

A study of the structure of the palate and the choana is instructive in as much as it serves to explain the condition obtaining in *Xantusia*, and, moreover, sheds light on the problem of the phylogeny of the anterior end of the ductus nasolacrimalis in Lizards. As in *Lacerta* a secondary palate bridges the primitive choana behind the organ of Jacobson in such a way that an open choanal groove is formed between the organ and the functional choana (Fuchs, 1908). This choanal groove has

retained its primitive character, since the organ of Jacobson and the ductus nasolacrimalis still open opposite each other into its extreme anterior end. (In fig. 35 the nasolacrimonal duct appears to open into the organ of Jacobson itself owing to the fact that the opening of the organ into the choanal groove is very wide). In this respect the Geckonidae, with the possible exception of the Iguania, are certainly the most primitive Lacertilian family. In the Lacertidae, where fairly primitive conditions also obtain, the opening of the ductus nasolacrimalis has moved back with the anterior edge of the choana, and the secretion of the Harderian gland is carried to the organ of Jacobson by the choanal groove.

The solum nasi is fairly extensive owing to the large size of both the paraseptal and the ectochoanal (fig. 33). The paraseptal closely resembles that of Azama atra: it consists of a broad strip of cartilage suddenly narrowing down opposite the duct of Jacobson's organ to allow for the possibility of movement in the ventral support of the organ (fig. 33). Behind the organ of Jacobson the paraseptal bears a vertical squame forming the posterior wall of the capsule of Jacobson. The ectochoanal is very large; as may be seen from fig. 33 and 34 it reaches back beyond the planum antorbitale. It serves as a support for the lateral edge of the choana and also for the anterior part of the choanal folds, which form the orbitonasal groove (Fuchs, 1908), transforming the latter into an open "ductus nasopharyngeus" (fig. 36). In Xantusia the ectochoanal is similarly

enlarged, but the edges of the orbitonasal groove overlap, so that the "ductus nasopharyngeus" is functionally closed off from the oral cavity (fig. 38). The participation of the ectochoanal in the formation of a "ductus nasopharyngeus" in the two families mentioned is unique for the Lacertilia. In *Anolis* the enlarged ectochoanal takes part in the formation of a "secondary palate" in front of the choana.

One is inclined to regard the Geckonid palate in which both the lateral and median edges of the choana are supported along their whole length by cartilage as primitive, although neither *Sphenodon* nor the *Iguania* bear out this hypothesis. In all other lizards the ectochoanal serves as a support for the palatal end of the nasolacrimal duct and, at most, a small part of the lateral choanal edge in the region of the duct.

The cartilaginous concha nasalis does not form a blind tube as in most *Autarchoglossa* and *Iguana* but consists of a flat plate, the inner, free edge of which undergoes a certain amount of scroll-like deflection (fig. 33). The glandula nasalis lateralis is therefore situated in a cavum conchale, the walls of which are only partly supported by cartilage. In several of the *Scincidae* the floor of the cartilaginous concha nasalis is also incomplete. Hafferl (1921) regards the Geckonid type of concha as primitive.

Xantusiidae.

Camp (1923) regards this isolated family as most important in establishing the affinities of the *Autarchoglossa*:

"Were it not for the intermediate position and relationships (with the Gekkota) of this family, one could derive the Scincomorpha and Anguimorpha from iguanid stock, as Cope has done". The Xantusiidae, however, combine an assemblage of typically Autarchoglossid characters, such as the musculature, ventral squamation and tongue, with a number of very primitive, definitely Geckonid characters. Investigation of the nasal capsule lends support to the theory of Geckonid relationship, as has been shown by Young (1942).

I am indebted to Dr. Atsatt of the University of California at Los Angeles for the specimens of Xantusia vigilis used in this investigation. To the best of my knowledge the only work which has appeared on the cranial morphology of Xantusia is that of Young (1942).

The nasal cavities are very similar to those of the Gecko, although the vestibule is somewhat shorter, and approximates more closely to the general Autarchoglossid type. The divergent type of oral roof and choana is clearly a specialized variant of that of the Geckonid pattern. The choanal groove of Geckonidae has become obliterated externally with the exception of a narrow canal, into the dorsal part of which the organ of Jacobson and the ductus nasolacrimalis open. A similar canal also occurs in Amphisbaenidae, Teiidae, Varanidae, Anguidae, Anniellidae and Anolis, and is often called "the duct of Jacobson's organ". It should be remembered, however, that it represents a persistent part of the primitive choana itself (Fuchs, 1908). The relations

of the openings of the ductus nasolacrimalis and the organ of Jacobson resemble the Geckonid type very closely (fig. 35).

The nasal capsule also recalls that of the Geckonidae, although it shows specialization in several instances (cf. figs. 33 and 37). A deep, narrow internasal cavity into which the fused premaxillaries are situated separates the two cupolae anteriores. The ramus medialis of the ethmoid branch of $\bar{V}$ passes through the medial wall of the cupola into this cavity through a large foramen apicale. A short processus alaris inferior is present, but, as in Geckos, no definite superior alar can be determined. A narrow strip of cartilage connects the upper border of the fenestra narina with the cartilage roofing the anterior part of the true nasal cavity, thus completely separating the fenestra narina proper from its postero-dorsal incisura through which the duct of the lateral nasal gland enters the capsule (fig. 37). Young (1942) regards the connecting strip as homologous with the processus alaris superior, and, judging by conditions obtaining in several Scincidae (cf. p. 71), the hypothesis seems correct. In Iguana, on the other hand, the foramen for the duct of the lateral nasal gland is formed by a fusion of the sides of the fissura lateralis, and it is impossible to determine whether the superior alar has any part in this fusion or not. In Microsaura, in which a separate foramen is also found, the fissura lateralis has disappeared and a definite processus alaris superior seems to be present in front of the fusion (fig. 27). The total length of the interrupted fissura

lateralis of *Xantusia* is comparable to that of *Geckonidae*, although it does not penetrate into the cavum conchale, as it does in *Pachydactylus* (fig. 34).

The fenestra superior nasi and f. lateralis nasi are absent (fig. 37), as in most *Ascalabota*. The concha nasalis, although better developed than in *Geckonidae*, similarly consists of a simple plate of cartilage with a scroll-like edge (fig. 37).

The region around the organ of Jacobson shows a number of adaptations calculated to bring about a greater structural firmness. Between the organs the paraseptals are fused (fig. 37): a condition unique among lizards. Also the vomers are fused, two posterior horns alone indicating their original paired nature. The septomaxillary is exceptionally well-developed, forming a protective buttress on either side of the septum and enclosing the ramus medialis in a bony canal. These strengthening devices would seem to be necessary (when the animal is chewing its food) to counteract the stress exerted upon the lamina transversalis anterior by the enormous ectochoanal which supports the flanges forming the floor of the "ductus nasopharyngeus". This seems especially significant, when the weakness of the posterior part of the paraseptal and of the lamina antorbitalis is compared with the massiveness of the ectochoanal (fig. 37).

As Young (1942) has shown, the most notable feature of the nasal region of *Xantusia* is the formation of a functional ductus nasopharyngeus behind the choanae by the large overlapping choanal folds (fig. 38). These are supported by the ectochoanals,

as in Geckonidae, where, however, they remain widely separated (fig. 36). In Xantusia the ectochoanals themselves overlap and are prolonged backward into the niveau of the planum suprasedale (fig. 37). Behind the ectochoanals the folds continue to overlap, and thus they transform the entire orbital groove into a "ductus nasopharyngeus". Behind the eyes they terminate as two free flaps of skin overlying the palato-pterygoid ledges. Güppert (1903) and Fuchs (1908) have demonstrated that the palatal folds and the palato-pterygoid ledges in combination with the tongue tend to separate the respiratory portion of the mouth cavity from the rest in all Lacertilians. In the other three super-families of the Scincomorpha; i.e. the Scincoidea, the Lacertoidea and the Amphisbaenoidea (Camp, 1923), the palatal folds exhibit a varying tendency to approach each other and to complete the separation of the respiratory tract. But in all these cases the ectochoanals take a negligible part in the support of the folds, the palatines being responsible for this function (cf. figs. 41, 42 and 43).

Scincoidea

Camp (1923) includes in this superfamily, in addition to the Scincidae, the three, small, degenerate burrowing Scincoid families: Anelytropsidae, Feyliniidae and Dibamidae. I was unable to obtain material of the last two families, and a specimen of Typhlosaurus vermis belonging to the Anelytropsidae, very kindly sent me by Dr. Fitzsimons of the Transvaal Museum unfortunately

proved to be so badly preserved as to be practically useless for purposes of microtomy. To my knowledge no detailed work has been done on the cranial anatomy of these rare forms, although they may be expected to be of considerable importance to the nasal adaptations of the limbless burrowing lizards.

The Scincidae are a large family with a world-wide distribution and have consequently formed the subject of numerous investigations. Solger (1876), Born (1879) and Göppert (1903) have all contributed to the knowledge of the nasal capsule and palate. In 1920 Rice published his work on the development of Eumeces quinquelineatus. More recently a number of genera have been investigated: Ablepharus pannonicus (Haas, 1935), Acontias meleagris (de Villiers, 1939; Brock, 1941 and van der Merwe, 1944), Chalcides guentheri (Haas, 1936) and Mabuia capensis (= trivittata) (Dick, *manusc.*). The work of Pearson (1921) on Lygosoma was unfortunately not available except for a comparison given by Brock with Acontias.

In the present investigation the following were examined: An adult specimen and a fairly complete embryological series of Mabuia capensis; adult specimens of Scelotes bipes and Ablepharus wahlbergii; and an adult and some embryological stages of Acontias meleagris.

The nasal region of the Scincidae resembles that of Lacerta so closely that a detailed account is unnecessary. The Scincid vestibule, however, is shorter than that of the genus Lacerta, and it commonly enters the true nasal cavity in

front of, (Agoutias and Ablepharus), or over the anterior portion of the organ of Jacobson. It, moreover, enters the nasal cavity partly from a lateral direction, not directly from the front. This condition is reminiscent of that of *Sphenodon* and may perhaps be taken as a proof of the primitive position of the Scincidae among the Autarchoglossa; the condition also obtains in the Anguidae, Amphisbaenidae and snakes. As a result of the shortness of the vestibule, the duct of the lateral nasal gland runs forward from the gland for some distance along the outer surface of the cartilaginous and bony nasal capsule before entering the nasal capsule through the postero-dorsal corner of the fenestra narina, behind the cartilago alaris superior. In *Ablepharus* the superior alar is fused to the anterior end of the cartilage roofing the lateral part of the true nasal cavity and supporting the side wall of the organ of Jacobson. The portion of the fenestra narina through which the duct of the lateral nasal gland enters, therefore constitute a separate foramen as in *Xantusia*, *Iguana* and the *Chamaeleontidae*. In the two latter cases it is not clear whether the processus alaris superior plays any part in the formation of the foramen. In *Scelotes* the two cartilages approach to within 60° of each other, but remain separate as a result of the intervention of the lateral tip of the septomaxillary. In *Mabuia* fusion is actually effected, but the condition is complicated by the disappearance of the cartilaginous bar separating the fenestra superior from the foramen for the duct of the lateral nasal gland.

The external naris of *Acontias* possesses an intricate closing mechanism as an adaptation to a sand-burrowing existence. The outer vertical portion of the vestibule runs obliquely forwards before opening into the true nasal cavity some distance in front of the organ of Jacobson. The cupolae anteriores are widely separated by the premaxillaries, and each of them is attached to the septum solely by means of two slender struts. Since the cupola and especially its processus alaris inferior are very large, the slightest pressure, such as would be exerted upon the tip of the snout when the animal is burrowing into loose sand, would tend to close the narial aperture. The processus alaris superior is, moreover, attached to the cupola by means of a slender basal portion, and is connected to the alaris inferior and the outer edge of the septomaxillary by means of a strongly developed dermal muscle, homologous to the narial muscle described for *Agama*. The contraction of this muscle would further serve to close the external naris. The foramen apicale is large and occupies the area between the two connecting struts mentioned above.

A fenestra superior nasi is present in all *Scincidae* investigated. The fenestra lateralis, on the other hand is uncommon, occurring only in *Acontias* and in *Scelotes*, in the latter of which it is a very small foramen placed postero-lateral to the foramen epiphaniale. According to Brock (1941) it is absent in the embryo of *Acontias* but de Villiers (1939) regards a large incisura in the posterior part of the side wall as the homologue of the fenestra lateralis.

The degree of adaptation to a burrowing existence has apparently no relation to the fusion of the median, paired dermal bones of the nasal region. The vomers are fused in the genus Eumeces (Kingman, 1932), Ablepharus pannonicus (Haas, 1935), A.wahlbergii (fig. 40), Chalcides guentheri (Haas, 1936), Lygosoma (Siebenrock, 1892), and Scelotes bipes (fig. 39); they remain separate in Mabuia capensis (Dick, manusc.), Acontias meleagris (fig. 41) and Scincus scincus (El-Toubi, 1938). The premaxillaries are fused in Scincus scincus and Scelotes bipes, but they remain separate in all the other genera mentioned above. According to Camp (1923) the premaxillaries are paired in some Geckonidae and Scincidae only. He inclines to the view that the unpaired nature of the median skull elements is primitive, but cites the opinion of Méhelij who regards it as a neotenic character ! Nor is the cartilaginous nasal capsule, except for the adaptation of the external nares of Acontias, affected by the burrowing habits, but is on the whole more complete than in Lacerta. The only adaptation exhibited by the burrowing forms is the compact build of the bony nasal case.

The cartilaginous capsule of Jacobson's organ is rudimentary. An anterior cupola is never present, since the septo-maxillary is closely applied to the flat plate-like lamina transversalis anterior in front of the organ of Jacobson. The paraseptal is complete in the embryo of Acontias, Mabuia and Eumeces (Rice, 1920), but tends to be interrupted opposite the organ of Jacobson in most adult scinks (fig. 40). The ectochoanal

is always small, as in *Lacerta*.

The concha nasalis shows similarity with the simple Geckonid concha, since the cavum conchale is rarely supported by a complete cartilaginous floor. The concha is, however, never continued as a simple plate behind the cavum conchale. Scelotes bipes is peculiar in the absence of a cavum extraconchale, the outer wall of the concha forming the side wall of the capsule (fig. 39). The processus maxillaris is generally well-developed (fig. 39), but is reduced to a mere knob of cartilage, plus minus 60μ in length, in *Acontias*.

As in *Lacerta* a short secondary palate converts the anterior part of the primitive choana into a choanal groove between the organ of Jacobson and the functional choana (Fuchs, 1908) (fig. 40). The ductus nasolacrimalis does not open into the choanal groove opposite the duct of Jacobson's organ as in *Sphenodon*, the Geckonidae (fig. 35), the Iguania and the Xantusiidae, but discharges the secretion of the Harderian gland into the anterior end of the functional choana, as in *Lacerta*. The secretion is carried thence along an open gutter in the roof of the choanal groove (fig. 40) to a point opposite the duct of Jacobson's organ. As in the case of the nasolacrimal duct in the Geckonidae, this "nasolacrimal groove" also appears to enter the organ of Jacobson itself, since the duct of the organ into the choanal groove is very wide (cf. fig. 35). In some genera these relations are very deceptive, since the anterior end of the "nasolacrimal groove" is transformed into a blind pocket,

which then appears to form part of the organ of Jacobson itself (e.g. Acontias: de Villiers, 1939). The "nasolacrimal groove" must therefore be regarded merely as a functional part of the nasolacrimal duct since the latter terminates in the choana. The occurrence of this "nasolacrimal groove" in the comparatively primitive Scincidae and Lacertidae is important for the interpretation of the palatal portion of the nasolacrimal duct in those families e.g. Teiidae in which the choanal groove has been obliterated externally (cf. ps. 80 & 121).

The nasal region of the Scincidae is chiefly remarkable in the possession of a functional ductus nasopharyngeus occurring in the various genera in different degrees of development. This fact is well-known from the works of Göppert (1903), Fleischmann and Beecker (1903) and Fuchs (1908). The nasal grooves ("Nasalmulde" - Fuchs, 1908), into which the choana opens on either side of the vomerine cushion, are practically closed off from the mouth cavity by a median increase in size of the choanal folds supported by the outer edge of the palatine (fig. 41). As a result the palatine acquires the form of a cylinder opening medio-ventrally (Brock, 1941). In *Lacerta* the palatine exhibits a moderate ventral flexure in this region, but becomes quite flat behind the vomerine cushion, so that the orbital groove appears as a wide, shallow depression in the roof of the mouth cavity. In many Scincidae, however, the entire orbital groove is formed into a "ductus nasopharyngeus" by the rolled-up outer edges of the palatines and occasionally by an approximation of the palatoptery-

-goid edges as well. In some genera, notably in *Ablepharus*, the palatopterygoid edges are in contact with each other (Haas, 1935), and in *A. wahlbergii* they actually overlap in the pterygoid region (fig. 43) so that the ductus nasopharyngeus is carried right up to the glottis. In *Scelotes bipes* and *Mabuia capensis* similar conditions obtain in the palatine region, but the palatopterygoid edges diverge to form a wide, shallow orbital groove. In a figure of *M. quinquetaeniatus* given by Fuchs (1908) the palatopterygoid edges are shown in contact with each other, so that conditions may apparently vary widely within a genus. In *Acontias meleagris* conditions are somewhat different as a result of the small size of the eye and the consequent abbreviation of the orbital region. The palatines possess along their entire lengths ventrally directed median squames closely applied to each other below the septum, and continuing the vomerine cushion into the orbital groove (fig. 41). The "ductus nasopharyngeus" is therefore paired over the whole orbital region. The palatopterygoid edges diverge as in *M. capensis* and *Scelotes bipes*. According to Brock (1941) the choanal region of *Lygosoma* (Pearson, 1921) resembles that of *M. capensis*, and judging from Kingman's figures (1932), this is also the case in the genus *Eumeces*.

Anelytropsidae.

According to Fitzsimons (1943) the genus *Typhlosaurus* can be derived from *Acontias* via *Acontophiops*, and consequently he places it with the *Scincidae*. The palate of *T. vermis* confirms

this view, since it agrees in most particulars with that of Acontias meleagris. It shows an advance over the Acontias condition in that the choanal folds are actually fused to the vomerine cushion, transforming the nasal grooves into completely closed-off ductus nasopharyngei (fig. 42). The free edges of each palatine tube are connected syndesmotically. This is a condition absolutely unique among lizards and is strongly reminiscent of the structure of the ophidian palate.

Lacertidae.

An account of the nasal region of the Lacertidae have been given in the introduction.

Gerrhosauridae.

The nasal region of this family closely resembles that of Lacerta (Camp, 1923 and Malan, 1940), and serial sections of Gerrhosaurus flavigularis, G. typicus and Tetradactylus tetradactylus show that as far as this region is concerned, the different genera exhibit little variation.

Teiidae.

Fürbringer (1900) was of the opinion that this New World family is closely related to the Xantusiidae which are endemic to North America. Gadow (1901) regarded the Teiidae as intermediate between the Xantusiidae and the Amphisbaenidae, but Camp (1923) classifies them with the Lacertidae and Gerrhosauridae under a superfamily Lacertoidea. He creates a separate superfamily for

the Amphisbaenidae which he regards as probably derived from the Teiidae. Except for references to the concha of Ameiva by Solger (1876) and to the palate of A. surinamensis by Fuchs (1908), no work has appeared on the nasal region of the Teiidae.

The following forms were examined in the present investigation: Teius teyo teyo Daudin, Ameiva undulatus Wiegmann and Cnemidophorus sexlineatus. The nasal capsule and cavities agree closely with those of Lacertidae and Gerrhosauridae but the structure of the palate and ductus nasolacrimalis points to a possible affinity with the Xantusiidae and/or the Amphisbaenidae. In the nasal region only slight differences characterize the three genera examined. Teius appears to be the most primitive, judging by the structure of the capsule of Jacobson's organ.

A well-developed rostrum or processus praenasalis occurs in all three genera; it is situated in a cavum internasale not flanked by the cupulae anteriores as in Sphenodon and the Iguanidae, but by two anterior cupolar processes (fig. 45). Among Autarchoglossa I have also found a rostrum in the genus Chamaesaura (Cordylidae) and in the Varanidae, where, however, a cavum internasale is entirely absent. To my knowledge the anterior cupolar process is peculiar to the Teiidae. It consists of a vertically placed lamina, pierced in Teius by three or four small branches of the ramus medialis where they leave the "internasal cavity" to supply the skin of the lateral parts of the snout (fig. 45). Although the processus alaris inferior is partly attached to this anterior process, the latter cannot be regarded as homologous with

the cartilago praenasalis inferior of Anura.

A fenestra superior nasi is absent, but a fenestra lateralis nasi occurs in all three genera investigated. This condition is the exact opposite of that found in the Scincidae, where a fenestra superior nasi is invariably present while a fenestra lateralis nasi is extremely uncommon.

A feature of exceptional interest in the cartilaginous capsule of Jacobson's organ of *Teius* is the occurrence of a roofing cartilage in the form of several thin, isolated strips closely applied to the lower surface of the septomaxillary (fig. 46). It has already been pointed out that this Rhynchocephalian character is found only in the family Iguanidae among lizards, although the presence of a septal ledge on which the inner edge of the septomaxillary rests, indicates its previous existence in quite a number of lizards belonging to the Lacertidae, Gerrhosauridae etc. A pronounced ledge occurs in *Cnemidophorus* and *Ameiva*. The specimen of *Teius*, although small, was undoubtedly adult, and the vestigial roofing cartilage must be regarded as a primitive character retained by *Teius*. Another peculiarity of Jacobson's capsule, which the Teiidae have in common with the Iguanidae, is the extensive cupola posterior forming a capsule to a large part of the posterior half of the organ (fig. 47). The nervus vomero-nasalis enters the organ of Jacobson through a large number of foramina situated in the hind wall of the cupola. The presence of a complete cupola anterior in this relatively primitive family serves to explain the occurrence of cartilaginous nodules in the

region behind Jacobson's organ in a large number of Autarchoglossid lizards belonging to the Lacertidae, Scincidae etc.

The paraseptal is not fused to the planum antorbitale, since its posterior portion is interrupted for a distance varying in the different genera. In the Autarchoglossa in general the paraseptal shows a tendency to degenerate in the region of the organ of Jacobson, while the posterior half is usually well-developed. This exceptional condition in the Teiidae may be connected with the large amount of cartilage retained in the capsule of Jacobson's organ. The ectochoanal is small as in *Lacerta*.

The cavum conchale is exceptionally large and occupies practically the whole length of the concha, which in the Geckonidae for instance terminates posteriorly in a simple flat plate. In *Teius* and *Ameiva* two longitudinal cartilaginous ridges project from the base of the concha into the nasal cavity. The anterior one is small (fig. 47), and in *Ameiva* it terminates directly behind the organ of Jacobson. The more posteriorly placed ridge is much longer and extends up to the hind end of the concha. The appearance in cross-section of the lateral nasal gland of Teiidae is quite typical of the family: the duct can be identified throughout the length of the gland, since it is very wide and runs along the centre of the mass of tubules which open into it at irregular intervals (fig. 47).

As in *Xantusia* the choanal groove present in Geckonidae, Scincidae, Lacertidae etc. between the organ of Jacobson and the functional choana is obliterated externally, so that what is

apparently the anterior end of the ductus nasolacrimalis runs below the epithelium of the oral roof for some distance (fig. 47). In the Teiidae, in contrast to the condition obtaining in Xantusia, the ductus nasolacrimalis opens into the anterior end of the choana exactly as it does in Lacerta. The duct which passes forward from the choana to the duct of Jacobson's organ must, therefore, represent a closed-off choanal groove, and it is only functionally a part of the ductus nasolacrimalis. It is evident that the Teiid condition should be derived from the Lacertid type of palate (fig. 44), while the condition found in Xantusia has probably arisen out of the Geckonid type, where the ductus nasolacrimalis still opens in the choanal groove opposite the duct of Jacobson's organ in the primitive position typified by Sphenodon (Fuchs, 1908).

With regard to the structure of a "ductus nasopharyngeus", the Teiidae occupy an intermediate position between the Scincidae, where the palatine is practically transformed into a tube, and the Lacertidae where it exhibits little ventral flexure. In the Teiidae this flexure is more pronounced than in the Gerrhosauridae which also represents a morphological link. The Teiid "ductus nasopharyngeus" never extends to the orbital groove as in many Scincidae.

Amphisbaenidae.

The older taxonomists have seldom attempted to express an opinion regarding the phylogenetic position of the

aberrant, burrowing family, the Amphisbaenidae. In the posthumous work of Cope (1900) they were relegated to a section "Annulati" containing a number of other limbless Lacertilian families eg. Anniellidae. Fürbringer (1900) separated them from his suborder: Lacertilia vera into a separate suborder, as was also done by Williston (1904). Gadow (1901) was the first to place them under "true lizards" (suborder: Lacertae) in a subgroup including the Xantusiidae and Teiidae. Camp (1923) places them in a separate superfamily of the suborder Scincomorpha, and states with reference to their affinities: "The resemblances (of the Amphisbaenidae) to the degenerate Teiidae are for the most part secondary but are nevertheless indicative of ancestral relationship to that family, as is also the fact that the anterior process of the basi-hyal is exceptionally long, as it is in all known Teiidae".

Investigation of the nasal region has provided little additional evidence with respect to the relationships of the family. The morphology of the anterior end of the ductus nasolacrimalis points to affinity with the Xantusiidae, but the resemblance may be secondary.

Von Bedriaga (1884) has given a detailed discussion of the nasal region in his work on the cranial anatomy of two species of the genus Amphisbaena. Cope (1892) has given a brief survey of the osteology of Rhineura floridana in his work: "The Osteology of Lizards", but I was unfortunately not able to consult it. Peter (1898) pointed out the adaptive resemblances existing in the skulls of Ichthyophis and of burrowing reptiles eg. Amphisbaenidae

and Typhlops. The only recent work on the cranial anatomy of the family is that of Kritzinger (in manusc.) on Monopeltis capensis.

For the present investigation microtomized sections were made of adult specimens of Monopeltis capensis and Rhineura floridana. The nasal region of Monopeltis is chiefly characterized in the very compact structure of the bony capsule, accompanied by a marked reduction of cartilage (Kritzinger, in manusc.). The absence of functional eyes and the consequent reduction in length of the orbital region has resulted in a secondary connection of the nasal region with the prootic bones, and an invasion of the nasal region by the rostrum parasphenoidale and the orbitosphenoid. This arrangement lends great resistance to the skull as a whole, in adaptation to a burrowing life.

As a further adaptation the external nares are placed ventrally, a short distance behind the tip of the snout. The vestibule and the anterior cupola of the nasal capsule reflect this unusual condition by their extreme specialization. The vestibule enters the true nasal cavity from below, is extremely short, and shows a marked reduction of the typical elastic muscular lining. A vestibule terminating in front of the organ of Jacobson characterizes the Scincidae and Anguidae. A mass of muscular tissue lying behind the narial opening between the processus alaris inferior and the side wall of the nasal capsule is probably homologous with the narial muscle, but its attachments could not be made out. The cupola anterior is connected to the anterior end of the septum solely by a cylindrical bar of cartilage

(cf. *Acontias*). Ventro-laterally the cupola is continued backward as two processes: the one lying medial to the external nares clearly represents the alaris inferior, while the more lateral one is continuous with the side wall of the nasal capsule. There is no indication of a processus alaris inferior. As a result of the enormous enlargement of the foramen apicale, the fenestra superior nasi and the fenestra lateralis nasi, the roof of the nasal capsule consists of a number of thin taenial bars connecting the septum with the side wall. The foramen epiphaniale is small and situated immediately behind the fenestra superior and above the aditus conchae.

The cartilaginous floor is markedly vestigial. As in several snakes (e.g. *Homalosoma*) the lamina transversalis anterior is not fused to either the side wall or to the septum, so that a zona annularis is wanting. The ectochoanal is large, but the paraseptal is interrupted over almost its entire length and is represented by a short anterior and a longer posterior rudiment. A greater amount of cartilage has been retained laterally, since the side wall supports the concha. The cavum conchale is small, and the horizontally inclined concha is attached to the middle of the paries nasi, so that strictly speaking, a cavum extraconchale is absent, as in *Scelotes*. The aditus conchae faces sideways and outward instead of forward and upward as in *Lacerta*.

The virtual absence of eyes and the need for a more closely-knit skull has resulted in an extreme degree of specialization in the posterior part of the nasal capsule. A clearly defined

cavum antorbitale is absent, since the nasal cavity gradually passes over into the "nasopharyngeal groove" (cf. Scincidae). As a result the planum antorbitale is in the form of a thin horizontal strip of cartilage connecting the paraseptal with the two taeniae representing at this point the roof and side wall. Owing to the telescoping of the orbital region the sphenethmoid commissures have been pushed so far forward, that they lie in the same horizontal plane as the planum antorbitale, thus simulating the fusion, present in snakes, between the planum antorbitale and the septum.

The orbitosphenoid ossification, limited in *Lacerta* to the pila methoptica (de Beer, 1937), has in *Monopeltis* invaded the planum suprasedale, the dorsal part of the interorbital septum and the postero-dorsal part of the nasal septum. The anterior limit of the ossification extends well into the conchal region. A curious feature, doubtless caused by secondary kinesis of the skull, is the fact that the orbitosphenoid is separated from the ventral cartilaginous part of the septum by connective tissue. Also the rostrum parasphenoidale reaches the nasal region; its anterior end is bifurcated: the upper prong lying inside the brain case above the medio-ventral suture of the frontals, and the lower one being situated underneath the septum. These processus unite behind the point where the trabeculae diverge from each other. As a result of the reduction in length of the orbital region, the divergence takes place at a point only about .3 m.m. behind the planum antorbitale in a specimen whose total nasal

capsule length is 1.9 m.m. (cf. Kritzinger, op.cit., fig.2).

With reference to the roofing bones of the nasal region it is of interest that the two nasals do not form a median suture, since they are separated by a long median process of the fused premaxillaries and two forwardly directed processes of the frontals. The frontals themselves are large and have encroached to a considerable extent on the region normally covered by the nasals.

The palate exhibits interesting adaptations to a burrowing habit. Both the premaxillary and the maxillary possess enormous palatal squames (Lakjer, 1927). The palatal squame of the former bifurcates in front of the organs of Jacobson and reaches back even further than do the ectochoanal cartilages. The organ of Jacobson is situated relatively far back, and an extensive secondary palate (Fuchs, 1908) supported by the vomer, the premaxillary and maxillary squames and the ectochoanal, separates the opening of Jacobson's organ from the functional choana (Kritzinger, op.cit). As in Xantusiidae, Teiidae, Varanidae, Anguidae and Anniellidae the choanal groove in front of the choana is obliterated externally. In Amphisbaenidae the ductus nasolacrimalis does not open into the choana (cf. Xantusiidae), as it does in the other four families mentioned. Without embryonic material it is impossible to determine whether the anterior palatal portion of the ductus nasolacrimalis running underneath the epithelium of the oral roof and opening opposite the duct of Jacobson's organ, represents a closed-off choanal groove, as in Teiidae, or part of the nasolacrimal duct itself, as in

Xantusiidae. If the former interpretation is accepted, it is necessary to assume that the actual opening of the ductus nasolacrimalis into the anterior end of the choana has secondarily closed up. The problem is discussed in detail on page 118.

The choanae are roughly circular instead of being slit-like and are situated behind the concha nasalis. They lead into two "nasopharyngeal" grooves supported by the ventrally flexed palatines, as in Scincidae.

With the exception of a few trivial differences the nasal region of Rhineura floridana very closely resembles that of Monopeltis. The foramen apicale is confluent with the fenestra narina, and the paraseptal is complete throughout its length. The rostrum parasphenoidale does not penetrate the nasal region and the orbitosphenoid ossification is not restricted to the dorsal part of the interorbital and nasal septum, these latter ossifying as a whole.

Varanidae.

The fossil record proves that the Varanidae have been a distinct family since Lower Eocene times (Camp, 1923). According to Fejérváry (1918), moreover, the Old World Varanoid fossils belong, without exception, to the genus Varanus which includes all the living forms as well. Camp (1923) is of the opinion that the Platynota, including the extinct Mosasauridae, Dolichosauridae and Aigialosauridae, are related to the Diploglossa, a group roughly comprising the Anguiroid and Cordyloid (= Zonuroid) lizards.

The existing species of Varanidae, however, form a peculiarly isolated group with a number of outstanding characteristics. The most important of these are the structure of the tongue which resembles that of snakes, and certain characters relating to the hyoid musculature and ventral squamation (Camp, 1923). In common with the Iguania, the Chamaeleontidae and the Teiidae, an upper temporal fossa is retained in Varanus. This character is, however, dependent on the loss, early in the phylogeny, of the cranial osteoderms and need not necessarily be indicative of affinity of the groups in which it occurs (Broom, 1935).

Born (1879) has given a brief account of the nasal region of "Monitor albigularis Gray" (= Varanus albigularis albigularis Daudin) in which he emphasized the unique structure of the vestibule and the concha. To my knowledge no other work has appeared on the nasal region of the Varanidae. For the present investigation microtomed sections were made of a 23 c.m. (total length) embryo of Varanus niloticus. The presence of a layer of extremely tough felt-like connective tissue in the skin over the dorsal surface of the head makes even a young embryo of Varanus a difficult object for microtomization. Satisfactory results were, however, obtained by removing the lower jaw and cutting the cross-sections from the direction of the palate.

The nasal organ of Varanus is highly peculiar, combining several unique features with a confusing mixture of Ascalabote and Autarchoglossid characters. The nasal cavities resemble those of the Iguania and Chamaeleontidae in the possession of a

greatly elongated vestibule, accompanied by a telescoping of those cavities constituting the posterior two-thirds of the Lacerta nasal organ (fig. 50).

The external nares are placed far back on the skull, somewhat nearer to the eye than to the end of the snout. In V.albigularis alb. Daudin the nostril lies much nearer to the eye than to the tip of the snout (Born, 1879 and Fitzsimons, 1943). The outer lateral sac of the vestibule runs obliquely forwards and inwards (fig. 50), being separated for a short distance from the main portion of the vestibule by the greatly enlarged processus alaris superior (figs. 48 and 51). The vestibule is thus doubled back upon itself, but in such a way, that a blind vestibular cavity, considerably longer than the main portion of the vestibule, occurs in the snout in front of the nostril (fig.50). The organ of Jacobson is placed underneath the anterior blind cavity. To my knowledge Microsaura pumila is the only other lizard in which the organ of Jacobson is situated in front of the external nares, although Iguana shows an approach to this condition. Although the length of the vestibule of Varanus is reminiscent of that of the Ascalabota, it lies in front of the true nasal cavity and enters the latter in the normal Autarchoglossid manner. A very peculiar feature of the vestibule, noted by Born in 1879, is the ventral blind pocket of unknown function situated behind the organ of Jacobson (fig. 50) and supported by a vertical, cupular squame of the septomaxillary. The elastic muscular tissue lining the vestibule is exceptionally well-developed particularly in the

area behind the nostril, but the narial muscle is apparently absent. The processus alaris inferior to which it normally attaches is rudimentary (figs. 48 and 51).

The true nasal cavity is small in comparison with the vestibule (fig. 50). The lateral nasal gland is situated in a cavum conchale as in all Aŭtarchoglossa (with the exception of *Celestus*, one of the Anguidae), Geckonidae and Iguana. As in Iguana, the concha is situated in the posterior part of the nasal capsule, and the aditus is placed dorsally and leads down into the cavum (figs. 48 and 49). As a result the cavum extraconchale communicates with the true nasal cavity behind and below the concha, and not above it, as in all lizards with a vertically placed aditus (fig. 54). The cavum extraconchale is unique among lizards in that it is largely extracapsular (fig. 53 and 54, right side). It is interesting in this respect to compare it with the middle turbinal sinus of *Crocodylus* (Meek, 1911), particularly since the middle turbinal is regarded as homologous with the concha nasalis of lizards (de Beer, 1937). In *Crocodylus* this diverticulum of the nasal sac passes out through a slit near the ventral edge of the side wall of the capsule and penetrates into the cavum conchale through the aditus (de Beer, 1930). The nasal gland of *Crocodylus* does not occupy the cavum conchale, but is situated in a shallow groove in the side wall cartilage underneath the maxillary (Gaupp, 1888). In my 7.5 c.m. embryo of *Alligator mississippiensis* the same relations obtain. In *Varanus* the cavum extraconchale passes out of the nasal capsule through a foramen lateral to the aditus

conchae and antero-lateral to the foramen epiphaniale (figs. 54, left side, and fig. 49). It slightly bulges over into the aditus (fig. 54), but does not actually penetrate the cavum conchale, since the latter is occupied by the lateral nasal gland. The extracapsular part of the cavum extraconchale lies median to the maxillary in a latero-dorsally facing trough formed by the side wall cartilage (figs. 49, 51 and 54 right side). Judging by the position of the foramen through which the sac issues, it represents the fenestra lateralis nasi of other lizards, and the trough has probably been formed by an extensive enlargement of this fenestra (fig. 49). The cavum antorbitale is large, and the "inner choana" (Born, 1879) is placed deep into the interior of the nasal organ with the result that the "choanengang" (Fuchs, 1908) is very large (fig. 50).

The structure of the nasal capsule is best understood by referring to the three graphical reconstructions (figs. 48, 49 and 51). The septum is prolonged in front of the capsule as a prenasal process or rostrum nasale. This is another instance of similarity with Iguanidae, but as a rostrum is also found in the Teiidae and the subfamily Chamaesaurinae, it must be regarded as a Rhynchocephalian character retained by several primitive Lacertilian families, rather than as a proof of affinity between Varanus and the Ascalabota. The foramen apicale is placed on the dorsal face of the capsule behind the prenasal process (fig. 49). The cupolae anteriores have been profoundly altered by the peculiar position of the external nares. The anterior parts of

the capsule are bent outward and backward to form a roof for the outer portion of the vestibule (fig. 52 and reconstructions); an internasal cavity is consequently absent. The processus alaris inferior is vestigial, but the alaris superior is represented by a large vertical lamina separating the two parallel portions of the vestibule (figs. 48, 51 and 52). The fenestra narina faces backward, because the processus alaris superior is overlapped by the cupola anterior, and it is incomplete posteriorly, since a zona annularis is absent through the failure of the lamina transversalis anterior to fuse with the paries nasi (fig. 51). The duct for the lateral nasal gland enters the nasal capsule through a ventrally facing incisura in the side-wall (fig. 51); as in *Lacerta*, this specialized part of the fenestra narina is separated from the rest by the alaris superior. Although conditions in the fenestra narina resemble those of the *Iguania* in all particulars, there is no fissura lateralis nasi because the zona annularis is incomplete (cf. figs. 51 and 8).

A fenestra superior nasi is absent, and the two cupolae are separated dorsally by a deep, median groove extending beyond the anterior half of the capsule and harbouring a median, dorsal process of the fused premaxillaries (figs. 49 and 52). The nasals are fused and very small leaving the cartilaginous roof of the nasal capsules unprotected; this fact probably accounts for the covering of felted connective tissue over the snout region.

The solum nasi is greatly reduced (fig. 48). As already pointed out, the lamina transversalis anterior is not fused to

the side of the capsule, but a long, slender process of the side-wall cartilage behind the entrance of the duct of the lateral nasal gland indicates that a fusion may formerly have existed in the group (fig. 51). The paraseptal is interrupted behind the organ of Jacobson, and it consists of a small posterior vestige on the lamina antorbitalis and a larger rudiment continuous with the lamina transversalis anterior (fig. 48). The ectochoanal is small and, as in *Lacerta*, it serves as a support for the anterior end of the "ductus nasolacrimalis". The anterior portion of the organ of Jacobson rests on the lamina transversalis anterior, and a large concha, continuous with the lamina, juts into the lumen of the organ. Behind the duct the cartilaginous capsule is represented solely by a slender bar supporting part of the side-wall (fig. 52), which is forked posteriorly, the ductus nasolacrimalis passing between the two prongs.

The nasal capsule of *Lacerta* may be divided into three approximately equal parts, the middle portion comprising the conchal region (Gaupp, 1900). In *Varanus* the conchal and posterior regions together form less than one third of the entire capsule (fig. 49). This is mainly the result of an enlargement of the vestibular region, but the relatively small size of the foramen olfactorium, the fact that it faces backward and the position of the foramen epiphaniale show that a certain amount of compression has taken place in the posterior part of the capsule. The relations of the various structures resemble those of *Iguanidae* although the foramen olfactorium is much larger in *Varanus*, in

which the foramen does not, however, encroach upon the tectum nasi as in *Lacerta* (cf. fig. 33).

The relations of the concha nasalis, the foramen epiphaniale and the fenestra lateralis nasi have already been treated in connection with the discussion of the nasal cavities.

As in *Microsaura* the processus maxillaris anterior and p.m.posterior are not continuous with the paries nasi in the developmental stage examined (23 c.m. total length) (fig. 51). The lamina antorbitalis and the sphenethmoid commissure are normal.

There is no choanal groove between the opening of the organ of Jacobson and the functional choana. This character *Varanus* has in common with the Xantusiidae, Amphisbaenidae, Teiidae, Anguidae, Anniellidae and snakes. As in Teiidae, Anguidae and Anniellidae the ductus nasolacrimalis opens into the choana itself (figs. 50 and 53, left side), and the anterior palatal portion of the duct (figs. 50 and 52) may consequently be regarded as a closed-off choanal groove, and it is therefore to be considered not as a morphological but merely as a functional part of the ductus nasolacrimalis. The ductus nasolacrimalis of *Varanus* is remarkable in that the division into the two orbital ducts takes place in the nasal region opposite the middle of the choana and immediately anterior to its opening into the latter (figs. 50 and 53, left side). As a result of this it appears as if the larger, upper duct draining the inner and posterior part of the eye opens into the choana, while the smaller, lower duct draining the anterior part of the eye is continued forward

as the closed-off choanal groove to open opposite the duct of Jacobson's organ (fig.50). The illusion is enhanced by the fact that the communication between the two orbital ducts is very small (fig. 50).

Anguidae.

Cope (1900), Fürbringer (1900), Gadow (1901), Willeston (1904) and Camp (1923) all agree that the Anguidae are closely related to the Cordylidae. A comparison of the nasal organs shows that in the Cordylidae they are relatively primitive, and conditions in the concha and the palate point to a possible derivation of the more specialized Anguidae from the Cordylidae.

Zimmermann (1913) in a paper on the chondrocranium of Anguis fragilis has recorded that Leydig investigated this species in 1872. To my knowledge no work on the cranial anatomy has appeared on any other genus of the Anguidae. I was able to examine specimens of Celestus pleii Duméril and Bibron and Ophisaurus ventralis Linné through the courtesy of Mr. A.Loveridge.

The nasal cavities and capsule are of the general Autarchaglossid type, but a certain amount of divergence is found in the structure of the concha and in the size of the ectochoanal. As in Scincidae the vestibule is short, consisting of little more than the outer vertical portion of that of other lizards, and it enters the true nasal cavity in front of the organ of Jacobson. A peculiar feature of the vestibule of the Anguidae is a large blind sac leading from the posterior wall of the external nares and lying beneath the anterior part of the true nasal cavity

term *Tissura lateralis nasi* for the structure so called by
 tissue-like shape is incidental. I have therefore retained the
 this opening is homologous to a fenestra lateralis nasi, and its
 Zimmerman the "*Tissura lateralis nasi*". Judging by its position
 concave and opening into the cavity extracochlear is called by
 and Lacerta. In Anguis a narrow slit placed behind the aditus
 typical position occupied by the fenestra superior in Sphenodon
 foramen in the rostrum nasi above the organ of Jacobson, in the
 absent in Crotalus. The latter genus, however, possesses a small
 olfactoria. A similar fenestra occurs in Ophisaurus but is
 foramen placed immediately in front of the edge of the fenestra
 Anguis Zimmerman designates as the fenestra superior a small
 Fenestra lateralis nasi vary greatly in the three genera. In
 The position and size of the fenestra superior nasi and
 apiculate.
 Genera I have examined the nerve issues through a normal foramen
 is also continuous with the fenestra nasalis, but in the two Anguid
 Fenestra nasalis. In Rhipidura (Amphispentidae) the foramen apiculate
 Anguis the nerve medialis leaves the nasal capsule through the
 and p.n. superior are normal. Zimmerman (1913) states that in
 The capsule anterior with its processes alaris inferior
 and the vestibule proper.
 nasal cavity to open on the boundary line between the latter cavity
 the lateral nasal gland runs between the blind sac and the true
 ly enclosed by the maxillary and the septomaxillary. The duct of
 and lateral to the organ of Jacobson. Its blind end is complete-

Hafferl (1926) in the Gecko and occurring throughout the other Ascalabota as well. In *Ophisaurus* a typical fenestra lateralis interrupts the side-wall in the region of the cavum extraconchale (fig. 55), but it is absent in *Celestus*.

The cartilaginous capsule of Jacobson's organ is incomplete posteriorly, there being no sign of the vestigial hind wall so common in the Scincomorpha. The paraseptal is interrupted in the region of the organ of Jacobson, and the ectochoanal is large and consists of a broad plate of cartilage supporting the outer wall of the palatal part of the ductus nasolacrimalis and the anterior end of the choanal groove (figs. 55 and 56). But in spite of its large size it is not continued into the choanal region itself, as in *Geckonidae* and *Xantusiidae*.

In *Celestus* and *Ophisaurus* the lateral nasal gland is extremely reduced, and the cavum conchale in which it is normally housed is correspondingly small; the greater part of the concha nasalis of *Celestus* consists of a flat horizontal plate of cartilage. The anterior third of its free edge is rolled up to form a small cavum conchale containing no more than three or four tubules of the nasal gland. The small aditus conchae is situated above the posterior end of the organ of Jacobson. As in *Scelotes* and the *Amphisbaenidae* a cavum extraconchale is non-existent; the concha merely divides the nasal cavity into two storeys.

In *Ophisaurus* the lateral nasal gland is even more degenerate and does not penetrate the cavum conchale at all. It consists of two or three tubules filling the cavity of a

small groove on the side-wall of the capsule in front of the aditus (fig. 55). The floor of the cartilaginous cavum conchale is completely absent, and a portion of the nasal sac has extruded through the opening and fills the cavity normally occupied by the gland (fig. 57). In the Geckonidae, many of the Scincidae and the Cordylidae the floor is also incomplete, but to my knowledge Ophisaurus is the only lizard in which the extracapsular cavum conchale is lined by sensory epithelium. In the Crocodile the middle turbinal sinus lies within the cartilage of the middle turbinal (homologous to the concha nasalis according to de Beer, 1937), but it enters the cavity through the aditus, having left the capsule through a foramen in the base of the side-wall (Week, 1911) (cf. also Varanus p. 90). As the aditus faces antero-laterally in Ophisaurus the fenestra in the floor of the concha also appears in the side-wall cartilage in front of the aditus, and a small portion of the sinus lies outside the cavum within the aditus (fig. 56). According to Zimmermann (1913) the cartilaginous cavum conchale of Anguis communicates with the general cavity of the nasal capsule through a long ventral slit. The nasal gland is not mentioned in his account or indicated in his drawings; but judging by his figure 5 on page 599 the nasal sac does not penetrate the cavum conchale. In the Cordylidae the lateral nasal gland is very large, but since the cavum conchale itself is small as in Anguidae, the greater part of the gland is lodged in a large groove in front of the aditus.

The palate and nasolacrimal duct of Celestus are of the

Teiid type: the choanal groove between the organ of Jacobson and the functional choana has disappeared, and the duct running underneath the oral epithelium in this region must represent a covered-in choanal groove (fig. 55), since the ductus nasolacrimal -is opens into the choana (fig. 57). A minor difference is the circumstance that the fusion between the sides of the choanal groove has occurred on a level deeper than the oral roof, so that a shallow depression still indicates externally the position of a former groove (figs. 55 and 56). As a result of faulty preservation the epithelium of the oral cavity of *Ophisaurus* was slightly macerated, but as far as could be made out the same conditions obtain in this genus.

Anniellidae.

The Anniellidae are almost unanimously considered as "degraded forms of Anguillidae" (Gadow, 1901) or, at least, as closely related to them (Fürbringer, 1900). Camp (1923) states that they show closest resemblance to *Gerrhonotus*, a form which I was unfortunately not able to examine. With the exception of the Pygopodidae they are the only burrowing Anguimorpha the rest of the limbless representatives of the group being grass-living, long-tailed forms (Camp, 1923). To my knowledge no work has been done on the nasal organ of this small Californian family. Serial sections of an adult specimen of Anniella pulchra was used in the present investigation.

The circumstance that the nasal organ of *Anniella* is

highly specialized and shows little or no resemblance to that of Anguidae may be due to divergence in habitat but e.g. the very different types of conchae may indicate that the two families are not quite as closely related as has hitherto been thought.

The organ of Jacobson is relatively large and although its anterior half is placed median to the vestibule it is not roofed by the tectum nasi, as in *Leiosaurus*, *Liolaemus* and partly in *Microsaura* (fig. 25) where similar relations obtain, but by the septomaxillary (fig. 59). The ramus medialis of the ethmoid branch of $\bar{V}a$ runs in a canal between the septomaxillary and the tectum in this region. Since the true nasal cavity is situated in the normal position next to the septum the vestibule enters it dorsal to the middle of the organ of Jacobson from a lateral direction. The lateral position of the vestibule lends an exceptional width to the anterior part of the nasal capsule (cf. figs. 26 and 58). The cupola anterior is rather small but its processus alaris inferior is large (fig. 58). A processus alaris superior is absent. Neither of the two nasal fenestrae is present.

The lamina transversalis anterior is well-developed (fig. 59) but both its connexion with the septum and with the paries nasi are reduced, and beyond a posterior rudiment on the lamina antorbitalis (fig. 58) the paraseptal is absent. The ectochoanal is broad as in Anguidae.

The structure of the concha is unique: the greater part of the glandula nasalis lateralis is situated in an open

conchal groove on the latero-dorsal face of the capsule (fig. 58). A small posterior portion of the gland penetrates the aditus conchae bound laterally by the paries nasi itself since no extraconchal recess is present (fig. 60). This condition is reminiscent of that of *Scelotes* (fig. 39). The close proximity of the foramen epiphaniale to the fissura orbitonasalis is illustrated by fig. 60, the right side of which represents a plane slightly in advance of that represented by the left side. The ethmoid branch of $\bar{V}a$ divides into its two components before entering the nasal cavity. The lamina antorbitalis is small (fig. 58) and that part of the paranasal cartilage forming the cavum conchale and the maxillary processes is situated lateral and posterior to it. The maxillary processes are exceptionally large.

The structure of the palate and ductus nasolacrimalis fully supports the theory of the close relationship existing between the Anniellidae and the Anguidae since it resembles that of the latter in all particulars (cf. figs. 55 and 56).

Cordylidae (= Zonuridae).

Gadow (1901) regarded the Cordylidae (= Zonuridae auctorum) together with the other families placed by Camp (1923) under the Diploglossa as closely allied to the Iguania, and in spite of the position which Camp (1923) assigns to the family he states that they exhibit closer resemblances with respect to details of tongue and hemipenal structure, pattern of the throat musculature and the structure of the teeth, with the Ascalabota than any other

Anguimorph. The temporal region closely resembles that of Gerrhosauridae in the loss of the temporal fossa and the relative sizes of the bones but Broom (1935) is of the opinion that the conditions in the temporal region have been determined by the presence or absence of osteoderms in the phylogeny and that this region may therefore have little taxonomic value.

The only work on the cranial anatomy of this African family is that of du Plessis (1944) on Chamaesaura anguina. In the present investigation the following forms were examined: an adult specimen of Cordylus cordylus and a fairly old embryo of Cordylus sp., and adult specimens of Platysaurus capensis and Chamaesaura anguina.

Camp (1923) divides the family into two subfamilies: the Chamaesaurinae (including only the genus Chamaesaura) and the Cordylinae (= Zonurinae). Conditions in the nasal region fully confirms Camp's conclusions as to their systematic position, and the fact that a prenasal process occurs in Chamaesaura but not in Cordylus or Platysaurus supports his subdivision of the family. The presence of a rostrum prenasale cannot be considered as a proof of special Iguanid affinity since it occurs also in Varanidae and Teiidae and as in these families it is not situated in a cavum internasale as it is in Iguanidae.

In general the nasal cavities and capsule closely resemble those of the Lacertoidea.

In Cordylus and in Chamaesaura the duct of the lateral nasal gland enters the nasal capsule through a foramen distinct

from the fenestra narina since the processus alaris superior is fused to the side-wall of Jacobson's organ (i.e. the lamina transversalis anterior), but in a fairly old embryo of *Cordylus* the fusion is not yet effected but only indicated by thickened connective tissue. A similar fusion occurs in some *Scincidae* and in *Xantusiidae*.

A fenestra superior nasi is present in all three genera examined but is absent in the *Cordylus* embryo. An insipient fenestra lateralis nasi is present in *Platysaurus* and *Chamaesaura*.

The anterior and posterior regions of the concha (Born, 1879) of *Platysaurus* and *Cordylus* are enlarged, and as in *Anguidae* the middle region comprising the cavum conchale is small. In contrast to the *Anguidae* the lateral nasal gland is large and as in *Anniellidae* is located principally in the open conchal groove representing the anterior third of the concha. The concha of the *Chamaesaurinae* more nearly resembles that of *Lacerta*.

The palate and the ductus nasolacrimalis of the *Cordylidae* resembles that of *Lacerta*.

Résumé and discussion.

The general type of the nasal organ occurring in the Lacertilia fully supports the division of the order into the two subdivisions of Camp (1923): the Ascalabota comprising the Geckonidae, Iguanidae, Agamidae and Chamaeleontidae, and the Autarchoglossa comprising all the remaining families. The latter shew the ordinary Lacerta type of nasal organ, that of the Varanidae only exhibiting any important variations, and these are mainly a matter of relative proportion of the various structures.

The Geckonid nasal organ represents an intermediate type which, though showing an approach to the Ascalabota condition in several characters, is yet so similar to that of the Autarchoglossa, that, with respect to the nasal region alone, the Geckonidae would certainly have to be included in the latter subdivision. In the remaining Ascalabota a very different type of nasal organ is found. As a result of a shortening of the nasal region, the vestibule and its protective cupola anterior have become greatly elongated and have come to lie dorsal to the rest of the nasal cavities and the capsule (figs. 7 and 8). This condition has resulted in the prolongation of the postero-dorsal corner of the fenestra narina into a fissura lateralis nasi, and, in most cases, to the loss of the concha nasalis. As a further result of the reduction of the posterior part of the nasal capsule the foramen olfactorium is small (fig. 6) as in Chelonia and Crocodilia, and the foramen epiphaniale is often lost (fig. 24).

A cavum conchale is also absent in *Sphenodon*, but since it is represented in *Iguana* its loss must be due to parallel evolution. In addition to these secondary differences present in all the *Ascalabota* (with the exception of the *Geckonidae*) a number of primitive *Rhynchocephalian* characters occur in the *Iguanidae*, such as the prenasal process and the roofing cartilage of Jacobson's organ.

The capsule of Jacobson's organ.

In *Lacerta* the capsule of the organ of Jacobson is partly bony and partly cartilaginous. The anterior portion of the organ rests upon the lamina transversalis anterior, from which a conchal cartilage juts into the lumen of the organ. The floor behind the entrance of the duct is supported partly by the vomer and partly by the paraseptal cartilage. The side-wall is formed by the lamina transversalis anterior in the region where it fuses with the paranasal to complete the zona annularis. Dorsally the organ is protected by the septomaxillary, whose inner edge rests upon a ledge of the septum nasi. The anterior edge of the lamina transversalis is flexed dorsally to form a shallow cupular protection for the anterior wall of the organ. Posteriorly, at the level immediately behind that represented by fig. 44 the side-wall becomes detached from the paranasal and having fused with the paraseptal, forms a ring of cartilage around the vomeronasal nerve (cf. fig. 47). The same type of capsule occurs in all the other *Autarchoglossa*, but, except in the

Teiidae, the cartilage shows a greater degree of reduction in most families, so that the vomer and the septomaxillary play a more important role in the formation of the capsule (figs. 40, 52, 55 and 59).

Among the Ascalabota the capsule of Jacobson's organ of the Geckonidae and the Agamidae resembles that of the Autarchoglossa, but Microsauria (the only Chamaeleontid possessing the organ) and the Iguanidae (with the exception of Anolis) has apparently preserved the primitive Sphenodon capsular type, the latter being provided with a cartilaginous roof (figs. 9, 11 and 25). Sphenodon has always been regarded as the only reptile possessing this character (figs. 1-3), and Broom (1906) has considered its presence as an indication of Sphenodon's mammalian affinities. The presence of thin strips of cartilage underneath the septomaxillary of Teius (fig. 47) and the occurrence of a septal ledge upon which the inner edge of the septomaxillary rests in some of the Lacertidae, Gerrhosauridae etc. proves that a roofing cartilage was probably present in all primitive lizards. Its secondary disappearance in most recent forms is probably due to the fact that the septomaxillary has taken over the function of a protective covering for the organ. The presence in Chrysemys marginata of a well-marked ledge on the anterior part of the septum (already described by Shaner in 1920) and projecting into the medial fold tending to separate a medio-ventral pocket of sensory epithelium (organ of Jacobson?) from the rest of the ventral respiratory portion of the nasal cavity (Seydel,

1896) indicates that a roofing cartilage was probably present in the capsule of all primitive reptiles, as it is in the primitive Mammalia. It is generally conceded that the Chelonians are the most primitive living reptiles.

The Monotremes differ, however, from Sphenodon, the Iguanidae and Chrysemys in that the roofing cartilage is not fused to the septum, the organ being provided with its own cartilaginous medial wall (Wilson, 1894 and 1901 and Broom, 1897). In Ornithorhynchus the two capsules are secondarily fused together probably as a result of the presence of what was formerly known as the "dumbbell-shaped bone" (Parrington, 1940). In the Marsupialia, Dasypus, Tubulidentata, Chrysochloris and in a modified form in the Rodentia a rudimentary roof occurs in the form of an "outer bar of Jacobson's cartilage" connecting the anterior medial wall with the side-wall behind the duct of the organ (Broom, 1896 and 1906). The mammalian condition in which the organ is provided with its own medial wall, may be considered as primitive and serves to confirm de Beer's opinion of the origin of the paraseptal. (See below).

It is interesting to compare the Sphenodon-Iguanid condition with that of Anura in which the crista intermedia, covering the recessus medialis (the supposed anuran homologon of the organ of Jacobson), is also continuous with the septum nasi in the same position as the roofing cartilage in the reptilian capsule.

Another peculiarity occurring in the Jacobson's capsule of some Iguanidae and Teiidae, and one which has apparently been

overlooked in *Lacerta* itself, is the circumstance that the side-wall cartilage becomes fused to the paraseptal immediately behind the duct of the organ for a short distance (figs. 13, 16, 44 and 47). The "secondary palate" of Fuchs (1908) bridging the primitive choana is therefore supported by cartilage in these forms. In a number of lizards rudiments of a more complete posterior capsule occur in the form of a vertical flange on the paraseptal (fig. 33), or as nodules of cartilage which may be isolated or fused to the paraseptal (fig. 22).

The Septomaxillary.

The septomaxillary is primarily an investing bone of the vestibular wall (Lapage, 1928) and as such appears on the outer surface of the skull in forms with a short vestibule e.g. *Anura*, *Rhynchocephalia* (figs. 1 and 2) and *Dasypus* (Wegner, 1922 and Fuchs, 1911). In the *Lacertilia* the vestibule has enormously increased in size and has carried the septomaxillary with it into the interior of the nasal organ where it forms a secondary bony roof for the organ of Jacobson (e.g. fig. 35), and causes the degeneration of the primary cartilaginous roof in all lizards with the exception of the *Iguanidae*. It may even cover the nasal cavity itself when the vestibule reaches back beyond the organ of Jacobson (fig. 10).

Nasal muscles.

Bruner (1896-1901) discovered in *Urodeles* the three,

smooth nasal muscles regulating the opening and closing of the external nares. The actual cutaneous opening is much smaller than the fenestra narina, which accomodates in addition the muscular apparatus. The musculus constrictor naris surrounds the posterior semicircle of the external narial opening, both ends being inserted on the anterior wall of the fenestra narina i.e. on the cartilago cupolaris. The m.dilatator naris and the m. dilatator naris accessorius originate on the posterior and lateral walls of the fenestra narina respectively. Both pass directly forward and upward to insert on the posterior margin of the cutaneous wall of the narial opening, among the fibres of the m. constrictor naris (Francis, 1934).

The mm. lateralis and medialis nasi of Anurans are homologous to the mm. constrictor and dilatator naris of Urodela respectively, but as a result of a complete change in function, their relations to the capsular elements have altered considerably (Gaupp, 1904). The external naris of Anura is, moreover, so highly specialized that it is of little morphological value.

Bruner was the first to discover the smooth nasal muscles in the Crocodile and he homologised them with those of the Salamandridae (Lapage, 1928). The relations of the muscles in a 7.5 c.m. embryo of Alligator mississippiensis are essentially the same as those in Salamandra.

Leydig (1872) was the first to describe the tissue lining the nasal vestibule of Lacerta. According to him it consists of a "geschichtetes Pflasterepithel", is allied to the

outer epidermis and contains no glands. The cutis layer resembles cavernous tissue (Born, 1879). Hoffman (1881) records the cuticular tissue as consisting of fine elastic fibres between which occur bloodvessels and simple blood lacunae, but containing no muscular elements. Lapage (1928), however, describes it as "a tissue composed of smooth muscle fibres and blood sinuses in connective tissue."

The cavernous cutis of the vestibule of all Lacertilians investigated consists chiefly of spindle-like, clearly nucleated cells, resembling smooth muscle fibres in all particulars. The fibres originate on either the edge of the fenestra narina or on the inner surface of the cupolar cartilage, run directly outward at right angles to the cartilage, and then insert on the ectodermal epithelial layer lining the vestibule. Among these muscle fibres, sparsely distributed ordinary connective tissue cells and a large number of fibres occur. These latter are apparently elastic, because in material treated with van Gieson's solution, they are not stained by the Fuchsin for which collagen fibres have a strong affinity. In material treated with borax-carmin and azan the elongated cells are stained the same dull purplish-blue as muscle, while the fibres assume a dark-blue colour. The tissue is interspersed with large blood lacunae between which the cellular elements form columnar trabeculae. The entire vestibule which in the Iguania and Chamaeleontidae may reach back right into the antorbital chamber is lined with this cavernous tissue.

No muscle apart from this peculiar tissue has to my knowledge been described for the Lacertilia. The work of Bruner (1896-1901) was unfortunately not available, but Lapage (1928) who quotes extensively from it, mentions no such muscle, although in snakes she describes a smooth m. subnasalis occurring in addition to the cavernous tissue lining the short vestibule. A smooth nasal muscle comparable with the m. subnasalis will, however, be shown to be present in all Lacertilians.

For snakes Lapage maintains that this musculus subnasalis corresponds in form to the musculus dilatator naris of Urodeles, thereby implying that she considers the muscular tissue lining the vestibule as homologous to the m. constrictor naris. The same implication is contained in the following statement: " a tissue composed of smooth muscle fibres and blood sinuses in connective tissue, which may by increase of muscular tension and pressure of blood, produce a thickening of the margin of the naris and thus bring about its closure." This interpretation appears to me to be entirely erroneous. The smooth muscle fibres run in a direction at right angles to both the cutaneous wall of the vestibule and the inner surface of the cupular cartilage. Their contraction would therefore obviously tend to enlarge the lumen of the vestibule, partly by their own action and partly by forcing the blood out of the lacunae. Functionally at least this tissue is therefore comparable with the dilatator muscles of Urodeles. Topographically it also corresponds to the m. dilatator naris,

since the muscle fibres arise from the edge of the fenestra narina and the inner surface of the cupola, and insert on the cutaneous wall of the vestibule representing a greatly elongated narial opening. Closure of the narial opening would be effected by a decrease in tension in the fibres and a filling of the lacunae with blood.

If this interpretation is correct, the *m. subnasalis* of snakes must either represent a part of the *m. dilatator naris* which has not been invaded by blood lacunae, or it must be homologous with the *m. constrictor naris*.

In the snake *Homalosoma* the *m. subnasalis* was found to be absent, unless it is represented by a small bundle of fibres running upward from the postero-lateral process of the premaxillary to insert on the plica nasalis. In the *Leptotyphlopidae* the muscle is likewise absent.

Since Lapage (1926) does not describe the anatomical relations of the muscle in snakes it is difficult to form any opinion regarding its homology with the muscle mass composed of smooth fibres and not invaded by blood lacunae found to be present in the region of the external narial opening in lizards. In the South African Lacertid genus *Eremias* the muscle is typically developed (fig. 62). Its anterior head originates on the dorsal surface of the cupola anterior bordering the fenestra narina. There are two heads posteriorly; the fibres composing the dorsal one insert on the postero-dorsal border of the fenestra narina,

while those of the ventral head pass downward behind the cutaneous narial opening to insert partly on the cartilago alaris inferior and partly on the maxillary where this bone contributes towards the formation of a ventral border to the fenestra narina. It is obvious that a contraction of the fibres would tend to lift the cartilago alaris inferior and thus close the narial opening.

In some of the larger adult specimens, in which it was found necessary to remove the skin before sectioning, this somewhat superficially lying muscle was unfortunately damaged, but it was possible to demonstrate its presence in a great number of representative genera. The muscle is exceptionally well-developed in the Agamidae (fig. 20 and p.46) and shows slight variations in the Chamaeleontidae (fig. 61 and p. 53). In Varanus niloticus, strangely enough, it appears to be absent.

In Lacertilia, therefore, there occurs in the cutis surrounding the external nares a smooth muscle, all the fibres of which attach to skeletal elements as also does the m. constrictor naris of Urodeles. The contraction of the muscle will cause the closure or at least a narrowing of the narial opening by lifting the cartilago alaris inferior, drawing down the cartilago alaris superior (p.46) and pulling forward the hind wall of the cutaneous narial opening itself. In various lizards one or a combination of two or all of these factors appear sufficient to effect a complete closure of the external nares. (See also p.72). Functionally, as well as morphologically therefore this muscle is

homologous with the m.constrictor naris of Urodeles.

The opening and closing of the external nares in Lacertilians, therefore, appear to be effected as in Urodeles and Crocodiles by the action of a pair of antagonistic muscles, of which the dilatator has become cavernous.

Bruner (quoted by Francis, 1934) maintained that the narial muscles in Urodeles, arise in situ from the mesoderm and not from any other muscle. In embryos of *Mabuia* and *Microsaura* the muscles are differentiated in the cutis fairly late in the ontogeny. It was hoped that the innervation might help to throw light on their morphology but since the dermal muscles are not clearly defined from the surrounding connective tissue, it was found impossible to trace the nerve endings in material not specially stained.

True dermal muscles, represented in the human being solely by the tunica dartos, apparently do not originate from the myogenic layers of either the myotome or the splanchnotome. They should therefore originate from the cutis layer of the myotome which is thus myogenic as well as desmogenic. The so-called dermal facial muscles in man belong in reality to the facialis musculature and are therefore splanchnotomic. To my knowledge nothing is known of the histogenesis and the ontogeny of the nerves passing to the tunica dartos in man. The erectile tissue of the vertebrate phallus according to Tonutti (1932) has resulted from the excavation of the retractors and propulsors of the Gymnophione prophallus but the author does not seem to

be certain as to the myogenic strata from which these muscles derive.

The ectochoanal.

The ectochoanal in typical Lacertilia consists of a small cartilaginous process projecting back from the lamina transversalis anterior and serving as a support for the lateral edge of the anterior portion of the choana (fig.33) or the choanal groove (fig.44), and also for the anterior end of the morphological (fig. 35) or functional (fig.47) ductus nasolacrimalis. (See below).

Gaupp (1900) confirms for *Lacerta Seydel's* (1895) statement that the ectochoanal ("Gaumenfortsatz") of Urodeles represents the first step towards the formation of a functional secondary palate. Among lizards the ectochoanal largely contributes towards the formation of two entirely non-related types of secondary palate: that of *Anolis* (fig. 18) and that of the *Geckonidae* and *Xantusiidae* (figs. 32 and 37). It is interesting to compare them with the Monotremes in this respect: in these primitive mammals the ectochoanal is relatively simple compared with that of higher mammals but it bends inward behind the ductus nasopalatinus to fuse midventrally with its fellow of the opposite side, thus forming a cartilaginous secondary palate ventral to the paraseptals and the septum (Broom, 1897). In higher mammals the ectochoanal is represented by the cartilago palatina which (in the more specialized forms in combination with the cartilago ductus nasopalatini) forms a support for Stenson's duct (de Beer,

1939).

The Paraseptal.

The origin of the paraseptal has been interpreted in various ways: Parker described it as being derived from the trabecular cornu, as is also the lamina transversalis anterior. Seydel (1895) and Gaupp (1900) considered the paraseptal as representing a remaining part of the solum nasi which has secondarily lost its connexion with the septum. Gaupp pointed out that it is horizontally situated in the young stages of ontogeny (cf. fig. 3) and only later acquires the normal Lacertilian relations (fig. 44). In *Lacerta* the early ontogeny affords no further clue as to its derivation, since the paraseptal originates as a separate cartilage (de Beer, 1930). In his "The development of the Vertebrate Skull", however, de Beer advances the opinion that the paraseptal is a vestige of the medial capsular wall, proceeding from the Selachian and Urodelan condition in which the median wall is still distinct from the trabecular septum. The type of nasal capsule retaining a free paraseptal and a free lamina antorbitalis (as in *Lacertilia*) should therefore be looked upon as primitive. In *Teius* (fig. 47) and in some *Iguanidae* a small posterior part of the capsule of Jacobson's organ is provided with its own median wall. This is true of the entire capsule of monotremes.

In the lizards investigated the paraseptal is continuous in the *Iguanidae*, *Geckonidae*, *Xantusiidae* and *Lacerta* but in the other families it tends to be discontinuous.

This is probably a functional adaptation caused by the pumping action of the organ of Jacobson. In the great majority of lizards it is discontinuous in the region of the organ of Jacobson (figs. 22 and 40). In the Chamaeleontidae it is completely reduced except in the development of *Microsaura* (fig. 30), while the *Teiidae* and *Varanidae* are exceptions to the general rule in that the paraseptal is interrupted in its posterior half. In *Xantusia* the paraseptals are fused in the region of the organ of Jacobson (fig. 37).

Lateral paraseptal.

In addition to the ordinary paraseptal a second bar of cartilage, also entochoanal in position and likewise extending from the lamina transversalis anterior to the lamina antorbitalis, occurs in the *Iguanidae* (fig. 10). In the genera examined it is complete in *Sceloporus* only (fig. 5), whereas it consists of anterior and posterior rudiments in the others (fig. 16). Its relations to the lamina transversalis anterior and the primitive choana is described on page 27 .

The occurrence of this "additional paraseptal" is an indication that a much more extensive solum nasi, comparable to that of *Chelonia* formerly existed in the *Lacertilia* since it is difficult to see how it could have arisen secondarily. In the absence of any homologous element in other groups it is proposed to call the cartilage the lateral paraseptal but its coincidence with the lateral part of the true paraseptal is not necessarily implied.

In birds remnants of the paraseptal have been described in *Apteryx* (Parker, 1888). In *Crypturellus* two or three parallel and isolated struts of cartilage occur on either side of the septum (de Villiers, in manusc.). The more lateral of these may perhaps be homologous to the lateral paraseptal of *Iguanidae* but it seems more probable that they represent vestiges of the hind wall of a capsule of Jacobson's organ (cf. fig.22). Parallel work on the paraseptal entities in *Anas* is in progress (Swart).

The ductus nasolacrimalis and the "secondary palate".

The primitive Diapsid relations of the ductus nasolacrimalis in *Sphenodon*, have been variously altered in the *Lacertilia*, as a result of a varying degree of development of a "secondary palate" bridging the primitive choana behind the opening of the organ of Jacobson (Fuchs, 1908).

In the development of *Lacerta* the *Sphenodon* condition is actually recapitulated: the anlage of the ductus nasolacrimalis originates in a groove in front of the eye as a solid epithelial cord growing inward towards, and eventually fusing with a lateral pocket (Beecker's "Winkeltasche") in the lateral wall of the anterior end of the primitive choanal slit ("Choanenspalte") opposite the duct of Jacobson's organ (Born, 1879) (cf. figs. 31 and 32). It opens into the respiratory choanal passage ("Choanengang") i.e. between the "inner" and "outer" choana connecting the nasal cavity proper with the choanal passage and the latter in turn with the mouth cavity (Güppert, 1903).

In all adult lizards, however, a secondary palate formed by a fusion of the sides of the choanal passage separates the opening of the organ of Jacobson from the functional choana (Fuchs, 1908). Theoretically the fusion may take place at either of two levels in the choanal passage, those corresponding to Born's "inner" and "outer choana" (See text fig. 6 in Fuchs, 1908). According to Fuchs, however, fusion is usually effected at the upper level as in *Lacerta*, with the result that a choanal groove ("Choanenrinne") is formed between the functional choana and the organ of Jacobson. He further states that in *Teiidae* and *Varanidae* the sides of the entire choanal passage in front of the functional choana have fused together so that the choanal groove is completely obliterated with the exception of an anterior tubular rudiment through which the organ of Jacobson opens into the oral cavity. A duct - which Fuchs considers by implication to be the ductus nasolacrimalis - opens into this anterior rudiment near the organ of Jacobson.

A study of the palate of *Anolis sagrei* (p. 42) and a careful analysis of the palates of those Lacertilian families in which no choanal groove exists would seem to prove that the absence of a choanal groove is only apparent and that the anterior palatal end of the ductus nasolacrimalis lying in front of the choana is homologous to a choanal groove, transformed into a duct by the presence of both the upper and the lower "secondary palates."

In the *Iguanidae* and *Agamidae* the "secondary palate"

and consequently the choanal groove are extremely short, and according to Fuchs (1908) the primitive *Sphenodon* type of palate obtains unchanged in the Agamid *Uromastix*. Where a "secondary palate" is present the ductus nasolacrimalis has the same relation-s as in *Geckonidae*.

In the other families examined a choanal groove is typically present in the *Geckonidae*, *Scincidae*, *Lacertidae*, *Gerrhosauridae* and *Cordylidae*. These families exhibit two orthogenetic directions each of which approximately constitutes the primitive type for each of the two principal subdivisions into which Camp (1923) groups the *Lacertilia*.

In the *Geckonidae* (and the *Iguania*) the ductus nasolacrimalis runs parallel to the choanal groove and opens into its anterior end opposite the organ of Jacobson, (fig. 35, right side), as in *Sphenodon*. In the other four families mentioned above the anterior end of the ductus nasolacrimalis together with the anterior end of the choana is posteriorly displaced during the ontogeny, and in the adult the secretion from the Harderian and lacrimal glands is carried to the organ of Jacobson along an open gutter in the choanal groove (homologous to the "Winkeltasche" of Beecker). As Fuchs (1908) has noted, the "Winkeltasche" is absent in *Geckonidae*. From these two relatively primitive types of palate the more specialized condition in which a choanal groove appears to be lacking may be derived.

In the aberrant *Chamaeleontidae* the organ of Jacobson is either absent or rudimentary and the choanal groove is

consequently completely obliterated, the ductus nasolacrimalis thus directly opening into the choana.

The condition found in *Anolis* (figs. 17 & 19) is clearly derivable from the first type, since two parallel ducts occur in front of the functional choana: the one representing a true nasolacrimonal duct, and the other a transformed choanal groove.

In all the other families investigated (*Xantusiidae*, *Teiidae*, *Varanidae*, *Amphisbaenidae*, *Anguidae* and *Anniellidae*) there is one palatal duct only (figs. 47, 52 and 55). In the *Teiidae*, *Varanidae*, *Anguidae* and *Anniellidae* the ductus nasolacrimalis opens into the anterior end of the choana (figs. 53 and 57), and it is evident that this condition has been derived from the *Lacerta* type through the development of an additional secondary palate closing up the anterior part of the "outer choana" as well. The duct carrying the secretion of the Harderian and lacrimal glands from the choana to the organ of Jacobson therefore represents that part of the choanal groove which, even in *Lacerta*, is functionally a part of the ductus nasolacrimalis i.e. the "Winkeltasche".

In the *Xantusiidae* and *Amphisbaenidae* the nasolacrimonal duct does not open into the choana, but is continuous with the palatal part of the duct.

Taking their close relationship with the *Geckonidae* and the great similarity of the opening of the duct into the organ of Jacobson (fig. 35) into account, the *Xantusiidae* (in spite of

being classified under the Autarchoglossa) must be derived from the Geckonid type, and the anterior portion of the duct would therefore represent the anterior part of the true nasolacrimal duct. If the presence or absence of an opening of the ductus nasolacrimalis into the choana is to be taken as a criterion, the Amphisbaenidae must also be derived from the Geckonid-Iguanid type. Significant in this respect is the opinion of Gadow (1920) with respect to their affinity with the Xantusiidae. The opening may, however, have been closed-up secondarily, and in view of Camp's theory of their Autarchoglossid affinities, the problem cannot be settled without reference to the ontogeny.

In snakes the eye is situated above the large organ of Jacobson; the nasal cavity itself is reduced, and the choana lies far back. The ductus nasolacrimalis extends downward from the orbital region and reaches the level of the palate lateral to and in the immediate vicinity of the organ of Jacobson. Instead of passing straight to the organ, it runs backward in the direction of the choana for a short distance, then turns back and enters the duct of the organ from behind. Snakes, therefore, resemble the Xantusiidae and Amphisbaenidae in as much as their duct does not actually open into the choana. The unusual direction taken by the duct would seem to indicate a previous connexion, lost through the modified relations of the eye and nasal cavities. Unfortunately the embryos of *Leptodeira*, kindly donated to the department by Dr.G.T.Brock, were too old to show whether this connexion is recapitulated in the ontogeny.

In the absence of younger embryonic material it is therefore impossible to come to any conclusion with respect to the homology of the anterior end of the ductus nasolacrimalis of snakes.

The investigation of the nasal organ and ductus nasolacrimalis confirms Camp's classification of lizards into two main groups, the Geckonidae occupying a somewhat obscure possibly "parental" position. In the Ascalabote, the Agamidae and Chamaeleontidae represent offshoots from already specialized Iguanid stock. Among Iguanidae Iguana itself is to be considered as primitive chiefly on account of the retention of a concha.

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Legend to the figures.

- Fig. 1 : Sphenodon. Cross-section through anterior part of Jacobson's organ. (from Broom).
- Fig. 2 : " Cross-section through region of Jacobson's organ. (from Fuchs).
- Fig. 3 : " Cross-section through region of Jacobson's organ. (from Fuchs).
- Fig. 4 : " Cross-section through conchal region. (from Fuchs).
- Fig. 5 : Sceloporus. Ventral reconstruction of nasal capsule.
- Fig. 6 : " Dorsal reconstruction of nasal capsule.
- Fig. 7 : " Lateral reconstruction of nasal sac.
- Fig. 8 : " Lateral reconstruction of nasal capsule.
- Fig. 9 : " Cross-section through posterior part of organ of Jacobson.
- Fig. 10 : " Cross-section through middle of nasal region.
- Fig. 11 : Phrynosoma. Cross-section through nasal opening.
- Fig. 12 : Iguana. Cross-section through anterior end of choana.
- Fig. 13 : " Cross-section through conchal region.
- Fig. 14 : " Dorsal reconstruction of nasal capsule.
- Fig. 15 : " Lateral " " " " .
- Fig. 16 : " Ventral " " " " " .
- Fig. 17 : Anolis. Cross-section through posterior half of nasal region.
- Fig. 18 : " Ventral reconstruction of nasal capsule and palatal bones.
- Fig. 19 : " Lateral reconstruction of nasal sac.
- Fig. 20 : Agama. Cross-section through region anterior to Jacobson's organ.

- Fig.21 : Agama. Cross-section through anterior end of choana.
- Fig.22 : " Ventral reconstruction of nasal capsule.
- Fig.23 : " Lateral " " " " .
- Fig.24 : " Dorsal " " " " .
- Fig.25 : Microsaura. Cross-section through organ of Jacobson.
(adult)
- Fig.26 : " Dorsal reconstruction of nasal capsule.
- Fig.27 : " Lateral " " " " .
- Fig.28 : Microsaura. Dorsal " " " " .
(3.1 cm. embryo).
- Fig.29 : Microsaura. Ventral " " " " .
(adult)
- Fig.30 : Microsaura. Cross-section through Jacobson's organ.
(5.4 cm. embryo).
- Fig.31 : Microsaura. Cross-section through nasal region.
(1.5 cm. embryo).
- Fig.32 : Microsaura. Cross-section " " " " .
(2.5 cm. embryo).
- Fig.33 : Pachydactylus. Ventral reconstruction of nasal capsule.
- Fig.34 : " Lateral " " " " .
- Fig.35 : " Cross-section through organ of Jacobson.
- Fig.36 : " Cross-section " "ductus nasopharyngeus".
- Fig.37 : Xantusia. Ventral reconstruction of nasal capsule.
- Fig.38 : " Cross-section through "ductus nasopharyngeus".
- Fig.39 : Scelotes. Cross-section through conchal region.
- Fig.40 : Ablepharus. Cross-section through posterior part of organ of Jacobson.

- Fig.41 : Acontias. Cross-section through "ductus nasopharyngei"
- Fig.42 : Typhlosaurus. Cross-section " " " "
- Fig.43 : Ablepharus. Cross-section " " "ductus nasopharyngeus"
- Fig.44 : Lacerta. Cross-section through posterior end of organ of Jacobson.
- Fig.45 : Teius. Cross-section through region of premaxillary.
- Fig.46 : " Cross-section through organ of Jacobson.
- Fig.47 : " Cross-section through anterior conchal region.
- Fig.48 : Varanus. Ventral reconstruction of nasal capsule.
- Fig.49 : " Dorsal " " " " "
- Fig.50 : " Lateral " " " " sac and nasolacrimal duct.
- Fig.51 : " Lateral reconstruction of nasal capsule.
- Fig.52 : " Cross-section through region immediately posterior to organ of Jacobson.
- Fig.53 : " Cross-section through anterior end of choana.
- Fig.54 : " Cross-section through conchal region.
- Fig.55 : Ophisaurus. Cross-section through anterior conchal region.
- Fig.56 : " Cross-section through extracapsular part of intraconchal recess.
- Fig.57 : " Cross-section through middle of conchal region.
- Fig.58 : Anniella. Dorsal reconstruction of nasal capsule.

- Fig.59 : Anniella. Cross-section through organ of Jacobson.
- Fig.60 : " Cross-section through conchal region.
- Fig.61 : Microsaura. Lateral reconstruction of fenestra narina
and narial muscle.
- Fig.62 : Eremias. Lateral " " " "
and narial muscle.

Abbreviations used in figures.

ac	: aditus conchae.
acp	: anterior conchal process.
apc	: anlage of parietotectal cartilage.
archg	: anterior rudiment of the choanal groove.
c	: concha nasalis.
ca	: cupola anterior.
cant	: cavum antorbitale.
cc	: cavum conchale.
ce	: cartilago ectochoanalis.
cec	: cavum extraconchale.
chd	: choanal duct.
chg	: choanal groove.
chodnl	: choanal opening of nasolacrimal duct.
cjo	: concha of Jacobson's organ.
co	: choanal opening.
cp	: planum antorbitale.
cpn	: paranasal cartilage.
cs	: cartilago sphenethmoidalis.
df	: dorsal fenestra in roofing cartilage.
dgl	: duct of lateral nasal gland.
dgpm	: dorsal groove for premaxillary.
dnl	: ductus nasolacrimalis.
dnl d	: dorsal division of ductus nasolacrimalis.
dnl v	: ventral " " " " .
dnph	: ductus nasopharyngeus.

drza	: dorsal rudiment of zona annularis.
ecric	: extracapsular part of recessus intraconchalis.
f	: frontal.
fa	: foramen apicale.
fe	: foramen epiphaniale.
fl	: fissura lateralis nasi.
fln	: fenestra lateralis nasi.
fn	: fenestra narina.
f.n.v.	: fenestra for nervus vomeronasalis.
f.ol.	: fenestra olfactoria.
f.or.	: fissura orbitonasalis.
f.r.m.	: foramen for ramus medialis.
fsn	: fenestra superior nasi.
gdl	: glandula nasalis lateralis.
grec	: groove for recessus extracapsularis.
Hg	: Harderian gland.
ic	: inner choana.
jc	: capsule of Jacobson's organ.
jd	: duct of Jacobson's organ.
jo	: organ of Jacobson.
l	: lacrimal.
ll	: lower eyelid.
lp	: lateral paraseptal.
lsp	: lower secondary palate.

lta	: lamina transversalis anterior.
m	: maxillary.
n	: nasal.
ne	: true nasal cavity.
nlg	: "nasolacrimal groove".
nm	: narial muscle.
no	: narial opening.
n.olf.	: nervus olfactorius.
oc	: outer choana.
ocav	: oral cavity.
odnl	: opening of ductus nasolacrimalis.
ojd	: opening of Jacobson's duct.
orbnc	: orbitonasal canal.
ordnl	: orbital rudiment of nasolacrimal duct.
p	: paraseptal.
pai	: processus alaris inferior.
pal	: palatine.
pas	: processus alaris superior.
pc	: parietotectal cartilage.
pca	: processus cupolaris anterior.
pch	: primitive choana (Fuchs).
pf	: prefrontal.
pm	: premaxillary.
pna	: processus maxillaris anterior.
pnp	: processus maxillaris posterior.

png	: primitive nasal groove.
pp	: prenasal process.
pr	: paraseptal rudiment.
prjd	: posterior recess of Jacobson's duct.
pss	: planum supraseptale.
pt	: pterygoid.
rc	: roofing cartilage.
rec	: recessus extracapsularis.
r.ethm.5	: ramus ethmoidalis of 5.
ric	: recessus intraconchale.
r.lat.	: ramus lateralis.
r.med.	: ramus medialis.
r.olf.	: ramus olfactorius.
rva	: anterior vestibular recess.
r.v.n.	: ramus vomeronasalis.
rvv	: ventral vestibular recess.
sc	: sclera.
sic	: interorbital septum.
sm	: septomaxillary.
sn	: septum nasi.
so	: supraorbitals .
sp	: secondary palate (Fuchs).
swjc	: side wall of Jacobson's organ.
t	: tongue.
tr	: transversum.

ul : upper eyelid.
usp : upper secondary palate.
v : vomer.
ves : vestibule.
za : zona annularis.
x : artefact.