Contributions

to the

Comparative Anatomy

of

Jacobson's Organ.

Being a Thesis presented to Senate of the University of Glasgow for the Degree of M.D.

By

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Preface.

While an undergraduate at college I became deeply interested, among other questions of anatomical importance, in the development of teeth and did a considerable amount of work with the view of possibly making this the subject of a graduation thesis. For a year or two after graduating, however, I had little or no opportunity of prosecuting my researches and it was only about a year ago ~~that~~ I was again enabled to continue my previous work. My original plan had been to prepare a treatise on the development and morphology of teeth, dealing largely with the mammalian organs and studying the question both ontogenetically and phylogenetically. I found however that the work was too great to enable me, with the time and material at my disposal, to do it as I thought justice, and so resolved on taking up some more practicable subject. In my transverse sections of foetal jaws I had often noticed the Organ of Jacobson and the scanty notices of it in our text books had led me to think that much remained to be done with regard to its Comparative Anatomy. While in a state of indecision I received through the kindness of Dr Hardcastle a copy of Prof. Symington's recent paper on the nose and organ of Jacobson in the Ornithorhynchus. My interest in the subject was at once rekindled and I resolved to make a careful study of the comparative anatomy of the organ in all the forms I could come across. The outcome of this research is the present thesis. Even with the subject of Jacobson's Organ however I have had to some extent the same difficulty that beset me in my study of the teeth — the inexhaustibleness of the work. Every new discovery, rather than bringing one nearer a conclusion seems but to open up fresh avenues for research. Still though the present thesis is little more than a preliminary study I have endeavoured to make it as complete as time and opportunity would permit, and as it contains a very large number of new facts, many of which lead up to conclusions of prime importance I think it well to present it in its present form leaving the account of further researches in the same line to a future occasion.

The line I have chiefly followed has been the study of the anatomical relations of the organ in the various forms of Reptiles and Mammals I had an opportunity of examining, and notwithstanding the numerous papers that have been published in recent times in connection with the organ the ground I have traversed has been very largely unexplored territory. Herzfeld in fact is the only author so far as I am aware who has made any comparative study of the organ. He has endeavoured to classify a number of the most typical mammals according to the condition of Jacobson's organ and Stenson's duct, and though he has as I endeavour to show fallen into some errors through over estimating the importance of certain facts and through having a very limited number of facts at his disposal, his paper is one of the most valuable contributions that have been made on the subject. To some extent my work among mammals is a revision and enlargement of his, and though I have based my classification on different lines my groups have been foreshadowed by Herzfeld.

Among the lizards and snakes I believe the present is the first attempt that has been made to deal with the comparative anatomy of the organ, and though my opportunities have been limited my work will probably be of some service as a preliminary to a more complete treatise on the subject

My best thanks are due to Prof. Wilson of Sydney for his kindness in allowing me the use of books from the Sydney University Library and for valuable assistance with the bibliography, to Mr Hamilton of Mount Kembla for the specimen of Perameles examined, and to my father Mr John Broom of Edinburgh who has spared no pains in abstracting and copying for me scientific papers I could not otherwise have had an opportunity of seeing.

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Introductory and Historical

As in Australia ones opportunities of studying the ancient literature of a subject are very limited and as some of the recent writers have entered into this point at sufficient length I will only briefly refer to the previous work that has been done in the study of Jacobson's Organ.

The organ was first discovered by Jacobson[25]* who communicated a paper on the subject to the French Academy entitled :- "Description anatomique d'un organe observé dans les Mammifères", and of which Cuvier rendered a report which appears in the Annales du Muséum d'histoire naturelle for 1811. Jacobson examined the organ in different forms and recognised that it is well developed in herbivorous animals, less so in carnivorous and but feebly developed in monkeys. Rathke[46] studied the development of the organ and considered that it arises as a diverticulum of the olfactory mucous membrane, a view which has since been abundantly confirmed. The next important work on the subject appeared in 1845, written by Gratiolet[17] (Recherches sur l'organe de Jacobson, Paris 1845) who appears to have studied the morphology and development of the organ in some detail. Unfortunately

* The figures after the authors names refer to the Bibliography.

I am only acquainted with his work through references in later authors. In 1860 Balogh[1] published his important paper (Das Jacobson'sche Organ des Schafes) in which he a very full account of the condition of the organ in the sheep entering into a description of both the anatomical relations and of the histological details. Within recent times numerous papers have been published dealing with various aspects of the subject. Born,[5-7] Fleischer[3] and Beard[21] have thoroughly studied its development especially among reptiles. Born[5-7] has published a series of lengthy papers on the nasal region in the higher vertebrates (Die Nasenhöhlen und der Thränennasengang der amnioten Wirbelthiere.) and in these he has besides discussing the development of the organ also examined its relations to the nasal cavities, to the lacrymal ducts and to the mouth. Though he has however examined the organ in the chief types of lizards he has neither figured the various conditions nor has he undertaken any comparative study. Fleisher[3] appears to have done some work to the comparative anatomy of the organ, but unfortunately (according to Beard) only a preliminary notice of his work has ever appeared.

In 1881 and /82 Klein[26-29] published four important papers giving a full description of the organ and more specially of its minute anatomy, in the Guinea Pig, Rabbit and Dog. The next important contributions to the subject appeared in 1889 in the same volume (Zoolog. Jahrb. III Bd.) including a paper by Beard[21] on the development of the organ in the Snake and a most valuable one by Herzfeld.[20] This latter author enters into a comparative examination of the mammalian organ and of the condition of Stenson's duct and classifies some of the chief mammalian types according to the various conditions presented. As Herzfeld's paper deals with the subject on somewhat similar lines to those followed in the present thesis, in one chapter I have entered into a discussion of it at some length.

Most of the other recent papers either deal with the condition of the organ in some special type or with its development, histological details or nervous connections

As a result of the various investigations it is now established that Jacobson's Organ is a highly specialized portion of the Nasal Mucous membrane and supplied like it by branches of the Olfactory and Trigeminal nerves.

Though found in the Urodela and also in the Gymnophiona it is in the higher groups that the

organ attains its greatest development. Being a sort of accessory olfactory organ it is generally most developed where the nasal cavity is simplest, and where the nasal organ is complex, the organ of Jacobson is usually rudimentary or absent. In the Reptilia it is highly developed among Snakes and Lizards, while among Turtles and Crocodiles it is typically absent, though in some forms of the latter a rudimentary organ appears to exist. In Birds hitherto no trace of a Jacobson's organ has ever been detected, though it is not improbable that such may yet be discovered, as in some forms septo maxillaries and cartilages resembling mammalian "recurrent cartilages" are found to occur — structures intimately associated with Jacobson's Organ.
In the Mammalia the organ is present in most typical forms, though its degree of development varies very greatly. As a rule it is best developed in the more primitive groups, and is generally much better developed in small species than in large.

In the present treatise I have endeavoured to make a comparative study of the organ and its relations in the groups in which it is best developed — Lizards, Snakes and Mammals in each case taking typical forms. Among Mammals I have entered more deeply into the detailed Examination of the organ in certain Groups, noticing the differences in closely allied genera and Species, while in the concluding chapter I have endeavoured to estimate the significance of the varying conditions

The Lacertilian Organ of Jacobson.

In the lizard the organ seems to attain its greatest degree of development.

The researches of Born[5], Beard[21] and others have shown that it is formed by an early outgrowth from the nasal cavity. This becomes more and more detached till ultimately it is completely partitioned off, and what was originally the large opening connecting it with the nasal cavity becomes reduced to form its duct and opens into the mouth.

From the floor of the primitive organ there arises an ingrowth or turbinal process invaginating the lower wall of the organ, and which though varying in different forms in its position is in all supported by a development of the cartilage of the trabecular horn. This latter is itself supported by the bone usually called "Vomer" but which I have elsewhere[8] shown might more appropriately be called "Prevomer". The chief other part of the skeletal framework of the organ is the Septomaxillary which forms the support of the partition between the organ and the nasal cavity. Though I have only examined a limited number of Lacertilian types, in these I have always found the nasal septum well developed and forming a part at least of the inner wall of the organ.

On the Organ of Jacobson in the Varanidæ

Type:– Varanus Gouldii Gray

In considering the comparative development of the organ among lizards it is most convenient to study in the first place its condition in this highly developed type, and taking it as the Lacertilian standard to contrast the other forms with it.

Born[3] briefly refers to the organ in Monitor albogularis Gray, and gives a figure of a longitudinal vertical section of the head showing roughly its position, but as the section is ~~not~~ for microscopical examination but mainly to show the condition of the nasal cavity, the details of the structure of Jacobson's organ are not well displayed.

I have studied the organ, as in most of the specimens I have examined, chiefly by means of a series of transverse vertical sections. By this means not only can the relation of parts be most satisfactorily made out but the uniformity enables one to notice even little peculiarities of relationship.

If a transverse vertical section be made immediately in front of Jacobson's Organ the following condition will be found. The nasal septum proper (see Plate I fig 1. S.N.) is short, the lower part being lost in the two very large lateral cartilaginous projections which form a large part of the framework of the organ and may be referred to as Jacobson's cartilage (J.C). At this plane the cartilage forms the anterior wall of the organ. Immediately above the cartilage and resting on it is the anterior part of the Septo-maxillary (Smx). Below the cartilages are the two Prevomers (P.Vo.) roughly triangular in section; while the Maxillary (Mx) is but slightly removed from the outer side of each cartilage. Below the outer angle of the Prevomer the oral epithelium is seen dipping in — this is the anterior opening of the Lacrymal and Jacobson's ducts.

Immediately behind this plane Jacobson's cartilage is found to be hollowed out by the anterior part of the organ, which separates the cartilage from the Septomaxillary and reduces it to the shape of a curved bar lying close against the Prevomer and curving round to meet the Septomaxillary.

A very short distance posteriorly (Plate I fig 2) the nasal septum (SN) is found fairly well developed and at its lower angles it is continued into the narrow curved plate of cartilage which forms the floor of this part of the organ. This cartilaginous plate on passing outward becomes greatly thickened and curving upward fits into the outer end of the Septomaxillary, which curves downwards to meet it. Between Jacobson's Cartilage and the Septomaxillary is an irregular ~~round~~ space in which lies the anterior part of Jacobson's Organ (J.O.). At the outer angle of the Prevomer the dipping in of the oral mucous membrane seen in fig 1, is here found leading upwards to an open duct (J.D.) ~~this is~~ the duct of Jacobson's organ in its forward course; and on its inner side it is found connected with another duct – the anterior part of the lacrymal duct. At this plane from the disposition of the mucous membrane of Jacobson's organ it is seen that the turbinal reaches practically to the front of the organ.

A little behind this plane, from the floor cartilage is seen passing into the greatly enlarged turbinal a very considerable cartilaginous projection; and at the outer part of the cartilaginous floor there is found a large downward development.

A few sections posteriorly the organ is found considerably enlarged and roughly crescentic in shape (Plate II). The mucous membrane is very thick on the upper and inner sides though comparatively thin around the turbinal process. The turbinal is here found supported not only by the process of of Jacobson's cartilage but also by a bony plate (T.Pv.) derived from the Prevomer. The inner part of Jacobson's cartilage which is connected with the nasal septum and rests on the Prevomer is here found detached from the outer mass of cartilage, and by the gap thus left the Prevomer sends up its supporting process to the turbinal. Later sections show that the bony plate forms a support round the inner and posterior sides of the turbinal. The outer mass of Jacobson's cartilage which was in previous sections seen much enlarged is here found still further altered. It is being divided by a downward extension of the cavity of the organ into an inner and an outer part. In succeeding sections the inner part of the divided outer mass is seen to become part of the framework of the greatly enlarged turbinal while the outer part (z y) becomes again divided into an upper part (z) which resting against the inner end of the Maxillary and the outer end of the Septo-maxillary forms part of the outer wall of the organ, and a lower part (y) which at first lying near the lower and inner angle of the maxillary is found to pass under the outer process of the Prevomer near the hinder part of the organ.

A little behind this plane the cavity

of the organ is found curving round the process and opening into the duct, so that the turbinal process is only connected with the wall by a narrow bridge of tissue on the lower and inner side supported by the process of the Prevomer which here passes right up and connects with the bony plate of the turbinal.

Almost immediately behind this the section reveals the turbinal quite detached from the walls and surrounded by the cavity of Jacobson's Organ (Plate III)

Behind this there is comparatively little alteration in the structure of the walls. Towards its posterior part the organ is walled in its whole upper half by the slender curved Septomaxillary. Externally it is supported by the detached portion of Jacobson's cartilage (Z) which becomes wedged between the Septo-maxillary and the Maxillary and by the inner process of the latter bone. Inferiorly the organ is supported by the Prevomer; and internally by the nasal septum and by the downward and lateral process extending from it. This inner portion of Jacobson's cartilage which rests on the Prevomer is at the anterior part of the organ attached to the base of the nasal septum but on passing backwards like the "Recurrent Cartilage" in the Mammal becomes detached, and at the posterior part of the organ they become considerably developed and passing outwards form part of the posterior wall of the organ (J.O.' Plate IV)

When the sections are considered together and in conjunction with a series of longitudinal vertical sections it is found that the organ is roughly spherical in shape with the anterior and inferior quarter occupied by the base of the turbinal process. The organ is connected with its duct by two openings, the one towards the middle of the lower part - the duct proper (J.D.), the other (J.D.') more external and on a lower level and opening into the duct proper near its union with the lacrymal duct. Instead of passing backward as figured by Wiedersheim (Grundriss der Vergleich. Anat.) in a "Lizard" the duct passes forwards and uniting on its inner side with the lacrymal duct the two discharge by a common opening.

Plate I. fig 1 fig 2 Plate II Plate III — Transverse vertical sections of the ~~Organ~~ of a small Varanus

Plate IV. — Longitudinal vertical section through Jacobson's organ in young Varanus.

On the Organ of Jacobson in the Agamidae
Type – Amphibolurus muricatus White.

In the Agamidae we find on the whole a simpler type of organ than in the Varanidae but though less developed it bears considerable resemblance to the more specialised form already described.

A transverse vertical section a little in front of the plane of Jacobsons organ shows the nasal septum at its base dividing into the two lateral cartilages as in Varanus. In this plane is to be seen the oral mucous membrane dipping up and dividing into an outer branch which passes up past the outer edge of the Prevomer and forming the anterior part of Jacobsons duct, and a branch which passes inwards below the Prevomer – the lacrymal duct.

In this group the anterior part of the organ excavates the cartilage becoming roofed by the upper part of it instead of directly by the Septomaxillary as in Varanus and in the other types to be described.

A little further back Jacobson's cartilage is found divided into an outer and an inner part – the outer forming the outer wall of the organ and the greater part of the floor. The organ is here roofed for the most part by the rather slender Septomaxillary. Inferiorly, the upper part of Jacobsons duct is formed passing inwards above the Prevomer and to be widely dilated and covered with typical Jacobson's organ mucous membrane. It is infact seen connected with the anterior projection of the lower part of the organ.

Immediately behind this the portion of cartilage which infront formed the floor of the organ becomes a transverse turbinal dividing the organ into an upper and a lower part as seen in Plate VI. The part of the organ previously seen attached to the duct is here seen continuous with the upper part of the organ.

Towards the posterior part of the organ it is again simple owing to the absence of the turbinal process. It is still roofed by the septo maxillary. On the floor there is found a cartilaginous projection passing from the outer part of Jacobson's Cartilage and meeting the outer part of the Prevomer.

The most important differences of the Organ from the previous type are the turbinal springing from the outer wall and dividing the organ into an upper and lower part, and the direct and wide opening of the organ into its duct on the inner and under side of the turbinal.

Born[1] in his work in this group took the Draco as his chief type, and gives a rather rough figure of a section through the organ of Jacobson (Taf. VIII, Fig 12) but which is sufficient to show that the organ in Draco is practically identical with that in the form I have described. In referring to the organ he says:— "Der Wulst, welcher bisher [Lacertidæ, Scincidæ und Geckonidæ(!)] immer am Boden des Jacobson'schen Organs gefunden wurde, ist hier an die laterale Wand gerückt und springt horizontal nach innen vor." He thus seems to consider the type of the Scincidæ and of the common Lizard the normal type whereas I regard it as an aberrant type.

The figures in Plate V. are of a rare North Queensland Agama, Diporophora australis Gray. As regards the organ itself there is practically no difference from the typical form, but the form is worthy of note from the Prevomers being unchylosed.

On the Organ of Jacobson in the Geckonidae.

Type:- Gehyra australis, Gray.

In the Gecko we have a type of organ which bears a very marked resemblance to that of the previous group.

A transverse section immediately in front of Jacobson's organ shows a moderately well developed Nasal Septum supported on either side in its lower part by the inner parts of the Septomaxillaries. The lateral masses forming Jacobson's cartilages are well developed and are overlaid by the Septomaxillaries. The anterior part of the organ passes between the cartilage and the Septomaxillary as in Varanus.

A section across the anterior part of the organ shows the following conditions. The organ is crescentic in shape, roofed above by the horizontal flattened septomaxillary, and walled externally by an upward process of Jacobson's cartilage. It is floored by the cartilage, the outer part of which forms an imperfect turbinal. At the outer end of the Prevomer Jacobson's duct is seen passing upwards.

Passing a little backwards the turbinal becomes much more marked, the organ curving round between it and the Prevomer to open into its duct.

Immediately behind this the organ is almost circular with the turbinal now rather delicate passing inwards from the outer side.

Towards the posterior of the organ the turbinal is absent. Here the organ is floored by the Prevomer chiefly and walled at its outer side by the outer part of Jacobson's cartilage, now simple.

On the Organ of Jacobson in the Scincidae

Type - Lygosoma lesueurii D. & B.

In the Scink we find a different type of Organ from that present in any of the previously examined groups, and though in its relationships there are many points of resemblance, it is the dissimilarity that chiefly strikes one. As already stated Born[(8)] considers this the normal type, but though it appears to be also the type in the Lacertidae, as it differs from that of the Varanidae, Geckonidae, Agamidae and of the various Snakes I have examined I think it is better to regard it as an abnormal type.

In the previous forms, in front of Jacobson's organ the nasal septum has been noticed to be very short; here it is present as a well developed flat vertical plate extending almost the whole depth of the skull.

In front of the organ, at its lower part it is found giving rise as in the previous types to two lateral cartilaginous developments, but these are much smaller than in the other forms examined. These lateral cartilages rest on the anchylosed Prevomers, and are covered by the well developed Septomaxillaries which here at their inner end extend upwards against the Nasal septum for about half of its extent (Pl VIII f. 1)

A section immediately in front of the organ shows the nasal septum at its base continued into two delicate curved plates which passing outwards become continuous with the alinasals – a character not found in the previous types. The Septomaxillary passes horizontally outwards from its vertical plate which abuts on the Nasal Septum, and curving downwards is fixed by a flattened base to the outer part of the flattened Jacobson's Cartilage.

Between the flattened floor cartilage and the curved Septomaxillary passes the anterior part of Jacobson's organ which here is quite devoid of a turbinal.

On passing a little backwards there is found passing into the organ from the inner side of the cartilaginous floor a very thick turbinal (Plate IX). Unlike the previous types this turbinal is supported almost entirely by that portion of the cartilaginous floor which rests on the Prevomer

A little distance behind this plane the organ is found opening into its duct (Plate VIII fig 2 J.D.). It is here the greatest peculiarity of this form is seen. In the previous forms the turbinal was found chiefly attached to the outer part of Jacobson's cartilage and the organ opening with its duct round the inner side of the turbinal, though in Varanus the duct opens into the lower and back part of the organ. Here we find the organ connected with its duct chiefly round the outer side of this turbinal though also at its posterior part. The organ in the Scink has therefore ~~much~~ more in common with that of Varanus than of either the Gecko or Agama.

The Ophidian Organ of Jacobson.

In the Snake the organ of Jacobson and its relations have been perhaps more studied than in any other group. Rathke,[46] Leydig,[36] Born[7] Wright[60] and Beard[2] have all contributed to the study of the organ as found in the Snake, while Parker[41] in his monograph on the Skull of the Snake has examined in detail the developments and structure of the supporting bones.

All the above mentioned authors have studied either solely or chiefly the common Snake (Tropidonotus natrix L); my researches have been on Australian Snakes alone and which belonging to different groups from the Common Snake will render my figures the more interesting for comparison.

The forms I have studied represent two genera of the Elapidae – Diemenia and Hoplocephalus and of the Typhlopidae a species of Typhlops itself. As however the two genera of Elapidae are closely allied I will only describe the organ in the one and use the other for comparison.

Notwithstanding the remarkable degree of specialisation met with in Typhlops the organ and its related structures differ but very little from the normal Ophidian type. The little degree of variation found in the organ in related forms no matter what be the different degrees of their specialisation illustrates as will be further shown the value of the organ as a factor in classification.

Of the Ophidian organ itself the chief characteristic is the peculiar grouping together of the rows of ganglionic cells into bundles — a feature so far as I am aware only present in snakes. The framework of the organ is characterised by the great development of the bony structures, and a corresponding reduction of the cartilages.

In front the lateral cartilages are quite rudimentary or absent; while in the region of Jacobson's organ the only portion of Jacobson's cartilage remaining is the plate which forms the chief framework of the well marked turbinal. Prevomer and Septomaxillary are highly developed and form usually between them the whole framework of the organ. Inferiorly the arrangement of ducts is very similar to that seen in Varanus.

On the Organ of Jacobson in the Elapidae
Type :- Denisonia superciliosa Fisch.

A section across the head of this form a little in front of Jacobson's organ shows a very small and short median nasal septum detached from the alinasals. The nasals send down, two plates close to each other forming a septum between the two nasal cavities and reaching at their lower ends the top of the rudimentary cartilaginous septum. By either side of the septum proper are greatly developed Septomaxillaries which curve outwards and form floors to the nasal cavities. On the inner side of each Septomaxillary below the nasal septum is the Prevomer - at this part rather small. Between the outer part of the Prevomer and the Septomaxillary is a small cartilaginous bar cut across - this is the rudimentary representative of the well developed lateral cartilaginous masses in the Lizards. In Hoplocephalus Ramsayi Krefft this lateral cartilage though still small is much better developed

In a section passing through the anterior part of Jacobsons Organ the Prevomer is seen separated from the Septomaxillary, not as in lizards by the separation of the one from the other directly, but by the great expansion of the Prevomer which is now found composed of a deep vertical plate and a horizontal one. In addition to this in Hoplocephalus there is an inward projection from the Septomaxillary towards the outer end of the Prevomer. On this plane also in Dicmenia the inner part of the Septomaxillary becomes greatly enlarged and constricted off from the outer part. In all sections further back this inner part of the Septomaxillary (Smx' in Plates X and XI) is found quite distinct from the outer part, and takes no part in the wall of Jacobsons organ. Between the outer part of the Prevomer and the Septomaxillary the rudiment of Jacobsons cartilage is seen on this plane much enlarged.

Plate X illustrates a section through the middle of the organ ~~showing its~~ near connection with the duct. It will be as well to consider it along with Plate XI which shows an almost corresponding section of Hoplocephalus. In Plate XI the mode of opening into the duct is shown, and it is seen that the duct is here also joined by the Lachrymal duct (L.D.) as in Varanus. The large turbinal is seen supported by a development of Jacobsons cartilage and also in Plate XI by a process of the Prevomer. This also exists in Dicmenia though the section figured does not show it. Superiorly the section from Hoplocephalus shows the nature of the wall, which is composed on the inner half of the upper part of the Prevomer, and in the outer half by the outer part of the Septomaxillary. In Diemenia the condition is very similar but becomes obscured by the Prevomer anchylosing above with the inner end of the outer part of the Septo-maxillary. Near the union of the two bones the roof is perforated for the passage of the nerves passing to the organ.

In both Genera the grouping of the rows of ganglionic cells is well marked. In Diemenia there is a very marked layer of pigment cells round the bases of the groups and passing slightly between them. In Hoplocephalus the ~~groups~~ groups of cells are more distinct and the pigment cells

On the Organ of Jacobson in the Typhlopidae
Type:- Typhlops Rupelli, Jan.

In Typhlops the organ is much more largely developed relatively than in ordinary snakes – most probably a provision of Nature to compensate for the deficiency of the sense of sight.

The cartilaginous nasal septum is rather better developed than in the ordinary type; while the Septo-maxillary attains a greater development than in any other form I have examined. In the anterior part of Jacobson's organ 4/5 of the wall is formed by the Septomaxillary, the only free part being where the organ on its inner side rests on the nasal septum. Below the inner part of the under plate of the Septomaxillary is seen the feeble Prevomer.

Plate XII represents a section near the middle of the organ. Even here the Septomaxillary forms fully half of the wall of the organ. On the underside the feeble Prevomer is seen divided as in the ordinary type of snake by Jacobson's duct. The turbinal is similar in structure to that the Elapidae, the framework being a process of the slightly developed Jacobson's Cartilage with the support of the Prevomerine process.

In other respects the organ resembles

the organ resembles that of the normal snake
The ganglionic rows are bunched together though
not so distinctly.

The duct connect with the organ on the inner
and posterior side and passes downwards and slightly
backwards.

A comparison of the Lacertilian + Ophidian Organs.

In comparing the organs in the two types the it will be noticed that organ of the Snake bears a very marked resemblance to that of certain lizards — especially Varanus. In both we have the turbinal constructed on exactly the same type — a process passing into the organ from the anterior and under side and supported by Jacobson's Cartilage together with a process of the Prevomer. That this condition should be common to Varanus and Snakes, and absent from most other lizards is remarkable, and lends much weight to the view that Lizards and Snakes belong to the one order.

The Agamidae and Geckonidae show the organ in its simplest condition, and it is clear that the two groups are moderately closely allied.

The Scincidae present a peculiar and aberrant type of organ — more highly developed and formed on different lines from the organ of the Gecko or of the Monitor.

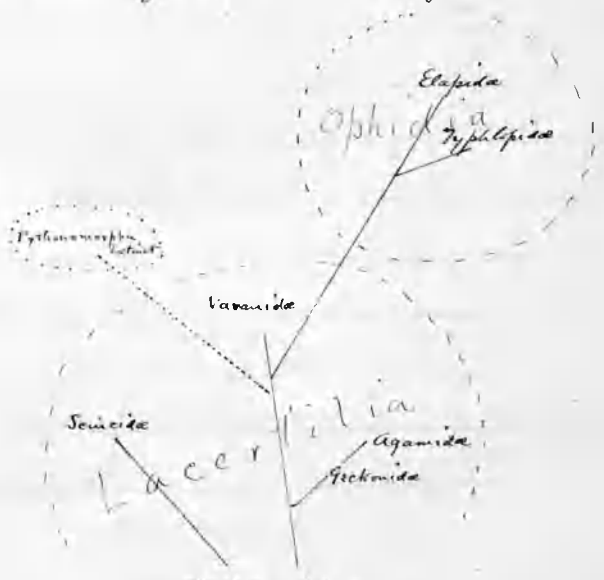
In the Varanus we have a type which is also highly developed but not so widely removed from the Gecko-type.

In Elapidae the framework of the organ is essentially Varanidean, but the organ is more highly developed in its intimate structure.

Typhlops though having an organ resembling that in the Elapidae, in the relations of the turbinal is a little nearer the Varanus type.

The adjoining table will roughly indicate what I consider the mutual relationships of the groups from the study of the Organ of Jacobson.

Evolution of Typical Groups of Squamata.



The Mammalian Organ of Jacobson.

In passing from the Reptilian to the Mammalian organ we at once note a complete change of type. Though the Mammal is much more highly organised as regards its viscera than the Reptile, as regards its skeleton it must be admitted that it is of a much more primitive form. Instead of the elaborate cup and ball vertebral joints the Mammal has but a series of simple padded bony blocks — instead of a lower jaw built up of a number of pieces, it has but a single bone which instead of articulating with a quadrate bone hinges on a little pad of cartilage. While instead of the brain being guarded by a series of bony arches formed by processes of the parietals post frontals, squamosals & occipitals, in the Mammal it is protected by but a single plate of bone. This same simplification is met with in the anterior nasal region, and we find the septomaxillary which played such an important part in connection with the Reptilian Organ of Jacobson quite absent. With this exception representatives of all the other structures in connection with the organ can be made out. As by way of compensation however there is present in the Mammal a secondary palate formed by the ingrowth of the Maxillaries and Palatines, a feature which though present in the Crocodile is absent or only rudimentary in the Squamata. This palate carries the nasal cavities far back and removes their posterior nares from direct connection with the mouth. Anteriorly however there is a small passage between the nasal cavity and the mouth by the duct known as Stensons' duct or the Naso-palatine Canal.

Jacobson's organ in the Mammal as in the Lizard lies by the side of the nasal septum and opens downwards towards the mouth, though instead of opening directly into it as in the Lizard it usually opens into Stenson's duct which is however the homologue of the anterior part of the Lacertilian palate. In the Lizard the organ is always more or less spheroidal or ovoid; in the Mammal it is almost always present as an elongated tube which has its opening at the anterior end. This tube has a cartilaginous support which is a development of the trabecular cornua and has been called by Parker the "Recurrent Cartilage". The cartilage which becomes the Cartilage of Jacobson is itself supported by a process of bone — the palatine process of the Premaxillary. In a paper I recently communicated to the Linnean Society of New South Wales[8] I adduced a number of facts confirming the view that the palatine process of the premaxillary is really a distinct element which though usually formed in connection with the Premaxillary, in many cases only becomes anchylosed with it later and in a few instances remains distinct throughout life. I further endeavoured to establish the homology of this element with the bone usually called "Vomer" in the Lizard — a view lately held by Kitchen Parker and also supported by Bland Sutton. While as it is developed in a manner exactly similar to the true Vomer but in connection with the trabecular cornua instead of with the septum and thus though closely related to the Vomer distinct from it. I have proposed for it and for its Lacertilian homologue the name of "Prevomer". For convenience however in the following pages I refer to it as the "Palatine process" except in those cases where it is in no way connected with the Premaxillary (Ornithorhynchus & Miniopterus)

Except in the lower Orders the organ of Jacobson is not in the Mammal the highly developed organ we find in the Lizard & Snake. In most forms however it is developed to some degree and even in those ~~animals~~ animals in which it is but slightly developed as regards the sensory membrane, the cartilaginous and bony supports are generally characteristically formed.

As regards the structure of the organ there is much similarity to the Reptilian form, but there is usually present a supply of mucous glands, and on the outer wall of the organ in the lower forms at least there is either a large vein ~~or~~ or a plexus of veins.

On the Organ of Jacobson in Ornithorhynchus

Ornithorhynchus anatinus (Shaw)

As the condition of the organ in the Platypus has been described but a few years ago by Symington,(56) and more recently in greater detail by myself,(9) I will only here refer to it at such length as will be necessary for purposes of comparison.

The Platypus is generally agreed to be the most primitive mammal at present alive, and the structure of its organ of Jacobson confirms this opinion. In all the higher mammals the organ is tubular and opens into the duct anteriorly; in the Platypus the organ is more than half as broad as it is long and extends in front of as well as behind its opening into the duct. The enormous development of the prenasal and lateral cartilages in connection with the flattened "beak" may to some extent account for the peculiar development.

As pointed out by Wilson & Martin there is an enormous development of the Prenasal Cartilage which stretches right across the anterior part of the Snout; and on passing backwards this is found to pass into the median Nasal Septum and two lateral cartilaginous plates which form the floor of the nasal cavities at their anterior parts.

A little behind the plane of the anterior nares the cartilages of the nasal floor which here meet in the middle line below the septum become considerably thickened at their inner parts and on passing still further back the thickened inner part becomes hollowed out by the anterior part of Jacobson's Organ. Even in its anterior part there is a well developed transverse turbinal present passing inwards from the outer side.

Plate XIII illustrates the relations a little further back. Here the inner part of the Cartilage of the organ rests on anterior part of the Prevomer or as it has hitherto chiefly been called "Dumb-bell shaped bone".

Plate XIV represents a section just in front of the naso palatine canal, and shows that the turbinal is really a part of the roofing cartilage.

Plate XV shows the relations at the opening into the canal. The Prevomer is here well formed and overlaps the cartilage above.

Plate XVI shows the condition of the organ behind the opening into the duct. Here the cartilage forms almost a ring with a rather delicate and curved turbinal passing inwards from the outer side. On its inner side the delicate cartilaginous wall rests on the Prevomer. The Prevomer itself rest inferiorly on a plate of cartilage which is of considerable interest. When the cartilage which formed the floor of Jacobson's organ and of the nasal cavity was divided by the naso-palatine canal the outer part though attached to the Alinasal is evidently a distinct element. This I suspected from various comparative-anatomy reasons, and my surmise has been proved correct by the discovery by Newton Parker that in the very young specimen this portion is distinct from the Alinasal. This small element on passing backwards becomes more developed and passes inwards below the organ and below the Prevomer forming with its neighbour the flat median plate.

Posteriorly the organ ends blindly though there are numerous ducts of glands opening into it.

In structure the organ itself shows

a high degree of development. Both in front of and behind the duct, the turbinal is covered by a network of veins forming a regular plexus. The epithelium of this part is strongly ciliated. The inner wall however is the chief seat of the sensory cells.

In contrasting the organ in this form with others we find that it is though on the whole a mammalian ~~type~~ somewhat intermediate. The anterior part of the organ in the situation of the turbinal and the relation of the duct recalls the organ in the Agamidae & Geckonidae; while the posterior part of the organ is typically mammalian except for the turbinal and the unusual degree of development.

On the Organ of Jacobson in Echidna
Echidna aculeata (Shaw)

In Echidna though in its general organisation closely allied to Ornithorhynchus we find a very considerable difference in the organ of Jacobson. The difference is so striking at first sight as to lead one almost to doubt the value of the organ as a factor in classification. In the first place however it must be borne in mind that though there is a great similarity between the two animals, in intimate structure they are probably not more intimately connected than are the Pig and the Dog. Then again as I pointed out in my paper "On the Organ of Jacobson in the Monotremata" the remarkable degree of specialisation of the snout probably to a large extent accounts for the condition of the organ in Ornithorhynchus. When this is taken into consideration really the only difference between the two organs is the extension of the organ in front of the duct in the Platypus. Study of the development of the organ alone can reveal whether this Reptilian character is the remains of an ancestral feature or an acquired condition in connection with the great development of the snout. Most probably it is an ancestral character which has become exceptionally developed. As it is, in Echidna, though we find the mesial & lateral cartilages similarly though but feebly developed, the organ of Jacobson scarcely extends any distance in front of its opening into the duct. Behind the duct the organ is present as a tube in section of very similar appearance to that found in Ornithorhynchus.

The figures on plates XVIII & XIX ~~the condition~~ illustrate the condition of the ~~anterior~~ relations of the organ. In fig. 1 in the first plate at the base of the nasal septum (N.S.) are seen the two cartilages which form the nasal floor (L.C.). At this point of simple structure. In fig 2. an anterior curve of the head of Stenson's duct (S.D.) is seen dividing the cartilage into an inner and an outer part. In fig 1 Plate XIX Stenson's duct is well shown and at its upper part it is seen connected with the anterior end of Jacobson's Organ. The cartilage is here quite divided in the inner part which forms Jacobson's Cartilage and a small outer (O.P.C.) which in succeeding sections is found well developed and forming the plate which passes below the organ just as was seen in Ornithorhynchus.

Fig 2 of the same plate is a little further back and shows the duct connected with the nasal cavity. Here Jacobson's cartilage is approximately a tube.

The organ itself is present as an elongated tube tapering at both ends. It is enclosed in a cartilaginous tube except at its posterior end where the organ is only supported by cartilage on the lower inner and outer sides. In the middle half of the organ there is a turbinal plate passing in from the outer side as seen in Plate XXI. In Echidna the plate is flattened, whereas in Ornithorhynchus it is very distinctly curved. Otherwise there is much resemblance between the two organs. One peculiar difference lies in the coursing of the veins of the turbinal plexus. In Echidna they run parallel with the organ, while in Ornithorhynchus they wind irregularly back and forwards over the cartilaginous process. Both organs are but feebly supplied with mucous glands though they receive the secretion of a large number posteriorly.

The Marsupial Organ of Jacobson.

In the Marsupialia we have a group of Mammals widely differing in details of structure, but which are united in a very natural division by the close agreement in their more fundamental organisation. Their developmental history besides many points in their anatomy show that they, though much more allied to the Placentalia, to some extent bridge over the gap between that group and the Monotremata. The structure of the organ of Jacobson gives further evidence of the same fact.

The only papers I am aware of referring to the organ in this group are that by Symington[57] on the organ in the Kangaroo and a very recent paper by Röse[50] on the organ in the Wombat and Opossum. The latter unfortunately I have not seen. Symington's paper briefly describes the organ in the young Macropus and in the closely allied Petrogale and concludes that "the organ of Jacobson in the Kangaroo closely resembles in its form and structure the same organ in the majority of Eutheria in which it has been investigated. Though this statement is in the main correct I hope to show that the Marsupial organ is of a much more primitive type than that found in the Placental and that in certain respects it resembles the Monotreme organ.

I have studied the organ in the following Genera — Phascologale, Dasyurus, Perameles Macropus, Trichosurus and Phascolarctos and in some forms the early fœtal as well as the adult condition. Though there is a general agreement between the organs in the different genera sufficient to show that they all belong to one group, there are certain distinctive differences between the Polyprotodont & Diprotodont types which will be referred to later. As the former appears to be the simpler and more primitive type I shall enter on its consideration first.

On the Organ of Jacobson in Phascolarctos
Mammary foetus of P. penicillata (Shaw)

My sections of this species were made on a very young mammary foetus, measuring in the curved condition 15 mm, the head being 6.5 mm.

Even at this early stage ossification is well advanced and the organ of Jacobson is well formed.

A transverse section immediately in front of Stenson's duct shows the nasal septum well developed, and the Alinasal curving round and becoming united with the nasal floor cartilage. These in turn passing inwards toward the base of the septum curve upwards and then outwards forming a sort of framework to the rudimentary turbinal on either side of the base of the septum. Below this nasal floor cartilage lies the Premaxillary.

Immediately behind this plane Stenson's duct is seen passing up dividing first the premaxillary into its outer part and whitens the anterior end of its palatine process, and in the succeeding section the nasal floor cartilage into an inner portion - the anterior part of Jacobson's cartilage, and a small outer portion which in posterior sections becomes lost.

Figure 2 of Plate XXIII represents a section in a plane a very little posterior. Here Jacobson's cartilage is seen quite removed from the outer part of the nasal floor cartilage (O.N.F.). At its lower end on the outer side is seen the anterior end of Jacobson's organ opening into the duct. On the median side of the base of Jacobson's cartilage is seen the small splint like palatine process of the Premaxillary (p Pmx) In this and the succeeding sections the close connection between the palatine process and the cartilage of Jacobson is well seen. the splint being moulded to suit the varying conditions of the cartilage.

Figure 1 Plate XXIV. illustrates the condition in the plane a little behind the preceding one and shows that the connection between the nasal cavity and the duct is a little behind the opening of Jacobson's organ

If this figure and fig 2 Plate XXIII be compared with fig 1 + 2 Plate XIX representing the corresponding parts in Echidna the agreement between the two will be found remarkable — The very small outer part of the nasal floor cartilage, the "C" shaped appearance of Jacobson's cartilage with the large head forming the support of the rudimentary turbinal, and further the ~~exact~~ wonderful similarity of the modes of connection of Jacobson's organ and the nasal cavity with Stenson's duct.

Further back as seen in fig 2 Pl. XXIV. the organ is well developed cartilage does not form a complete investment but only a support on the inner and lower sides of the organ and further there is no turbinal as in Echidna, though there is a slight depression more marked at some parts than others of the outer wall caused by the vascular ridge.

On the Organ of Jacobson in Dasyurus

Dasyurus viverrinus (Shaw)

Of this form my sections were made in an almost adult specimen; and as this genus is very closely allied to the preceding as would be expected the organs are very similar.

A little in front of Jacobson's Organ as seen in Plate XXV fig 1 the nasal floor cartilage is well developed and moderately flat and those of either side pass inwards and almost meet below the nasal septum. By the side of the septum a little higher up is seen a delicate portion of cartilage — this a delicate precurrent spur from the upward extension of the nasal floor cartilage seen a little further back. On this plane Stenson's duct is seen passing upwards and inwards below the inner part of the Premaxillary.

In fig 2 is seen the relation of parts a little posteriorly; the nasal floor cartilage will be noticed much more curved.

Almost immediately in front of the anterior part of Jacobson's Organ the lowest part of the nasal floor cartilage becomes considerably thickened and into this passes the upper part of Stenson's duct. The duct can hardly be said to divide the nasal floor cartilage, as the part outside the duct becomes quite lost; and in subsequent sections only Jacobson's cartilage is to be seen.

In the next succeeding section Jacobson's cartilage is found to be irregularly "C" shaped. The upper part of the "C" is fairly developed and still forms the support of the rudimentary turbinal, while inferiorly the upper part of Stenson's duct passes into the lower hollow, but this not yet part of Jacobson's organ being coated with squamous epithelium. The cavity of the "C" is still connected with the outer nasal wall by a bridge of tissue which conveys the large blood vessel which in succeeding sections is found occupying the vascular ridge on the outer wall of the organ.

In figure 3 plate XXV is represented the appearance immediately behind the place where Stenson's duct merges into the nasal cavity. Here and for some little distance behind this place the cartilage of Jacobson still retains the "C" shape, though on passing backwards the lower limb becomes the larger, through joining with what before was the outer part of the upper limb, while the latter becomes detached from it. Jacobson's

Organ is roughly kidney shaped and has its outer wall pushed in by the large vein which runs parallel with the organ. The whole cartilaginous capsule is practically filled up by the organ and the large vein there being an absence of mucous glands. The palatine process of the Premaxillary is seen supporting the inner and lower side of the cartilage of Jacobson.

In a section through the middle of the organ as represented in plate XXVI the cartilage is seen much reduced while the palatine process of the Premaxillary is greatly developed and to a large extent replaces it. The organ itself has the typical mammalian features. The outer wall of the organ has columnar epithelial cells with long cilia, while the inner wall as far as can be made out in my sections appears to be constructed on the normal type. Cilia are either absent or very minute. Mucous glands appear to be absent

On the Organ of Jacobson in Perameles
Perameles nasuta, Geoffr.

In the Bandicoot we have another type of the Polyprotodont group of Marsupials — a ~~group~~ type remarkable for having with teeth of a carnivorous or insectivorous type feet constructed after the same pattern as the Kangaroo. The organ of Jacobson and its relations bear out to the full the view of Thomas and others that the bandicoots are a specialised branch of the Polyprotodont group and in no way nearly related to the Diprotodont Marsupials. The peculiar development of the foot is thus almost certainly an instance of parallelism and probably the most remarkable in the Animal Kingdom.

There is a marked resemblance between the organ in this form and that of Dasyurus. Like in that genus the cartilage plays a secondary part, but here the reduction of the cartilage of Jacobson is very much more marked, and towards the posterior part of the organ there is no cartilage at all.

In a transverse section just in front of the point where the Premaxillary gives off its palatine process is seen in Fig 1 Plate XXVII we have the great reduction of the cartilaginous elements well marked. Even here in front of Stenson's duct we have only the inner part of the nasal floor cartilage remaining, and that is present as three detached fragments — the two inner representing the lower part of the inner moiety of the nasal floor cartilage of Dasyurus the outer, the bar supporting the maxillo-turbinal turbinal. Inferiorly Stenson's duct is seen passing up.

In Fig 2 a very short distance behind the previous one the Premaxillary is seen distinct from its palatine process and in the cleft between the two portions of the bone there is formed a minute portion of cartilage — a downward process from Jacobson's cartilage — which is specially interesting as being the first indication of this downward process which becomes so well developed and important in the higher forms.

In fig 3 Stenson's duct is seen passing upwards into the hollow of the palatine process and uniting with the anterior part of Jacobson's Organ.

In fig 4 which is a little distance farther back, Jacobson's organ is distinct from the duct, whose upper part is now seen merged into the nasal cavity. The organ is here small and has on its outer side the large vein of the vascular ridge (v). On the extreme outer side is seen a small precurrent spur of the palatine process. In succeeding sections this is found united with the inner part and the palatine process then assumes the appearance on section of an "L" as seen in Fig 1 plate XXVIII.

Fig. 1 plate XXVIII shows a section through the main part of the organ. The cartilage is here seen to be very rudimentary forming an imperfect lining to the "L" shaped palatine process. The organ itself is fairly well developed and has in section the usual kidney shape. The vascular ridge on its outer wall is occupied as in Dasyurus by a single large vein. There is also as in that genus an absence or great scarcity of mucous glands

Towards its posterior end as seen in Fig 2 plate XXVIII. The section reveals below

The septum the large vomer while the palatine process is much reduced in size but still retains the "L" shape. The organ itself is much rounder in section, and has on its inner side a large number of nerves.

Taking the forms just described as typical members of the Polyprotodontia, it will be noticed that the organ is characterised by (1) the simple and rather rudimentary condition of the Cartilage of Jacobson, (2) simple condition of the vascular ridge & (3) the absence or scarcity of mucous glands.

On the Organ of Jacobson in Trichosurus

Trichosurus vulpecula (Kerr) = Phalangista vulpina Desm.

Part I – Very young mammary foetus.

I have examined the condition of affairs in mammary foetuses of 18 mm and 30 mm but as there is much similarity between the two I will only describe the larger form as in it the tissues are more clearly differentiated.

In this as a representative of the Diprotodont division we have some typical distinguishing features from the ~~previous~~ forms. The most striking peculiarity lies in the great development of the nasal-floor cartilage. Still well seen the highly developed Jacobson's cartilage of the adult Diprotodont.

In a section made through the plane where there is the first indication of Stenson's duct the nasal-floor cartilage is large and but slightly ~~curved~~. Near the septum it is thinner and curves slightly upwards. The septum passes down a little way between the inner ends of the nasal-floor cartilage ending between the inner parts of the Premaxillaries.

A very short distance behind this plane as seen in Fig 1 Plate XXIX the inner part of the nasal floor cartilage becomes complicated by a large downward process and a small process pointing upward and outwards. The inner, not part of the cartilage forms with the downward process an obtuse angle in which lies the palatine process of the Premaxillary.

In fig. 2, plate XXIX we have presented the condition almost immediately behind. Stenson's duct is found passing up and opening into the very large anterior end of Jacobson's organ. On this plane the Recurrent or Jacobson's cartilage (R.C.) is only slightly curved in section with the palatine process of the Premaxillary resting on the middle of the concavity. ~~The~~

Figure 3 Plate XXIX shows the condition still further back. Here the nasal cavity is merged into the upper part of Stenson's duct. The organ of Jacobson is large and extends upwards considerably and is supported on its inner side by the recurrent cartilage (R.C.) here present as a flattened plate. The palatine process of the Premaxillary (p. Pmx) is still present as a small round rod resting on the middle of the inner side of the cartilage.

Near the posterior part of the

organ there is found attached to its upper side a number of developing mucous glands.

In comparing this form with the early mammary foetal Phascologale we find there are many common features and some important differences. Firstly the duct of Stenson opens into the organ and the nasal cavity in exactly similar ways in each type and in a way precisely similar to that found in Echidna but quite different from that of any of the Placentalia in which the organ has been examined. (It is possible the Edentata may agree with the Marsupialia in this feature, as the Rodentia another low-group of the Placentalia though having a peculiar arrangement of their own present certain resemblances to the Marsupial type) On the other hand there is a difference in the development of the cartilage and of the relations of the palatine process of the premaxilla – a difference quite as great as that found between the Cat and the Sheep.

On the Organ of Jacobson in Trichosurus

Trichosurus vulpecula (Kerr) = Phalangista vulpina, Desm.

Part II – Adult.

Having studied the organ and its relations in the early foetal specimens the changes we here note are chiefly brought about by a further development of the cartilages and the related bones.

In Plates XXX and XXXI are presented a series of sections illustrating the appearances in successive planes and showing the various alterations in the condition of the nasal-floor cartilage and organ of Jacobson.

In front of the plane passing through the point of exit of Stenson's duct the nasal-floor cartilage is present as a curved plate turning upwards at the base of the septum.

In Fig 1 Plate XXX through the plane of the anterior part of Stenson's duct the nasal-floor cartilage is becoming altered in shape. There is a small process pointing upwards and outwards below the glandular ridge, and another near the middle of the cartilage passing downwards. This downward process ripens into the anterior part of the large downward projection which lies in the cleft between the Premaxillary and its Palatine process. In the palatal region is seen the peculiar median palatal cartilage (M.P.C) already similar to that already seen in Perameles and which probably represents the Prenasal element.

Immediately behind figure 1 the downward process is much enlarged and extends downwards to the base of the palatine process.

In the next succeeding plane as seen in Fig 2 plate XXX we find the downward process cleft for the upward extension of Stensons duct.

Fig. 3 plate XXX shows a step further back. with the cartilage cleft in two. The inner part is moderately flat and rests on the palatine process of the Premaxillary (P.Pmx), while the outer part includes besides the outer part of the nasal floor cartilage, also the cartilaginous supporting the glandular ridge. Between the glandular ridge process and the flattened plate is found a small anterior part of Jacobson's organ. The organ does not pass much in front of the duct but in both this genus and Macropus it has a slight anterior projection.

Fig 1 Plate XXXI represents a section through the plane where the organ opens into Stenson's duct.

The cartilaginous elements are here the inner plate which rests on the palatine process of the Premaxillary and on the outside of Jacobson's Organ the glandular ridge support in the form of a small bar of cartilage cut across.

In Figure 2 Plate XXXI the organ is seen detached from the duct whose upper part is now as in all similar marsupial Sections merged in the lower part of the nasal cavity. On the concave outer wall of the organ are two large veins cut across; and a third is found below the lower part of the inner wall.

Fig 3 Plate XXXI is a little further back and here we find the organ much increased in size and crescentic in section. Its cartilage is no longer only a plate on its inner side but passes below as well and curving outwards and upwards joins the glandular ridge element. On the outer wall of the organ the vascular ridge is found well developed, being formed of three or four large veins running parallel. A large vein is also present below the inner wall

The organ is very elongate and throughout its whole length varies very little in structure.

From front to back the vascular ridge is well developed and above, the organ is covered with an abundant supply of mucous glands. These seem to open chiefly into the lower and outer angle of the organ.

Plate XXXII illustrates a section near the middle of the organ. The cartilage is here as in Fig 3 Plate XXXI an irregular half circle. It rests on a flat expansion of the palatine process of the Premaxillary, while at its upper and inner end it is supported by the vomer. The nasal septum in this plane is seen partly ossified — this is the anterior part of the Mesethmoid. The organ itself has still an irregular crescentic shape. The inner wall is the sensory layer and in structure seems practically identical with that in the Rabbit as figured by Klein. In fact the whole organ in this genus bears a very marked resemblance to that of the rabbit, though the relations are very different. The outer wall is bulged in by the vascular ridge which here is composed of two large and two small veins. Near the upper angle of the

Organ are two large nerve bundles and at the lower angle another very large one. On the inner wall are two or three small bundles. All the remaining space nearly is packed with mucous glands (G) or their ducts (D), A few small nerves lie in the outer part of the glandular ridge under the Epithelium.

On the Organ of Jacobson in Phascolarctos.

Phascolarctos cinereus Goldf.

In Phascolarctos the organ is small and the palatine process of the Premaxillary short and stout while the Vomer is well developed and passes right forwards above the palatine processes as far as the point where the Premaxillary gives off its palatine process. Notwithstanding these peculiarities the cartilage of Jacobson in its relations and structure presents a wonderful resemblance to that of Trichosurus and affords additional evidence of the reliability of the development of Jacobson's cartilage for purposes of classification.

Anteriorly the nasal floor cartilage is found undergoing almost the exact same changes as were noticed in Trichosurus. On the whole however the cartilage though simpler is more strongly developed. There is the same downward process which receives on its outer side the anterior part of the organ.

At a plane a little in front of Jacobson's organ the nasal-floor cartilage consists of a large outer part resting on the Premaxillary and forming part of the outer wall of the nasal cavity, and an inner part irregularly "i" shaped and united by its outer limb to the inner end of the outer part of the cartilage.

On the plane of Fig. 1 Plate XXXIII the two parts of the nasal-floor cartilage are separated and the organ is seen opening into the duct. On the inner side above of Jacobson's cartilage is the Vomer (Vo) while below and internal is the palatine process of the Premaxillary (p Pmx)

In Fig. 2 Plate XXXIII the upper part of the duct is seen as part of the nasal cavity.

Fig. 3 Plate XXXIII shows the condition a little further back where the cartilage of Jacobson forms a complete capsule. The organ itself is small but has on its outer wall a vascular layer very similar to that seen in Trichosurus. There are only a few mucous glands.

On the Organ of Jacobson in Macropus

Macropus sp?

Part I. Mammary foetus 29mm.

Though this type in many respects resembles that found in Trichosurus there are a few differences of interest. In some points this is a simpler form, while in others it is more complex.

The nasal floor cartilage is narrow and only its inner part is well developed. In Fig 1 Plate XXXIV. it is seen attached at its outer part to the lower part of the alinasal. The inner part is rather thickened where it meets the septum.

Immediately behind this the inner part only is represented which though thick at its inner end is pointed at its outer and directed downwards and outwards. On its inner and under side is seen on section the palatine process of the Premaxillary ossifying in the midst of a nest of cells.

A few sections further back as seen in Fig 2 Plate XXXIV Stenson's duct is seen passing up and opening into Jacobson's organ. Practically on the same plane the duct also opens into the nasal cavity. Jacobson's cartilage resembles that in the foetal Trichosurus in being a flattened plate and in having on its inner side near the middle the palatine process of the Premaxillary.

In Fig 3 Plate XXXIV almost immediately behind the opening of Jacobson's organ, the cartilage is seen sending out a small process below the organ. In this and in the sections figured in Fig 2 and Fig 4 the organ of Jacobson is seen considerably less developed than in the similar sections of the foetal Trichosurus.

In Fig 4 Plate XXXIV near the posterior part of the organ, the palatine process of the Premaxillary is lost and there is seen the developing plates of the Vomer (Vo). The cartilage of Jacobson is also absent.

On the Organ of Jacobson in Macropus

Macropus walabatus (♂ and ♀.)

Part II. A well developed pouch specimen (head 50 mm.)

This stage of the young Macropus illustrates well all the features of the adult, and in some respects shows the relationships better. The largest specimen examined by Symington had the head 37 mm and though his illustrations show to some extent distortions and displacements due to his imbedding process, the main characters are very similar to those seen in my preparations. In Symington's specimens however minute details seem to be but imperfectly shown. In his Fig 1. he omits to show the median palatal cartilage which is certainly present in the plane he figures, while the part mark P.P. (palatine process of the Premaxillary) is the body of the Premaxillary itself. Otherwise his figures are correct so far as they go. In passing I may here remark on the usual imbedding process. Symington says "all the specimens were imbedded in paraffin." Many years ago I found I could make much better sections without imbedding. Imbedding seems always to cause some distortion whereas by proper hardening all the cells are kept in exact relations and the tissue can easily be cut by hand. In my sections across foetal jaws almost invariably in the developing teeth the Enamel cells are to be seen directly passing into the Enamel prisms and the Odontoblasts are almost always in contact with the dentine. My process has also the advantage that I can mount in a Glycerine medium and am thus enabled to see details that are rendered almost invisible by Balsam.

Symington seems to regard the nasal floor cartilage as part of the Alinasal with which it is very often united. In this Howes seems to agree with him. From my very extended series of preparations of various mammals I cannot agree with them and have little doubt but Kitchen Parker is right in regarding the Recurrent or Jacobson's Cartilage as a development directly of the Trabecular Cornu. If in any form the mode of development seems doubtful it is not in Macropus.

In the Diprotodont Marsupials the powerful incisors give rise to a greater development of the Premaxillary than among the Polyprotodonts. This in turn removes the nasal cavity at its anterior part further from the palate. Hence in sections across the snout in front of Stenson's duct the base of the septum and the nasal floor cartilage is far removed from the mucous membrane of the mouth.

Figure 1 Plate XXXV represents a section a little in front of Stenson's duct. The Nasal-floor cartilage is here very simple, It is slightly curved and comparatively thick where it approaches the nasal septum. In the palatal region between the entrances of Stenson's ducts lies a broad flat plate of cartilage similar to that already seen in other Marsupials and which I believe to be the Prenasal Element.

In Fig. 2 Plate XXXV which is but a very short distance behind there are many marked changes. The nasal septum is still the same distance from the palate but in the nasal floor cartilage there are some marked changes The palatine process is becoming separated from the Premaxillary and the nasal floor cartilage is found dipping down toward the palate and filling up the gap between the two portions of bone.

Figure 3 Plate XXXV represents the condition in a section through the plane immediately behind the separation of the palatine process from the premaxillary. The differentiation of the nasal floor cartilage has gone still further and it differs from the previous section in being hollowed out to accommodate a small anterior projection of Jacobson's organ (J.O). If this section be compared with the similar one in Trichosurus (Fig 3 Plate XXX) the only important difference is that in the latter the anterior projection of Jacobson's organ is not supported by any cartilage inferiorly, while in Peramys the inner part of the cartilage curves round below the organ and is attached to the outer part.

Figure 1 Plate XXXVI shows the opening of the organ into Stenson's duct and is essentially similar to Symington's fig 2. though it differs in showing the opening of the organ a little anterior to the connection of the duct with the nasal cavity. On comparing this section with the corresponding one of Trichosurus (Fig 1 plate XXXI) the resemblance between the two is most remarkable in almost very particular. The chief difference is the very slight one of the relative development of the organ. The organ is lined with Columnar Epithelium which ends as the organ opens into the duct of Stenson where the Epithelium becomes Squamous. Though there is some resemblance with the corresponding section in Perameles (Fig 3 Plate XXVII) there are many very marked differences, especially in the condition of the cartilage of Jacobson

Figure 2 Plate XXXVI is in the plane a little further back where the duct of Stenson has become merged in the nasal cavity and where the organ is quite removed from the duct. Here the cartilage is found passing round below the organ and forming the little detached piece forming on section the appearance of a "V" as shown by Symington. In this respect it resembles the condition in Trichosurus (Fig 3 Pl. XXXI) though there the "V" is much broader and the organ larger. There is a further difference in the scantiness of the Mucous glands compared with the Phalanger. In Macropus the vascular ridge is present but the veins are very much smaller.

As described by Symington the

organ at its hinder end passes upwards in a level with the lower part of the nasal septum, and is separated from it by the Vomer. Fig 3 Plate XXXVI illustrates this condition. Here the organ is surrounded on its outer side by mucous glands which discharge into the cavity of the organ, which is very much flattened. On its inner side is a series of nerve bundles. The Vomer is well developed and has two peculiar outward processes. The palatine processes of the Premaxillaries are seen to the sides.

The Placental Organ of Jacobson

The Placental group of the Mammalia contains the vast majority of all the Mammals and comprises a large number of subdivisions to which the rank of Orders is usually given. In these Orders, which are formed of groups of very dissimilar animals, ~~and~~ as the organ of Jacobson is present sometimes well developed and at others quite absent. Where the organ is present it is remarkable how it is sometimes developed very similarly in two orders which comprise animals very unlike.

At present our knowledge of the organ in some Orders is a blank and in others the only notices are very unsatisfactory. But in the various Orders that have been well studied where the organ is present it is constructed on one of three types, and of these three types two are related, while the third is entirely dissimilar. This third type is that found in the Rodents and we shall consider it first. The other types are those found in the Cat and Bat. In both the Organ opens into Stenson's duct, and in both the duct has a cartilaginous support on both its outer and inner walls. There is a great difference however between these two types and that of the Rodent, which in some respects resembles the Marsupial condition. The details and the peculiarities of the forms will be dealt with under each form when studied.

On the Organ of Jacobson in Lepus.
Lepus timidus L.

As the result of the excellent papers by Klein[28] we know more of the Organ of Jacobson in this genus than in any other. He has described and fully figured the conditions of parts in the Rabbit and made a detailed examination of the minute anatomy. In the Hare the differences are so slight that it will be unnecessary to do more than notice them. The great mass of cartilage which forms the anterior wall of the capsule of the organ is even more developed in the Hare than in the Rabbit, but on the whole its relations are similar. The duct of Stenson is similarly provided with the curious curved cartilage on its outer wall – Stenson's cartilage. In the Rabbit it is only at the anterior part that the capsule is completely closed in by cartilage but in the Hare the capsule is enclosed for the greater part of its extent. Posteriorly the Vomer comes further forward and lies between the septum and the inner part of Jacobson's cartilage almost in the middle line. In details of structure there is little to note – ~~both~~ the species being practically alike in this respect.

In the Guinea Pig as figured by Klein though the type is rather simpler the structure is in the main the same.

Taking these as typical Rodents the characteristic features are :-

1. The opening of Jacobson's Organ into the anterior part of the nasal cavity and not into Stenson's duct

2. Stenson's duct opening into the nasal cavity at a lower plane and considerably behind the opening of Jacobson's Organ.

3. The absence of any downward process of cartilage towards Stenson's duct.

4. Outer wall of Stenson's duct supported by a cartilage (Stenson's Cartilage) which may (Lepus) or may not (Cavia) take part in the flooring of the nasal cavity.

5. Organ provided with a well developed cavernous layer on its outer wall.

6. A rich supply of mucous glands emptying into the lumen of the organ.

When the condition is compared with that of the Diprotodont Marsupial the only point of difference are the mode of opening of the organ and the presence of a Stenson's Cartilage. But as will be shown later the latter is not a constant feature in the Rodentia being absent in Mus and Hydromys. The fact of the Organ opening into the anterior part of the nasal cavity is not due to any peculiarity in the relation of the organ which is situated in regard to the cartilage of the nasal floor very much as in the Marsupial, but to low position of Stenson's duct.

It will thus be seen that the only marked point of difference between the condition in the Rodent and Marsupial is one of relationship.

On the Organ of Jacobson in Mus.
Mus musculus L.

The organ of Jacobson has been studied in the Rat ~~Mouse~~ by Herzfeld[10] who in his paper gives four very careful drawings of sections at different planes. In the mouse as in some other small mammals (e.g. the mole and bat) the osseous elements are well developed and to some extent replace the cartilaginous. There is here unlike the Rabbit or Guinea pig no Stenson's cartilage, and the cartilage of Jacobson is only present at the anterior part of the organ. The palatine process of the* Premaxilla is unusually well developed and for a considerable distance sends up both an outer and inner plate which form a complete capsule even roofing the organ above.

The organ opens into the anterior nasal cavity exactly as in the Guinea Pig. In my sections the organ itself seems much more developed than in those figured by Herzfeld; in many of sections the organ almost fills the whole capsule. On the outer wall there is a single large vein which runs parallel with the organ, and represents the cavernous layer of the Rabbit. It is interesting that in this Rodent there is but a single large vessel as this is exactly the condition in the Polyprotodont Marsupials.

There is a large development of mucous glands towards the posterior part of the organ.

On the Organ of Jacobson in Hydromys.

Hydromys chrysogaster

In the common Australian Water-rat or Beaver-rat as it is frequently called, the organ of Jacobson is so essentially similar to that of the Mouse that little need be said of it. The palatine processes of the Premaxillaries are formed after the same plan though they are scarcely so well developed above. The organ itself does not occupy so large a part of the capsule as in the mouse but like it has a single large vein on its outer wall. There is a large supply of Mucous gland opening into the organ.

Plate XXXIX illustrates a section through the largest part of the organ.

On the Organ of Jacobson in Bos.

Bos Taurus L.

Specimens examined 1. Foetal calf 65 mm (Head 20 mm)

2. Foetal calf 200 mm (about) (Head 55 mm)

The organ of Jacobson in the cow resembles very closely that in the sheep, which scarcely differs from that in the goat. So that we may assume that there is a general resemblance throughout the group.

In the Sheep the organ has been carefully studied by Balogh[1] who minutely examined not only the general relations of the cartilages and the organ, but also the histological details. His paper in fact may almost be regarded as one of the classics on the subject of Jacobson's organ.

Before however entering into an examination of his work it will be well to consider briefly the leading features of the organ in this group.

Unlike any of the previous groups studied the Duct of Stenson is long and narrow and passing upwards and backwards very obliquely. In the lower mammals the duct might almost be regarded as an anterior and downward projection of the nasal cavity, which is only constricted at its opening into the mouth. Here Stenson's duct is a long very narrow tube which is quite small even at its opening into the nasal cavity. In its anterior part this narrow duct receives on its inner and upper side the duct of Jacobson's organ. In most of the lower mammals the organ opens into the Stenson's duct quite abruptly the columnar epithelium giving place to the squamous only at the opening into naso-palatine canal. In this group, as is also the case though to a less extent in the Rodent, the organ has a distinct duct of its own lined with squamous epithelium. For a considerable distance this duct runs parallel or almost so with Stenson's duct, the two becoming one near the anterior end of the duct of Stenson.

In the Rabbit Hare and Guinea-Pig Stenson's duct was seen to be protected on its outer wall by a curved plate of cartilage. A similar portion of cartilage exists in this group, but it is complicated by being united above with a second plate which lies on the inner side of the duct. As the duct of Jacobson becomes separated from Stenson's duct the two plates of cartilage become disconnected. The inner which curves round below the duct of Jacobson becomes on passing backwards attached to the inner part of the nasal-floor cartilage and we have a Jacobson's organ lying in a cartilaginous capsule very similar to that of the Rodent or Marsupial. The outer plate on passing backwards becomes attached to the outer part of the nasal floor cartilage and behind the plane of the opening of Stenson's duct into the nasal cavity the two together form the outer wall of the lower part of the cavity.

Balogh though his figures are somewhat diagrammatic describes the relations of the cartilages correctly. The external cartilage he calls Stenson's cartilage, the inner one Jacobson's cartilage. The nasal-floor cartilage he calls "die obere Bogenlamelle des

Intramaxillartheiles des Jacobsonschen Knorpels" the lower part ~~being~~ which protects the duct being "die untere Bogenlamelle". Klein[26] considers Balogh's arrangement of the cartilages unnecessarily complicated. In the forms studied by Klein there is very little difficulty with regard to the cartilaginous structures. In the dog in which the type is similar to that in the sheep the cartilages are simpler and Klein has made the condition appear simpler still by failing to recognise the importance of the different elements. The cartilage on the outer side of Stenson's duct he recognises as Stenson's cartilage but where it curves round and forms the support of Jacobson's duct he says it "is now no more Stenson's but Jacobson's cartilage." Herzfeld[20] avoids all difficulty by calling the various elements according to their position.

With a view to determine the significance of the various elements I have examined the structures in two early stages of the foetal calf, in the smallest of which the snout was only 5mm ~~across~~ in breadth. The other specimen was about three times as large.

In these the very early condition of the cartilages is well seen.

Figure 1 Plate XI shows the condition of Stenson's duct near its anterior part. The duct is here about to give off at its upper part Jacobson's duct. On its outer side is seen a small piece of cartilage (S.C) – this is Stenson's cartilage. On the inner side is another cartilaginous element – Jacobson's cartilage (J.C) These two are quite distinct at this stage and are not in contact either in front or behind this plane. Above the duct is seen the Premaxillary giving off its palatine process (p.Pmx). Higher still is seen the well developed nasal-floor cartilage or trabecular cornu given off from the base of the septum which here shows indications of the two trabeculae.

In Figure 2 Plate XI. Stenson's duct (S.D) is seen separated from Jacobson's duct (J.D) Stenson's cartilage is seen united with the outer part of the nasal floor cartilage; showing that it is merely an anterior process of the outer part of the nasal floor cartilage. Jacobson's cartilage is well developed and quite distinct. On its inner side is seen the slender palatine process of the premaxillary (Pmx). The nasal-floor cartilage is rather reduced and sends a process upwards on the outer wall of the nasal cavity. It is here also detached from the septum here.

Figure 1 Plate XLI shows the condition a little further back. Here the nasal floor cartilage is divided into two. The outer part has retreated up the outer wall of the nasal cavity, while the inner has become attached to Jacobson's cartilage. Jacobson's cartilage or rather the anterior part of it is thus seen to be an anterior process of the inner moiety of the nasal floor cartilage.

In Fig. 2 Plate XLI. Stenson's duct has opened into the nasal cavity and the palatine process has become much reduced but otherwise the section resembles the previous one

If this section be compared with Fig 3. Plate XXIX representing the similar part in Trichosurus there will be noticed a wonderful resemblance, a resemblance so remarkable as to leave no doubt as to the homology of the parts. Even the palatine process takes up a similar situation. The main difference then between this type and that of the Diprotodont Marsupial is that here both Jacobson's duct and Stenson's have a long convex oblique direction and the former is supported by a process of Jacobson's cartilage which passes forward below the premaxillary, while Stenson's duct is similarly supported by a forward process from the outer margin of the nasal-floor cartilage.

In Plates XLII and XLIII the condition is seen in the larger foetus. Here in the anterior sections Jacobson's and Stenson's cartilages are seen united above. While in Fig 5 Pl XLIII Stenson's cartilage is seen again present as a free process this time a posterior one.

On the Organ of Jacobson in Felis

Felis domestica L.

In the study of the organ in the Carnivora we have the assistance of the valuable monograph by Klein[29] on the Organ of Jacobson in the dog. He points out the difference of this type from that of the Guinea Pig and Rabbit which he had previously examined in the peculiar mode of the opening of the organ and in its relations to Stenson's duct. By a series of sections he well illustrates the characteristics of the type, how the cartilage supporting Stenson's duct on the outer side is formed in passing backwards to curve round and join the cartilage of Jacobson. He describes in detail the peculiarities of the organ and points out as the most noteworthy points of difference from the condition in the Rabbit (1) the difference in the shape of the cartilage (2) the scarcity of the mucous glands and (3) the absence of cavernous tissue on the outer wall of the organ.

Dr. Harvey[8] refers very briefly to the condition in the cat and calls attention to the remarkable deepening of the nasal cavity behind the Premaxillary bone and also to the complete ring formed by the cartilage of Jacobson.

Having myself made a careful study of the organ in the Kitten I will take it as my type of the Carnivora and as it agrees closely with the condition in the dog I will not describe it at any great length, but rather following on the lines of Kleins paper call attention to the points of resemblance and difference.

In the first place with regard to the Cartilaginous wall of Stenson's duct we find some difference in the arrangement in the cat from that figured by Klein for the dog. In the dog Stenson's duct at its opening "is surrounded on its outer side by a trough shaped plate of hyaline cartilage .... this is Stenson's cartilage." In the cat (Fig 1 Plate XLIV) even at the anterior part of the duct there is an inner as well as an outer plate of cartilage. Passing backwards the inner and outer plate join above (Fig 2 Plate XLV) forming on section an inverted

"V". Still further back the inner part becomes again detached from the outer (Fig 3 Plate XLIV). On this plane the duct of Stenson is giving off Jacobson's duct in exactly the same manner as seen in the Cow. The inner cartilage is Jacobson's cartilage and well developed, while the outer or Stenson's cartilage is but small.

On arriving at the plane where the palatine process becomes distinct from the Premaxillary (Fig 4 Plate XLV) the nasal floor cartilage is found divided into an inner and an outer part. Jacobson's cartilage almost surrounds the organ, while Stenson's cartilage is still to be seen as a small piece on the outer side of Stenson's duct now opening into the nasal cavity.

In succeeding sections Jacobson's organ becomes completely enclosed by the cartilage ~~which became attached to the inner part of the nasal floor cartilage.~~

In the dog throughout the whole length of the organ it is merely supported by a curved plate.

The organ itself in the cat is better developed than in the dog but resembles it very closely in most of its details. Here it is much more distinctly kidney shaped and the walls are much more regular. In the cat the organ occupies about 1/3 of the space of the capsule; in the dog it only occupies about 1/5. The scantiness of the glandular tissue is a characteristic of both and in both there is an absence of a distinct cavernous layer.

Taking then the dog and cat as typical Carnivora we may regard the following as the characteristics of the organ and its relations in that group.

(1) The nasal-floor cartilage though well developed in front near the plane of the hind end of Stenson's duct divides into an inner and an outer part both of which become lost though the tract of the inner part becomes occupied by the upper part of Jacobson's Cartilage.

(2) Stenson's duct is long and passes forward very obliquely. It is supported by Stenson's cartilage in its whole length.

(3) Jacobson's organ discharges into the anterior part of Stenson's duct. In

its forward course Jacobson's duct is supported by an anterior process of Jacobson's cartilage.

(4) Absence of a cavernous layer

(5) Scarcity of mucous glands.

On the Organ of Jacobson in Miniopterus.
Miniopterus schreibersii Natt.

One of the most interesting observations I have been enabled to make has been the discovery in the common Australian Insectivorous Bat of a well developed organ of Jacobson. This is the more remarkable as Herzfeld (20) states that in the German Insectivorous Bat (Species undetermined) the organ is quite absent, and on his authority Wiedersheim in his latest Edition of "Grundriss der Vergleich. Anat. der Wirbelthiere" refers to the organ being absent in the Cheiroptera.

In the Australian bat not only is the organ well developed but it is formed on a different type from that of any other observed form. It has some resemblance to the type found in the cow and cat, but comes nearer the marsupial type in the shortness of the duct of Stenson and its almost straight upward course.

There is also in this form another most interesting feature to which I have elsewhere called attention — the existance of a distinct Prevomer as in the

Platypus. The two bones are anchylosed together in the middle and bear the exact same relations to the Cartilages of Jacobson as do the palatine processes of the Premaxillaries in most mammals and the united Prevomers have much resemblance to the homologous bone in the Platypus – the "Dumb-bell-shaped bone." Though the Premaxillaries are well developed and bear the incisor teeth they do not meet in the middle line and this is probably the reason why the Prevomers remains as "distinct element. As it is this little median bone has attachment either in front with the Premaxillaries or behind with the Vomer.

A section through the anterior part of Stensons duct shows the ducts passing inward and constricting off a well marked median papilla. Above each duct is a little piece of cartilage (Stensons cartilage) and in the middle line between the inner parts of the ducts there is a well developed mesial element which gives off two downward and outward processes towards the outer angles of the papilla. This is probably the homologue of the median palatal cartilage in the Marsupial. The nasal Septum is only moderately developed and a little removed from its base are two well formed nasal floor cartilages.

Almost immediately behind this the mesial element becomes reduced to a mere rudiment. Stenson's duct is seen passing upwards more, and while Stenson's cartilage is still present on its outer and upper side, it is also seen connected with an inner element – Jacobson's cartilage.

In the next succeeding section Stenson's duct curves round and inwards ~~and~~ reaches the anterior end of Jacobson's duct. This is completely surrounded on its inner side by Jacobson's cartilage, which above is becoming attached to the inner part of the nasal floor cartilage, while Stenson's cartilage at its upper part is becoming attached to the outer part of the nasal-floor cartilage.

In Figure 1 Plate XLVI the condition is seen in the succeeding section where Stenson's duct is ~~becoming lost in~~ opening into the nasal cavity. The outer part of the nasal floor cartilage

is here almost lost in Stenson's cartilage &c.
The small medial element still persists.

In Figure 2 Plate XLVI. immediately behind the preceding Jacobson's cartilage is becoming better formed and Jacobson's organ or duct is both roofed and floored by cartilage. The organ is still lined here with squamous epithelium. On this plane between the cartilages of Jacobson there are no bony elements whatever.

In almost the next section however there is seen on the inner side of each cartilage of Jacobson a small bony plate and a very little distance back these are seen united into a single median bone.

The whole organ of Jacobson is much shorter than ordinary mammal in comparison with its diameter, and in this resembles more the organ in the Platypus

Plate XLVII. illustrates a section through the most developed part of the organ. Here the cartilages of Jacobson almost surround the organ and in some specimens there is even a sort of rudimentary turbinal process. Below the two cartilages is seen the median Prevomer (P.Vo). Stenson's cartilage forms a sort of floor to the nasal cavity and passes inwards below Jacobson's cartilage in a similar manner to that seen in the Monotremata. At this place there is an absence of mucous glands in connection with the organ, though at the posterior part there seem to be some in connection with it. There is a rudimentary cavernous layer composed as in the Polyprotodont Marsupials of a single vein.

For a short distance near the posterior part of the organ there is no bony support to it, then it becomes supported by the vomer proper. (Plate XLVIII)

In reviewing the condition here presented it will be noticed that it is somewhat intermediate between the condition found in the cat with and that of the Polyprotodont Marsupial, with some of the features of the Monotremata.

The Marsupial features are

(1) The opening of the organ into Stenson's duct immediately behind its connection with

the nasal cavity.

(2) the shortness and almost vertical direction of Stenson's duct.

(3) the presence of a single vein as representing the cavernous layer.

(4) a distinct median cartilage between Stenson's ducts — a prenasal Element (2)

The Monotreme features are.

(1) The shortness of the organ

(2) the flattened condition of Stenson's cartilage in its posterior part and its passing below the cartilage of Jacobson forming a sort of support for it.

(3) the absence of a palatine process to the Premaxillary, attached and its place occupied by a separate ossification as in Ornithorhynchus.

The features in common with the Cat are

(1) the anterior and downward ~~prop~~ process of Jacobson's cartilage

(2) the presence of an anterior process from the outer part of the nasal floor cartilage — Stenson's cartilage anterior part

(3 the union in front above

the anterior part of Stenson's duct of the anterior processes of Jacobson's and Stenson's cartilages.

On the absence of the Organ of Jacobson – Pteropus
Pteropus poliocephalus Tem.

Herzfeld[(21)] records the absence of the organ in Pteropus Edwarsi, and in the Australian flying fox I find the same condition to hold. In my sections I cannot find even a rudiment of the organ.

Though the organ is absent Jacobson's cartilage is present as is also Stenson's, and these cartilages in their relations almost exactly correspond with those in the bat. It is thus seen that the mere presence or absence of the organ is not a point of great importance, but that the relations of the cartilages are similar in even dissimilar members of the same order and that this is a character so fixed that even the absence of the organ does not affect it. (Plate XLIX)

Another interesting fact with regard to this genus is the absence of palatine processes on the Premaxillae though they are as well developed as in the cat. There is not even a distinct foramen present. In the dried skull the Premaxillae appear to unite, but in the fresh state, in P. poliocephalus at any rate there is a distinct space between the two bones, though it is small.

One point of difference from the bat is the absence of the Median Cartilage.

On the Human Organ of Jacobson
Human foetus of 10 weeks

Various observers have studied the small duct found by the side of the nasal septum in man and while the majority agree that it is rudimentary Organ of Jacobson, Gegenbaur[14] has expressed the opinion that is a rudimentary gland duct.

I have studied the point in a 10 week human foetus which is younger than any previously examined so far as I am aware, and my observations go to confirm the view of Meckel, Kölliker[21] and Herzfeld[20] that we have in man a true rudimentary Jacobson's organ.

In Plate XL illustrates a section through the best developed part of the duct. Jacobson's cartilage or the "Ploughshare cartilage of Huscke" is as well developed relatively as in the early foetal Phalanger (Trichosurus). The organ it is true lies wholly above the cartilage, but in the very young marsupials the main part of the organ is often removed up the septum a little distance, cf the condition in the young Macropus Fig 4 Plate XXXIV or the young Trichosurus Fig 3 Plate XXIX. In fact on comparing this last section with Plate L there will be noticed a marked resemblance between the two other forms.

On the importance of the condition of the Organ of Jacobson and its relations as an aid to the classification of the Mammalia.

Herzfeld[20] in his paper on the Organ of Jacobson attempts a classification of the higher Mammalia from the condition of the organ and Stenson's duct. He forms six groups all differing as regards the duct or the organ. In his first group he includes representatives of the following orders:- Carnivora, Ungulata, Insectivora &c. In his third group he has three species of the Rodentia. His other four groups are characterised by various degrees of rudimentary development either of the organ or the duct.

In criticism of Herzfeld's groups I should like in the first place to call attention to the fact that the presence or absence of Jacobson's organ is of very little importance for purposes of classification. The truth of this will perhaps be best seen in the case of the bats. Herzfeld examined a German bat (species undetermined) and found the organ to be quite absent, and in this agreeing with the Flying fox. But in the common insectivorous bat of Australia (Miniopterus) the organ is unusually well developed. So that in two closely allied members of the same order the extreme differences of development are met with. In other orders great differences of development are to be seen in closely allied genera.

While the relative degrees of development of the organ are of little or no value for purposes of classification, when the organ is well developed in a species it seems to be as far as my researches go always constructed on the type characteristic of the group to which the animal belongs. In an order where the organ is generally well developed such as the Rodentia it is found that in such varied genera as Cavia, Lepus, Mus & Hydromys, it is always constructed on the same plan, and as this plan is quite distinct from that of any members of the other higher orders that have been examined, the organ is seen to be of some considerable value in the classification of the Mammalia. In the Carnivora as represented by the Cat and Dog we have quite a different type of construction from that in the Rodent. In the Australian bat we have a third type which though resembling that found in the Carnivora is still quite distinct. Into one of these three types can be place the organs of any of the higher mammals as yet examined. In the Marsupialia the organ is developed on a plan distinct from that of any of the known Placental types. It has however some resemblance to the type found in Echidna. In the Monotremata still another type is found.

While in any natural classification there must be taken into consideration a number of characters, so that individual peculiarities may count for little, it is of the greatest service to have one character which varies little within a group, and where if it does vary the variation is one of development and not of type. Such a character we have in the palate of the Bird, which has been of such service in the classification of the Aves. In the Mammalia I believe in the Organ of Jacobson we have a character of equal importance.

At present the class Mammalia is divided into three subclasses which are generally regarded as of equivalent value — Monodelphia or Placentalia, Didelphia or ~~Mamsupialia~~ Marsupialia and Ornithodelphia or Monotremata. The structure of the organ of Jacobson confirms this threefold division. But further, it enables us to subdivide the groups more definitely than any other known character.

Of the subclass Monotremata we have only two well marked genera — Ornithorhynchus and Echidna. These two though constructed on very similar lines are sufficiently diverse to suggest their being placed ~~in dist~~ if not in distinct orders at least in different sub-orders. In my paper on the Organ in the Monotremata and in the previous part of this thesis I refer sufficiently to the characters of the organ and the points of difference between the two genera. found in the

In the Marsupial type in its simplest form we have the cartilage of the nasal floor divided by Stenson's duct into a large inner part which becomes Jacobson's cartilage and a small outer, somewhat after the fashion in the Echidna. The chief differences are due to the greater depth of the snout in the tooth bearing Marsupial which removes the nasal floor at its anterior part a considerable distance from the palate. This causes Stenson's duct to be a moderate length, while the outer and inner divisions of the nasal floor cartilage take on a greater development in a vertical direction, passing downward somewhat by the sides of the duct. In the very young foetal Phascolarctos this downward extension of the cartilage is not observable, suggesting that in all probability this development was not present in the early Marsupials, which would thus have an organ of the Echidna type. In the Polyprotodont genera Dasyure and Perameles the downward development is only slightly marked. In the Diprotodont members of the group as the depth of the snout is much greater to accommodate the large incisors the characteristic Marsupial development indicated in the Dasyure is here seen in a greatly accentuated degree. Even in the very early mammary foetal Trichosurus the more highly developed type is clearly seen in the downward extension of Jacobson's cartilage. The difference is very noticeable on comparing the relative position of the palatine processes of the premaxillae and Jacobson's cartilage in the young Phascologale and Trichosurus. In the former the process is at the lower inner corner of the cartilage; in the latter it runs along the middle of the inner side. Otherwise there is a general agreement between the two types.

The group Placentalia includes the vast majority of the Mammals. Though this is one of the most clearly marked groups in the animal kingdom. It comprises such a variety of forms that great difficulties beset the attempts at a satisfactory classification. Many orders are more or less clearly marked, but the inter-relationships of these and the limits of others have given rise to very varied opinions. Flower in the second edition of his "Osteology of the Mammalia" says, "It is very difficult to subdivide the Monodelphia into any larger groups than orders or to arrange these orders in anything like a linear series as most of them have affinities in many directions". He recognises the Edentata as distinct from the others but makes no ~~attempt~~ to classify the remaining ten orders.

It is perhaps here that the value of Jacobson's organ is best seen as it enables us to group the numerous orders in a few divisions. At present our knowledge is too meagre to make the classification anything like complete. In many typical forms Jacobson's organ has not yet been studied while in others it is absent or rudimentary and thus not available; but in the representative forms I have studied I have found three, and only three distinct types. These are found typically developed in the Rabbit, Cat and Bat.

Herzfeld recognised the distinction of the relations of the organ in the Rabbit from those in Dog, Sheep &c in the organ opening into the anterior part of the nasal cavity instead of into Stenson's duct. This peculiarity not being present in any other known group, and here as it is present in all the Rodents yet examined we have our first distinct group in the Rodentia.

The second type – that seen in the Cat – is very interesting. Here we have a long oblique Stenson's duct with the the organ of Jacobson opening by means of a duct into the anterior part of Stenson's duct. The anterior part of Jacobson's duct is supported internally by an anterior process of Jacobson's cartilage, while Stenson's duct is supported on the outside by a cartilage. The two cartilages meet above the union of the two ducts. Notwithstanding the complexity of this arrangement in the cat and dog, it is rather remarkable to find that Exactly the same type is present in the Cow and Sheep. It would thus seem that notwithstanding the many apparent differences between the Ungulata and the Carnivora they are really related. When the relationship is once suggested it will at once be noticed that the characters which seem to separate the groups are really secondary in importance. In the Didelphia Flower says there is but one order the Marsupialia. Yet in this one order there are as great differences in teeth, alimentary canal and even bones as between the Carnivora and the Ungulata. I would thus be inclined to lower the Carnivora and the Ungulata to the rank of Sub-orders and to form a new order to include the two – which from the elongated condition of the nasal structure might be called the Dolichorhinata. In this order in all probability will also be included the Insectivora, though I have not had an opportunity of examining any member

The Bat represents the third type and is characterised by the short Stenson's duct with the organ of Jacobson opening into it at its upper part, by the organ itself being constructed on the type of the Polyprotodont Marsupial and by the presence of a median palatine cartilage. For this type I would propose the name Brachyrhinata. This order will include the Cheiroptera and probably the Primates. It is interesting to note that in this division the organ is very often absent or rudimentary. According to Herzfeld's figures of the anterior part of Jacobson's organ in Lemur it is probable that it belongs to this type. He found a well developed organ in the New world Monkey, Hapale, but failed to discover any organ in the Old world monkeys Cercopithecus and Inuus. In Man the organ is rudimentary.

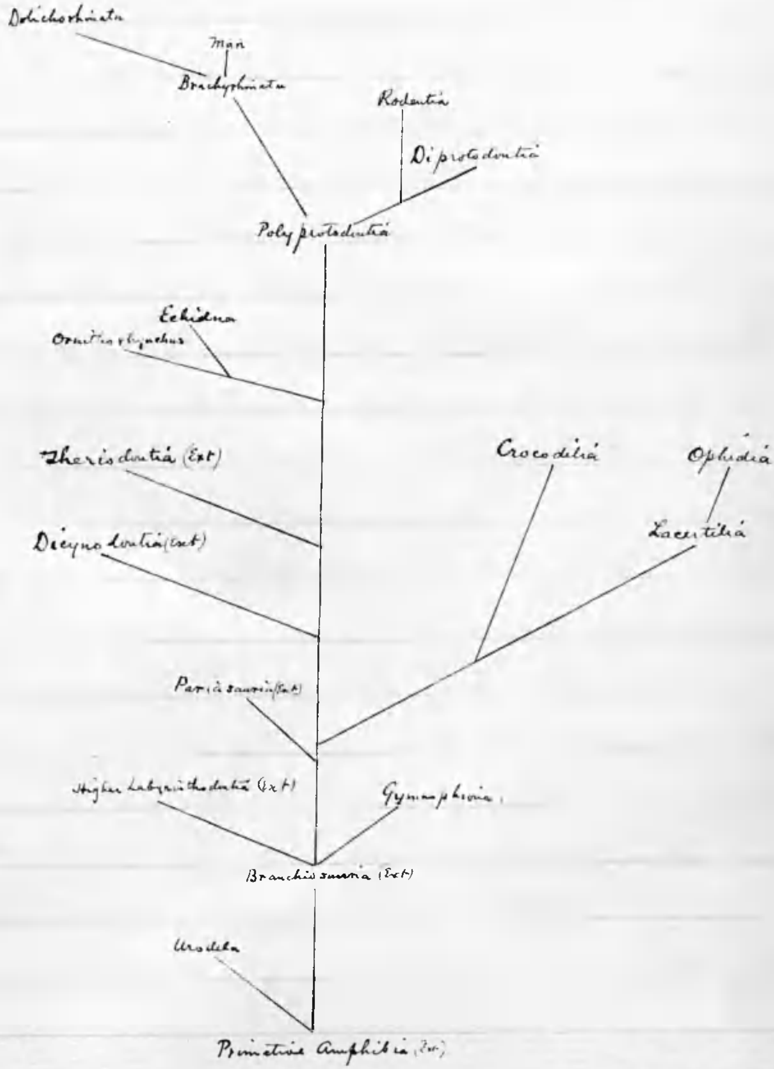
Taking into consideration the above facts in addition to the other known points in their anatomy I would suggest the following scheme as a provisional and necessarily imperfect classification of the Mammalia.

Class Mammalia.

Subclasses	Orders	Suborders
Monodelphia	Edentata (?)	
	Rodentia	
	Dolichorhinata	Carnivora
		Ungulata
		Insectivora (?)
	Brachyrhinata	Cheiroptera
		Primates (?)
Didelphia	Marsupialia	Polyprotodontia
		Diprotodontia
Ornithodelphia	Monotremata	Echidnia
		Ornithorhynchia

With the additional light derived from the study of the organ of Jacobson as to the relationships of the various groups I have endeavoured to construct a table of the descent of the typical groups.

Table illustrating the Evolution and affinities of the higher Vertebrates which possess an organ of Jacobson



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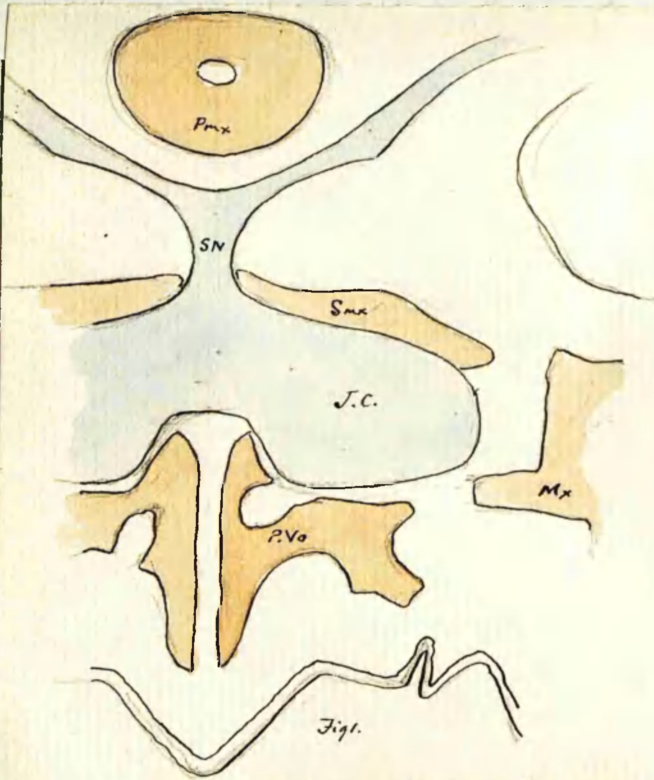
Plates.

References.

S.N. or N.S.	Nasal septum.
J.C.	Jacobson's Cartilage
S.C.	Stenson's Cartilage
A.N.	Alinasal Cartilage
M.P.C.	Median palatal Cartilage
N.F.C.	Nasal floor Cartilage.
Mx	Maxillary
Pmx	Premaxillary
p. Pmx	Palatine process of Premaxillary
Vo	Vomer
P.Vo	Prevomer
Na	Nasal
SMx	Septomaxillary
T.V. or T.P.V.	Turbinal plate of the Prevomer
N.V.	Nasal Valve
G.R.	Glandular ridge
G.	Gland
V.	Vein.
J.C.	Jacobson's Cartilage
J.D.	Jacobson's duct
S.D.	Stenson's duct.
L.C.	Lachrymal Canal.
R.C.	Recurrent Cartilage = Jacobson's Cartilage.
D.	Duct.

Plate I.



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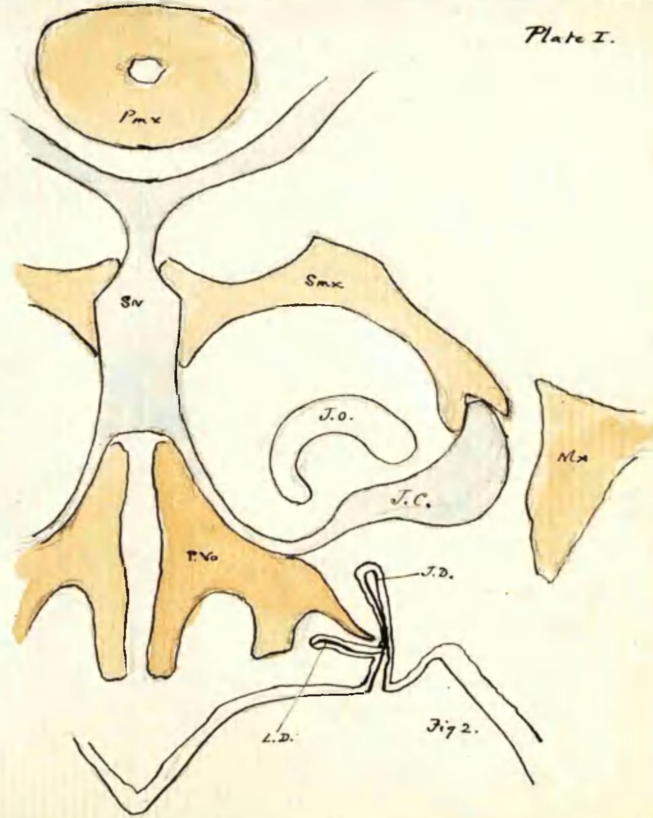
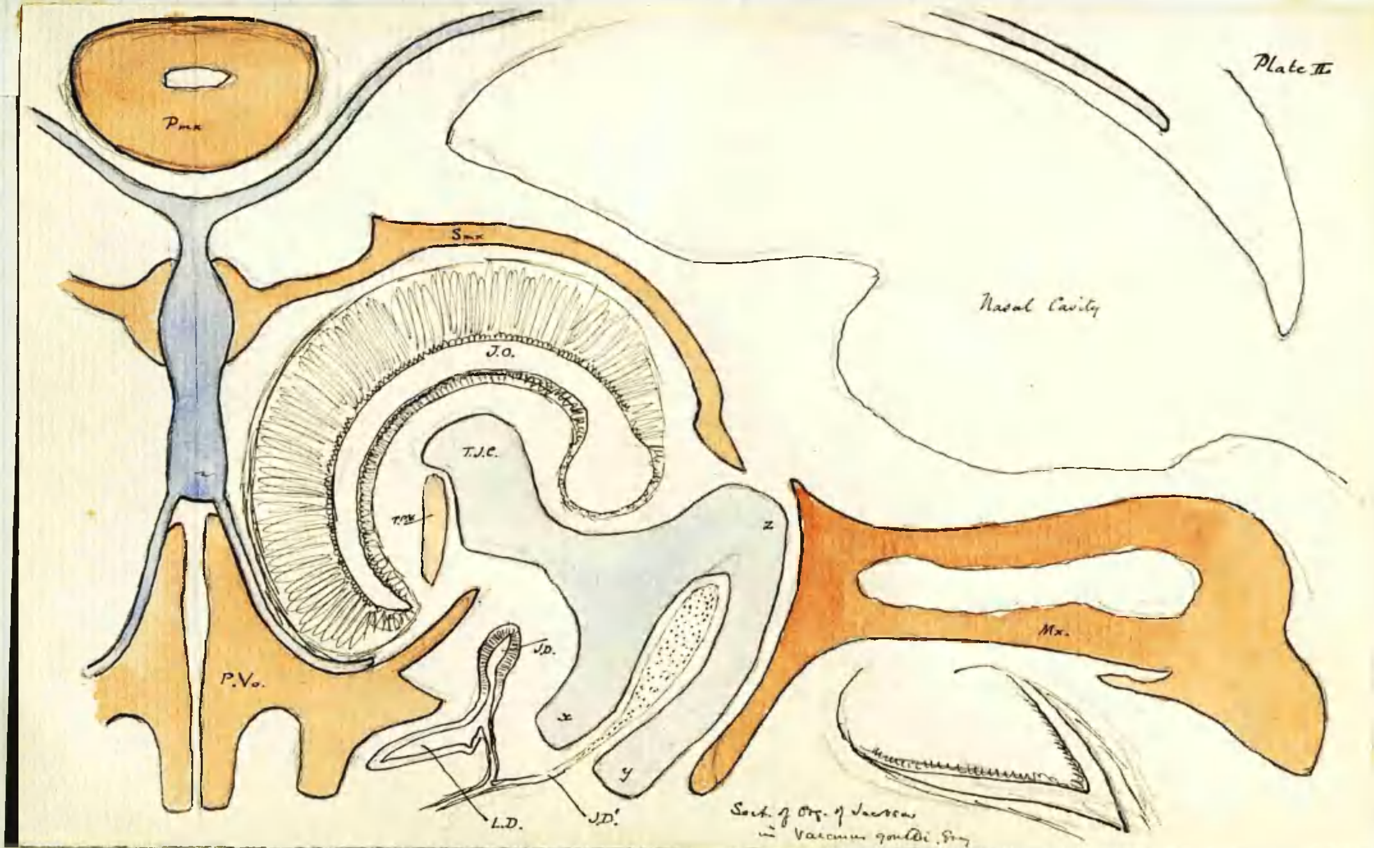


Fig 2.

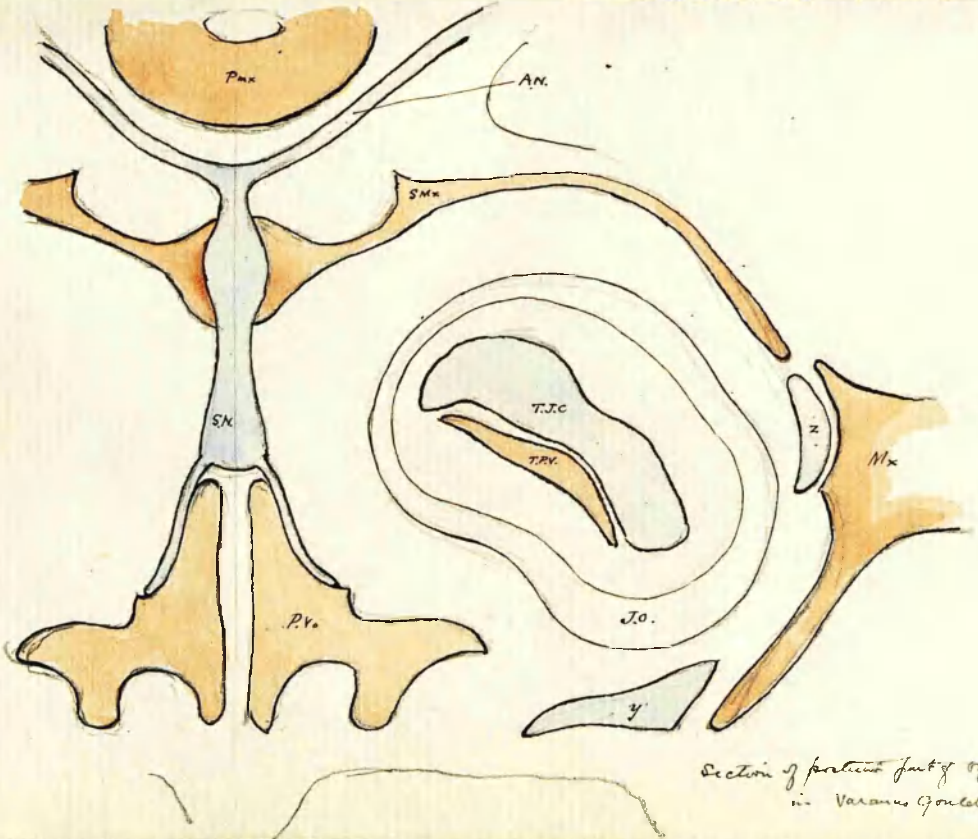
Section of the org. of Jacobson of
Varanus Gouldi, Gray

Plate II



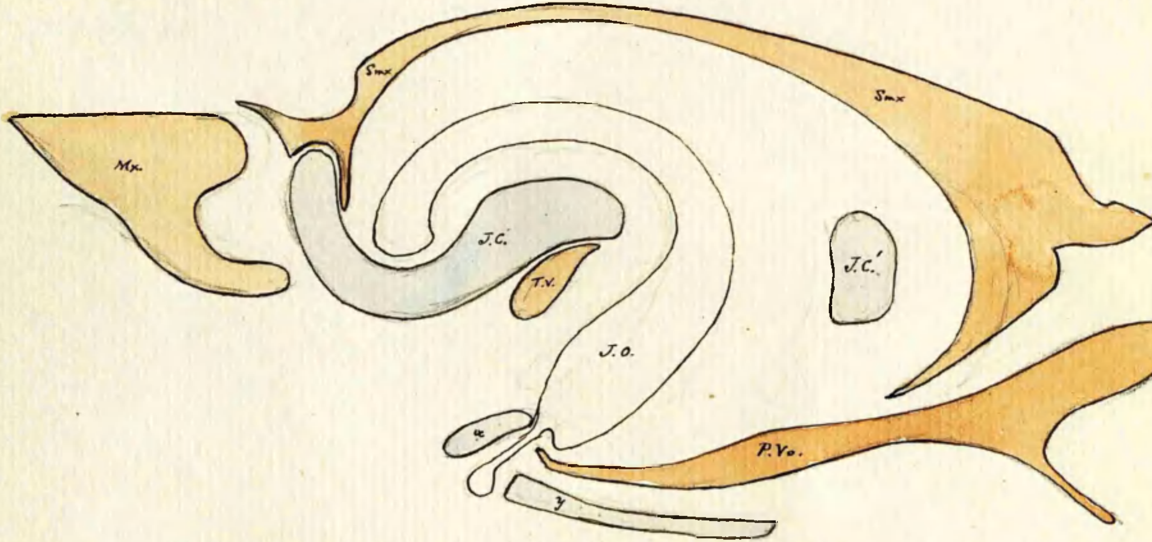
Sect. of Org. of Jacobson
in Vacuum gouldi, Gray

Plate III



Section of posterior part of organ of Jacobson
in Varanus Gouldi Gray.

Plate IV.



Longitud. Section of Organ of Jacobson in Varanus Gouldii, Gray

Plate V.

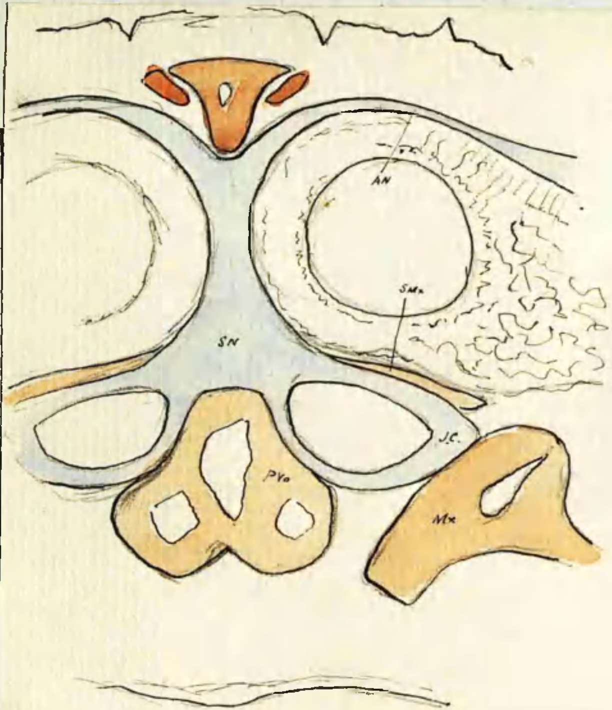


Fig. 1.

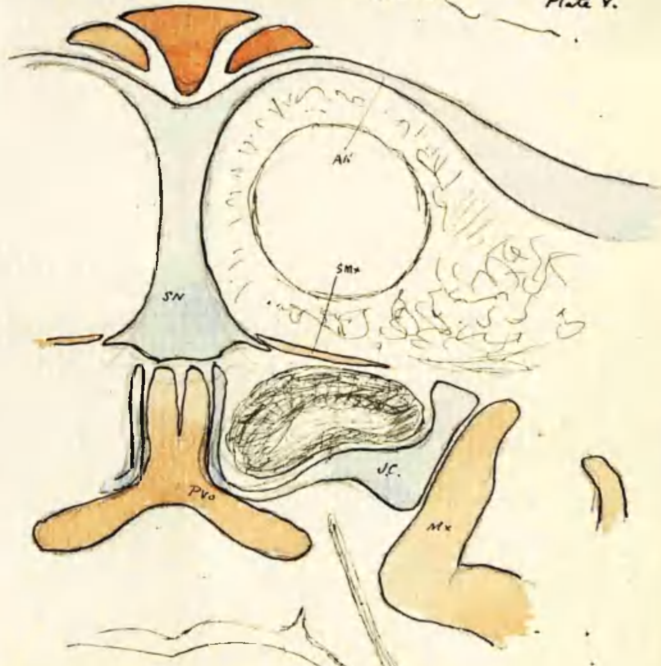
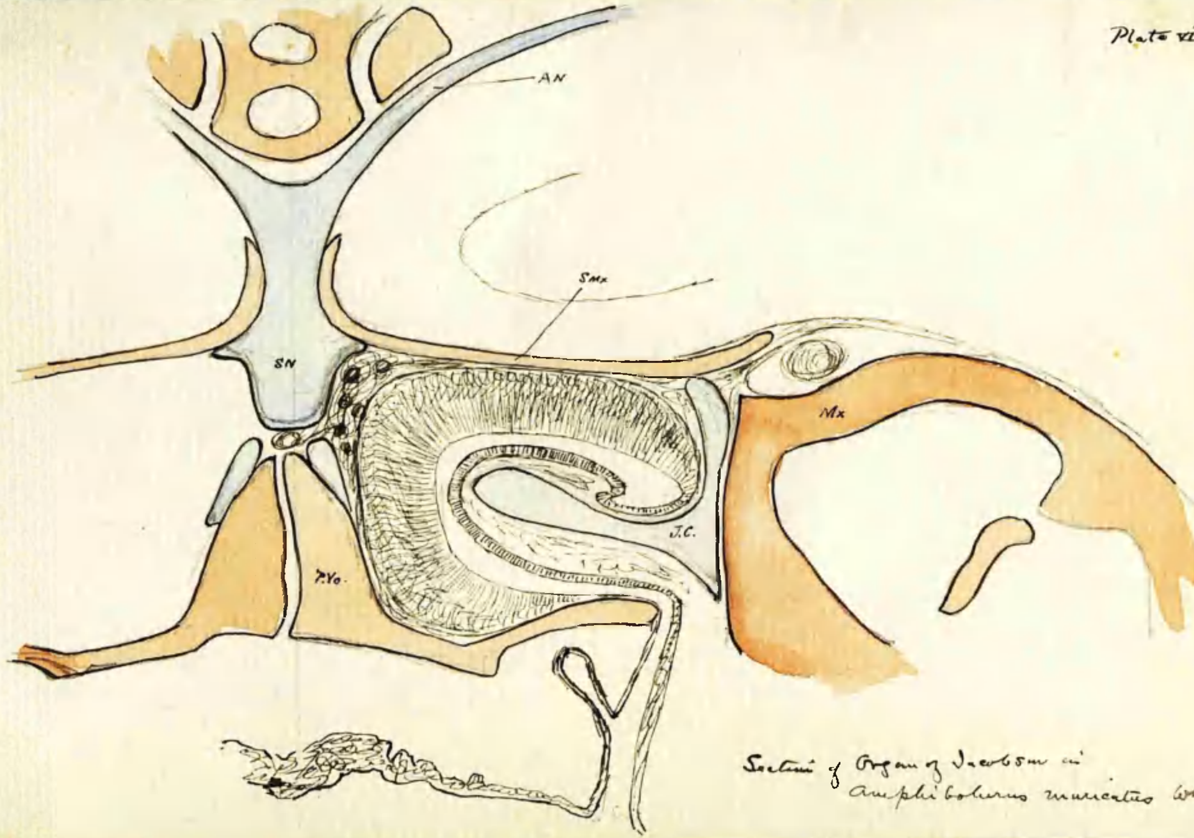


Fig 2.

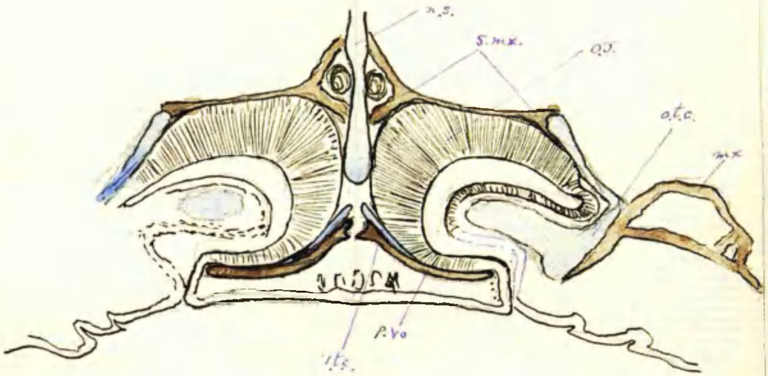
Sections across front of Jacobson's organ in *Diporophora australis*, Gray.
(a rather rare Queensland Agama)

Plate vi.



Section of Organ of Jacobson in
Amphibolurus muricatus White

Plate VII.



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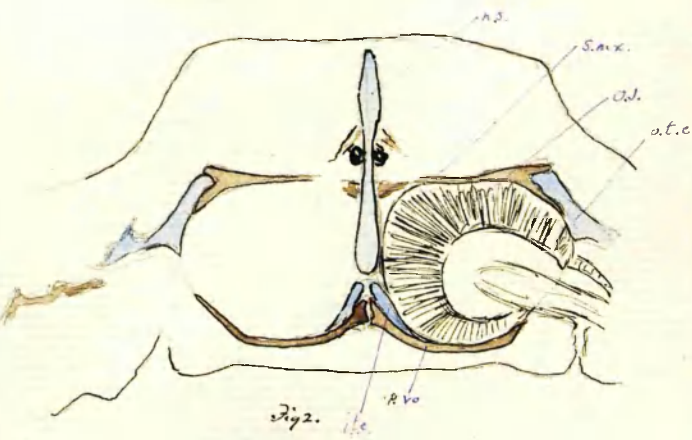


Fig 2.

Sections through Jacobson's Organ in newly hatched House Gecko

Plate VIII.

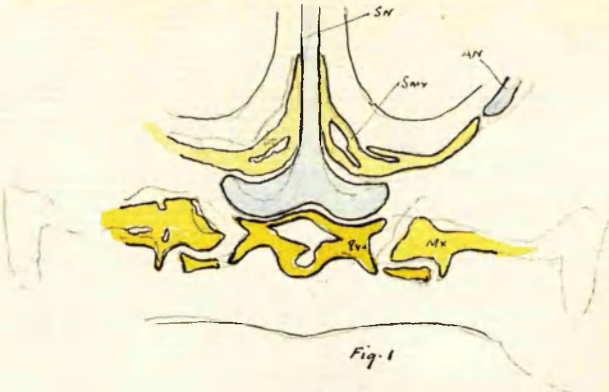


Fig. 1

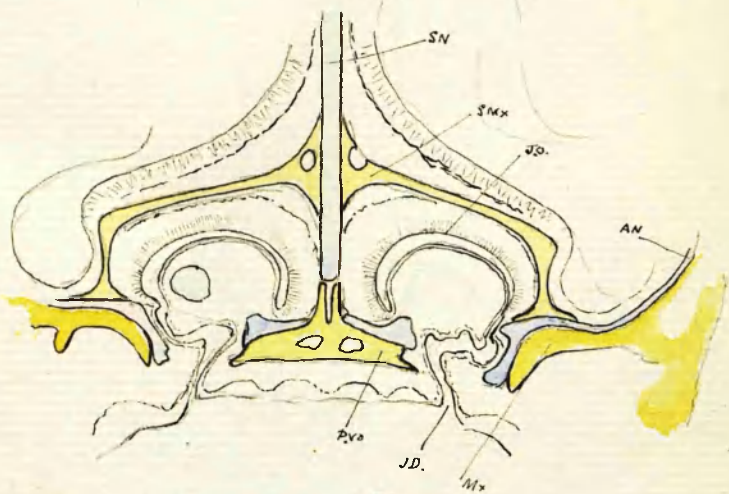
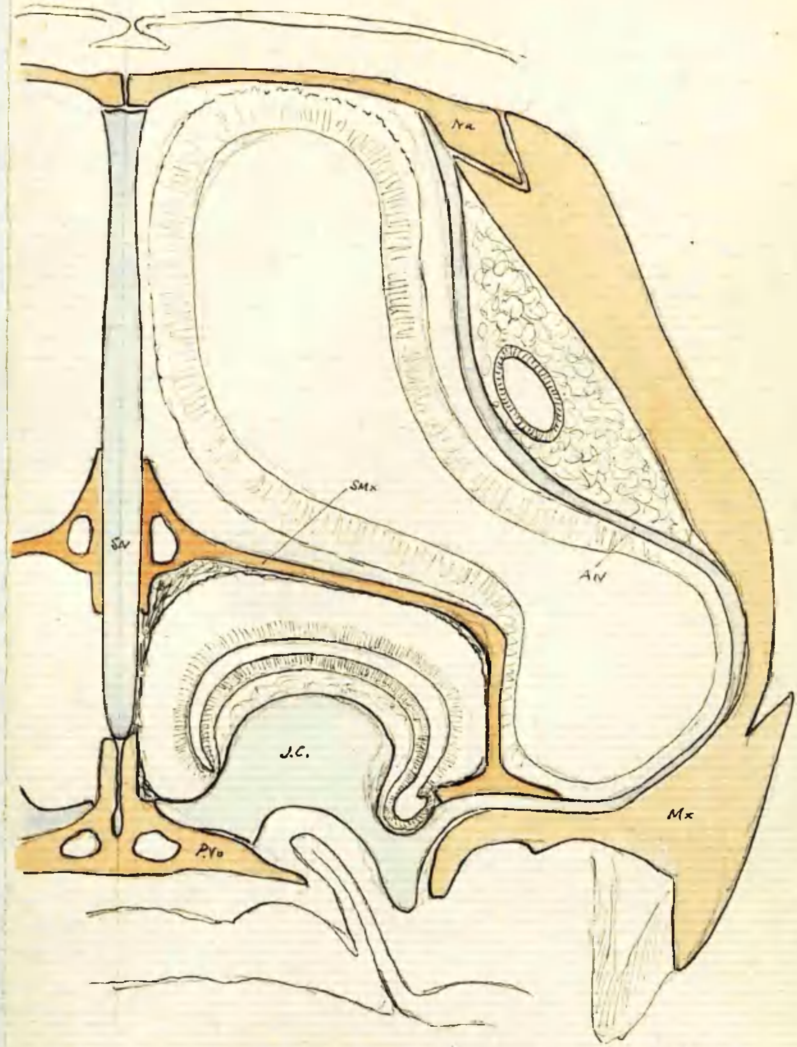


Fig 2.

T.S. across nose of Common little Australian Skink
Lygosoma lesueurii D.+B. ×30.

R.B. del ad nat.

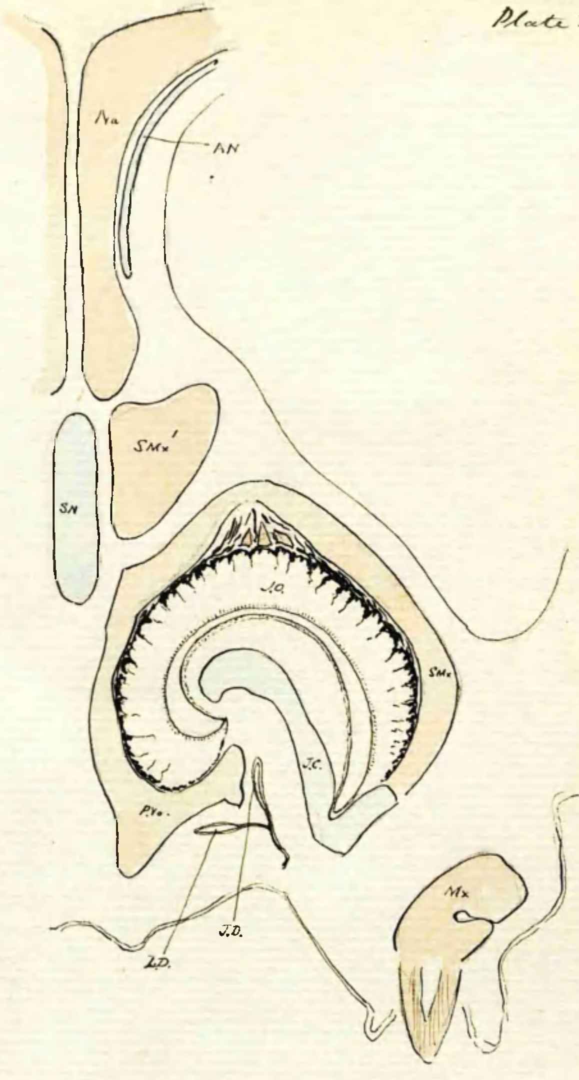
Plate IX.



T.S. of Organ of Jacobson in the Common Australian Skink
Lygosoma lesueurii D. & B. × 48.

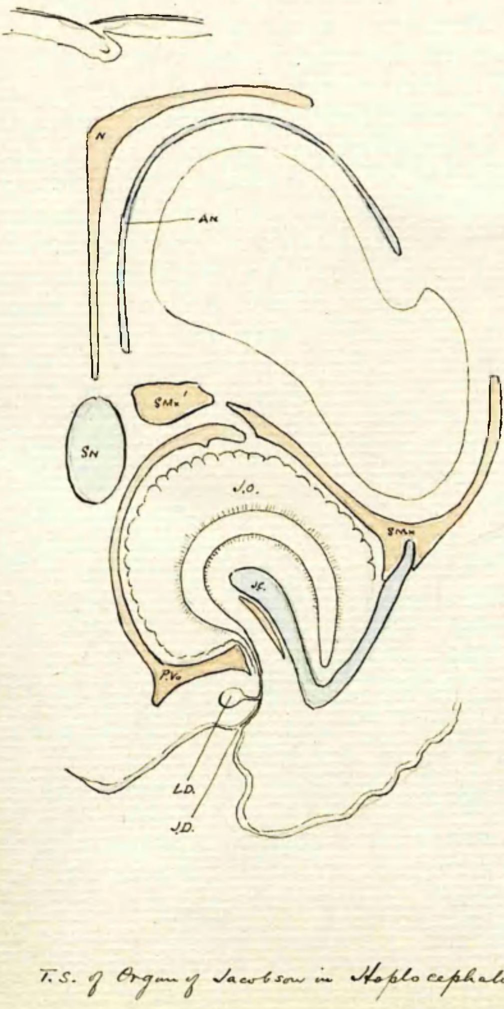
R.B. del ad nat.

Plate X



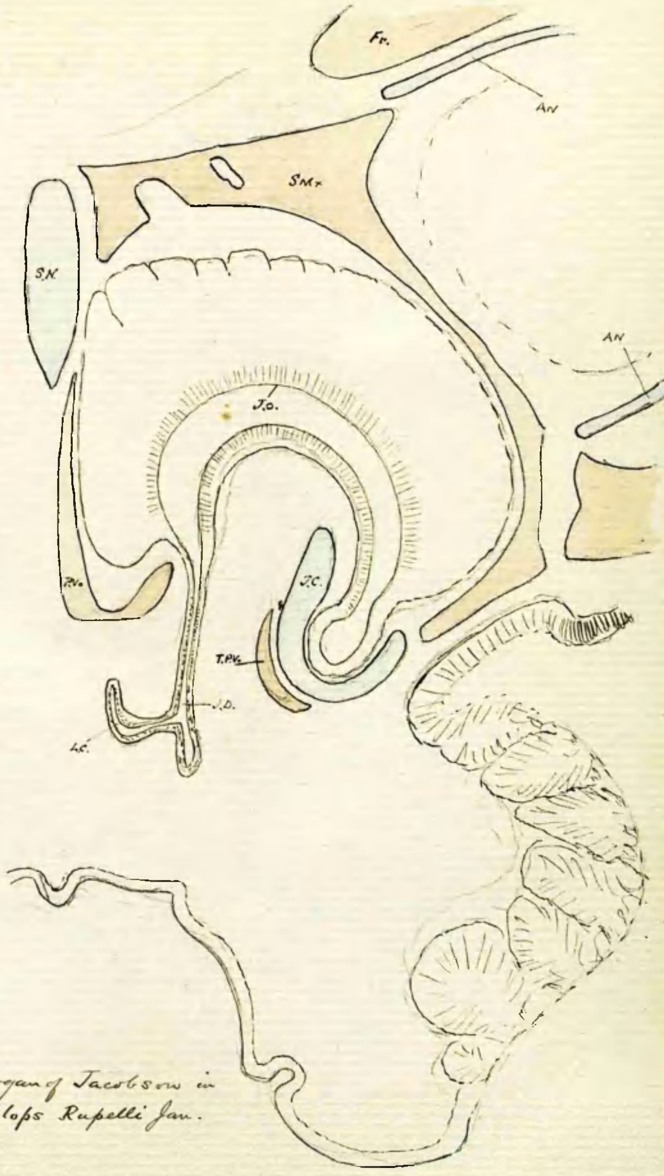
T.S. of Organ of Jacobson in the Australian Brown Snake
Diemenia superciliosa Fisch. × 26.

Plate XI.



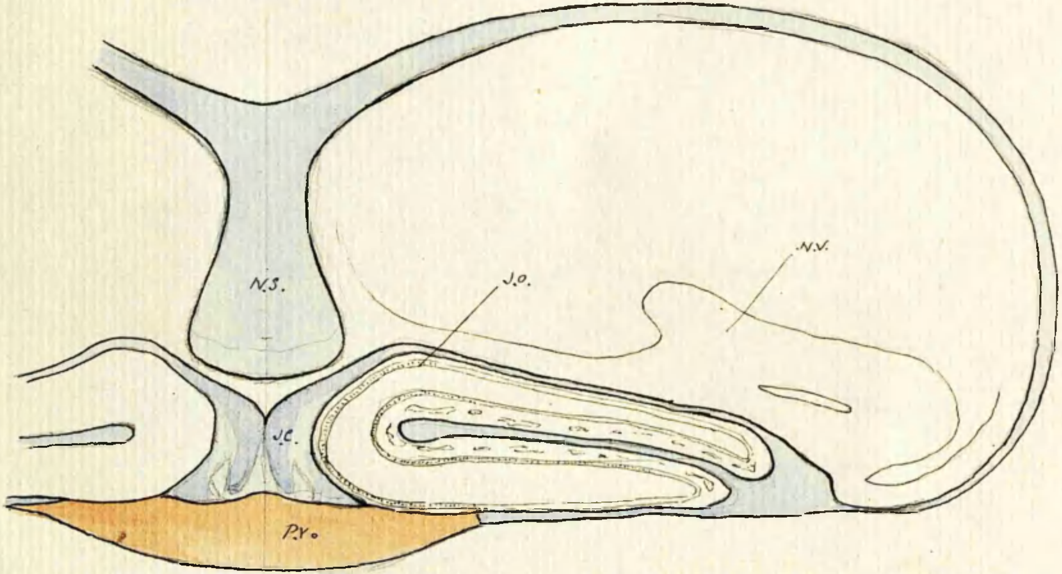
T.S. of Organ of Jacobson in Hoplocephalus Ramsayi Krefft

Plate XII.



T.S. of Organ of Jacobson in
Typhlops Rupelli Jan.

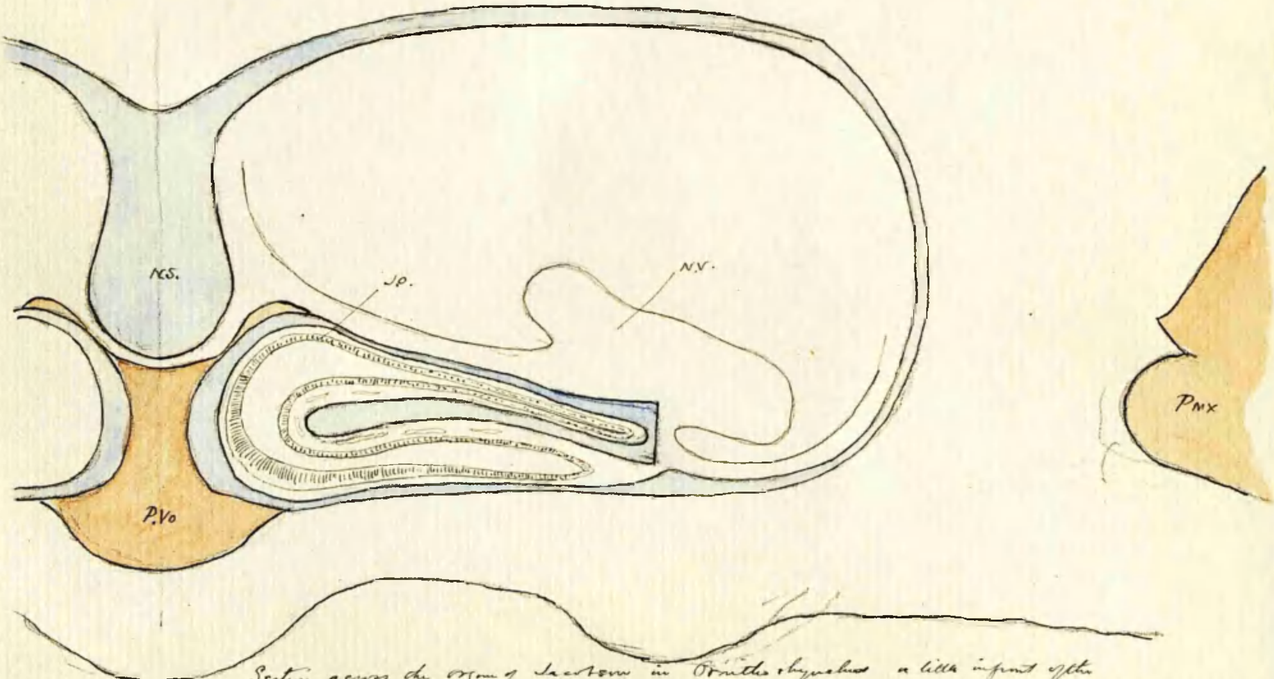
Plate XIII.



Section across the anterior part of Jacobson's Organ in Ornithorhynchus × 18.

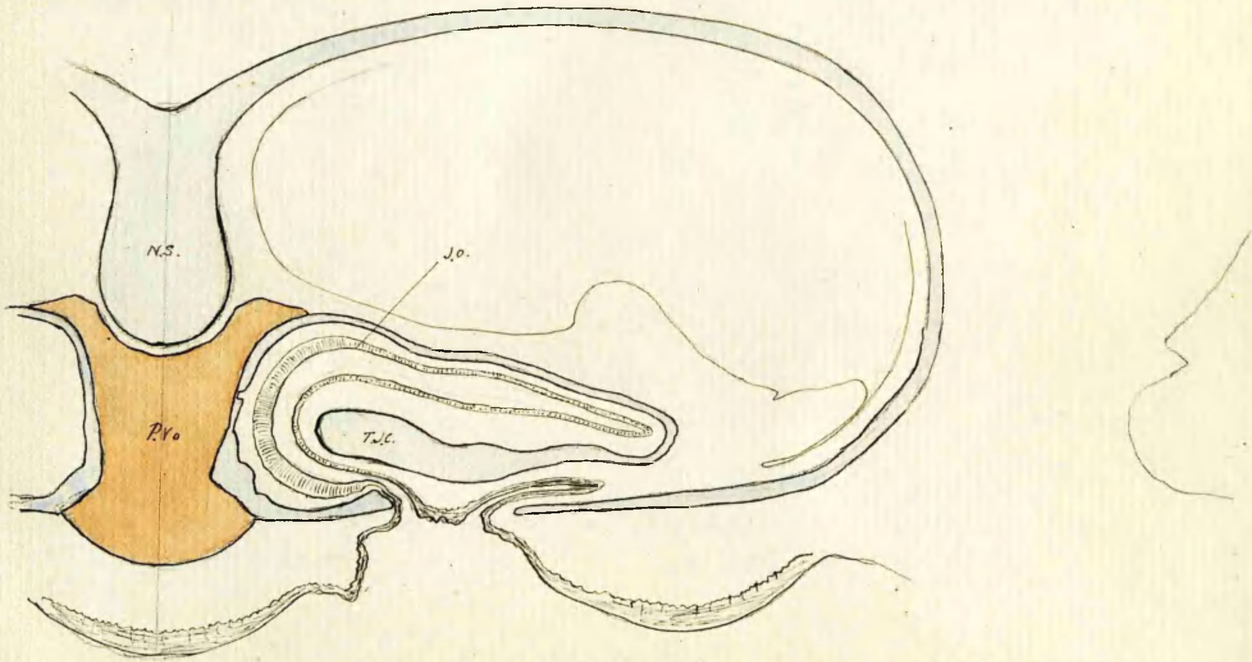
R. B. del. ad nat.

Plate XIV.



Section across the organ of Jacobson in Ornithorhynchus a little in front of the opening into the duct. × 18

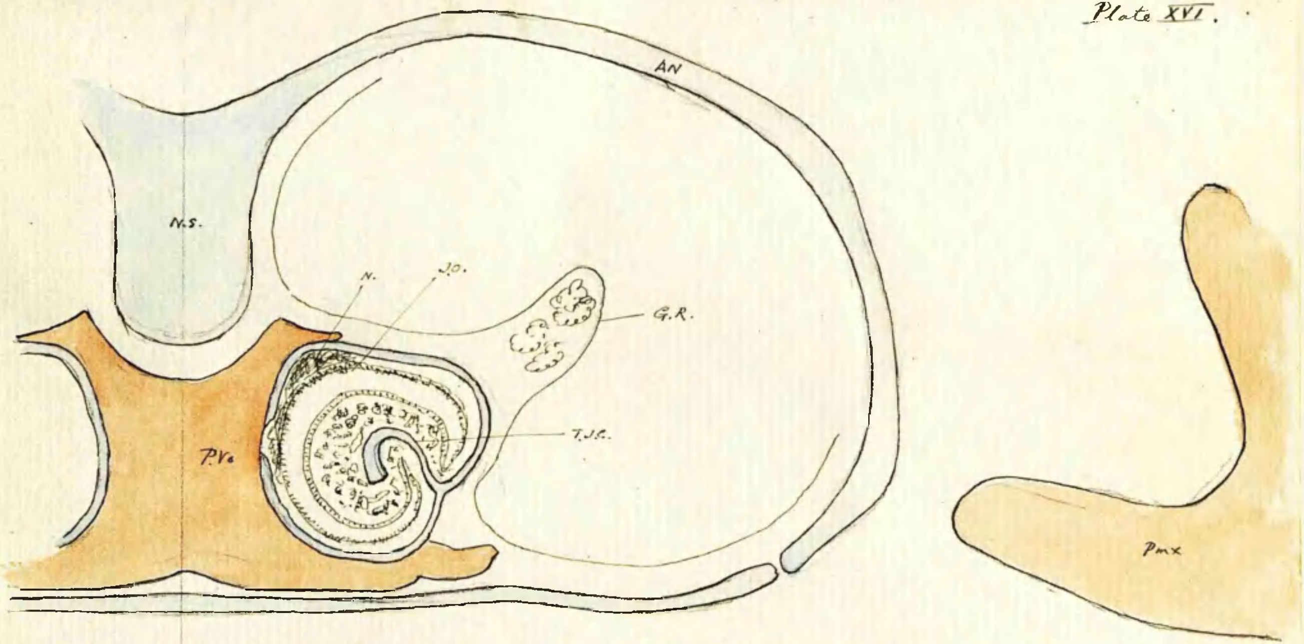
Plate XV.



Section through Jacobson's Organ in Ornithorhynchus, after its opening into its duct. x 18

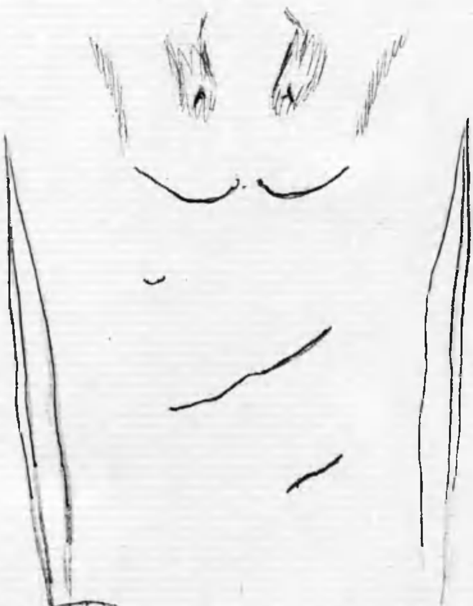
R.B. del. ad nat.

Plate XVI.



Section through the posterior part of Organ of Jacobson in Ornithorhynchus × 18.

Plate XVII.



x 3.

Nat. Size

View of the Anterior Palatal Region in Ornithorhynchus with relative size of Organ of Jacobson

Plate XVIII

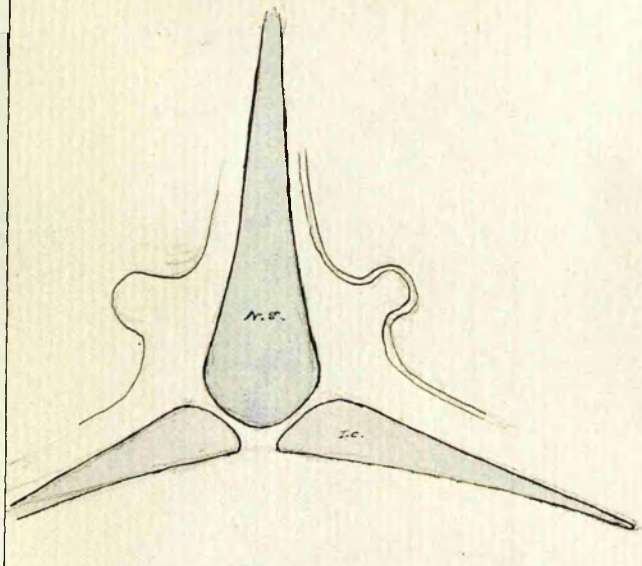


Fig 1.

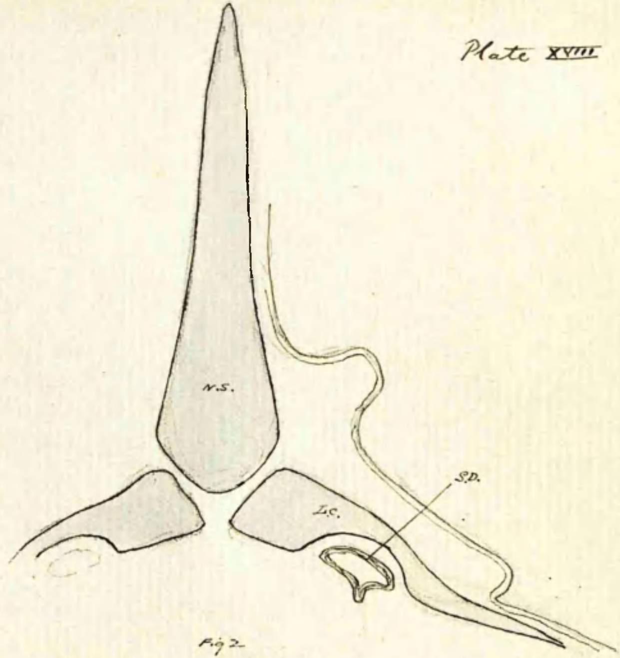


Fig 2.

Sections of Snout of Echidna illustrating the relations of the Cartilages at anterior part of Jacobsons Organ × 45

Plate XIX.

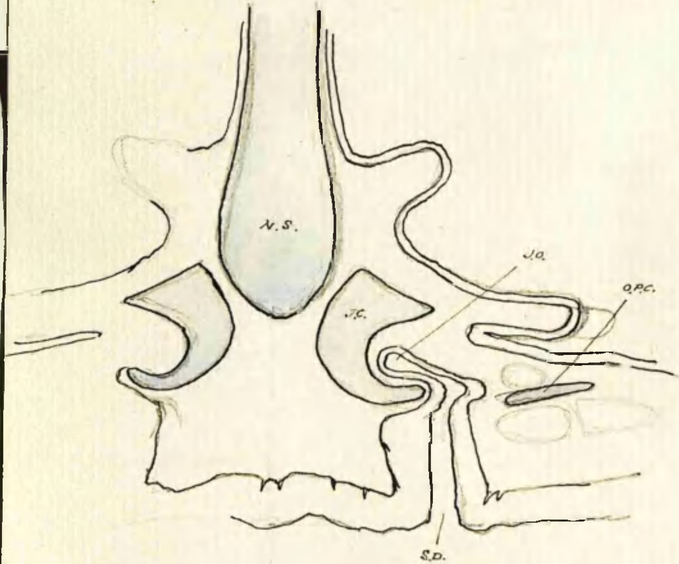


Fig 1.

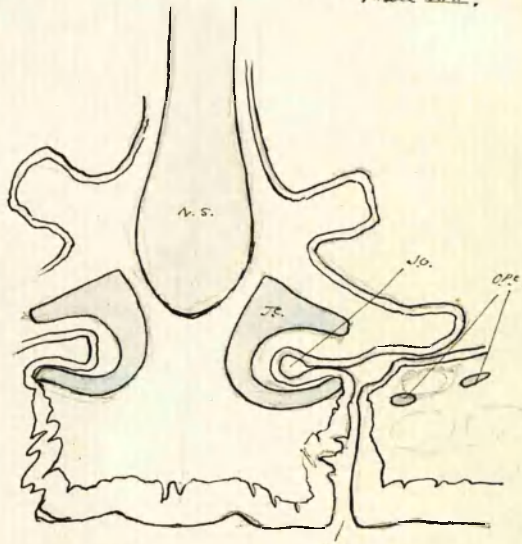
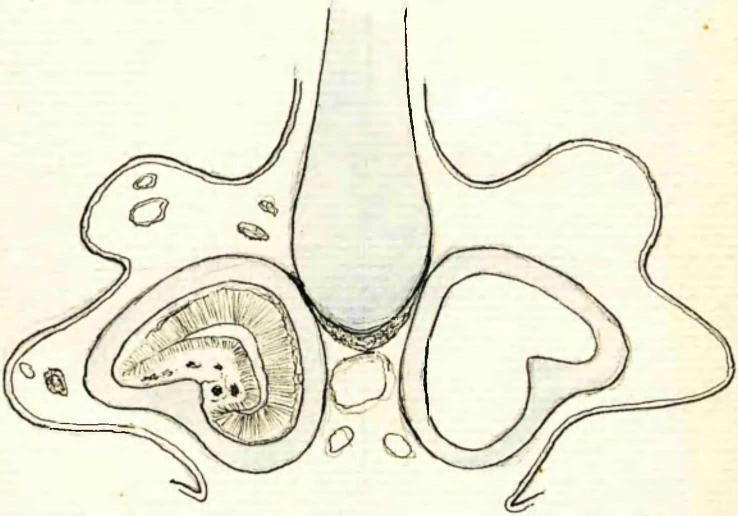


Fig 2

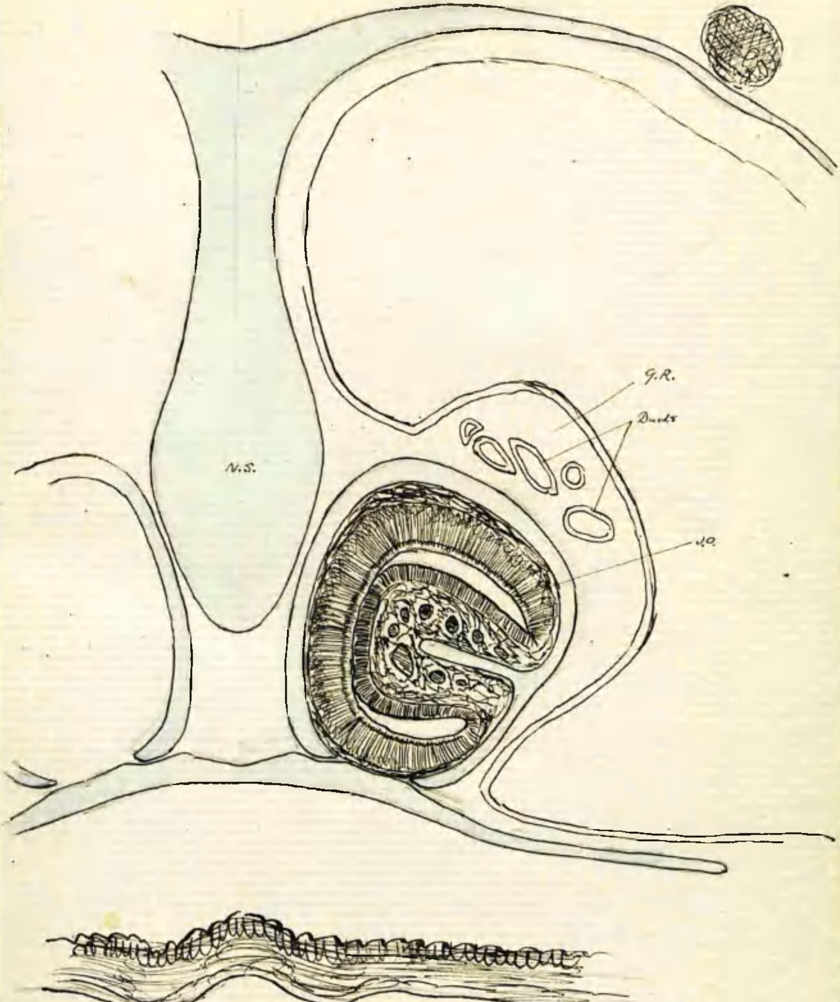
Transverse Sections of underpart of Snout of Echidna illustrating the connection of Jacobson's Organ with Stenson's duct. ×

Plate XX.



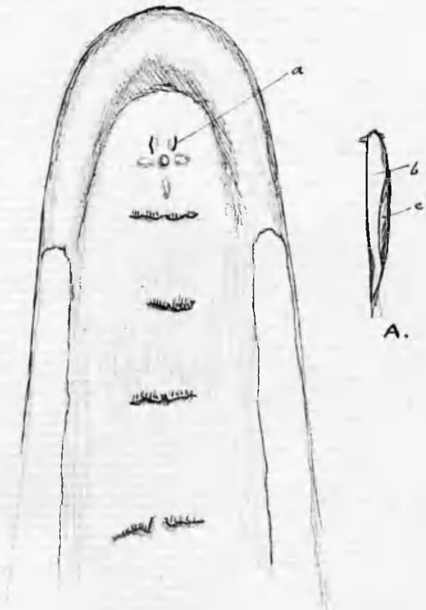
Transverse Section of Jacobson's Organs in Echidna, ¾ grown on the plane passing through posterior border of anterior Nares. × 45

Plate XXI.



Section across the organ of Jacobson in Echidna ×45.

Plate XXII



Front of Palate of Echidna ×3.
Showing at (a) the Nasopalatine foramen.

A represents the corresponding extent of the Organ of Jacobson. c, the turbinal plate.

Plate XXIII.

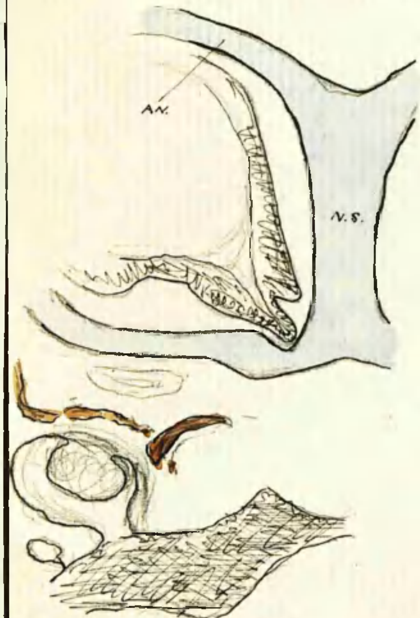


Fig 1.

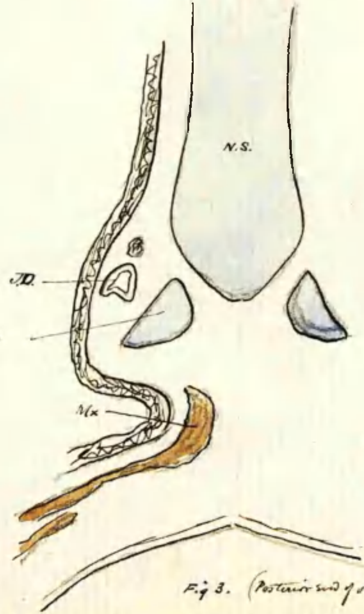


Fig 3. (Posterior end of organ)

Fig 2.

Sections across the nose of mammary foetus of Phascologale penicillata Shaw.

Plate XXIV

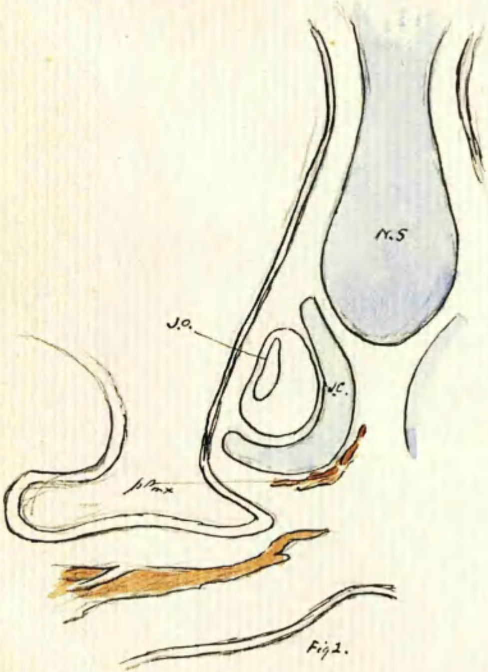


Fig 2.

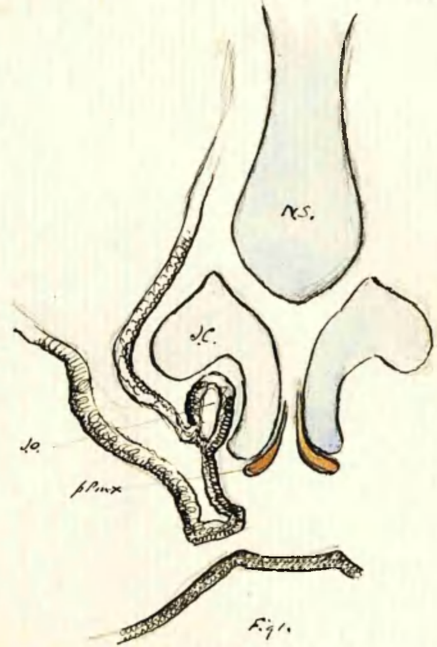


Fig 1.

Section across the Organ of Jacobson in mammary foetus of Phascologale penicillata ([illegible])

Pl. XXV.

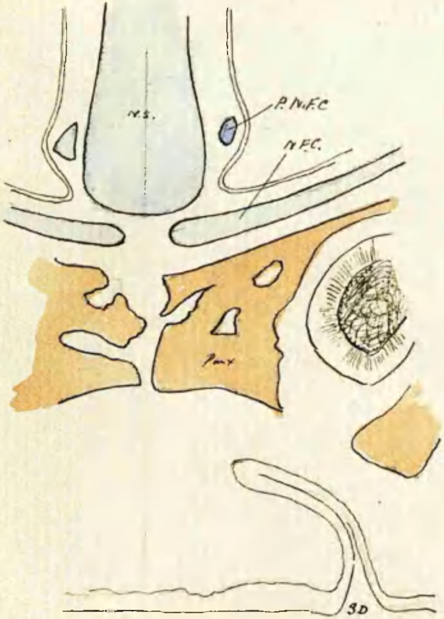


Fig 1.

Fig 2.

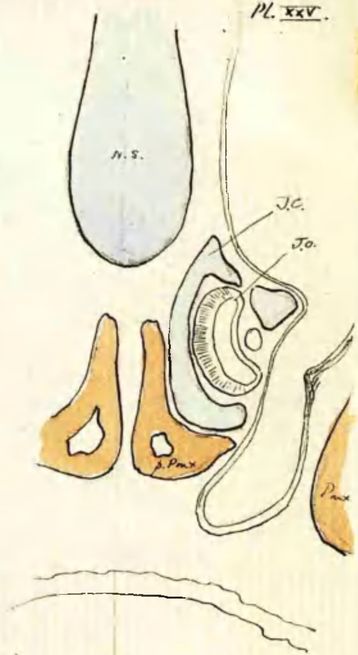
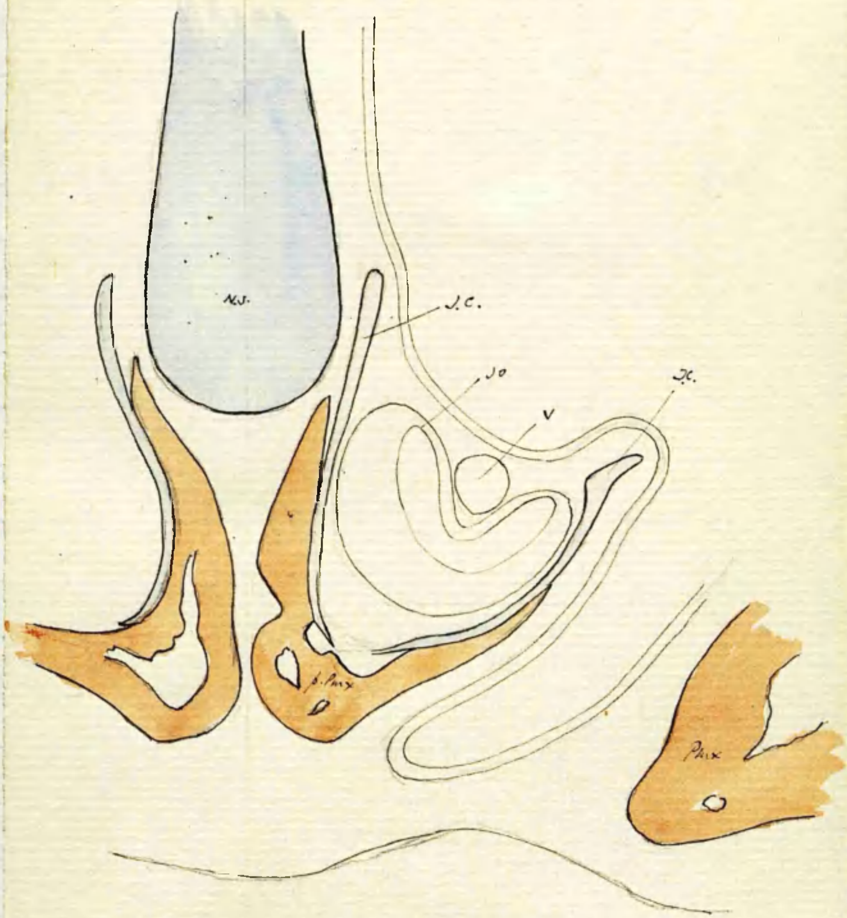


Fig 3.

Sections across the nose of almost adult Dasyurus viverrinus (Shaw) × 20.

Plate XXVI



T.S. of Org. of Jacobson in Dasyurus viverrinus (Shaw)

Plate XXVII

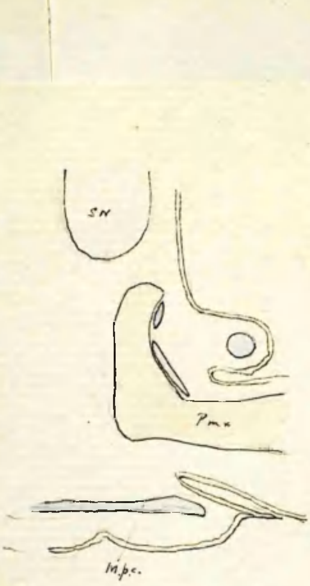


Fig 1.

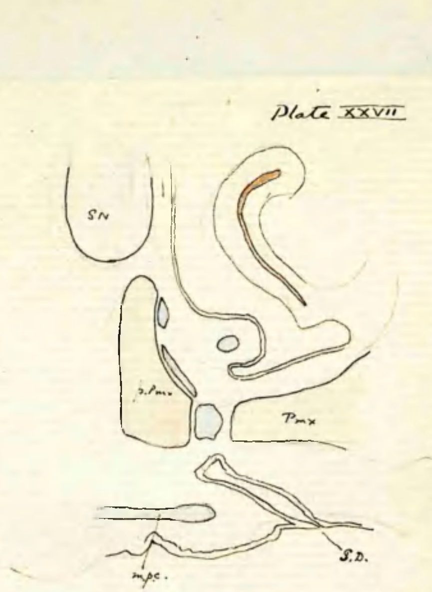


Fig 2.

Fig 3.

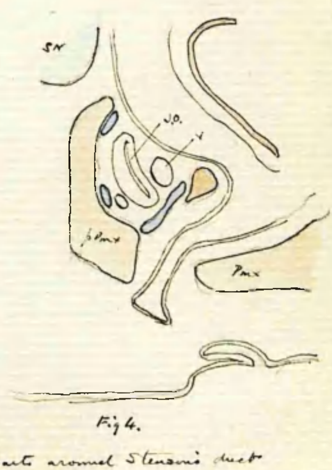


Fig 4.

Trans. Sects. illustrating the condition of parts around Stenson's duct and anterior end of Jacobson's Organ in adult Perameles nasuta

Plate XXVIII.

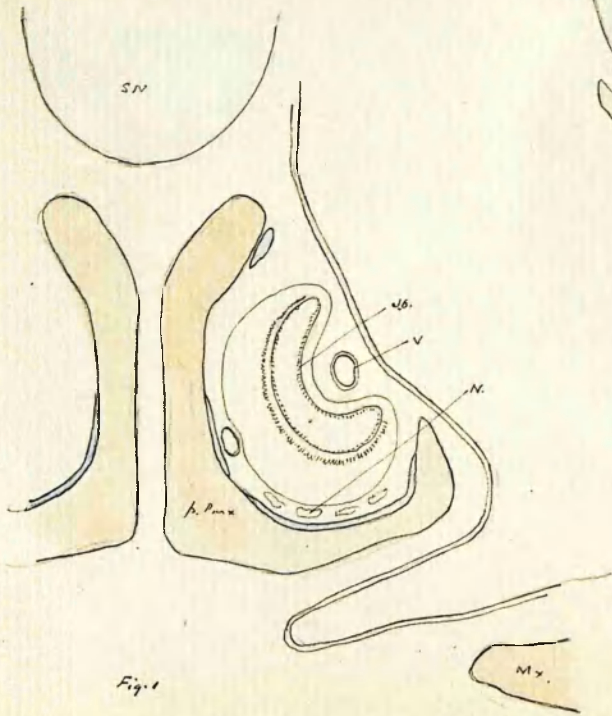


Fig. 1

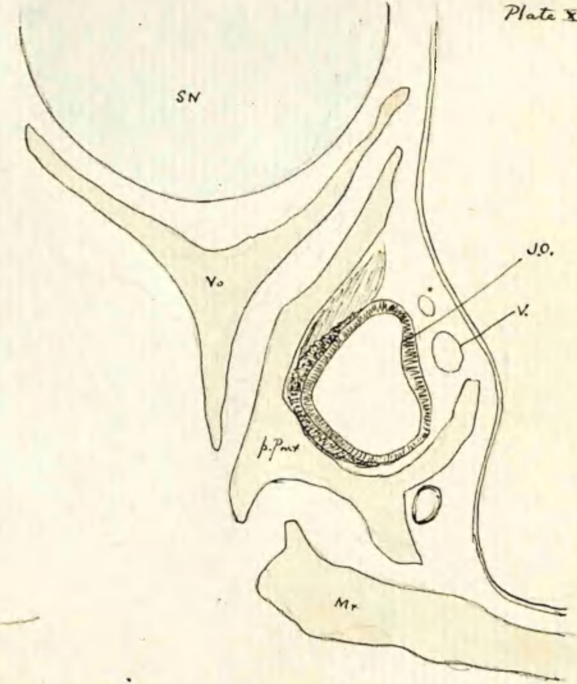


Fig. 2.

Trans. Sects. of Organ of Jacobson in adult Perameles nasuta

Plate XXIX

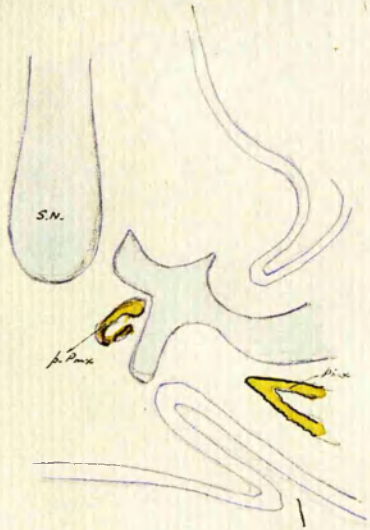


Fig. 1

Fig 2

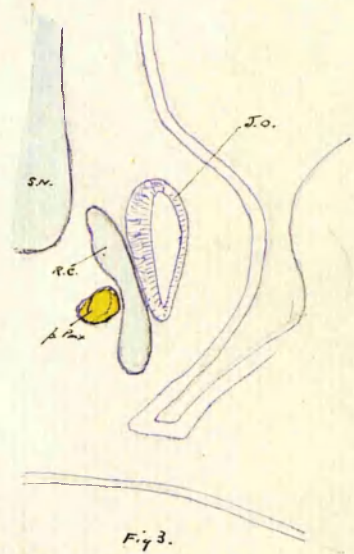
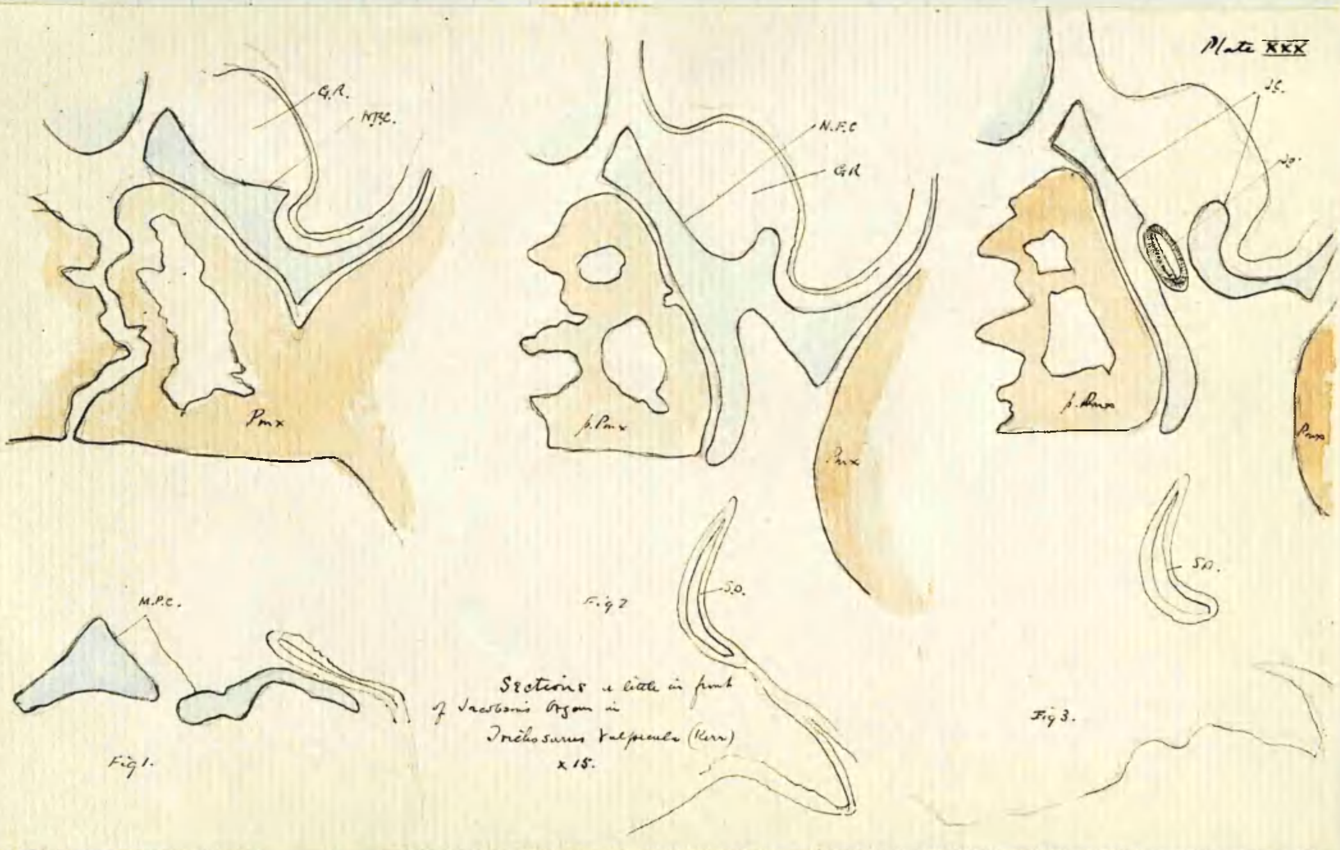


Fig 3.

Sections across nose of mammary foetus of Trichosurus vulpecula (30 mm) 26

(Head length (10.5 mm)

Plate XXX



Sections a little in front
of Jacobson's Organ in
Trichosurus Vulpecula (Kerr)
x 15.

Plate XXXI.

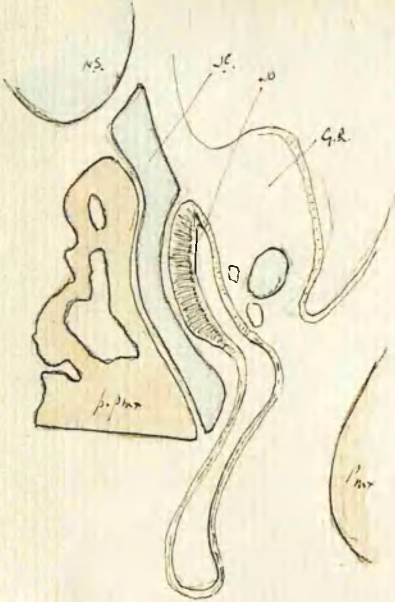


Fig 1

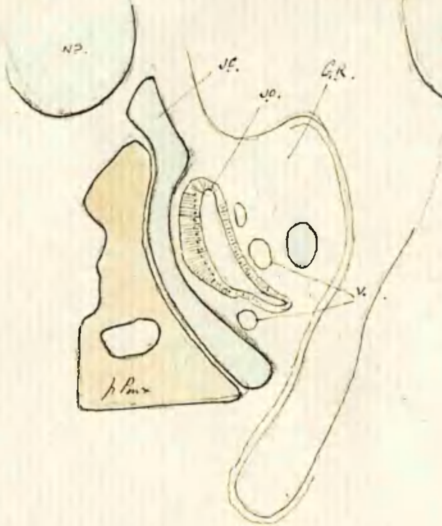
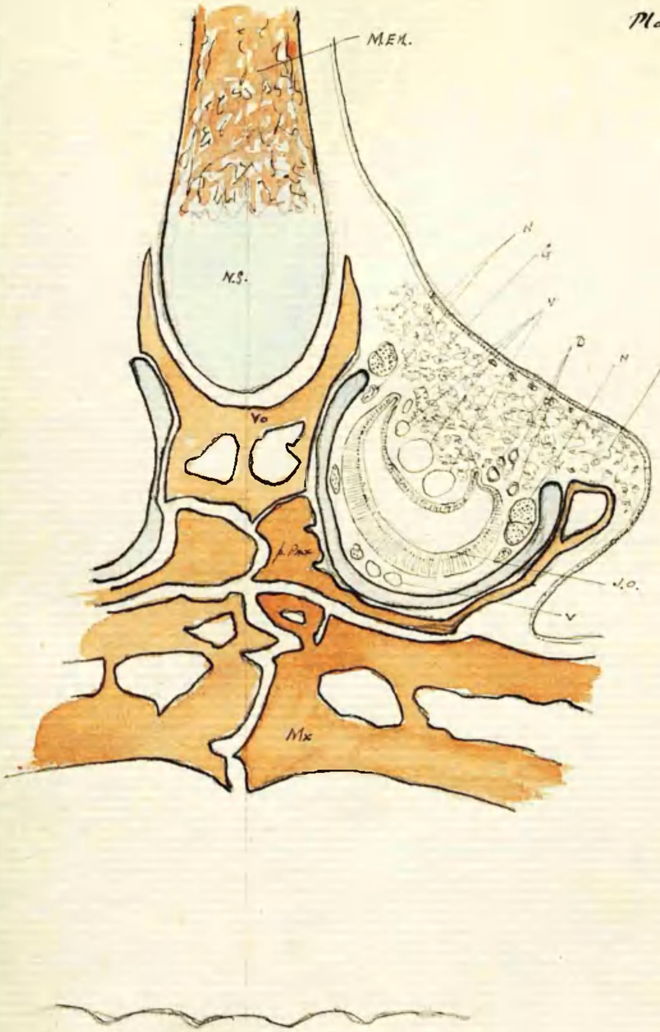


Fig 2

Fig 3

Sections through the anterior part of Jacobson's Organ in Trichosurus vulpecula (Kerr) × 15

Plate XXXII.



Transverse section through the main part of Organ of Jacobson in adult Trichosurus vulpecula (Kerr) = Phalangista vulpina Desm. × 15

Plate XXXIII.

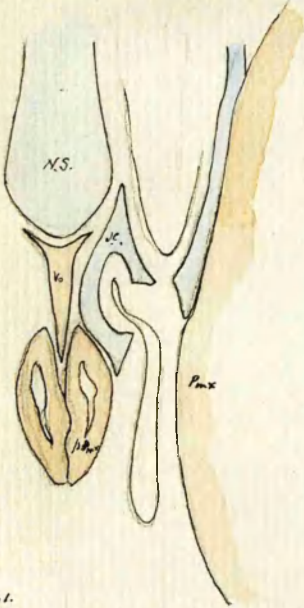


Fig 1.

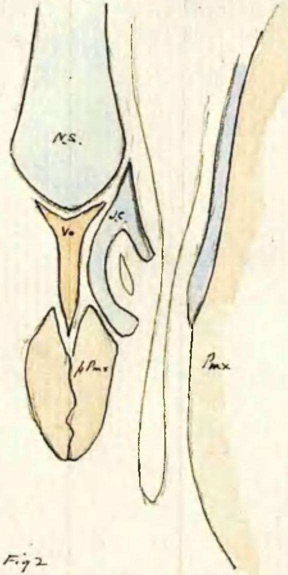


Fig 2

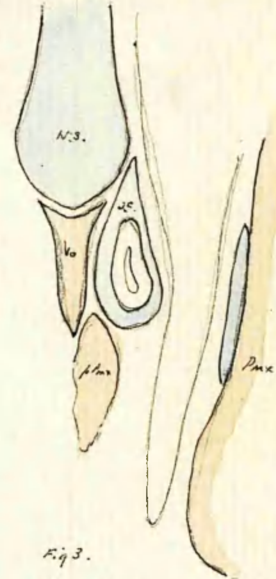


Fig 3.

T. V. Sections through anterior part of Jacobson's organ in adult
Phascolarctos cinereus Goldf. ×

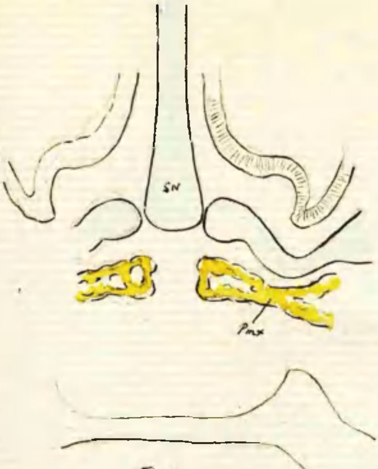


Fig. 1.

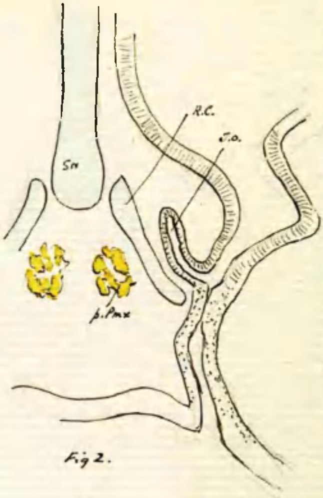


Fig 2.

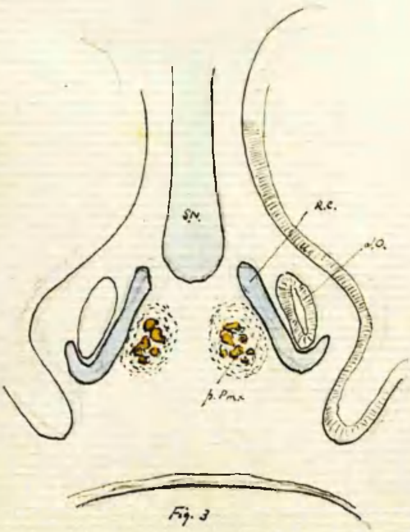


Fig. 3

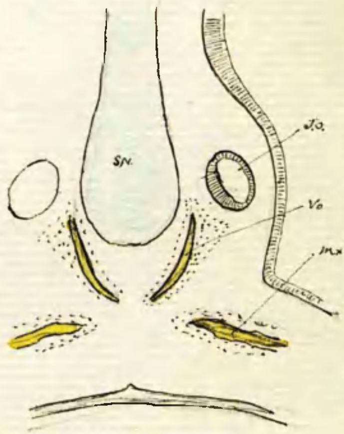


Fig. 4.

Sections through nose of mammary foetus of Macropus (29 mm)

Plate XXXV

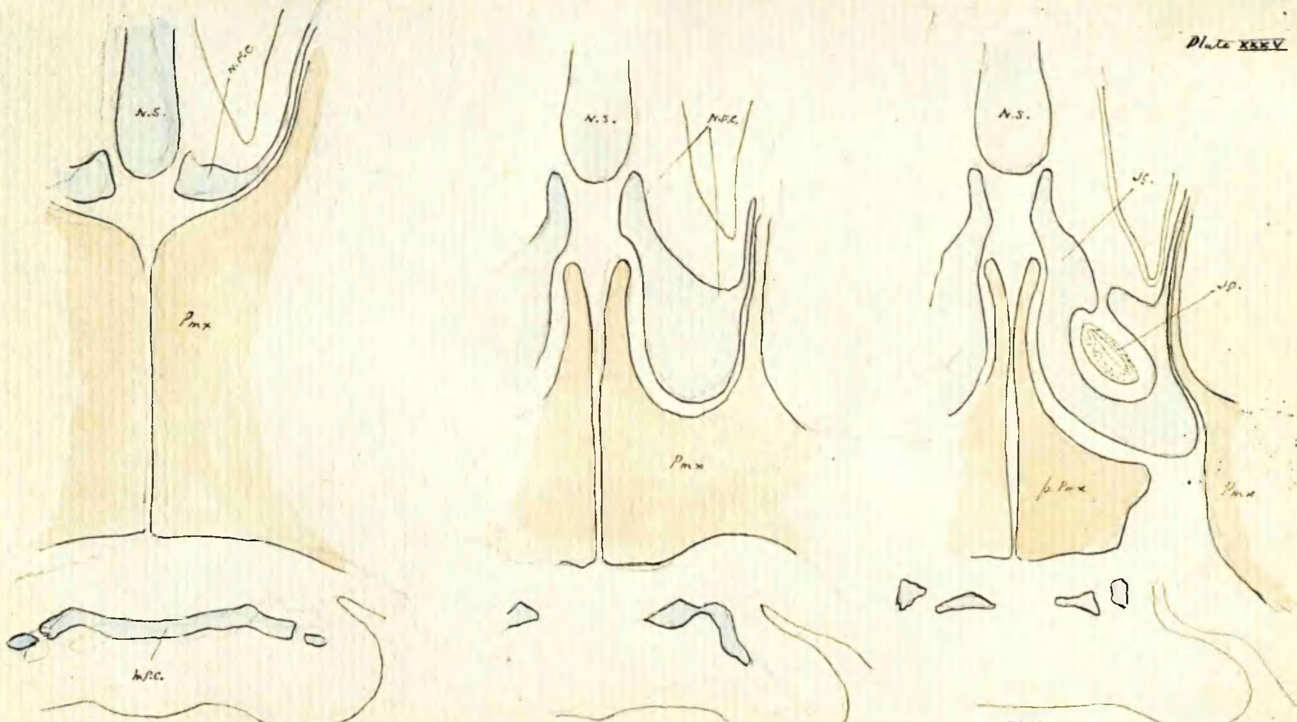


Fig. 1. Fig. 2. Fig. 3.

Transverse section immed.ly in front of Jacobson's organ in well developed pouch specimen (head 50 mm) of Macropus ualabatus (L+G.)

Plate XXXVI

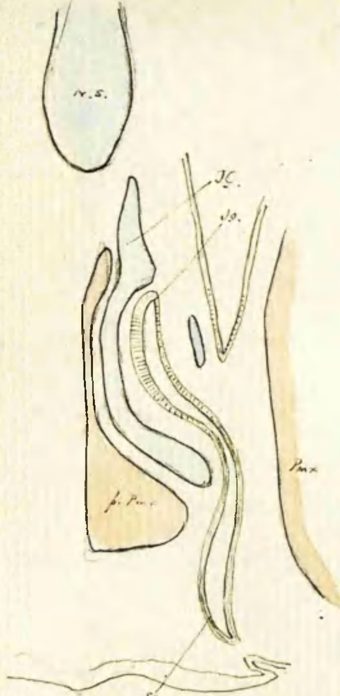


Fig 1

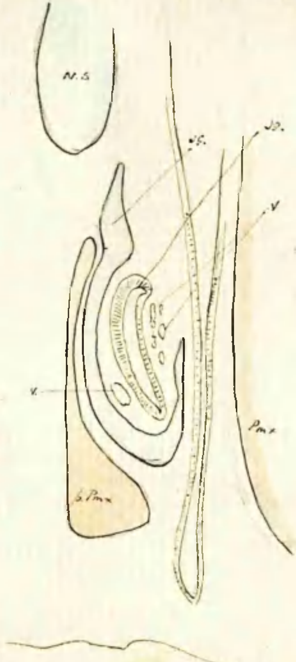


Fig 2

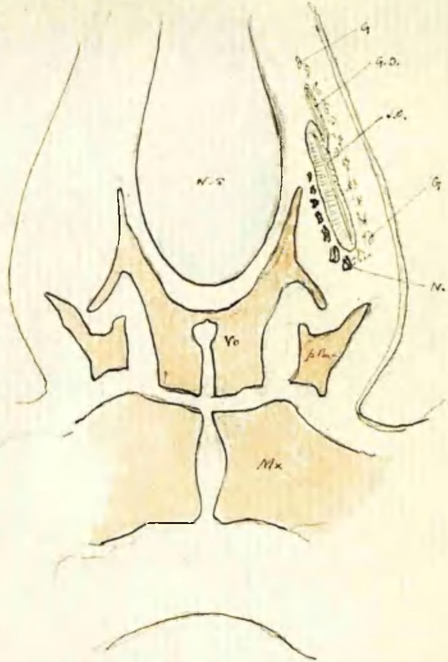
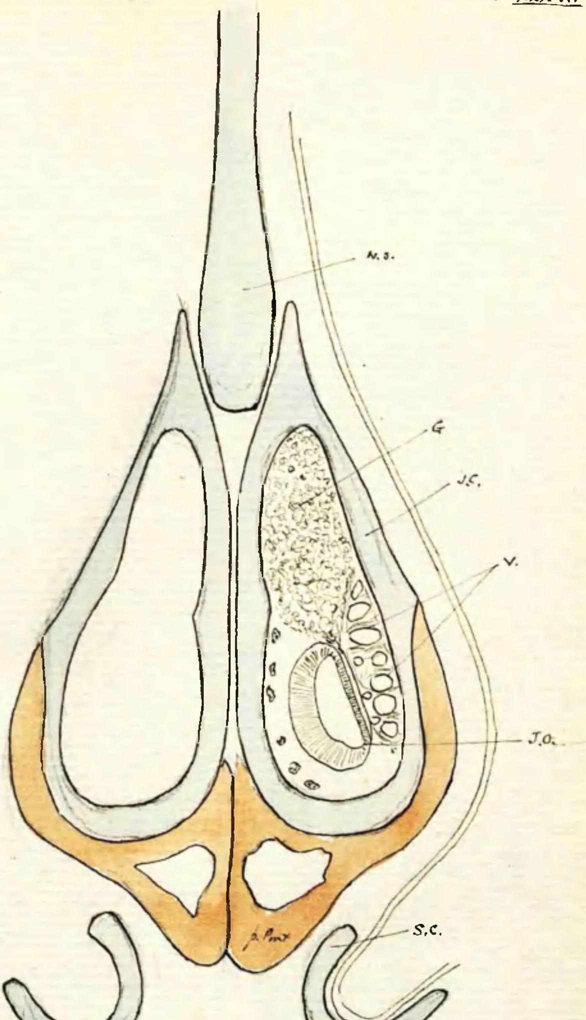


Fig 3.

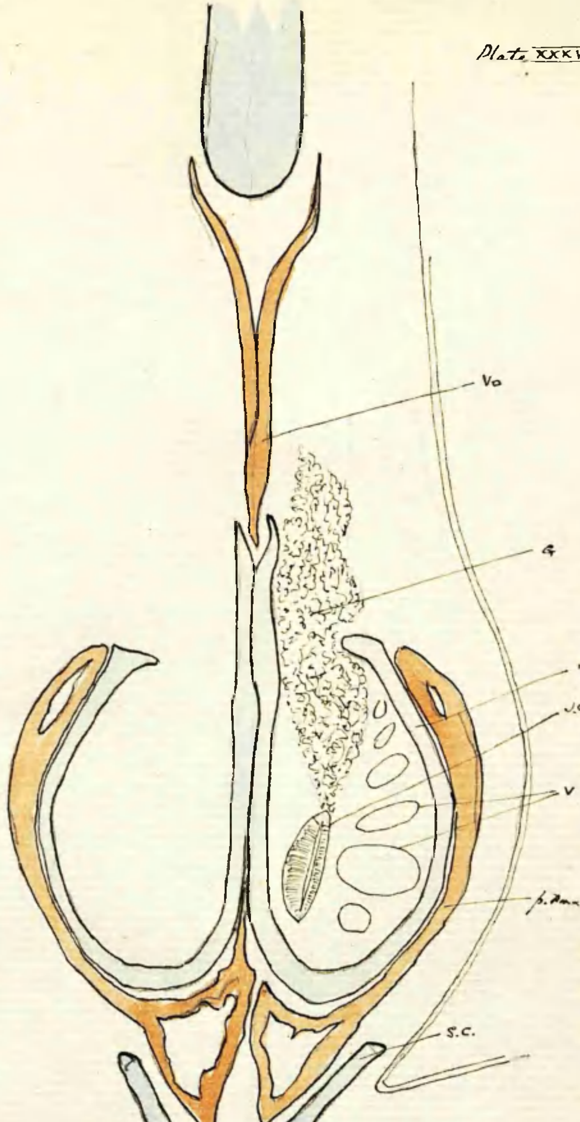
Transverse sections of Jacobson's Organ of well developed pouch specimen (head 50mm) of **Macropus ualabatus** (L+G.)

Plate XXXVII.



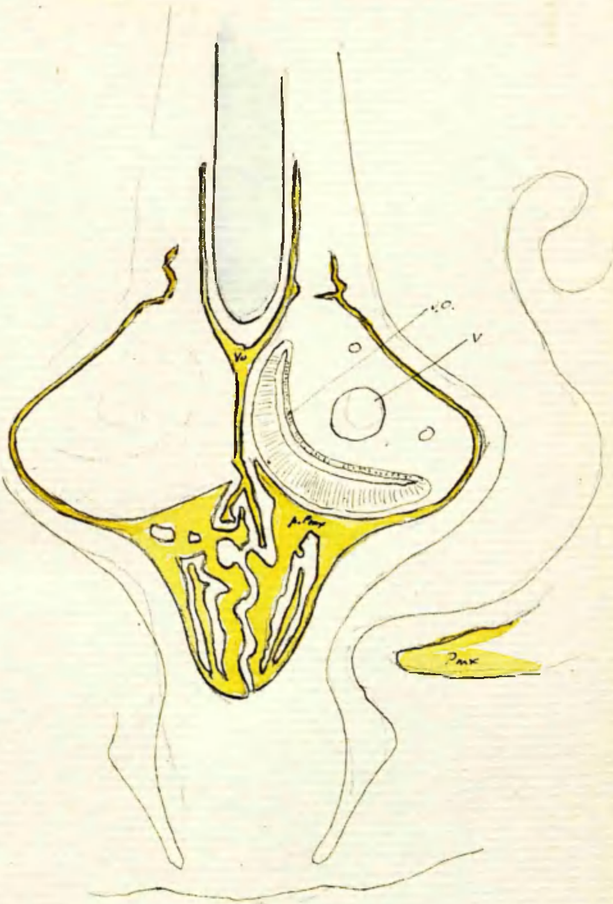
Section through the anterior part of Jacobson's Organ
in a young Hare   Lepus timidus L.

Plate XXXVIII.



Section through the hinder part of Jacobson's Organ in a young Hare — Lepus timidus L.

Plate XXXIX.



Organ of Jacobson in Hydromys chrysogaster Geoff.

Plate XL.

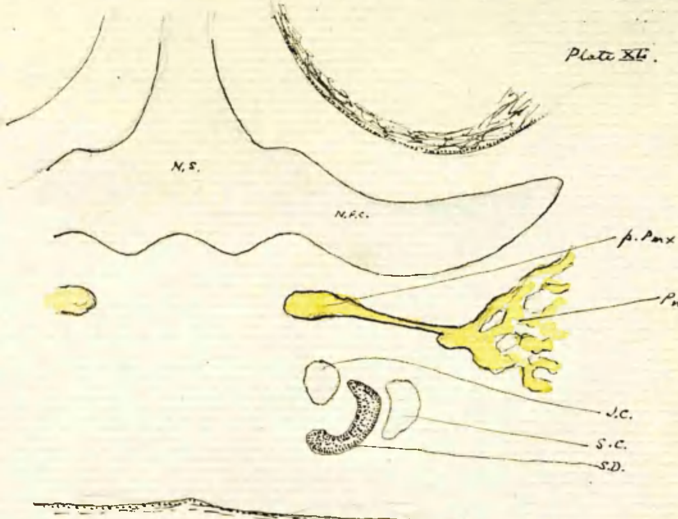


Fig 1.

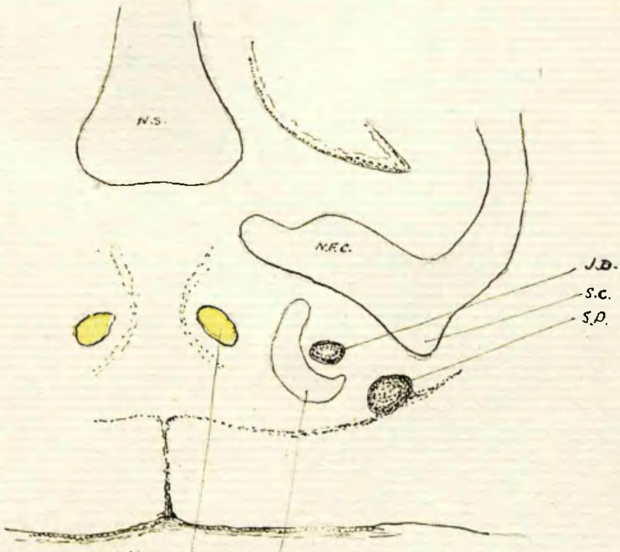


Fig 2

Sections illustrating Stensons and Jacobsons ducts in foetal calf (Bos Taurus L) 65mm
× 50

Plate XLI.

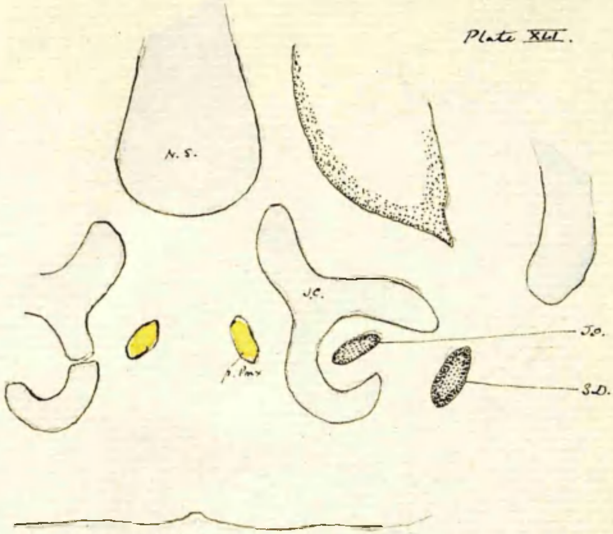


Fig 1.

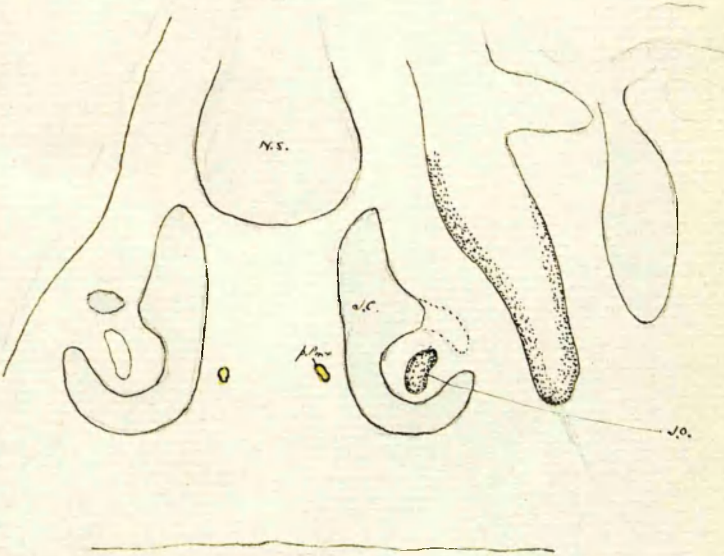


Fig 2.

Sections illustrating the anterior part of Jacobson's organ in foetal calf of 65 mm.

×50.

Plate XLII

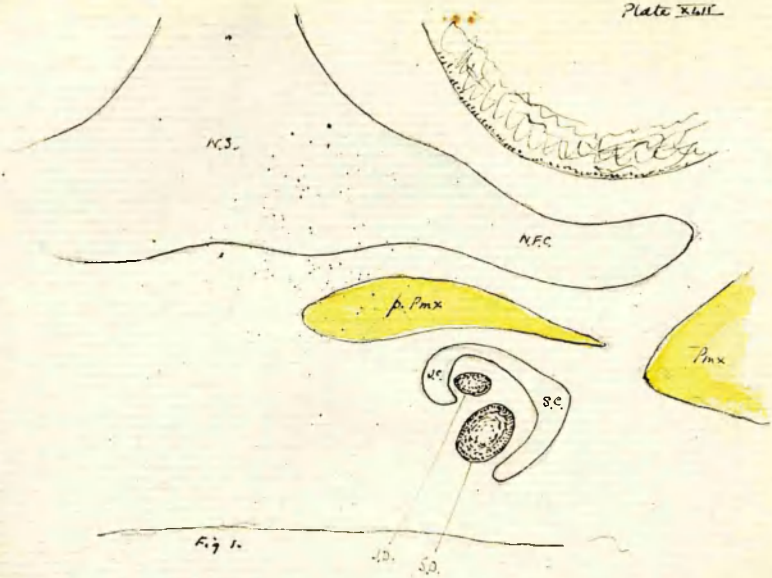


Fig 1.

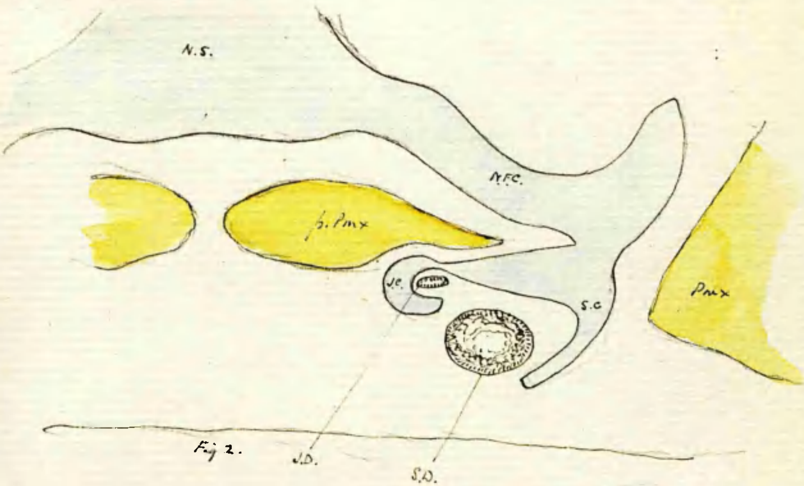


Fig 2.

Sections of the anterior region of Jacobson's organ in a foetal calf (about 200 mm in length)
×20

Plate XLIII.

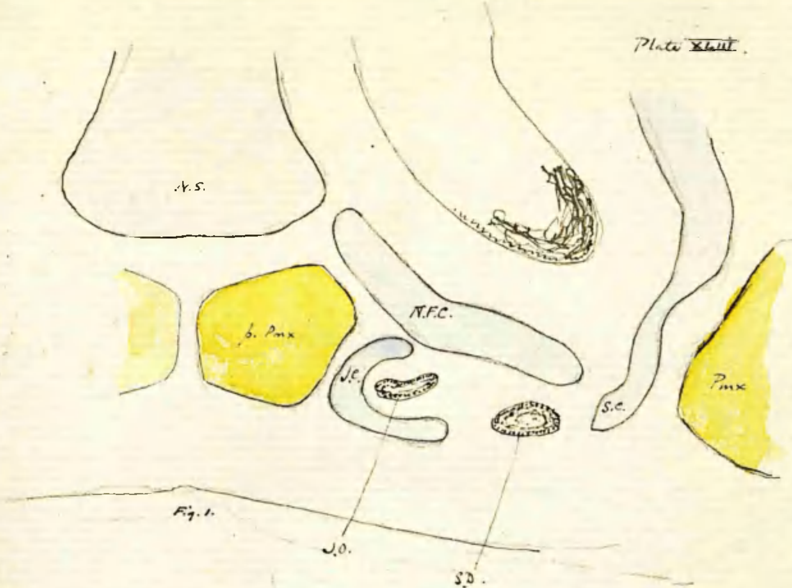


Fig. 1.

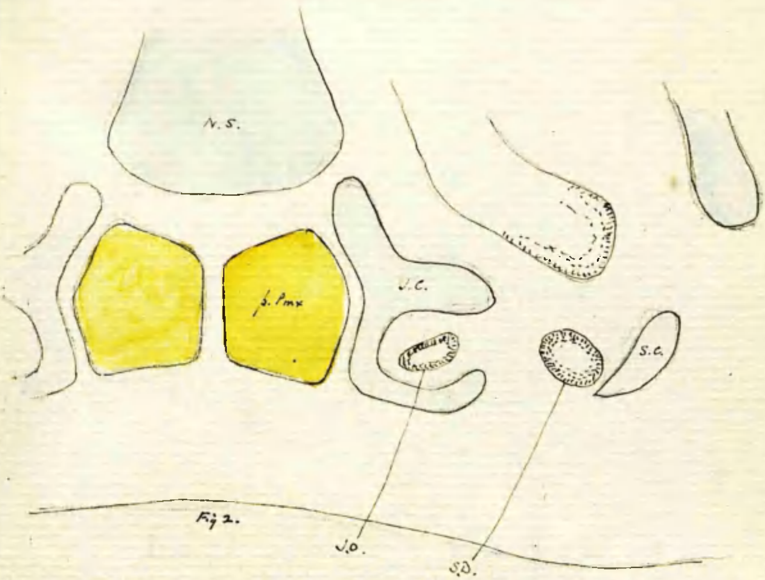


Fig 2.

Sections of anterior part of Jacobson's Organ in foetal calf (about 3.00 cm in length)

x 20

Plate XLIV

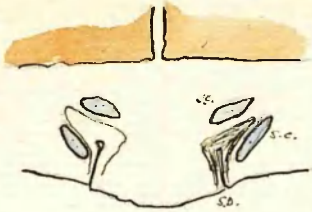


Fig 1.

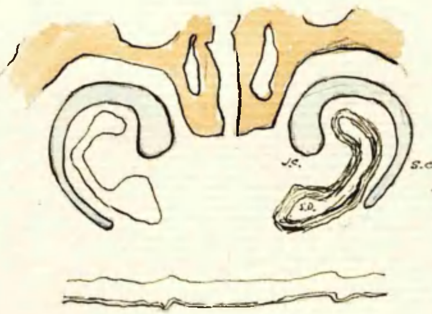


Fig 2.

Fig 3.

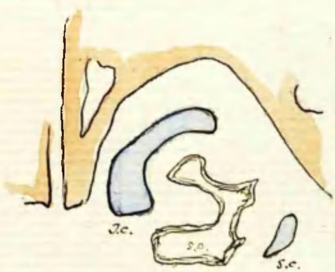
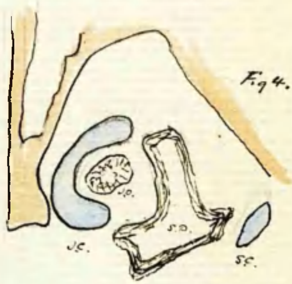


Fig 4.



Transverse sections across Stenson's duct and anterior part of
Jacobson's duct in young Kitten
Felis domestica

Plate XLV.

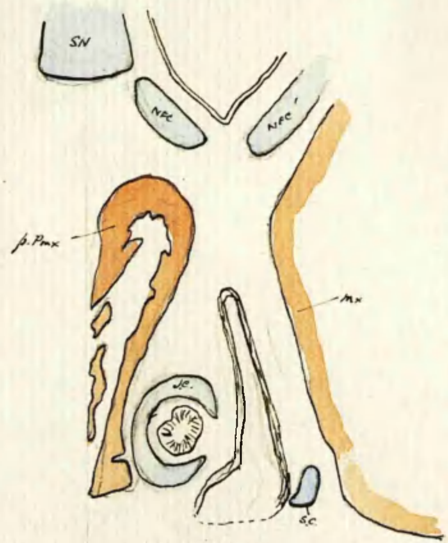


Fig 1

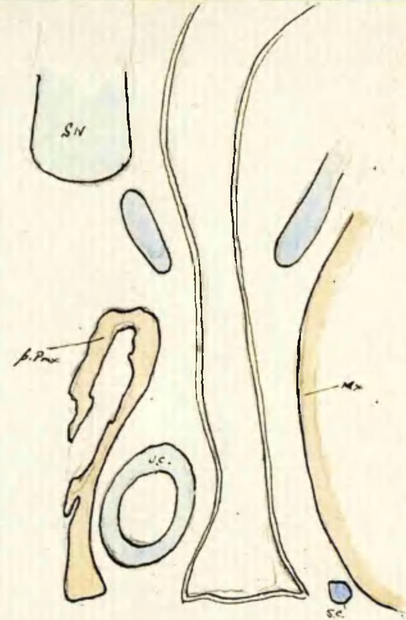


Fig 2

Sections across the anterior part of Jacobson's organ in young kitten.

Plate XLVI

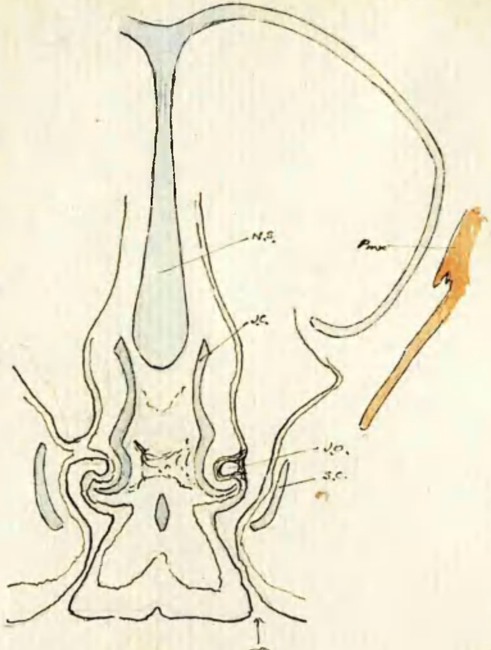


Fig. 1

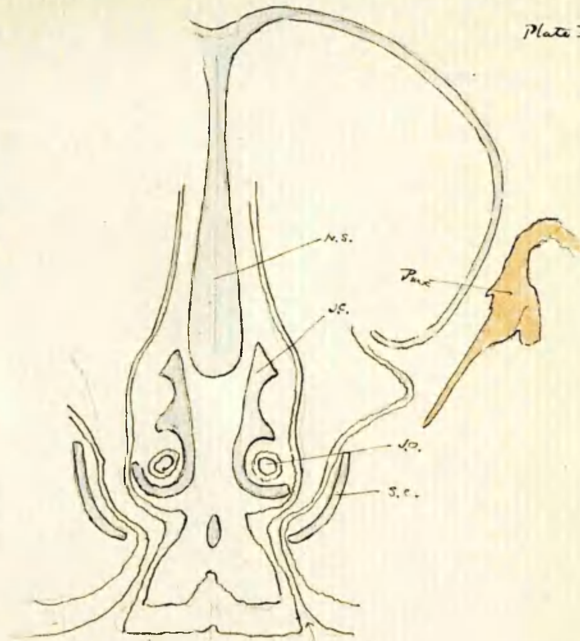
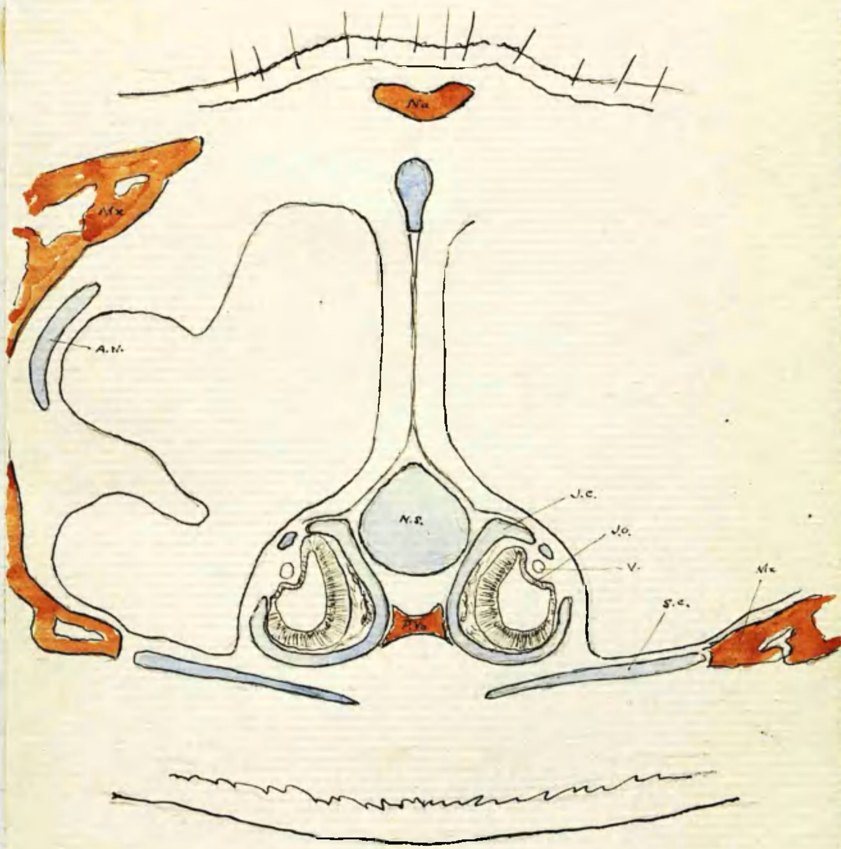


Fig. 2

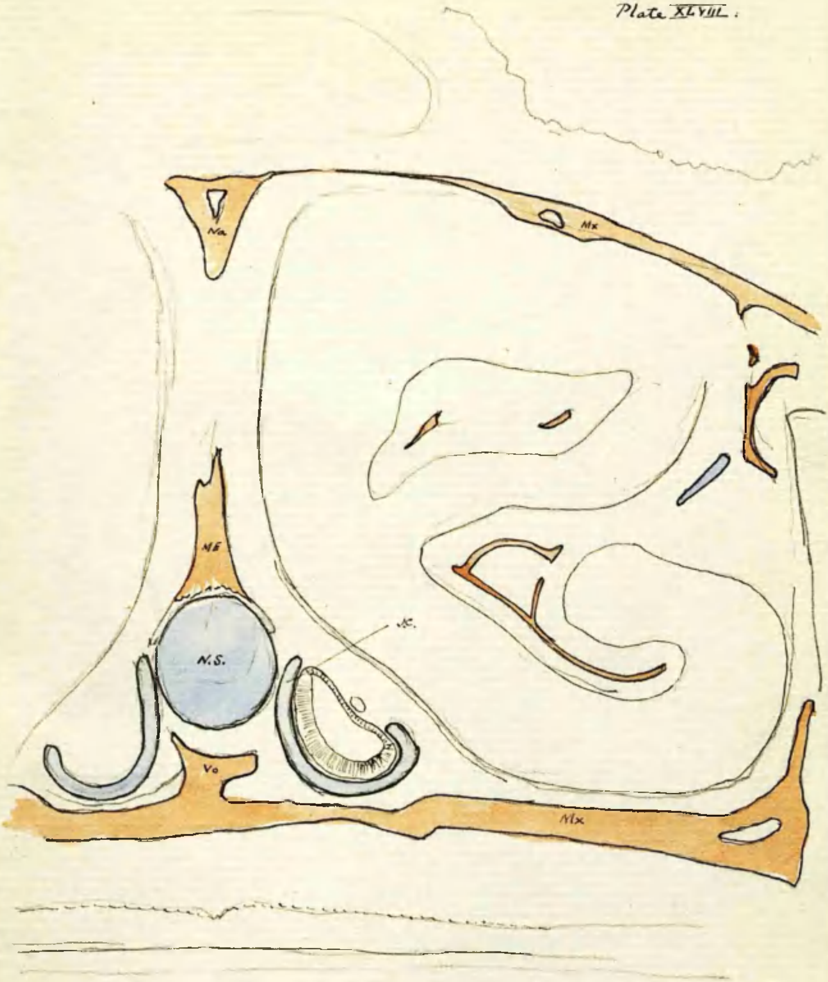
Anterior part of Organ of Jacobson in Australian Bat
Miniopterus schreibersii Natt × 45

Plate XLVII



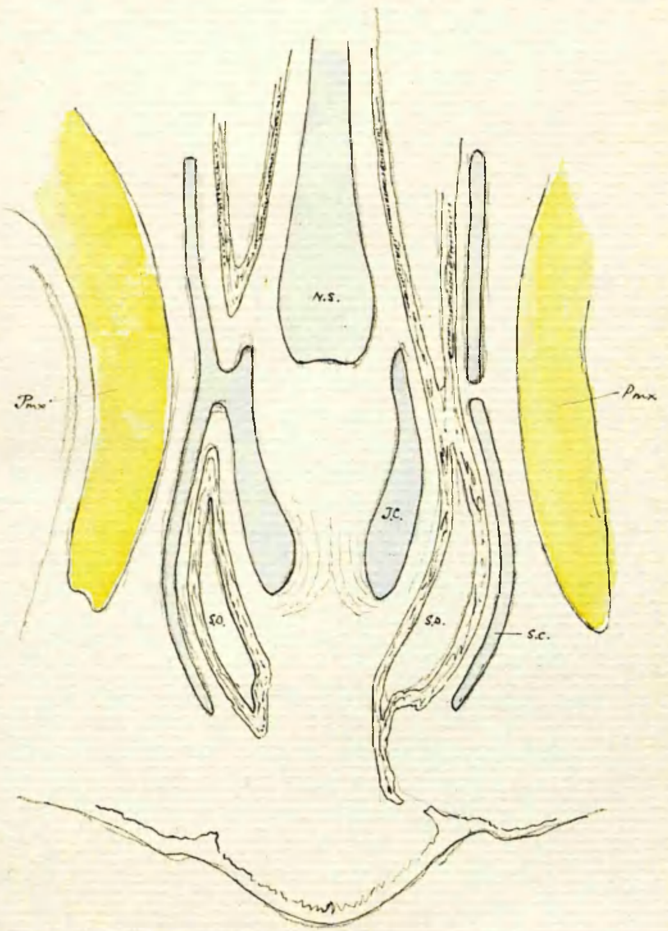
The organ of Jacobson in the Australian Bat
Miniopterus Schreibersii Kuhl
×45

Plate XLVIII.



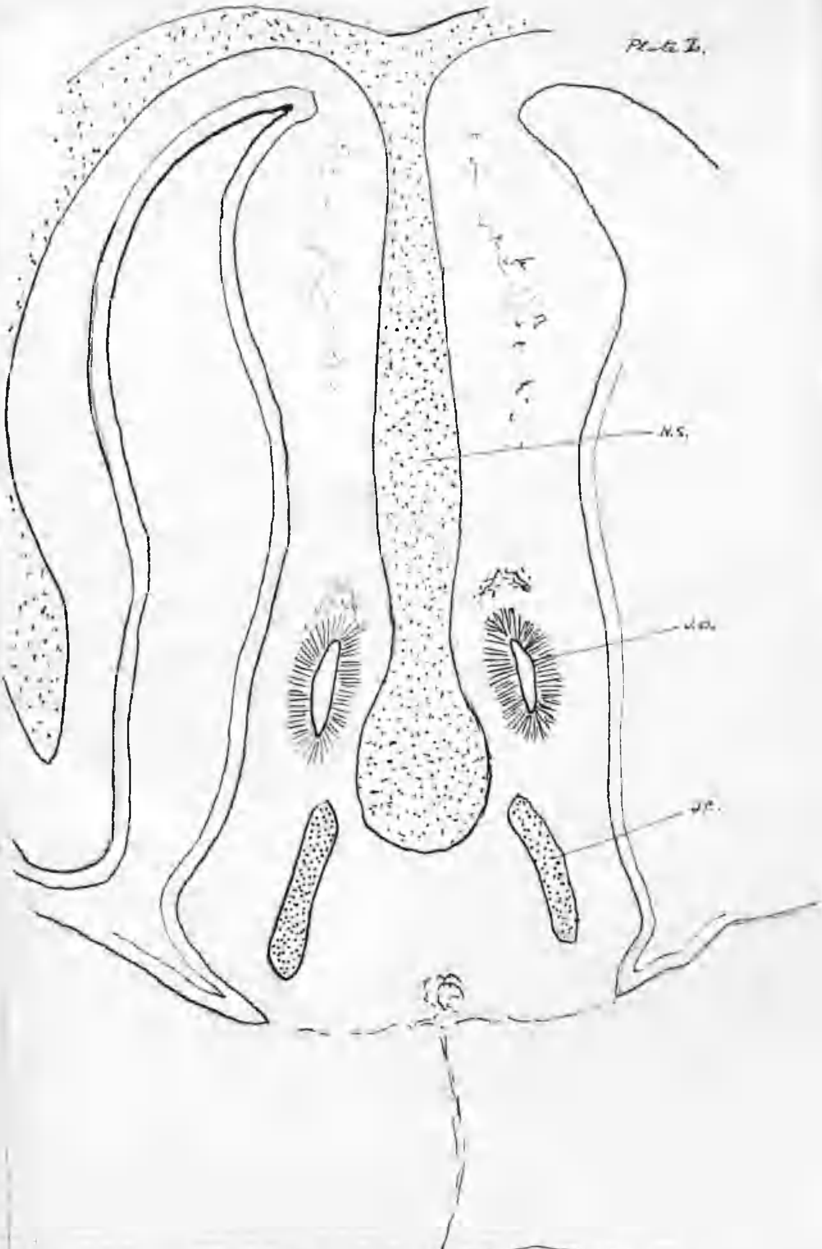
Hinder part of the Organ of Jacobson in
Miniopterus schreibersii, Natt. × 45

Plate XLIX.



Vert. Sect. in the plane of Stenson's duct in the Flying fox
Pteropus poliocephalus Tem

Plate II.



Organ of Jacobson in Human Foetus of 10 weeks.