VIII.—*A Contribution to the Comparative Anatomy of the Mammalian Organ of Jacobson.* By R. Broom, M.D., B.Sc. Communicated by Sir Wm. Turner. (With Two Plates.)

(Read 7th June 1897.)

Since the Organ of Jacobson was first described in 1811, a large amount of study has been given to its structure, development, and morphology; and as a result of these investigations, we have now a very good idea of the distribution of the organ in the animal kingdom, of its relations in many typical forms, and of its minute anatomy in a few representative types. With the exception, however, of Seydel's work among the Amphibia, very little has been done to the study of the comparative anatomy of the organ, and it is hoped that the present contribution will assist towards a clearer understanding of its comparative anatomy in the Mammalia.

The organ is present in the large majority of mammals, and is generally fairly well developed. The most important investigations into the general anatomy of the organ and its relations have been those of Gratiolet, Balogh, Klein and Herzfeld. Gratiolet has apparently examined the organ and its relations in a considerable number of the higher mammals, but, unfortunately, I have been unable to see his paper. Balogh has made a very careful study of the relations and minute anatomy of the organ in the sheep, and has shown the complicated arrangement of the cartilages in connection with the organ and its duct and with the naso-palatine canal. To Klein we are indebted for a very careful study of the organ and its relations in the guinea-pig, the rabbit and the dog. Though Herzfeld has also added considerably to our knowledge by the examination of some interesting new groups, his most important contribution to the subject has been in connection with the comparative anatomy of the organ. He has apparently been the first to recognise that, according to the various relations of the organ and its duct found in different mammals, it was possible to arrange the animals examined into a few not altogether unnatural groups. Owing to observations having up to that time been made in an insufficient number of forms, he has, unfortunately, over-estimated the importance of certain points, and thus to a large extent has rendered his grouping unsatisfactory.

The present communication deals with the results of an extended examination into the general relations of the mammalian organ—its distribution, varying degree of development, and extent of variation in allied forms. In all the forms I have studied, I have made the examination by a series of vertical transverse sections, which seems the most satisfactory method, and gives uniformity in the results.

The following is the list of forms I have examined :—

MONOTREMATA.

Ornithorhynchus anatinus; adult.
Echidna aculeata; adult.

MARSUPIALIA.

Dasyurus viverrinus; mammary fœtal, and $\frac{2}{3}$ grown.
Dasyurus maculatus; adult.
Phascologale penicillata; mammary fœtal.
Didelphys murinus; mammary fœtal.
Didelphys marsupialis; mammary fœtal.
Perameles nasuta; mammary fœtal, and adult.
Petaurus breviceps; almost adult.
Petauroides volans; adult.
Pseudochirus peregrinus; mammary fœtal, and adult.
Trichosurus vulpecula; intra uterine, mammary fœtal (3 stages), and adult.
Phascolarctus cinereus; $\frac{2}{3}$ grown, and adult.
Phascolomys mitchelli; $\frac{1}{2}$ grown.
Macropus ualabatus; large mammary fœtal.
Macropus sp.?; early mammary fœtal.
Æpyprymnus rufescens; mammary fœtal.

EDENTATA.

Dasypus villosus; adult.

RODENTIA.

Lepus europœus; young.
Lepus cuniculus; fœtal (3 stages).
Mus musculus, adult.
Hydromys chrysogaster; adult.

UNGULATA.

Sus scrofa; fœtal.
Bos taurus; fœtal (2 stages).
Equus caballus; fœtal.

CETACEA.

Delphinaptera leucas; fœtal.

INSECTIVORA.

Erinaceus europœus; fœtal and adult.
Talpa europœa; early fœtal.

CARNIVORA.

Felis domestica; young.

CHIROPTERA.

Miniopterus schreibersii; adult.
Nyctophilus sp.?; adult.
Pteropus poliocephalus; adult.

PRIMATES.

Homo sapiens; early fœtal.

GENERAL OBSERVATIONS.

In its typical form the mammalian organ of Jacobson is a specialised portion of the nasal mucous membrane, situated in the anterior part of the base of the nasal septum, and forming a tubular process, blind posteriorly, but opening in front in the region of the naso-palatine canal. The inner wall of the tubular organ is lined with highly specialised neuro-epithelium, while the outer wall is composed of ciliated columnar epithelium, considerably resembling that of the nasal passage. Into the organ there open a large number of mucous glands, which are situated chiefly at its posterior part. Along the outer wall, which generally bulges into the lumen of the organ, there run one or more blood-vessels, frequently forming a sort of plexus. On its inner and under sides, at least, the organ is supported by a curved cartilaginous plate—the recurrent cartilage—which is itself supported by a curved bony plate, the palatine process of the premaxillary.

While, as a rule, the organ is fairly well developed, in a number of animals it is quite absent, and in others only a rudiment is present. It is difficult at present to account for the remarkable differences in the degree of development of the organ in different mammals, as absolutely nothing is known for certain as to its special function; still, from comparative observations, a few interesting general conclusions can be arrived at. In the first place, the organ is, as a rule, better developed in the lower forms than in the higher. Thus, in both the Monotremes the organ is exceedingly well developed, and in all the Marsupials yet examined it is at least fairly well developed, while among the Primates, it is absent, according to HERZFELD, in Cercopithecus and Inuus—the only old world monkeys examined—and in man it is quite rudimentary. Another conclusion that may be safely arrived at is, that in large animals the organ is, relatively, considerably less developed than in the smaller sorts. For example, in the two species of Dasyurus, *D. maculatus* and *D. viverrinus*, though the former is about twice the size of the latter, the organs are absolutely about the same size in each; the cartilaginous capsule of the organ, however, is much larger, and the extra space is filled up by a great development of glandular tissue. In all forms in which the organ is developed it receives the secretion from numerous mucous glands, which lie chiefly towards the posterior part of the organ, and in most small animals, *e.g.*, the mouse, where it fills the greater part of cartilaginous capsule, only at that part. In the larger animals, *e.g.*, rabbit, dog, etc., where the organ only occupies a small portion of the space enclosed by the cartilage, it receives the ducts of glands throughout its whole length.

While it will thus be noticed that there may be a very considerable difference in the degree of development of the organ in even closely allied forms, I have been led to a much more important conclusion, viz., that though the degree of development may vary greatly, there is throughout large groups a very marked constancy of the type, followed by the organ in its general relations and connections. For example, in all the Marsupials that have been examined, with one exception, which will be referred to later, the organ opens into the upper end of the naso-palatine canal, near the point where the canal opens out into the nasal cavity, while there is never more than a rudimentary cartilaginous support given off to support the naso-palatine canal either from Jacobson's cartilage or from the nasal floor cartilage. While this holds good for practically all Marsupials, of no Eutherian that has yet been examined can the same be asserted. The two known Monotremes have in their organs a number of features in common, but which differ from those of any other animal. And the same can be said of the different Rodents which have been examined. Again, in all the higher Eutheria in which Jacobson's organ is well developed, there is a very complex development of the nasal floor cartilage, giving rise to a cartilaginous support for the naso-palatine canal as well as to a posterior nasal floor cartilage, while Jacobson's cartilage is produced downwards and forwards to form a support to Jacobson's duct; and so unvarying is this type, that even in forms in which the organ of Jacobson is completely aborted, as in Pteropus, the cartilages still retain the same general arrangement. From the small tendency to variation in the organ and its cartilages, we have in them a factor of considerable value in the classification of the Eutherian orders, probably of more value than either dentition or placentation.

In the following pages the relations of the organ in the principal orders will be considered, and the affinities and significance of the various arrangements dwelt upon.

MONOTREMATA.

The differences of the organ in the two Monotremes are such that it will be more convenient to consider the two separately.

Ornithorhynchus.—The presence of the organ in the Platypus was recognised by Sir W. TURNER in 1885, but was first described in detail by SYMINGTON in 1891. Since then further details have been supplied by WILSON, WILSON and MARTIN, W. N. PARKER, ELLIOT SMITH, and myself.

It is unfortunate that in Ornithorhynchus—the most primitive mammal at present existing—there is a most remarkable degree of specialisation of the structures in the anterior part of the snout, and that this specialisation is in a direction entirely dissimilar to that found in any other known vertebrate. This peculiar development in the snout to some extent affects the organ of Jacobson and its cartilages, and renders it difficult to say whether certain of the peculiarities presented are due to the specialisation, or are retained primitive characters.

The condition of the cartilages of the snout may be briefly described as follows. In the hinder part of the nasal region the nasal septum is a short, thick, simple cartilage, which gives off above two well marked alinasals, as in higher mammals. On passing forward, when we reach the plane passing through the anterior part of the prevomer or dumb-bell shaped bone, the nasal septum becomes divided into a very slender upper part supporting the alinasals, and a thick lower part. This lower part is here in close contact with the inner parts of the well developed nasal floor cartilages, while a little in front it becomes united with these, and forms a well developed flat cartilage, stretching right across from the one premaxillary bone to the other. About 3 mm. in front of the plane of the anterior nares the large flat plate of cartilage becomes thickened and arrested in the middle line, but laterally it passes out to the margins of the beak, and sending developments in front and behind forms the support of the beak throughout its whole extent. Though in none of the higher vertebrates is there any cartilaginous development similar to the large rostral cartilage of Ornithorhynchus, there is reason to believe that it is a very great development of the prenasal element.

With regard to the nasal floor cartilages, which on passing back are separated off from the median or septal part of the main cartilage, there is little or no doubt but they are the homologues of the nasal floor cartilages of the higher mammals, though in some respects they differ from those of any higher form. In the typical mammalian condition we have the inner part of the nasal floor cartilage quite simple and curving up by the base of the septum ; in Ornithorhynchus alone among mammals the nasal floor cartilage at its inner part is thickened and excavated to receive the anterior part of the organ of Jacobson.

The organ itself differs from that of any other known mammal in being made up of an anterior and a posterior part with the opening near the middle, as was shown by SYMINGTON. In fig. 1, Plate I., we have represented a transverse vertical section through the anterior part of the organ. The large organ (J.O.) is seen completely surrounded by the nasal floor cartilage, and almost completely divided into an upper and a lower part by a large turbinal plate (t.J.c.). The inner part of the nasal floor cartilage rests on the anterior part of the prevomer or dumb-bell shaped bone (Pvo), and at the outer side of the nasal passage the cartilage is seen united with the alinasal (a.n.). In this section is also seen the hinder part of the nasal valve (val.).

On approaching the region of the naso-palatine canal and the opening of the organ, the turbinal plate becomes considerably thickened, while the cartilages surrounding the two organs become separated by the body of the prevomer. On reaching the plane passing through the opening of the organ, as seen in fig. 2, the cartilage is found to be open below, and the outer part of the cartilage surrounding the organ is seen to be free from the nasal floor cartilage. The organ is here made up of an upper part lying above the turbinal plate and an inner part. Inferiorly, the inner part may be said to open directly into the mouth, as the little pocket into which it opens in common with the naso-palatine canal is frequently so shallow that the ducts practically open independently into the mouth.

Behind the plane represented by fig. 2 the organ becomes much less expanded laterally, while the outer part of the cartilage of the organ becomes united with the lower part of the inner portion, forming a complete capsule to the organ; and the organ becomes almost cylindrical instead of flat as in the anterior part. Fig. 3 illustrates a section across the posterior part of the organ. The turbinal plate, which in the anterior and middle region is moderately flat, here passes upwards and inwards, and then downwards, being to a considerable extent folded on itself. Below the prevomer, which here attains its maximum development, is seen a large thin plate of cartilage (o.n.f.c.) stretching across from one side to the other, but distinct at the sides from the alinasals. This cartilage is a backward continuation of the part of the nasal floor cartilage on the outer side of the naso-palatine canal, which, on passing backwards, becomes distinct from the alinasal, and sweeping inwards below the prevomer unites with the cartilage of the opposite side, and forms the large plate which supports the back part of the dumb-bell.

It is exceedingly difficult, as already remarked, to pick out which characters of the organ are inherited from reptilian ancestors and which are specialisations peculiar to the genus or order. Unfortunately the order of reptiles, which probably contained the ancestors of the Monotremes—the Theromora—is long since extinct, and the only living reptilian order in which the organ is known to be well developed—the Squamata—is only but distantly related to the Monotremes. Among lizards the organ of Jacobson is usually very well developed, but there are great differences in the structure and relations of the organ in different groups. In the Varanidæ and in snakes a most complex and highly specialised arrangement is found; in the Scincoidæ a different mode of specialisation is met with; while in the Agamidæ and Geckonidæ, on the other hand, though the organ is well developed, it is comparatively simple both in structure and its relations, and it is in these latter simple Lacertilian types that we recognise some affinities to the organ of the Monotremes. In the Gecko we find the opening of the organ situated inferiorly, almost exactly as in Ornithorhynchus, while we have an even more remarkable resemblance in the presence of a large cartilaginous turbinal process invaginating the organ from the outer side. It would thus seem probable that the mode of opening of the organ and the well-marked turbinal in Ornithorhynchus are reptilian heirlooms. The anterior extension of the organ would seem at first sight to be also a reptilian character, seeing that the organ extends slightly in front of the duct in lizards, but it is possible that the specialisation of the beak may be sufficient to account for this peculiarity, and until the very early development is known it had better be regarded as a doubtful reptilian character. Another reptilian character is to be noticed in the prevomer or dumb-bell shaped bone being quite distinct from the premaxillary, and not united with it as a palatine process, as is usually the case in mammals.

Echidna.—In Echidna the organ is considerably simpler than in Ornithorhynchus, and it is uncomplicated by any remarkable cartilaginous developments. W. N. PARKER has studied the structure of the organ and its relations in the young animal, while the adult condition has been described by myself.

The most striking point of difference of the organ in Echidna from that of Ornithorhynchus is the absence of any anterior development. The nasal floor cartilage is comparatively simple, and, in the adult, but feebly developed, and quite distinct from the alinasal. Immediately in front of the region of the naso-palatine canal, the nasal floor cartilage is a small cartilaginous plate which abuts against the base of the nasal septum by its thickened inner edge, and becomes rapidly thinned away on passing outwards, only forming a support to the inner third of the nasal floor. On passing a little backwards the thickened inner part becomes divided off from the slender outer part by the naso-palatine canal passing upwards (figs. 4 and 5). At first the inner part is irregularly square shaped, but a little farther back it becomes hollowed out on the outer side for the reception of the duct of Jacobson's organ, as it opens into the naso-palatine canal (fig. 5). On passing still farther back this inner cartilage becomes very distinctly "C"-shaped, with the anterior end of Jacobson's organ in its concavity. The cartilage is about uniform in thickness, but at the outer end of the upper part of the "C" there is a very distinct thickening. A very little beyond this plane the lower part of the "C" joins with the thickened outer rim, and Jacobson's organ becomes completely enclosed in cartilage. The naso-palatine canal receives the duct of Jacobson anterior to its opening into the nasal cavity, so that the organ only communicates with the nasal cavity indirectly by the upper part of the canal. Fig. 6 represents a section through the posterior wall of the naso-palatine canal. To the outer side of the cartilage of Jacobson the thickened portion will be observed (rud.t.); this is found, on examining the succeeding sections, to be continuous with the turbinal, and is, no doubt, the remnant of a turbinal which once extended to the front of the organ as in Ornithorhynchus. The organ itself at this plane is found on section to have the ordinary mammalian kidney shape. The outer part of the nasal floor cartilage is still seen as a small inconspicuous fragment. A short distance behind the plane of fig. 5 the organ is met with in its full development, and assumes an appearance which it retains to near its posterior end. On section it is found to be nearly circular with the outer wall so completely invaginated as to leave very little lumen in the organ. It is completely surrounded by cartilage, and the invaginated wall is supported by a flat turbinal plate of cartilage passing inwards from the outer wall of the capsule. The capsules of each side rest on a flat cartilaginous plate, which passes right across from the one side to the other, and completes what would otherwise be a little gap in the lower wall of the cartilage of Jacobson. This cartilaginous plate is exactly comparable with the similar plate in Ornithorhynchus, and is developed from the small outer portions of the nasal-floor cartilage, which become greatly enlarged, and pass inwards.

On comparing the structure of the organ and its relations in Echidna with that in

Ornithorhynchus, it will be observed that in the posterior parts of the organ there is a close agreement between the two forms. In Echidna, the whole organ being posterior to the duct, this region is naturally developed to a greater extent than in Ornithorhynchus, where the organ extends in front of the duct as well as behind, but otherwise the only points of difference at present worthy of note are the absence of the prevomer in Echidna, and the different degrees of development of the turbinal plates—in Ornithorhynchus large and curved; in Echidna small and flat. The anterior part of the organ in Echidna differs remarkably from that in Ornithorhynchus, and yet it is not difficult to imagine an intermediate or ancestral form from which both would be derived—the Echidna type by simplification and the Ornithorhynchus type by specialisation. In this hypothetical ancestral form the organ probably extended little, if at all, in front of the duct opening, but had a well-developed turbinal which extended right to the front of the organ. If in Echidna the turbinal were carried forward to the front of the organ, and the part of the organ in the neighbourhood of the naso-palatine canal, instead of being reduced to a duct, were well developed, there would be as great a resemblance to the Ornithorhynchus condition even in this region as is to be seen in the posterior part. The well-developed anterior part of the organ in Ornithorhynchus is but a continuation forwards of the various structures met with in the region of the duct rendered possible by the great development of the nasal floor cartilage in the anterior region.

MARSUPIALIA.

The marsupial organ of Jacobson was apparently first described in 1891 by SYMINGTON, who studied the condition in pouch specimens of the kangaroo and rock wallaby. At that time the organ in Echidna was undescribed, and SYMINGTON, comparing the Marsupial organ with that in Ornithorhynchus, concluded that its affinities were more with the higher Eutherian type than with that of the Monotreme. With the exception of a short note by C. RÖSE on the organ in the wombat and opossum, and a few incidental references in one or two of my own papers, nothing further had been written on the subject till last year, when I communicated a paper "On the Comparative Anatomy of the Organ of Jacobson in Marsupials" to the Linnean Society of New South Wales. This paper, which will appear in the *Proceedings* of the Society, contains a description of the organ in representative genera of the principal groups, and of the changes met with at different stages of development. From my study of the organ in the various marsupials, it was seen that in all the diverse forms the organ conformed more or less to one main type. Of this main type, however, there are two minor varieties—the simpler one found in the Polyprotodonts, the more complex in the Diprotodonts. In the present paper I will take Dasyurus as the typical representative of the former group, and Petaurus of the latter.

Dasyurus.—In Dasyurus we meet with the simplest form of the marsupial organ. As the structure of the organ and its relations have been described in some detail in the above-mentioned paper, a brief account will here suffice. The nasal floor cartilage is well developed and simple in its structure. Fig. 8 represents a transverse section just in front of the naso-palatine canal. Here the nasal floor cartilage is seen as a curved plate of cartilage resting on the premaxillary bone, and with its inner end curved upwards by the side of the base of the septum, and then slightly outwards, forming a support to the inferior septal ridge. The naso-palatine canal on passing upwards passes slightly backwards, and in fig. 9 it is seen cut across as it lies between the premaxillary and its palatine process, and dividing the nasal floor cartilage into an inner and an outer part. The inner part, which becomes Jacobson's cartilage, is very irregularly "C"-shaped, there being an inner curved portion for the reception of the organ and a well-marked little process passing out into the septal ridge. In fig. 10 the canal is found first opening into the anterior end of Jacobson's organ, and then communicating with the nasal cavity.

If the three sections of Dasyurus figured be compared with the corresponding figures representing the condition in Echidna, the wonderful agreement will be at once evident—the simple condition of the nasal floor cartilage, its division into two parts by the naso-palatine canal, and the mode of communication of the canal with the anterior end of Jacobson's organ and with the nasal cavity. Even the details of structure of Jacobson's cartilage are exceedingly instructive. The outer end of the upper part of Jacobson's cartilage is in fig. 10 seen detached from the inner plate, forming a bar along the concavity of the organ. A very short distance, however, behind the plane of fig. 10 the lower end of the inner plate of Jacobson's cartilage passes outwards and unites with the bar. This interesting little bar of cartilage, which is present in nearly all Marsupials, I have elsewhere called the "outer bar of Jacobson's cartilage." Its chief interest lies in the fact that there is not the slightest doubt but it is exactly homologous with the rudimentary turbinal found in the anterior part of the cartilage in Echidna, and that it is thus the remnant of an ancestral turbinal. The posterior and main part of the body of the organ lies in an open curved plate of cartilage, which only supports the organ on its inner and under sides. We thus have in this primitive marsupial type a series of structures which are in all details easily traceable to the monotreme condition. In Ornithorhynchus the ancestral monotreme type is complicated by excessive cartilaginous developments, while in Echidna the primitive condition is obscured by the rudimentary condition of the cartilage in the anterior region. In Dasyurus, on the other hand, we probably have a nearer approach to the proto-mammalian proportions than in either of the existing monotremes, but, unfortunately, the organ has become much more feebly developed, and the cartilages are so reduced that at first sight one fails to observe the traces of their former grand developments.

Didelphys agrees very closely with Dasyurus as regards its organ and cartilages; Perameles, on the other hand, while agreeing fairly well with these more normal polyprotodonts, shows some slight peculiarities, which have been considered in my above-mentioned paper.

Petaurus.—Petaurus I have chosen for consideration, as it shows the diprotodont marsupial characteristics in their most typical form. The main part of the organ agrees very closely with that in Dasyurus, as will be seen by comparing fig. 15 with fig. 11. In front, however, there are some remarkable differences. The nasal region, generally at its anterior part, is somewhat more expanded laterally than in Dasyurus, and the inferior septal ridges are much more developed. It is probably in connection with this broadening out of the base of the septum that the inner part of the nasal floor cartilage assumes its characteristic development. In front of the naso-palatine canal the nasal floor cartilage, as seen in fig. 12, closely resembles the condition in Dasyurus (fig. 8). In fig. 13, in the plane just behind the point where the palatine process divides off from the premaxillary, the nasal floor cartilage is seen in its characteristic form. Its outer part is very much reduced, but the inner part, which becomes Jacobson's cartilage, is much better developed than in Dasyurus. By comparing this figure with fig. 9, the following points of difference will be noticed. Instead of the cartilage being composed of a vertical curved plate, with a short process passing to the inferior septal ridge from the upper end, we have here a moderately flat plate passing markedly outwards, and resting on the palatine process of the premaxillary, while from near its middle there passes upwards and outwards a well-marked process, which passes into and supports the well-developed inferior septal ridge. The interpretation of the morphology of the different structures here seems at first sight rather difficult, but an examination of the succeeding planes gives a satisfactory solution of the problem. In fig. 14 we have represented a transverse section through the point where Jacobson's organ opens into the naso-palatine canal and into the nasal cavity. It will be observed that there is a much more marked connection between the organ and the nasal cavity than in Dasyurus. In the ridge we find a portion of cartilage which we have no difficulty in recognising to be the outer bar of Jacobson's cartilage, and we are thus driven to the conclusion that the ridge support seen in fig. 13 is the homologue of the short plate which passes out to the little ridge in Dasyurus. This being so, we see that two of the peculiarities of the Petaurus arrangement are (1) a great development of the ridge process, and (2) its arising from near the middle of the inner plate instead of from its upper end, which probably means that in Petaurus the upper part of the cartilage is developed to a much greater degree than in Dasyurus. A third peculiarity, and probably the most important, is that the inner plate of the cartilage at its lower end passes down on the outside of the palatine process of the premaxillary, and forms the inner wall of part of the naso-palatine canal. In almost all other respects the details of the anatomy in Petaurus agree with those in Dasyurus. One feature worthy of note is, that in the diprotodonts the organ almost always has a well-marked vascular plexus, while in the polyprotodonts the plexus is more or less rudimentary. In my paper above referred to I have pointed out the peculiarities of the different diprotodonts, and here need only call attention to one, viz., Æpyprymnus. In this rat-kangaroo we have a peculiar arrangement found in no other marsupial yet examined, namely, that the organ opens directly into the nasal cavity slightly in front of the point where the naso-palatine canal ends. In every other respect the characters agree perfectly with the Marsupial type, and the peculiarity is probably due to the lengthening of the front of the snout in connection with the well-developed front incisors. It will be noted later that the opening of Jacobson's organ into the nasal floor in front of the naso-palatine canal is one of the most noticeable characteristics of the rodents, and it is interesting here to notice a parallel development in an animal which to a considerable degree approximates to the rodent type of dentition.

Edentata.

With the exception of Parker's Monograph on the development of the skull in the Edentata, practically nothing has been published on the organ of Jacobson in this order, and Parker's figures, though showing the presence of the organ in different forms, do not enable us to form any idea of the more delicate relations. Symington, who has made sections of the snout of the Peba armadillo, and of a fœtal 3-toed sloth, but has not yet published his results, kindly informs me that he finds the organ well developed in the armadillo, and that in the sloth it is rudimentary, and opens into the nasal cavity. Through the kindness of Mr F. E. Beddard, F.R.S., I recently obtained the head of an adult hairy armadillo (*Dasypus villosus*), and have since made a study of the organ of Jacobson and its relations in that form. In this species the organ is moderately well developed, and though it is possible that in such a varied group as the Edentata there may be some considerable variations in the relations of the organ, *Dasypus villosus* may provisionally be taken as the type of the order; and, judging by the structure in this form, it seems probable to me that the other genera will not depart very greatly from the Dasypus type.

Dasypus.—In a short paper recently published I described the condition of the nasal floor cartilage in its anterior region, and more especially the remarkable little nasal floor bone which is associated with it. The cartilage differs in some respects from that of any of the lower mammals, and also from the majority of the higher forms. In most mammals the nasal floor cartilage arises as two lateral plates from the base of the nasal septum: here, in front, they appear to rise by a splitting up of the lower third of the nasal septum. In the plane passing through the anterior part of the papilla the cartilages are quite below the base of the septum, and do not form any floor to nasal cavity, the floor being formed by the little nasal floor bone.

Fig. 16 represents a transverse section near the middle of the papilla. Here the nasal floor cartilage has almost its normal development, for though the outer and inner parts appear detached by the posterior part of the nasal floor bone, they are quite united round behind the bone. The nasal floor cartilage and bone both rest on the peculiarly flattened out premaxillary. The inner part of the nasal floor cartilage is very large, and is seen curving upwards and outwards almost exactly as in Dasyurus; there is here, however, practically no inferior septal ridge, the large glandular ridge being apparently the homologue of the upper of the two ridges in Echidna, and not of the lower, which corresponds to the inferior septal ridge of marsupials. A very short distance behind the plane of fig. 16 the inner part of the nasal floor cartilage, or Jacobson's cartilage, becomes much thinner, and the upper part curves outwards and downwards, thereby forming a cavity for the reception of Jacobson's duct, which in fig. 17 we find lying in the concavity thus formed, and opening into the floor of the nasal cavity. In this latter figure we find the outer part of Jacobson's cartilage detached as a little flat plate which, though different in shape, is, there is little doubt, the homologue of the outer bar of Jacobson's cartilage in marsupials. The duct of the organ is seen to have a plentiful supply of vascular tissue, especially on its upper side. A little behind this plane the outer bar becomes united with the lower part of the inner plate, and the organ rests in a sort of "V"-shaped trough. For a short distance Jacobson's cartilage still retains its connection with the outer nasal floor cartilage, then becoming detached the "V" becomes gradually rounded into the normal "C" shape, and the outer nasal floor cartilage becomes more and more reduced. Fig. 18 represents a section just beyond the point where the naso-palatine canal opens into the nasal cavity, and it will be observed that there is no connection whatever between the canal and Jacobson's organ. The two cartilages of Jacobson are separated by the vomer, and rest on the palatine processes of the premaxillary. The organ has the usual mammalian kidney-shape, and in structure does not differ apparently from the marsupial organ. Along the concavity of the organ there is a rudimentary plexus composed of one large and three or four small blood-vessels.

From the consideration of the above-mentioned details, it will be seen that there is little to distinguish the Edentate organ from that of the Marsupial. The most striking difference is the opening of the organ into the nasal cavity much in advance of the naso-palatine canal, but this is only an extreme exaggeration of the condition met with in the rat-kangaroo, *Æpyprymnus.*

Rodentia.

In no order of mammals has the organ and its relations been studied so thoroughly as in the Rodentia, and yet in no order is the difficulty of interpreting its affinities so great. Klein has fully described the details of the anatomy in the rabbit and guinea-pig, while Herzfeld has examined the organ in the rat. I have myself examined the organ in the hare, at birth, two stages of fœtal rabbit, the mouse, and the Australian water-rat, Hydromys.

Though the organ is probably better developed throughout this order than in any other of the Eutheria, there are certain peculiarities both in the organ itself and in its relations which distinguish it from that of any other mammal. At present I will leave out of consideration the minute structure of the organ, the well-developed plexus, and the glandular connections, and confine myself to the study of the relations of the organ and its cartilages.

The most striking characteristic of the organ is that it apparently always opens on to the floor of the nasal cavity in its anterior part, and well in advance of the naso-palatine canal, with which it has no connection. This peculiarity has been found in all the rodents yet examined, and from the examination of Dr BEARD's sections of the embryo rabbit of 13 mm. described in his recent paper "On Certain Problems in Vertebrate Embryology" I find that the characteristic peculiarity is already distinctly marked even at this early period.

Lepus.—To illustrate the Rodent type of organ I have taken a fœtal rabbit (head length 19 mm.), as in adult animals the great development of the premaxillaries to some extent mar the cartilaginous arrangements. In front the nasal floor cartilage presents no remarkable peculiarity, differing little from the simple marsupial type, except in that the development is confined chiefly to the inner part, which curves up close to the base of the feeble nasal septum. In fig. 36 we see the much compressed nasal cavity passing down and curving into the outer concavity of the nasal floor cartilage, or, as it may be here called, Jacobson's cartilage. Almost immediately beyond this plane the duct of Jacobson is found passing off from the nasal cavity, and occupying the concavity of the cartilage. In fig. 37 we find Jacobson's organ quite separated from the nasal cavity, and almost surrounded by cartilage. It will be noticed that there is a rudimentary outer bar, on the one side united above, on the other below, resembling more the condition in Dasypus than in Marsupials. On the palate the extreme anterior part of the naso-palatine canal is cut across. Fig. 38 represents a section near the posterior part of the naso-palatine canal. Jacobson's organ and cartilage are found in their normal form, and the cartilages are supported by the palatine processes of the premaxillary. Below and on the outer side of the naso-palatine canal is seen a small cartilaginous element, the explanation of the significance of which is the most troublesome problem in the snout of the rodent. The little cartilaginous process passes forwards almost to the front of the canal, supporting it on its outer side. Behind, it supports chiefly the lower wall of the canal, and when the canal opens into the nasal cavity the cartilage forms a true nasal floor cartilage. As it passes still further back it curves inwards and upwards, and forms an inner wall to the lower part of the nasal cavity. Throughout its whole length it is quite unconnected with either Jacobson's cartilage or the alinasal. In the lower mammals the only cartilage with which homology can be claimed is the outer nasal floor cartilage of the Monotremes. In the higher Eutheria, however, we have a somewhat similar cartilaginous development complicated in front by the presence of an anterior process of Jacobson's cartilage, which is absent in the rodents. By a comparison with the simple higher Eutherian type, as found in Miniopterus, it will be seen that the peculiar process of cartilage is a much modified outer nasal floor cartilage.

From the consideration of the above features it will be noticed that in the rodent we have a number of lower mammalian characters together with what would seem to be a higher Eutherian feature. The well-developed condition of the organ, with its large vascular plexus and its numerous glands, all point to an affinity with the lower mammals —Monotremes and Marsupials, and the structure of Jacobson's cartilage with its rudimentary outer bar gives strong support to this affinity. The mode of opening of the organ is similar to that in Dasypus, and is but an extreme degree of the condition in Æpyprymnus. The well-developed naso-palatine canal, and the process of the outer nasal floor cartilage passing forward with it, reveals a character which seems to remove the rodent from its lower relatives, and suggests an affinity with the higher Eutheria. Taking the various points into consideration, one of two conclusions seems to be possible—(1) Either the rodents are an aberrant group sprung off from the main Eutherian stem somewhat earlier than the development of the common ancestors of the higher Eutheria; or (2) they are a modified and specialised branch of the higher Eutheria. From the primitive characters of the organ and its cartilage found in the rodents and in none of the higher Eutheria, and from the fact that in no known higher Eutherian has a condition similar to that of the rodent arisen by secondary development, the first of the two conclusions, viz., that the rodents are a specialised offshoot from the early ancestors of the higher Eutherians, seems much the more probable.

Higher Eutheria.

In a few typical members of the higher Eutheria the organ has been carefully studied, but though much has been done in the way of describing the details of the anatomy practically no attempt has been made to indicate the significance of the various details. Not taking into consideration the Anthropoidea, in which the organ is generally rudimentary or absent, I have studied the organ in the following orders:—Chiroptera, Insectivora, Carnivora, and Ungulata (Artiodactyla and Perissodactyla). Notwithstanding the great differences in the general structure of the members of these different orders, the organs of Jacobson are formed on a common plan, and the differences are very slight. In the bat, when the organ is developed, we have the same type as in the pig, while the organ in the ox scarcely differs in one detail from that in the cat.

The affinities are such as to lead irresistibly to the conclusion that, in spite of the great outward differences in structure and the differences in habits and dentition, we have the various groups connected by ties of a common ancestry. And, furthermore, not only do the common ties indicate a close relationship, but they distinguish at once the higher Eutheria from the lower mammals. The simplest form of the higher Eutherian type that I have met with is that found in the Chiroptera; it will, therefore, be convenient to consider first the structure in its simple form as seen in Miniopterus.

Chiroptera.—Until recently it was believed that there was no organ of Jacobson in the Chiroptera, but in 1895 Messrs Duval and Garnault discovered a moderately developed organ in *Vesperugo pipistrellus*, and in the same year I found a very well-developed organ in *Miniopterus schreibersii.* Though the organ is thus seen to be occasionally present, it must be admitted to be more normally absent: it is interesting, however, as showing the value of the general anatomical arrangement of parts as a factor in classification, that even when the organ is quite absent (Pteropus, Nyctophilus) the cartilages still follow the same general arrangement as in Miniopterus where the organ is so well developed.

Though Miniopterus gives us the simplest form of the Eutherian type, and though it has certain affinities with the Marsupial arrangement, it is further removed from the Marsupial type than is the Marsupial from the Monotreme.

If a transverse vertical section be made through the posterior part of the papilla an appearance will be presented like that shown in fig. 19. The nasal septum is rather slender, and from a little below its base on each side there passes out a thin nasal floor cartilage, which is present here as a moderately flat plate, curving slightly upwards at its inner end. In the middle line, a considerable distance below the base of the septum is a small oval cartilage—a development of the prenasal. By the side of the papilla is seen the naso-palatine canal passing upwards and inwards, and at its upper part curving first outwards, then inwards. The upper portion is considerably dilated, and represents really the anterior prolongation of the lower part of the nasal cavity. Round this dilated portion there is a curved cartilaginous support which surrounds it on its outer, upper, and inner sides. On tracing the curved cartilage forwards the inner part becomes lost, only a small portion of cartilage remaining on the outer side of the canal at its upper end. If we trace the curved cartilage backwards we find a most remarkable development. Fig. 20 represents a section a very short distance behind fig. 19, and here the naso-palatine canal is found freely opening into the nasal cavity. What in fig. 19 represented the nasal floor cartilage is here divided into two parts, while the outer part of the curved roof of the naso-palatine canal is likewise separated from the inner, and, furthermore, the inner part of the nasal floor cartilage is found united with the inner part of the curved roof of the canal, forming one piece, which is really Jacobson's cartilage. Jacobson's cartilage thus consists of an upper moderately flat portion and a lower portion, which is markedly concave, and which has in its concavity the anterior continuation of the duct of Jacobson's organ. The outer part of the nasal floor cartilage proper becomes lost shortly behind this plane, but the outer part of the cartilage which supported the canal (*o.n.f.c.*) becomes well developed. In fig. 21 we have a section a little way behind the naso-palatine canal. Jacobson's duct is seen almost surrounded by the well-developed Jacobson's cartilage, while what was the outer canal cartilage becomes a very well developed nasal floor cartilage. On the inner side of each cartilage of Jacobson is seen the anterior part of the prevomer. In this region Jacobson's duct is a pure duct lined with squamous epithelium. Fig. 22 represents a section through the most developed part of the organ. The organ is here almost surrounded by a cartilaginous capsule; while the nasal floor cartilage forms a large flat plate which, to some extent, passes below Jacobson's cartilage. The broad posterior part of the prevomer is seen stretching from the one cartilage of Jacobson to the other.

In tracing the affinities between this type and that of the Marsupials we have at first a slight difficulty. With regard to the main body of the organ and its cartilaginous capsule the agreement between the two is close, but as we pass to the front the differences become more marked. The organ has a fairly long distinct duct, and even after it opens into the upper part of the naso-palatine canal it preserves for a short distance its individuality as a distinct groove. One of the main characteristics of the Miniopterus type, and of the higher Eutherian type generally, is due to this anterior extension of the duct of Jacobson being supported by an anterior process from the cartilage of Jacobson. Then, again, the outer part of the nasal floor cartilage is much better developed than in the Marsupials, and in some respects it has more resemblance to the Monotreme type, especially where the posterior part becomes well developed and passes in below the organ of Jacobson. The great development, however, of the outer part of the nasal floor cartilage gives rise in front to a special process passing forward on the outer side of the naso-palatine canal. The anterior process of Jacobson's cartilage, and that from the outer nasal floor cartilage, unite in front by their upper edges, the united cartilages forming the support to the upper part of the naso-palatine canal. Though there is no similar development in Marsupials, there is frequently present in Diprotodonts a downward process of Jacobson's cartilage by the side of the naso-palatine canal, which is apparently a rudimentary homologue of the anterior process in Miniopterus and the higher Eutheria. Different modifications of this downward development of Jacobson's cartilage are found in Perameles, Trichosurus, Phascolarctus, Macropus, and Phascolomys. The posterior and anterior developments of the outer nasal floor cartilage are no doubt homologous with the outer nasal floor cartilage and its anterior process in the rabbit, but whether the rodent condition represents a degeneration from the elaborate arrangement found in the higher Eutheria, or a pure parallel development, it is difficult to decide definitely, though the latter alternative appears the more likely.

Lemuridæ.—I have not had an opportunity of examining personally any member of this group, but fortunately HERZFELD has made an examination of the organ and its cartilages in Lemur, and so far as he has figured his sections the type followed differs in no essentials from that of Miniopterus.

Insectivora.—The organ in members of the Insectivora has been examined by HARVEY and HERZFELD, while PARKER in his monograph on the development of the skull gives numerous figures of sections through the organ. PARKER's figures, however, are on too small a scale to give more than rough indications of the arrangements. HARVEY has noted the general features in the hedgehog, and HERZFELD has figured the organ in the mole, though this latter animal is a much less satisfactory insectivorous type than the former.

Taking the hedgehog as the insectivorous type, we find in it an organ which differs but little from that of the bat, except that in a few points there are indications of a more advanced stage of organisation. As in the majority of the higher Eutheria the naso-palatine canal is long, and passes very obliquely upwards and backwards, and the great length of the canal is one of the points in which we have an advance on the Chiropterus condition. The other main points of difference are due to a less degree of development of the organ in the hedgehog, and a greater of the bony tissues. Though the naso-palatine canal passes up very obliquely, it is supported by cartilaginous walls almost exactly as in Miniopterus, and unquestionably of the same nature. Fig. 23, which represents a section of the snout of the hedgehog cut slightly obliquely, shows on the one side the naso-palatine canal almost surrounded by cartilage. The upper and inner corner of the canal is really the continuation of Jacobson's duct. If this figure be compared with fig. 19 the close agreement of the two will be at once manifest. In the hedgehog the nasal floor cartilage is represented only by the inner part above, and by the feebly developed outer wall of the naso-palatine canal. In the other side of fig. 23 the section passes through the point where the naso-palatine canal opens into the nasal cavity, and Jacobson's duct is likewise seen opening into the nasal cavity at this point. Jacobson's cartilage is here represented in two portions—a lower small concave portion which lodges the duct of Jacobson, and a small upper plate which is the continuation of the nasal floor cartilage proper. This section may be compared with fig. 20 of Miniopterus. Almost immediately beyond this plane the two portions of Jacobson's cartilage unite, and we soon get on section an appearance like fig. 24, with the organ well protected by a large cartilage. This section may be seen to agree fairly closely with fig. 21 from Miniopterus, the outer nasal floor cartilage being unrepresented in the hedgehog.

Carnivora.—As a result of KLEIN'S work we have a very complete account of the organ and its relations in one of the members of this order, the dog. Though the arrangement of the cartilages in the dog is quite characteristic of the carnivorous type, their development indicates some degree of degeneration, and in the cat we have a much better representative of the order, as the cartilages here attain their full development.

As in the hedgehog we have an advance upon the Miniopterus condition, so in the cat we have a further stage in the specialisation of the same type; and the hedgehog condition stands almost intermediate between the primitive bat condition and the more specialised condition of the cat.

In the cat we have a very long naso-palatine canal supported by cartilaginous walls as in the hedgehog. The mutual relations of the canal and its cartilaginous walls are well shown by KLEIN in his paper on the organ in the dog, and the condition in the cat is essentially similar. In both the bat and hedgehog the organ was seen to open into the nasal cavity as well as into the naso-palatine canal; in the cat the duct of the organ opens into the canal well in advance of the posterior end of the canal, and thus only communicates with the nasal cavity indirectly by means of the naso-palatine canal. In fig. 25 the naso-palatine canal is supported by cartilage almost exactly as in the hedgehog; the nasal floor cartilage is, however, much better developed. Fig. 26 represents Jacobson's duct separating off from the canal, and already the inner part of the cartilage —the anterior process of Jacobson's cartilage—is seen distinct from the outer portion or the process from the outer nasal floor cartilage. In fig. 27 we see the whole four elements which are derived from the cornual cartilages all distinct. The section is made in a plane a little behind the point where the naso-palatine canal opens into the nasal cavity, and the palatine process has just become detached from the premaxillary bone. The nasal floor cartilage proper is seen divided into an inner and an outer part, and at the outer and lower corner of the naso-palatine canal is the remains of the outer canal cartilage. Though in this type this little cartilage which supports the outer wall of the canal is quite unconnected with the outer part of the nasal floor cartilage above, a comparison with the condition in Miniopterus, and especially with higher Ungulate types, leaves little doubt but that it is morphologically a part of the outer nasal floor cartilage. Beyond the plane of fig. 27 the inner part of the nasal floor cartilage proper unites with the lower part to form Jacobson's cartilage, which now presents an appearance similar to that in the hedgehog.

Ungulata.—Notwithstanding the numerous points in the anatomy of the Ungulates, which would seem to mark them off from the rest of the Eutheria as a well-defined group, it is remarkable that in the relations of the organ of Jacobson and its cartilages there is the closest agreement even in small points of detail with the condition found in other higher Eutherians such as the Carnivora and Insectivora. The agreement is more marked than between the Polyprotodont and Diprotodont Marsupials, and one is forced to the conclusion that there is a more intimate relationship between the Ungulates and some other of the so-called orders of the Eutheria than is at present believed.

The different groups of Ungulates seem to be related to each other in much the same way as are the Chiroptera, Insectivora, and Carnivora; and in the types which have been examined so far we find evidences of a parallel development, the pig representing the simpler condition and the cow the more specialised.

Sus.—The general anatomy of the snout of the pig has been fairly well illustrated by PARKER, but he has not entered upon the details of the anatomy of the structures related to the organ of Jacobson or the naso-palatine canal. I have myself examined the snout of a fœtal pig (head length 19 mm.), which will be found to illustrate fairly well the Ungulate type in its simplest form. On the whole there is a marked agreement with the condition in Miniopterus, except that the outer nasal floor cartilage and the anterior process which it normally gives rise to is likewise undeveloped. In fig. 28 we have a section through the point of entrance of the naso-palatine canal. By the side of the base of the septum is the inner part of the nasal floor cartilage. Above the upper part of the naso-palatine canal, and towards its inner side, is the well marked anterior process of Jacobson's cartilage, and between this and the nasal floor cartilage and a little internally is situated the palatine process of the premaxillary. The close agreement with Miniopterus will be evident on comparing this figure with fig. 19. In fig. 29 we have the condition of parts a little further back. Here Jacobson's cartilage is complete, the anterior process being in contact with the upper part or nasal floor cartilage exactly as is seen in Miniopterus (fig. 20). On the one side the duct of Jacobson has just become separated off from the naso-palatine canal, and on the other side the canal is opening into the nasal cavity. From this section it will thus be seen that Jacobson's duct opens into the naso-palatine canal just as the canal is opening into the nasal cavity. In this it agrees with Miniopterus and the hedgehog, and also with most Marsupials. In fig. 30 we have a section through the body of the organ, and showing the normal relations of the organ, the cartilage, and the palatine process.

Bos.—In the Ruminants the condition has long ago been carefully studied, and the structure and relations of the cartilages, etc., were fully described by BALOGH in 1860, though his illustrations unfortunately are exceedingly diagrammatic. Of the ruminant type I have examined two stages of fœtal calf and a young goat, but the peculiarities of the arrangements are perhaps best shown in the larger of the fœtal calves—one about six inches in length. As in the pig, the condition of parts closely agrees with that in Miniopterus, so in the Ruminants we have an arrangement as closely corresponding with that of the Carnivora. In the cat we have a long naso-palatine canal, and the duct of Jacobson opening into the canal much in front of the union of the canal and the nasal cavity. In the Ruminant a precisely similar condition is found; but the agreement of the cartilaginous structures is even more remarkable. Fig. 33 represents a section through the anterior part of the naso-palatine canal, and even in this plane the duct of Jacobson is already seen to be split off from the canal. The nasal floor cartilage is very well developed, and still attached to the nasal septum. Around the naso-palatine canal and Jacobson's duct is a curved plate of cartilage in which there is no difficulty in recognising the two elements—the inner, which embraces Jacobson's duct, being the anterior process of Jacobson's cartilage, the outer, the anterior process of the outer nasal floor cartilage. Between these anterior cartilaginous processes and the nasal floor cartilage lies the delicate palatine process of the premaxillary. In fig. 34 we find the nasal floor cartilage almost united with the anterior process of Jacobson's cartilage, and farther out the outer nasal floor cartilage separated from the inner is seen united with its anterior process. Fig. 35 shows the appearances just anterior to the opening of the naso-palatine canal into the nasal cavity. Jacobson's cartilage has now attained its normal form, and has as its support on the inner side the premaxillary palatine process. The lower part of the outer nasal floor cartilage again forms a sort of nasal floor, as is found in Miniopterus, and in the rabbit. The close agreement between the condition of parts in the calf with those in the cat will be well seen by comparing figures 33 and 35 with 25 and 27 respectively.

Equus.—In the horse we have an aberrant modification of the Ungulate type brought about probably by the great development of the premaxillaries. As I have elsewhere described the peculiarity in detail, I will only here briefly mention the main features.

In the horse the naso-palatine canal does not open into the mouth, but ends blindly after passing forward for a short distance. The organ of Jacobson, which is normally formed, opens into the canal which carries the secretion back into the nasal cavity. In connection with the rudimentary canal and the well-developed premaxillaries, the cartilages are modified considerably anteriorly. The nasal floor cartilage is much compressed laterally, and instead of an inner and an outer process being sent forward to support the ducts, we have these processes rudimentary, and retaining their attachment to the nasal floor cartilage throughout their whole extent. Fig. 31 shows Jacobson's duct and the naso-palatine canal distinct, while the cartilaginous supports are seen as outgrowths from the laterally compressed nasal floor cartilage. In fig. 38 the structures are all seen in their usual relations.

CETACEA.

Through the kindness of Professor D'Arcy Thompson, I have been enabled to make an examination of the snout of a young fœtal Beluga. It has long been known that the organ of Jacobson is absent in the whale tribe, but I was anxious to see if the arrangement of the cartilages would give any evidence of the affinities of the group. My work for the most part confirms KÜKENTHAL'S recent researches. Before conclusive results can be obtained, however, younger embryos than any yet studied will have to be examined.

The peculiarities of the Cetacean are due to the nasal openings being shifted from their normal situation in the anterior part of the snout to the upper region of the head. The palatal region does not depart much from the normal type, there being even a small papilla in the anterior part; there is, however, no trace of a naso-palatine canal by the side of the papilla. Fig. 39 represents a curved section cut so as to approximate to the transverse in both the region of the nasal cavities and the snout. Above are seen the two nasal cavities separated by the cartilaginous nasal septum, which passes right down to near the palatal region where it rests on the vomer. On each side of the nasal septum is seen a peculiarly developed cartilaginous plate. At its upper part it forms a floor to the nasal cavity, but its chief part is closely placed against the nasal septum which it supports down almost to its lower end. This cartilage is, with little doubt, the true nasal floor cartilage, and its peculiar development is evidently the result of the shifting of the anterior nares. It passes well forward in advance of the region of the nasal cavities still resting by the side of the nasal septum, and ends about midway between the nasal passage and the papilla.

The only mammal in which I have met with a nasal floor cartilage at all comparable with that in the whale is the horse, where, owing to a sort of rostrum being formed by the well-developed premaxillaries, the nasal floor cartilage becomes laterally compressed somewhat as in the Cetacean. Though the evidence afforded by the condition of the cartilages is too slight to lead to any conclusions, so far as it goes it suggests affinities with the higher Eutheria.

Conclusion.

From the careful examination of the relations of the organ in the various groups of mammals it will be observed that not only is there a close agreement in the details of the anatomy in allied forms, but that the anatomical details of the structures related to the organ are so little affected by variations in the habits of the animals that, even in allied orders, evidences of affinity are here manifested when lost in most of the other characters. It will also be seen that in the organ and its cartilages we have a steady evolution which has apparently been only but slightly influenced by the great changes in external structure.

In the Prototheria we have an organ in a highly-developed condition, well supplied with glandular tissue, and having a large vascular plexus along its outer side. In the Marsupialia, though there are numerous little modifications—specialisations and degenerations—when these are examined it is found that they all point back to the Prototherian type, and leave little doubt but that in the Marsupial organ we have only a degenerate and slightly specialised variety of the type found in the Monotremes. In the Edentata, so far as known, the organ might be regarded as a more degenerate and slightly aberrant variety of that seen in Marsupials. In Jacobson's organ and its relations we thus have a feature which reveals an affinity between the Monotremes, the Marsupials, and this the lowest order of the Eutheria, notwithstanding the great differences manifested in their modes of development. In the Rodentia we have a well developed organ whose cartilage bears some resemblance to that both in the Marsupials and in the Edentata, with the additional feature which has not been observed in either of these groups—a posterior nasal floor cartilage which is continued forwards as a supporting cartilage to the naso-palatine canal. As this cartilage is found in the higher Eutheria, *e.g.*, Miniopterus, we see a certain affinity with this higher group. On the whole, however, the agreement is more with the lower than with the higher forms.

The examination of the organ in the higher Eutheria also reveals some striking relationships. As a rule, the organ itself is more or less rudimentary, the plexus absent. and the glandular tissue much reduced. In the cartilages, however, it has been seen that there is almost invariably a peculiar and characteristic development by which any higher Eutherian in which the organ is developed, and the majority of those even in which it is absent, can be at once distinguished from any of the lower mammals. In the complex development of the nasal floor cartilage we have, apparently, a thoroughly reliable character by which the higher Eutheria can be divided off from the lower into a distinct group by themselves. For this group I would propose the name *Cœnorhinata*, while for those Eutheria which have the primitive arrangement of the cartilages of the nasal floor the distinguishing name *Archœorhinata* might be given. In the former group would be included the following orders:—Primates, Carnivora, Insectivora, Chiroptera, and Ungulata; in the latter, the Edentata, and probably the Rodentia. There should be no difficulty in placing the Sirenia in its proper group, as in it there is known to be a well-developed organ of Jacobson. The position of the Cetacea will have to be decided by other characters.

In the Marsupialia or Metatheria there is no doubt we have a most satisfactory sub-class, but there seems reason from the present investigation to divide it into two sub-orders, the Polyprotodontia and the Diprotodontia. The position of the Bandicoots has frequently been a matter of doubt, and there are unquestionably some Eutherian characters to be met with in the group, as the presence of an allantoic placenta, as discovered by J. P. Hill, the ossified patella, and a character which I have observed in no other marsupial, the intercommunication of the two nasal cavities behind the region of Jacobson's organ. Notwithstanding these advanced characters, there is little doubt but that the Peramelidæ are rightly placed with the other Polyprotodonts, as has been done by Thomas.

The Rodents, as has already been shown, have the organ so specialised that it is a little difficult to decide whether we have an advancement of the early condition, or a specialisation of the later; the evidence, however, mostly points to the former conclusion, and at present we may tentatively regard the Rodentia as belonging to the Archæorhinata. This being so, we may classify the Mammalia thus :—

Class—Mammalia.

Sub-class I.	Protheria.		Order Monotremata.	
Sub-class II.	Metatheria.		Order Marsupialia.	S. O. Polyprodontia.
				S. O. Diprotodontia.
Sub-class III.	Eutheria.	Group 1. Archæorhinata.	Order Edentata.	
			Order Rodentia (?).	
		Group 2. Cænorhinata.	Order Chiroptera.	
			Order Insectivora.	
			Order Carnivora.	
			Order Primates.	
			Order Ungulata.	
			Order Sirenia.	
			Order Cetacea.	

A further subdivision of the orders in the group Cænorhinata might be made, the Chiroptera, Insectivora, Carnivora and Primates being apparently more nearly allied to each other than to the Ungulata.

In conclusion, I must express my thanks to the following gentlemen for their kindness in assisting me with specimens and in other ways:—Sir William Turner, Sir William Flower, Mr F. E. Beddard, Dr Elliot Smith, Mr A. G. Hamilton, Professor Wilson, Professor D'Arcy Thompson, and Dr Beard.

REFERENCES TO LITERATURE.

ANTON, W., "Beiträge zur Kenntniss des Jacobson'schen Organs der Erwachsenen," *Z. F. Heilk*, B. 16, H. 4.

ANTON, W., "Beiträge zur Kenntniss des Jacobson'schen Organs bis Erwachsenen," *Vhdlgn. d. Deutsch., otolog. Ges. 4 Vers.*, Jena.

BALOGH, C., "Das Jacobson'sche Organ des Schafes," *Sitzungsb. d. K. Akad. d. W. Math. naturw.*, 1860.

BAWDEN, H. H., "The Nose and Jacobson's Organ, with special reference to the Amphibia," *Jour. Comp. Neurol.*, vol. iv., 1894.

BEARD, J., "The Nose and Jacobson's Organ," *Zool. Jahrb. Anat. u. Ontog.*, Bd. iii., 1889.

BÉRANECK, E., "Sur le développement des nerfs craniens chez les Lézards," *Recueil. Zool. Suisse*, vol. i. (1884), p. 519.

BORN, G., "Ueber die Nasenhöhlen und der Thränennasengang der Amphibien," *Morph. Jahrb.*, Bd. ii., 1877.

BORN, G., "Die Nasenhöhlen und der Thränennasengang der Amnioten," Theil I., *Morph. Jahrb.*, Bd. v.

BORN, G., *Ibid.*, Theil II., *Morph. Jahrb.*, Bd. vi.

BORN, G., *Ibid.*, Theil III., *Morph. Jahrb.*, Bd. viii.

BROOM, R., "On the Homology of the Palatine Process in the Mammalian Premaxillary," *Proc. Linn. Soc. N.S.W.*, 2nd ser., vol. x., 1895.

BROOM, R., "On the Organ of Jacobson in the Monotremata," *Jour. Anat. and Phys.*, vol. xxx. p. 70, 1895.

BROOM, R., "On the Organ of Jacobson in an Australian Bat. (Miniopterus)," *Proc. Linn. Soc. N.S.W.*, 2nd ser., vol. x., 1895.

BROOM, R., "Observations on the Relations of the Organ of Jacobson in the Horse," *Proc. Linn. Soc. N.S.W.*, 1896.

BROOM, R., "On the Comparative Anatomy of the Marsupial Organs of Jacobson," *Proc. Linn. Soc. N.S.W.*, 1896.

BRUNN, AV., "Die Endigung der Olfactorius Fasern und Jacobson'schen Organe des Schafes," *Arch. f. mikr. Anat.*, Bd. xxxix.

DURSY, E., "Zur Entwickelungsgeschichte des Kopfes des Menschen und der höheren Wirbelthiere," Tübingen, 1869.

DUVAL, M., and GARNAULT, P., "L'Organe de Jacobson des Chiroptères," *Compt. Rend. Hebd. des Séances de la Société de Biologie*, 10th ser., 28th June 1895.

FISH, P., "The Cerebral Nervous System of *Desmognathus fusca*," *Journ. of Morph.*, pt. i., 1895.

FLEISCHER, E., "Beiträge zu der Entwickelungsgeschichte des Jacobson'schen Organs," etc., *Sitzungsberichte Phys. Med. Soc. Erlangen*, 1878.

GEGENBAUR, C., "Ueber das Rudiment einer septalen Nasendrüse beim Menschen," *Morph. Jahrb.*, Bd. xi., 1885.

GOLGI, C., "Nervous System," Merkel & Bonnet's Ergebnisse, Bd. ii., 1892 (pub. 1893).

GÖTTE, A., "Die Entwickelungsgeschichte der Unke," 1875.

GRATIOLET, "Recherches sur l'Organe de Jacobson," Paris, 1845.

HARVEY, R., "Note on the Organ of Jacobson," *Q. J. M. S.*, 1882.

HERRICK, C. L., "Topography and Histology of the Reptilian Brain," *Journ. of Comp. Neurol.*, vol. iii.

HERZFELD, P., "Ueber das Jacobson'sche Organ des Menschen und der Saugethiere," *Zool. Jahrb. Abth., f. Anat. u. Ontog.*, Bd. iii., 1889.

HILL, J. P., "Preliminary Note on the occurrence of a Placental connection in *Perameles obesula*, and on the fœtal membranes of certain Macropods," *Proc. Linn. Soc., N.S.W.*, vol. x., 2nd series, Nov. 27, 1895.

HOFFMAN, C. K., (On Jacobson's organ in Reptilia). Bronn's *Thierreich*, Bd. vi., *Abth.* iii.

HOWES, G. B., "On the probable existence of a Jacobson's Organ among the *Crocodilia*," etc., *Proc. Zool. Soc.*, 1891.

JACOBSON, "Rapport de M. Cuvier sur un mémoire de M. Jacobson," in *Annales Muséum d'Hist. Naturelle*, tom. xviii., 1811.

KLEIN, E., "Contributions to the Minute Anatomy of the Nasal Mucous Membrane," *Quart. Jour. Micr. Sci.*, vol. xxi., 1881.

KLEIN, E., "A further Contribution to the Minute Anatomy of the Organ of Jacobson in the Guinea-pig," *Ibid.*, 1891, vol. xxi.

KLEIN, E, "The Organ of Jacobson in the Rabbit," *Ibid.*, 1881, vol. xxi.

KLEIN, E., "The Organ of Jacobson in the Dog," *Ibid.*, 1882, vol. xxii.

KÖLLIKER, A. v., "Ueber das Jacobson'sche Organ des Menschen," *Grat. Schr. des Würz. Medic. Facultät für Rinecker*, Leipzig, 1877.

LEBOUCQ, H., "Le Canal naso-palatin chez l'homme," *Arch. de Biologie*, vol. ii., 1881.

LEGAL, E., "Die Nasenhöhlen und der Thränennasengang der Amnioten Wirbelthiere," *Morph. Jahrb.*, Bd. viii., 1883.

LENHOSSÉK, M. v., "Die Nervenursprünge u. Endig. im Jacobson'schen Organ des Kaninchens," *Anat. Anz.*, 1892.

LEYDIG, F. v., "Die in Deutschland lebenden arten der Saurier," 1872.

LEYDIG, F. v., "Zur Kenntniss der Sinnesorgane der Schlangen," *Arch. für. mikrosk. Anatomie*, Bd. viii., 1872.

MACALLUM, A. B., "The Nasal Region in Entaenia," *Proc. Canad. Inst. Toronto*, 1883.

MARSHALL, A. M., "The Morphology of the Vertebrate Olfactory Organ," *Q. J. M. S.*, 1879.

MEEK, A., "On Jacobson's Organ in *Crocodillus porosus*."

MERKEL, F. v., "Das Jacobson'sche Organ und Papilla palatina beim Menschen," *Anat. Hefte.*, Bd. *Abth.* i., i., Heft. iii., 1892.

PARKER, W. K., "On the Structure and Development of the Skull in Lacertilia," *Phil. Trans.*, part ii., 1879.

PARKER, W. K., "On the Structure and Development of the Skull in the Common Snake," *Phil. Trans.*, part ii., 1878.

PARKER, W. K., "On the Structure and Development of the Skull in the Pig," *Phil. Trans.*, 1874.

PARKER, W. K., "On the Structure and Development of the Skull in the Mammalia," part ii., *Edentata*; part iii., *Insectivora* (*Phil. Trans.*, part i., 1885).

PARKER, W. N., "On some Points on the Structure of the Young of *Echidna aculeata*," *Proc. Zool. Soc.*, 1894.

PIANA, G. P., "Contribuzione alla Conoscenza della Struttura e della Funzione dell' Organo del Jacobson," Bologna, 1880.

RAMON Y CAYAL, S., "Neue Darstellung von Histologischen Bau des Centralnervensystems," *Archiv. f. Anat. und Phys.*, *Anat. Abth.*, Heft vi., 1893.

RATHKE, H., "Entwickelungsgeschichte der Natter," Königsberg, 1838.

RAUGÉ, P., "Anatomie Microscop. de l'Organe de Jacobson chez bœuf," etc. *Arch. intern. de laryng.*, Année 6.

RAUGÉ, P., "Le Canal incisif et l'Organe de Jacobson," *Arch. intern. de laryng.*, 1894.

RUYSCH, "Thesaurus anat. tertius," Amstelod, 1744.

RÖSE, C., "Ueber das Jacobson'sche Organ von Wombat und Opossum," *Anat. Anz.*, 1893.

RÖSE, C., "Ueber das rudim. Jacobson'sche Organ der Crocodile und des Menschen," *Anat. Anz.*, 1893.

SARASIN, P. und F., "Zur Entwickelung Gesch. und Anat. der Ceylon Blindwühle," Wiesbaden, 1890.

SCHWINK, F., "Ueber den Zwischenkiefer und seine Nachbarorg. bei Säugethiere," München, 1888.

SEYDEL, O., "Ueber die Nasenhöhle der höheren Säugethiere und des Menschen," *Morph. Jahrb.*, Bd. xvii., p. 44.

SEYDEL, O., "Ueber die Nasenhöhle und das Jacobson'sche Organ der Amphibien," *Morph. Jahrb.*, Bd. xxiii., p. 453.

SLUITER, C. PH., "Das Jacobson'sche Organ von *Crocodilus porosus*," *Anat. Anz.*, 1892.

SMITH, G. ELLIOT, "Jacobson's Organ and the Olfactory Bulb in Ornithorhynchus," *Anat. Anz.*, 1895.

SOLGER, B., "Beiträge zur Kenntniss der Nasenwandung," etc., *Morph. Jahrb.*, *Bd.* i.

SYMINGTON, J., "On the Nose, the Organ of Jacobson, and the Dumb-bell shaped Bone in Ornithorhynchus," *Proc. Zool. Soc.*, 1891.

SYMINGTON, J., "On the Organ of Jacobson in the Kangaroo and Rock Wallaby (*Macropus giganteus* and *Petrogale penicillata*)," *Journ. Anat. and Phys.*, vol. xxvi., 1892.

SYMINGTON, J., "On the Homology of the Dumb-bell shaped Bone in Ornithorhynchus," *Journ. Anat. and Phys.*, vol. xxx., 1896.

Turner, W., "The Dumb-bell shaped Bone in the palate of Ornithorhynchus compared with the Prenasal Bone of the Pig," *Journ. of Anat. and Phys.*, vol. xix., p. 214, 1885.

Wiedersheim, R., "Die Stammesentwickelung des Jacobson'schen Organes," *Tagbl. Versamml. deutscher Naturforsch v. Aertze in Salzburg*, 1881.

Wiedersheim, R., "Die Anatomie der Gymnophionen," 1879.

Wilson, J. T., "Observation upon the Anatomy and Relations of the Dumb-bell shaped bone in Ornithorhynchus, etc.," *Proc. Linn. Soc. F.S.W.*, 1897.

Wilson, J. T., and Martin, C. J., "Observations upon the Anatomy of the Muzzle of the Ornithorhynchus," Macleay Mem. Vol., *Linn. Soc. N.S.W.*, 1893.

Wright, R. R., "On the Organ of Jacobson in *Ophidia*," *Zool. Anz.*, No. 144, 1883.

Zuckerkandl, E., Das periphere Geruchsorgan der Säugethiere, *eine Vergleichend. Anat. Studie*, Stuttgart.

REFERENCES TO PLATES.

General.—*a.J.c.*, anterior process of Jacobson's cartilage; *a.n.f.c.*, anterior process of the nasal floor cartilage; *g.*, glands; *i.t.*, inferior turbinal bone; *J.c.*, Jacobson's cartilage; *J.d.*, Jacobson's duct; *J.o.*, Jacobson's organ; *l.d.*, lachrymal duct; *mx.*, maxillary bone; *n.f.b.*, nasal floor bone; *n.f.c.*, nasal floor cartilage; *n.p.c.*, naso-palatine canal; *n.s.*, nasal septum; *o.b.J.c.*, outer bar of Jacobson's cartilage; *o.n.f.c.*, outer part of the nasal floor cartilage; *p.c.*, papillary cartilage; *p.n.*, prenasal cartilage; *Pmx.*, premaxillary bone; *p.Pmx.*, palatine process of the premaxillary; *Pvo.*, prevomer; *rud.t.*, rudimentary turbinal cartilage; *u.c.c.*, united canal cartilages; *i.e.*, anterior processes of Jacobson's cartilage and of the outer nasal floor cartilage; *t.p.*, turbinal plate; *v.*, blood-vessel; *val.*, nasal valve; *vo.*, vomer; *v.s.*, vascular space.

The parts shaded in lines are bones; whilst the dotted structures are cartilages.

Plate I.

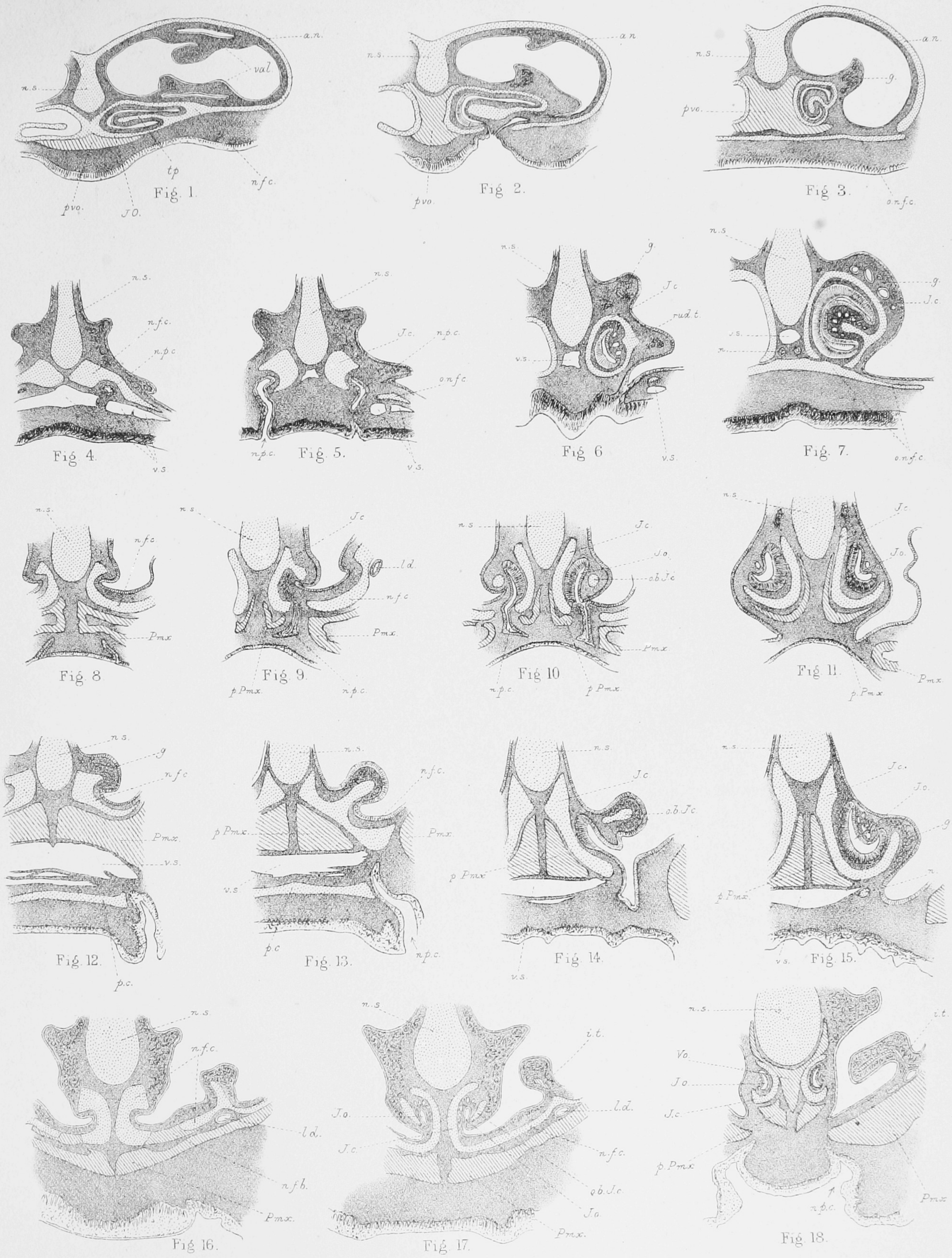
Fig. 1–3.	Transverse sections of the organ of Jacobson in			*Ornithorhynchus anatinus*, × 5.
Fig. 4–7.	,,	,,	,,	*Echidna aculeata*, × 20.
Fig. 8–11.	,,	,,	,,	*Dasyurus viverrinus* (mammary fœtal specimen), × 20.
Fig. 12–15.	,,	,,	,,	*Petaurus breviceps*, × 20.
Fig. 16–18.	,,	,,	,,	*Dasypus villosus*, × 5.

Plate II.

Fig. 19–22.	Transverse sections of the organ of Jacobson in			*Miniopterus schreibersii*, × 25.
Fig. 23–24.	,,	,,	,,	*Erinaceus europœus*, × 10.
Fig. 25–27.	,,	,,	,,	*Felis domestica* (Young), × 10.
Fig. 28–30.	,,	,,	,,	*Sus scrofa* (fœtal), × 20.
Fig. 31–32.	,,	,,	,,	*Equus caballus* (fœtal), × 7.
Fig. 33–35.	,,	,,	,,	*Bos taurus* (fœtal), × 10.
Fig. 36–38.	,,	,,	,,	*Lepus cuniculus* (fœtal), × 20.

Fig. 39. Transverse section of snout of *Delphinaptera leucas* (fœtal), × $1\frac{1}{2}$.

Dr R. BROOM ON MAMMALIAN ORGAN OF JACOBSON — PLATE I.



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ORNITHORHYNCHUS, ECHIDNA, DASYURUS,
PETAURUS, DASYPUS.

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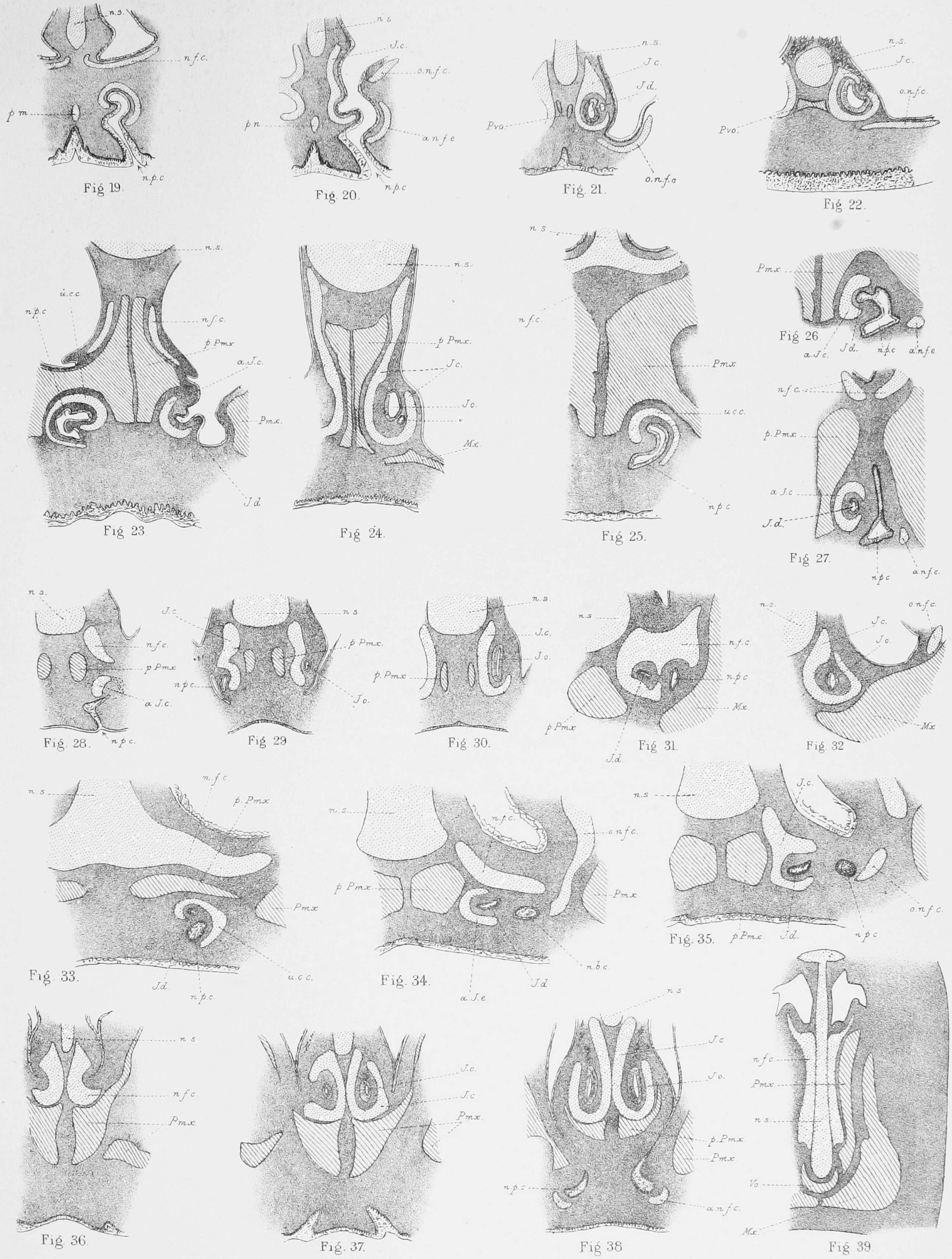

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MINIOPTERUS, ERINACEUS, FELIS, SUS, EQUUS, BOS, LEPUS, DELPHINAPTERA.