ON THE COMPARATIVE ANATOMY OF THE ORGAN OF JACOBSON IN MARSUPIALS.

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(PLATES XLI.-XLVIII.)

Although the researches of Gratiolet, Balogh, Klein, and others had made us familiar with the structure and relations of Jacobson's organ in a number of the principal types of higher Mammals, until very recent years no examination appears to have been made of the organ in any of the Marsupials.

In 1891, Symington published a paper "On the Organ of Jacobson in the Kangaroo and Rock Wallaby," in which he points out the main features of the organ and its relations, and gives figures of transverse sections at the opening of the organ and also at its most developed part. He concludes that the Marsupial organ agrees very closely with the Eutherian type, and differs markedly from that found in the Prototherian Ornithorhynchus. It is unfortunate that when his paper was written only the aberrant Platypus type had been carefully studied, for had he compared the Marsupial organ with the simpler Monotreme type as found in *Echidna*, his conclusion would probably have been different.

In 1893, Röse, apparently ignorant of Symington's work, published a very short paper on the organ in the Wombat and Opossum. He gives two good figures of the organ in the young Wombat, but makes no remarks on the peculiarities of the organ or its relations.

The only other papers, as far as I am aware, in which the Marsupial arrangement is touched on are, Symington's recent paper "On the Homology of the Dumb-bell-shaped Bone in

Ornithorhynchus," and some papers of my own where various references are made to points in the Marsupial anatomy for purposes of comparison.

In the present paper I shall confine myself mainly to the consideration of the general morphology of the organ and its duct, with their cartilaginous and bony relationships, and their vascular and glandular connections in typical members of the chief groups of Marsupials, and to the morphological significance of the various peculiarities met with. In discussing the various forms, I shall adopt tentatively the classification as given in Thomas' "British Museum Catalogue of Marsupials and Monotremes"; and as the polyprotodont Marsupials have long been recognized as the more generalised—a view which is confirmed by the study of the region under consideration—it will be convenient to examine these first.

DASYURIDÆ. (Plate XLI.)

Of this group I have studied, (1) Early mammary foetal *Phascologale penicillata*, (2) mammary foetal *Dasyurus viverrinus*, (3) two-thirds grown *D. viverrinus*, and (4) adult *D. maculatus*.

If a series of transverse sections be made of the anterior part of the snout of *Echidna*, it will be found that there passes out from each side of the base of the septum a flat cartilage, forming a floor to each nasal cavity. In the very young animal, as shown by Newton Parker, this cartilage is well developed, but in the adult it only remains as a floor to the inner half of the nasal cavity. On reaching the plane of the naso-palatine canal, this nasal floor cartilage is found to divide into an inner and an outer part. The inner becomes the cartilage of Jacobson's organ, while the outer, much reduced just behind the region of the naso-palatine canal, on passing backwards becomes more developed and passes inwards below Jacobson's organ, uniting with the corresponding cartilage of the other side. Although there is no similar development of the posterior outer part of the nasal floor cartilage in any Marsupial yet examined, the mode of division of the two parts and the structure and relations of the anterior part of Jacobson's cartilage will be found to have an almost perfect counterpart in the corresponding structures of the Daysure and its allies.

Phascologale penicillata, Shaw, (mammary foetus, head length 9 mm.). The nasal-floor cartilage in front of the naso-palatine canal is present as a well developed, slightly curved plate of cartilage passing outwards from the base of the septum and forming a complete floor to the nasal cavity, uniting laterally with the alinasal. On nearing the naso-palatine canal, its inner end becomes detached from the septum and curves upwards and slightly outwards (Pl. xli. fig. 10). The naso-palatine canal passes somewhat obliquely backwards, as well as upwards, so that in vertical section it is seen connecting the nasal cavity with the mouth. On its passing upwards the premaxillary is seen to separate from its palatine process as if to make a passage (fig. 10), and a little behind this the nasal-floor cartilage divides into its inner and outer parts. The outer part, which is small, disappears almost immediately behind this plane; but the inner part, or Jacobson's cartilage, is well developed and appears as an upright plate with a large process passing outwards from its upper end and forming a support to the *inferior septal ridge*.* The lower part is supported on its lower and inner side by the developing palatine process of the premaxillary.

In fig. 11 the naso-palatine canal has lost its connection with the mouth, and above is seen to receive the opening of Jacobson's duct on the inner side, and on its outer side to be connected with the nasal cavity. Jacobson's cartilage is here well developed, receiving Jacobson's duct or organ in its concave outer side. If this section be compared with the similar section in the young

* This ridge, which extends along on each side of the base of the septum, has been generally referred to as the "glandular ridge." The term, however, is inappropriate, as the ridge is often quite devoid of glandular tissue, and I have therefore proposed the above term instead and in contradistinction to a much more typically glandular ridge frequently present in the upper and middle septal region, which may be called the "superior septal ridge." In the present paper, as only the lower septal region is under consideration, when the term "septal ridge" occurs, the inferior septal ridge will be understood.

Echidna as figured by N. Parker, or in the adult as figured by myself, the striking agreement will be manifest.

In fig. 12 is seen the condition of the organ and its relations in the region of its greatest development. The organ is almost oval in section, there being but a very slight indentation of the outer wall: the inner and lower walls of the organ are about 4-6 times the thickness of the outer. Jacobson's cartilage is a curved plate which supports the organ on its inner and lower sides. The palatine process of the premaxilla, here just commencing to ossify, occupies the lower and inner side of Jacobson's cartilage.

Near its posterior part the organ is reduced to a duct with simple columnar epithelium, and the cartilage is present as a narrow thick plate passing more outwards than downwards, and forming a floor to the duct and its neighbouring developing glands.

Dasyurus viverrinus, Shaw, (mammary foetus, head length 15 mm.). In the somewhat older foetus of the common Dasyure we have the same type, but with the later stage of development the details are better seen. The nasal-floor cartilage is very similar to that seen in the foetal Phascologale, but an additional feature is revealed. From the point where the ascending inner plate of the nasal-floor cartilage sends out the plate to support the basal ridge a detached process of cartilage passes forward supporting the feeble anterior part of the ridge. This is better seen in the adult, and is interesting from the fact that a similar pre-current process has not been found in any other form, except Didelphys.

Figs. 1 and 2 illustrate sections in the anterior part of the nasal-floor cartilage. In fig. 2 the outer part of Jacobson's cartilage is seen detached from the inner on one side. This little detached bar is seen in fig. 4 to become connected with the lower part of Jacobson's cartilage, and from its being almost invariably present throughout the Marsupialia connecting the upper with the lower parts on the outer side, it will be referred to in the following descriptions as the "outer bar of Jacobson's cartilage."

In fig. 3 the naso-palatine canal is seen, on the right side opening into the anterior end of Jacobson's organ. The organ has a very

short duct lined with squamous epithelium. On the left side, which is further back, the opening of the organ into the naso-palatine canal is closing, while the connection between the canal and the nasal cavity is seen. Immediately beyond this plane Jacobson's organ is closed and the lower part of the inner plate of Jacobson's cartilage becomes connected with the outer bar, forming a floor to the organ; and what was the naso-palatine canal becomes lost in the general nasal cavity.

Fig. 4 represents a section through the body of the organ. The cartilage on section assumes the appearance of an irregular L or a U with the outer side shorter than the other—an appearance very common in Marsupial types. It is supported on its lower and inner sides by the scroll-like palatine-process of the pre-maxilla. The organ on section is kidney-shaped, with a much indented hilus, which accommodates the rather large blood vessel.

Dasyurus viverrinus, Shaw, (two-thirds grown). In the grown Dasyure the condition of parts is essentially similar to that in the young. Fig. 5 shows a section in the region of the hinder part of the papilla—a portion of the papillary cartilage being seen. The nasal-floor cartilage is moderately flat, and somewhat above its inner end by the side of the septum is seen the small precurrent process of cartilage supporting the septal ridge. In fig. 6 the pre-maxillary is about to give off its palatine process. The naso-palatine canal is seen cut across below the isthmus, while above it the nasal-floor cartilage is dipping down into the hollow. The outer part of the nasal-floor cartilage behind this becomes lost in *D. viverrinus*, though in *D. maculatus* it is seen for a short time as a very small fragment on the outer side of the naso-palatine canal. The organ opens into the naso-palatine canal almost immediately behind the plane of fig. 7. Fig. 8 is just behind the opening of the organ and immediately in front of the plane where the naso-palatine becomes part of the general nasal cavity. Here the organ is roofed over by the union of the inner plate of Jacobson's cartilage with the outer bar. In fig. 9, a little further back, the upper union with the outer bar is lost and the lower connec-

tion complete, giving the cartilage the typical appearance on section.

The organ itself at its best developed part has on section a moderately regular kidney shape, the hilus being directed almost quite upwards and having in it a single large blood vessel. There is extremely little glandular tissue in connection with the anterior and middle part of the organ. The sensory layer is unusually well developed, being about $3\frac{1}{2}$ times as thick as the nasal epithelial layer. The outer wall of the organ has small columnar cells only about half the size of those of the nasal epithelium.

Dasyurus maculatus, Kerr, (adult). The organ in this species differs considerably in a number of ways from that of *D. viverrinus*. In almost all large animals the organ is less developed proportionately, and appears to have less of a sensory function, and to become to a greater extent a glandular duct; and yet with the difference in the character of the organ the cartilaginous relations remain very constant in allied species and genera. The only difference in the cartilaginous developments of the two species of *Dasyurus* is a very slight one of degree; *e.g.*, in *D. maculatus* the cartilage is rather more developed in front, and rather less posteriorly than in the smaller species. As regards the organs, however, the differences are marked. The sensory layer is present quite characteristically, but much less developed than in *D. viverrinus*, while the whole organ is absolutely smaller in lumen, which means that it is relatively only about half the size. Instead of occupying almost the whole of the cartilaginous hollow as in the smaller species, it fills only about one-third the available space, the rest being almost quite filled up by a great development of mucous gland tissue, except that occupied by the large hilar vessel.

DIDELPHYIDÆ. (Plate XLII.)

In the American carnivorous genus *Didelphys*, we have a number of points of close agreement with *Dasyurus*, and also a few features suggesting a considerable gap between them. This genus I have been able to study through the kindness of Sir. W.

Flower in supplying me with three mammary fœtuses—one small and two moderate-sized—of which I have sectioned the small one and one of the large.

Didelphys murina, L., (mammary fœtus, head length 14 mm.). In the young fœtal Opossum the anterior portion of the nasal-floor cartilage agrees very closely with the condition in the *Dasyure*; not only is it comparatively flat, but from its ascending inner plate it gives off a precurrent process to support the anterior part of the septal ridge. In the plane of the papilla (fig. 1) the premaxilla is seen giving off its palatine process. The nasal-floor cartilage is here curved, the inner end passing up by the side of the septal base into the septal ridge, while it is slightly depressed into the hollow between the premaxilla and its palatine process. A broad but not very thoroughly chondrified papillary cartilage is seen in the section; and by its edge the naso-palatine canal is seen opening. In fig. 2—a little distance behind—the nasal-floor cartilage is found to have become divided as in *Dasyurus*, the inner part having become a well developed Jacobson's cartilage, while the outer part has on this plane become lost. If this figure be compared with fig. 2 of the *Dasyure* the close agreement between the forms will be seen in the structure of Jacobson's cartilage. There is, however, a slight difference in the relations borne by the developing palatine processes to the cartilages. In *Dasyurus* the palatine process is mostly inferior; while in this form it lies within the lower half, the bottom end of the cartilage being unsupported by bone. This though apparently a small matter will be seen to be of considerable interest in connection with the condition in the other forms to be described. In *Didelphys murina* the septal ridge is more marked, the lower corner of the nasal cavity passing well in below it. The naso-palatine canal will be noticed to have an almost vertical direction, the obliquity being very slightly marked. The connections of the canal with Jacobson's organ and with the nasal cavity are as in *Dasyurus*, except that in *Didelphys murina* the organ becomes constricted into a little roundish duct-like canal before opening into the naso-palatine canal. This little constricted part is not a

true Jacobson's duct, as it is lined with columnar epithelium. The organ where best developed, as seen in fig. 3, almost completely fills the large hollow cartilage. On section it is kidney-shaped, but the two poles are approximated so as to give the organ an almost circular appearance, folding the small outer wall closely on itself. The cartilage is supported by the small curved palatine process at its lower and inner side.

Didelphys marsupialis, L., (?)* (large mammary foetus, head length 37 mm.). Between this form and the foetal *D. murina* there are a number of little differences, in addition to what can be accounted for by difference of age. The nasal-floor cartilage is nearly flat, and on passing backwards turns up at the base of the septum as in *D. murina*. The inferior septal ridge is here less developed, and the precurrent cartilaginous process, present in *D. murina*, is practically absent. In fig. 4 is shown a section in the plane of the opening of the naso-palatine canal. Though the papilla is well developed there is no trace of a papillary cartilage, which is interesting as this is the only Marsupial I have met with where it is quite absent. In fig. 5 the nasal-floor cartilage is found divided and the premaxilla distinct from its palatine process; and in the space between the divided structures is seen the anterior part of the almost vertical naso-palatine canal. The outer part of the nasal-floor cartilage is still distinct. A few sections behind this plane, as seen in fig. 6, show the outer end of the upper part of Jacobson's cartilage becoming detached, forming the outer bar. The palatine process will be seen to bear the same relation to the cartilage as in *D. murina* (fig. 2). In fig. 7 the naso-palatine canal is seen opening into the nasal cavity, as well as into Jacobson's organ. This last connection is effected by means of a very short duct of Jacobson. In the next figure the organ is closed from the canal which still connects the nasal cavity with the mouth.

* The species of this specimen was unknown, but there is very little doubt that it is the young of the Common Opossum, *Didelphys marsupialis*, L.

The organ itself in the region of best development (fig. 9) has on section the usual kidney shape. There is some resemblance to the organ in *Dasyurus*, with which it agrees in having a single vessel along the hilus; in *Didelphys*, however, the blood vessel is considerably smaller. The sensory region is well developed, the upper and lower ends of which curve towards each other constricting the hilar region slightly. In the hilar region are a few mucous glands which open into the organ at the point of union of the upper end of the sensory wall with the non-sensory. The main nerves lie as usual in the little triangular space above the organ.

PERAMELIDÆ. (Plate XLIII.)

In the Bandicoots I have confined myself to the study of one species, *Perameles nasuta*; of which I have examined—(1) a young mammary foetus; (2) a half grown specimen; and (3) an adult. To Mr. A. G. Hamilton, of Mt. Kembla, N.S.W., I am indebted for the foetus and the adult specimen.

Perameles nasuta, E. Geoff., (mammary foetus, head length 21 mm.). In a section through the developing first upper incisor, and also a little in front of and behind this plane, the nasal-floor cartilage will be found to be well developed and moderately flat. By each side of the base of the septum is a rather large inferior septal ridge, and into the base of it, at least, passes an ascending plate of the nasal-floor cartilage, lying close to the septum. This ascending plate is better developed anteriorly in this genus than in either *Dasyurus* or *Didelphys*. On reaching the papillary planes the septum is found to have retreated, and its place to have become occupied between the two ascending plates of the nasal-floor cartilage by the two palatine processes of the premaxillary (fig. 1). This very marked retreating of the base of the septum is greater than in the other Marsupials, and recalls the condition in the Insectivora. In fig. 1 is shown the moderately developed papillary cartilage, by the edge of which the naso-palatine canal is seen entering. Here also the well developed nasal-floor cartilage is seen passing up and curving round into the septal ridge forming

its support. In the immediately succeeding planes the inner plates of the nasal-floor cartilages about to become Jacobson's cartilages are seen approaching somewhat and the palatine processes becoming more curved along their inner sides; while the process of cartilage supporting the ridge becomes a detached bar. This bar thus becomes detached further forward than in either *Dasyurus* or *Didelphys*. A very short distance behind the plane of the posterior part of the papilla, the naso-palatine canal is found passing inwards below the lower edge of Jacobson's cartilage and even below the lower edge of the palatine process. From this point it passes outwards, upwards, and slightly forwards into the hollow of the lower half of Jacobson's cartilage, where it meets a short but distinct Jacobson's duct. It also passes outwards and backwards, as seen in fig. 2, opening into the nasal cavity. On this plane the short duct of Jacobson is replaced by the lower part of the organ proper, which is almost shut off from the naso-palatine canal. In the relations of the canal to the lower part of the palatine process and of the cartilage of Jacobson there is a marked agreement with *Didelphys*, though the lower unsupported part of Jacobson's cartilage is much greater here than in that genus, and clearly suggest the development met with in both the *Phalangers* and the *Kangaroos*. Almost immediately beyond the plane of the closing of the organ the lower end of the inner plate of Jacobson's cartilage curves round and unites with the outer bar, giving on section the usual U-shaped hollow trough.

The organ itself closely resembles that in *Didelphys* in the folding together of the feeble outer wall. There is, however, a marked difference in the support the cartilage obtains from the palatine process. In *Perameles* the palatine process is largely developed, and forms a bony support to almost the whole inner and lower sides of the cartilage. About the middle region of the organ, in fact, with the exception of a very small portion at the upper angle, the palatine process not only completely surrounds it, but at its outer edge even replaces the cartilage. On nearing the posterior end of the organ the cartilage becomes completely lost in the whole lower region being replaced by the palatine

process, and ultimately all that is left of it is a small plate lying over the upper and inner side of the reduced posterior end of the organ.

Perameles nasuta, E. Geoff., (half grown and adult). Between the adult and half grown condition the chief differences are due to the fact that in the adult the bony development is greater and the cartilaginous elements more degenerate. In the following account it is the half grown specimen that is being described unless otherwise stated.

In the region immediately in front of the incisor teeth, the nasal septum is rather broad and at its base has on each side a well developed inferior septal ridge. The nasal-floor cartilage is relatively feeble on the whole, but its inner part is better developed and turns up close against the septum, then curves outwards to form the support of the septal ridge. On reaching the plane of the first pair of incisors, the only difference worth noting is that the septum has retreated somewhat, and only the inner part of the nasal-floor cartilage remains.

In the adult, even in the region of the premental portion of the premaxillary, the nasal-floor cartilage is represented by little more than the inner part.

In the plane of 2nd incisor in the half grown specimen the nasal-floor cartilage is represented only by the skeleton of the ridge, while on the same plane the premaxilla is seen sending up a process towards the base of the septum. In the anterior papillary region, as seen in fig. 5, the cartilage is found present as an inner plate and an outer bar. Though this is in front of the naso-palatine canal, as there is no outer part of the nasal-floor cartilage, it will be better to call it Jacobson's cartilage, for though there is no organ at this point, from the condition of the cartilages and other structures it is highly probable that the organ once extended forwards considerably in advance of its opening into the naso-palatine canal, as is the case in *Ornithorhynchus*. As it is, the organ still extends some little way in front of its opening into the naso-palatine canal, and on one side of fig. 6 the anterior extension is seen cut across.

In fig. 6 and fig. 7 the very short naso-palatine canal is seen first opening into Jacobson's organ and then connecting the nasal cavity with the mouth in the usual manner. In both figures the enormous development of the palatine processes is the most noticeable feature. On the outer side of the outer bar of Jacobson's cartilage is seen in section a precurrent process from the outer part of the palatine process of the premaxillary. On the left side of fig. 7 the inner plate of Jacobson's cartilage is seen sending down a process by the side of the canal; on the right side, which is a little further back, the inner plate of Jacobson's cartilage has united with the outer bar.

In the adult in the region just considered the palatine process of the premaxillary is very similar, but the cartilage has degenerated into a few irregular patches. It is interesting that the downward process of Jacobson's cartilage by the side of the naso-palatine canal is persistent (fig. 9).

In the region of greatest development the organ is very similar to that in the other Polyprotodonts. In the adult the cartilaginous capsule is scarcely observable, the organ being almost entirely supported by the well developed palatine process. The sensory wall is fairly well developed, though less so than in either *Dasyurus viverrinus* or *Didelphys*. Along the hilus there runs a single moderate-sized vessel, and a rather large vein runs along the inner and under side of the organ. There are no glands in connection with the anterior part of the organ.

PHALANGERIDÆ. (Plates XLIV.-XLVI.)

Although the Phalangers are probably not the Diprotodonts most nearly related to the Polyprotodonts, yet as they represent most distinctly the typical differentiation of the structures found in the Diprotodonts, it will be more convenient to consider them first.

Sub-family PHALANGERINÆ. (Plates XLIV.-XLVI., figs. 1-6.)

Of this group I have examined, (1) early mammary fœtus, *Pseudochirus peregrinus*; (2) adult *P. peregrinus*; (3) adult

Petauroides volans; (4) adult *Petaurus breviceps*; (5) very early mammary fœtus, *Trichosurus vulpecula*; (6) early mammary fœtus, *Trichosurus*; (7) large mammary fœtus, *Trichosurus*; and (8) adult *Trichosurus*.

In all these genera the same type is followed, and the close agreement between the different genera is remarkable.

Pseudochirus peregrinus, Bodd., (mammary fœtus, head length 8.5 mm.). In the anterior papillary plane and a little in front the nasal-floor cartilage is well developed, but not of very great lateral extent. The nasal septum comes well down and anteriorly the nasal-floor cartilage abuts squarely against it; but in the middle region of the papilla the septum has begun to retreat, and the inner end of the nasal-floor cartilage curves up towards it somewhat. There is on each side a well developed septal ridge, and the nasal-floor cartilage sends a feebly developed process towards it. In Pl. XLIV. fig. 1, the ridge process is not so well developed as just in front. In this section will be seen a feature which is developed in all the Diprotodonts as distinguished from the Polyprotodonts, in the great lateral development of all the structures. The inferior septal ridges project more, making the base of the septal region much broader; the nasal-floor cartilages are further apart at their inner ends, and the palatine processes which are developed in connection with Jacobson's cartilages are, in their early development instead of closely together as in the Polyprotodonts, widely apart. The naso-palatine canal passes obliquely upwards and backwards, and opens into Jacobson's organ on practically the same plane as that in which it becomes part of the general nasal cavity. In Pl. XLIV. figs. 2 and 3, the nasal-floor is found divided. Jacobson's cartilage is hollowed slightly on the inner side, and in the hollow lies the palatine process of the premaxilla. In the region of best development Jacobson's cartilage is present as a slightly concave plate, which inclines markedly outwards as well as downwards from the base of the septum. The palatine process is present as a small ossified bar lying along the middle of the inner side. The organ itself is almost oval on section; the inner wall of which is

more than half the diameter, while the lumen is slightly crescentic, owing to the outer wall being much better developed at its central than lateral portions.

Pseudochirus peregrinus, Bodd., (adult), *Petauroides volans*, Kerr, (adult), and *Petaurus breviceps*, Waterh., (adult). These three genera agree with each other so markedly that it will only be necessary to describe the condition in one—*Petaurus*—and call attention to the points in which the others differ from it.

In a plane immediately in front of the papilla, the condition of the nasal-floor cartilage is found to agree very closely with that described in *Perameles*, each inner end having an ascending plate closely placed against the sides of the base of the septum. The only marked difference is that the lateral part of the cartilage is much curved; this, however, is rendered necessary by the largely developed first incisors. In the plane passing through the middle of the papilla the inner ascending plate of the nasal-floor cartilage is much shorter, but has become broadened out, while the inferior septal ridge, which anteriorly was developed considerably vertically, is here a much more defined ridge, and from the outer angle of the irregular square-shaped inner part of the nasal-floor cartilage a slight process passes into the ridge. The outer part of the nasal-floor cartilage becomes almost entirely lost. Pl. XLIV. fig. 10 represents a section through the third incisor or the posterior part of the papilla. Here the nasal-floor cartilage assumes an appearance which may be regarded as typical of the *Phalangers*. The inferior septal ridge is removed from any direct connection with the septum, and the process from the inner part of the nasal-floor cartilage (which may even here be regarded as Jacobson's cartilage) supporting it, instead of coming from the inner part of the cartilage, springs from a point considerably farther out, while an independent continuation of the nasal-floor cartilage extends on to the base of the septum. In *Petaurus* Jacobson's cartilage lies very obliquely outwards on the palatine process, but in *Petauroides* and *Pseudochirus* the cartilage is much more vertical (*cf.* fig. 4); otherwise, however, the structures are similar. Inferiorly the cartilage plate extends downwards considerably

past the lower edge of the palatine process, a condition more apparent in *Pseudochirus* than in *Petaurus*. On passing backwards the outer part of the cartilaginous process of the ridge becomes detached as the outer bar of Jacobson's cartilage. In Pl. XLIV. fig. 11 the anterior part of Jacobson's organ is indicated, with the naso-palatine canal connected with the short duct of the organ. In Pl. XLIV. fig. 12 the organ communicates freely with the nasal cavity at the plane where the naso-palatine canal becomes part of the cavity.

From Pl. XLIV. figs. 5 and 6 it will be seen that in *Pseudochirus* the opening of the organ is more directly into the upper part of the canal, while in *Petauroides* (fig. 8) the condition agrees more nearly with that in *Petaurus*. The difference, however, is only a very slight one of degree.

After the closing of the organ the lower part of Jacobson's cartilage unites with the outer bar in the usual manner. In *Pseudochirus* the ridge is considerably lower than in the other Phalangians, so that when the lower part of Jacobson's cartilage is complete, instead of an irregular U-shaped appearance we have a very regular L, as in Pl. XLIV. fig. 7. In *Petauroides* (fig. 9) the cartilage has the more usual appearance.

The organ in all these genera is well developed, and has on section a rather elongated kidney shape. In the small *Petaurus* the sensory wall is larger proportionally than in the other two genera. The hilus is very broad and only but slightly depressed, leaving a larger lumen to the organ. In all three genera there is a distinct venous plexus usually composed of one, two, or three vessels anteriorly, which branch into six or more posteriorly. There are but few glands in connection with the organ, except at the posterior part.

Trichosurus vulpecula, Kerr, (mammary fœtus, head length 7.5 mm.). In this very small mammary fœtus, which may be taken as the size at birth, the cartilages are all fairly well developed, and the ossification of the premaxillary bones quite distinctly marked. In the plane of the developing incisors the nasal-floor cartilage is very well developed, as seen in Pl. XLV. fig. 1.

At its inner end it sends up a process by the side of the septum, which latter at this early stage descends down between the inner ends of the premaxillaries. At the outer ends the nasal-floor cartilage unites with the alinasal. On reaching the plane of the papilla the nasal-floor cartilage divides into its inner and outer parts; before dividing, however, the downward process of the inner part makes itself manifest. On the left side of Pl. XLV. fig. 2, representing the plane a little behind the division of the nasal-floor cartilage, Jacobson's cartilage is seen as a curved plate with, near the middle of the inner concave side, the developing palatine process, present as a minute spicula of bone. The downward process, it will be seen, is more marked than in the young *Pseudochirus*. The naso-palatine canal has the usual relations, opening first into Jacobson's organ and then becoming merged in the nasal cavity. The organ is present as a small oval tube with the inner wall considerably thicker than the outer.

Trichosurus vulpecula, Kerr, (mammary foetus, head length 10.5 mm.). In this more developed mammary foetus the relations of parts are better seen. In Pl. XLV. fig. 4 is shown the complex structure of the inner part of the nasal-floor cartilage just before division. From this figure it will be seen that the descending process is a structure superadded to the simple nasal-floor cartilage as seen in the *Dasyure*. The same can probably also be said of the internal ascending process. In Pl. XLV. fig. 6 Jacobson's cartilage is an almost vertical plate with the rod-like palatine process along the middle of the inner side. The organ is here very large.

Trichosurus vulpecula, Kerr, (mammary foetus, head length 20 mm.). In the series of sections from this specimen we have the steps intermediate between the condition in the early foetus and the adult. The nasal-floor cartilage before division as seen in Pl. XLV. fig. 7 may be compared with Pl. XLIV. fig. 4, illustrating the similar part in *Pseudochirus*. The only marked difference is due to the unusually well developed posterior outer part of the nasal-floor cartilage. In the Ringtail the outer nasal-floor cartilage is only a rudiment, but here it is larger than the inner part.

The ridge process, on the other hand, so large in the Ringtail and Flying Phalangers is only slightly developed in *Trichosurus*. The descending process is very distinct; and the palatine process more developed vertically than in the younger fœtuses. In Pl. XLV. fig. 8 the naso-palatine canal passes up almost vertically and opens into Jacobson's organ. At this stage there is no chondrification of the outer bar. In the following figure the organ is closed; and the naso-palatine canal is merged in the nasal cavity. Even in this plane the outer part of the nasal-floor cartilage is still well developed. Jacobson's cartilage is an almost vertical plate, and the organ lies against it much flattened from side to side.

Trichosurus vulpecula, Kerr, (adult). In the adult common Phalanger there is considerable agreement with the condition in the adult *Petaurus*. All the main peculiarities are due to two facts—(1) a much less degree of development of the inferior septal ridge in *Trichosurus*; and (2) a greater development of the outer nasal-floor cartilage.

In Pl. XLVI. fig. 1 through the posterior papillary region, the inner part of the nasal-floor cartilage is very similar to that in *Petaurus*, except that the ridge process is more feeble here; the outer part of the nasal-floor cartilage though small is, however, better developed than in *Petaurus*. The papillary cartilage is well seen in this plane and is interesting from its having a distinct median ridge. In Pl. XLVI. figs. 2, 3 and 4, is seen the mode of division of the nasal-floor cartilage, which is more complicated than in any of the other common Marsupials. In the most anterior part of the gap between the premaxilla and its palatine process there is a most distinct, rather large, descending process filling up the whole gap. On the naso-palatine canal passing up, and on the premaxillary being farther removed from the palatine process, the descending cartilaginous process remains only as a narrow internal plate lying close against the palatine process (Pl. XLVI. fig. 2). In this plane the ridge process though small is distinct, and is connected with both the inner plate of Jacobson's cartilage and the outer part of the nasal-floor cartilage. In Pl. XLVI. fig. 3, a very little behind the previous plane, an anterior prolongation of

Jacobson's organ makes its appearance between the outer end of the ridge process and the inner plate of Jacobson's cartilage, dividing the one from the other; but though the outer part of the ridge process—clearly the outer bar of Jacobson's cartilage—becomes detached from the inner plate, it still retains its connection with the outer part of the nasal-floor cartilage. In Pl. XLVI. fig. 4, however,—a little further back still—the outer bar is free from the nasal-floor cartilage which is now lost. On this plane the appearance quite agrees with that in the Ringtail—the organ connecting with the naso-palatine canal in quite a similar way. In Pl. XLVI. fig. 5 the organ is closed, and the naso-palatine canal is merged in the nasal cavity. In the following figure the usual appearances are presented. The inner plate of Jacobson's cartilage has united below with the outer bar, and an irregular U-shaped hollow is formed for the reception of the organ.

The organ is large and has an irregular crescentic shape; with a well developed sensory wall. The hilus is large and contains two or three large veins and one or two small; while all along the outer side of the organ is an enormous amount of glandular tissue, in which it differs from that of the other Phalangers.

Subfamily PHASCOLARCTINÆ. (Plate XLVI. figs. 7-9.)

Phascolarctus cinereus, Goldf., (two-thirds grown). In *Phascolarctus* we have a very highly modified type which differs in many ways from that of the Phalangers just described.

The naso-palatine canal is very long and oblique. In Pl. XLVI. fig. 7 we have represented a section through the plane a little in front of the point where the premaxillary gives off its palatine process. In this and the following sections the most striking peculiarity is the depth of the secondary palate. The nasal-floor cartilage is well developed, but with the narrowing of the nasal cavity only a very small portion is really a floor. At its inner end it is very simple and abuts against the base of the septum. Below the septum will be seen the vomer, a most exceptional occurrence, this being the only Marsupial known in which the vomer is directly in contact with the body of the premaxillary.

In the lower part of the section the naso-palatine canal is seen cut across.

On reaching the plane where the premaxillary gives off its palatine process the nasal-floor cartilage is found to bend down into the gap formed, as seen on the left side of Pl. XLVI. fig. 8. There is no more than a slight indication of a downward process apart from the general dipping down and thickening of the nasal-floor cartilage. The palatine process is by the side of the lower third of the downward bent cartilage; while the naso-palatine canal is seen almost in contact with the lower part of the cartilage. On the right side of the same figure is seen the condition a little farther back. The large solid downward extension has given way before the ascending naso-palatine canal, and there is formed a well marked inner plate, extending from the side of the base of the septum, down past the vomer and along the upper half of the palatine process. From the upper end of this plate there passes an outward and downward process which becomes continuous with the outer part of the nasal-floor cartilage. In Pl. XLVI. fig. 9 we see the inner part of the nasal-floor cartilage or Jacobson's cartilage separated from the outer. It has a well developed inner concave plate, with above a downward and outward sloping roof. In the hollow is the anterior part of Jacobson's organ connected with the naso-palatine canal near the point where it merges into the nasal cavity.

Beyond this plane there is found passing up from the lower edge of the inner plate a process meeting the lower edge of the roof and forming a complete cartilaginous tube for the organ.

The organ itself, however, is very feebly developed relatively, though it possesses the usual sensory wall. There are very few glands in the tube; but it is extremely interesting to find a plexus of five or six large veins on the outer side of the organ. The whole length of the organ is somewhat less than 10 mm.

MACROPODIDÆ. (Plate XLVII.)

Of the Kangaroo group, Symington, as already stated, has examined the small mammary foetus of *Macropus giganteus* and

of *Petrogale penicillata*, and found that the condition in both forms is "practically identical." Of this group I have examined (1) a series of sections prepared by Prof. Wilson, of a very small mammary foetus of *Macropus sp.*?; (2) a large mammary foetus of *M. ualabatus*; and (3) a small mammary foetus of *Epyprymnus rufescens*.

Sub-family MACROPODINÆ. Plate (XLVII. figs. 1-9.)

Macropus sp.? (mammary foetus, total length 29 mm.). In this very young foetus the condition of parts agrees very closely with that in *Trichosurus*. The nasal-floor cartilage is well developed in the anterior part (Pl. XLVII. fig. 1), but before reaching the upper opening of the naso-palatine canal the outer part is lost. There is a distinct though small downward process. The naso-palatine canal passes up almost vertically, and the organ of Jacobson opens into it on the same plane as that in which it unites with the nasal cavity (fig. 2). The palatine process is represented as in *Trichosurus* by an ossifying rod near the middle of the inner plate of Jacobson's cartilage. Posteriorly the condition agrees with that in the early foetal *Trichosurus*.

Macropus ualabatus, Less. & Garn., (large mammary foetus, head 50 mm.). This specimen may be taken as the type of the Kangaroo.

In front of the naso-palatine canal (Pl. XLVII. fig. 3) the nasal-floor cartilage is rather feebly developed and very simple in structure. There is no distinct septal ridge, and in consequence the inner end of the floor cartilage remains more simple than in the Phalangers. Inferiorly a broad papillary cartilage is seen. In fig. 4, where the naso-palatine canal begins to be seen, the nasal-floor cartilage becomes very much thickened and dips down in the hollow formed where the palatine process is about to divide off from the premaxilla. The condition resembles in general appearance that of *Phascolarctus* more than that of the Phalangers. On reaching the plane where the palatine process becomes quite distinct from the premaxilla the following condition is seen on section (Pl. XLVII. fig. 6). The large dipping down portion of

the nasal-floor cartilage is hollowed out to accommodate an anterior projection of Jacobson's organ, but we are thereby enabled to understand the different parts. If this section be compared with Pl. XLV. fig. 3, the Trichosure condition, there is no trouble in making out the homology of the different parts. The inner plate corresponds to that in Trichosurus, except that it does not curve downwards at its lower end, but retains its connection with the outer part of the nasal-floor cartilage. On the outer side of the opening in the cartilage above the organ is seen a distinct knob attached to the outer nasal-floor cartilage; this is unquestionably the outer bar of Jacobson's cartilage, agreeing closely with the condition in Trichosurus; while the upper opening in the cartilage is due to the customary detachment of the outer bar from the inner plate of Jacobson's cartilage. In Pl. XLVI. fig. 4 we have the more usual condition revealed; almost the only difference, in fact, from the similar section in Trichosurus (Pl. XLV. fig. 4) is due to the absence or reduction of the inferior septal ridge in Macropus. The naso-palatine canal opens into the organ and the nasal cavity in the usual way.

At its hinder end, as seen in Pl. XLVII. fig. 9, the organ is situated well up the side of the septum, a condition recalling the appearance in the human foetus.

The organ itself is on the whole rather feebly developed, and has the appearance of a degenerate Phalanger type. There are few glands anteriorly, and in the hilus are only a few small blood vessels.

Sub family P O T O R O I N Æ. (Plate XLVII. figs. 10-12.)

Æpyprymnus rufescens, Gray, (mammary foetus, head length 15.5 mm.). In the Rat-Kangaroo, though we have a fairly close agreement with the condition in Macropus, we have some remarkable differences. Pl. XLVII. fig. 10 represents a section in the plane of the 2nd upper incisors. The nasal-floor cartilage is well developed, and at its inner part is found turning round to support the inferior septal ridge more after the manner of the Polyprotodonts than of the Phalangers. In the plane through the point

where the palatine process is first seen distinct from the premaxilla, the inner part of the nasal-floor cartilage curves markedly upwards and sends out a well marked though feeble plate into the inferior septal ridge. At the lower angle of the nasal-floor cartilage there is sent down a short process into the gap between the premaxilla and its palatine process.

Immediately following this plane we have the remarkable condition shown in Pl. XLVII. fig. 11. The outer part of the nasal-floor cartilage is detached from Jacobson's cartilage, which is present as an inner plate and an outer bar. In the hollow is found the anterior portion of Jacobson's organ opening directly into the anterior part of the nasal floor, and in no way directly connected with the naso-palatine canal. It is only some sections posterior to this, after the organ is quite closed, that the naso-palatine canal unites with the nasal cavity. In other respects the ordinary arrangement is followed.

The relation of the palatine process to the cartilage is more like that found in *Petaurus* than in *Macropus*.

In the early foetal specimen the vascular and glandular relation of the organ cannot be made out very satisfactorily, but there is apparently nothing remarkable about the organ itself.

PHASCOLOMYIDÆ. (Plate XLVIII).

Of the *Wombat* I have only had an opportunity of examining the condition in a half grown specimen, but Röse has fortunately published two very good sections of an early mammary foetus, which I have taken the liberty of reproducing.

Phascolomys wombat, Per. & Less., (very early foetus, body length 19 mm.) [after Röse]. In this early foetus the condition most strikingly resembles that in the *Dasyure*. Indeed, if Pl. XLVIII. fig. 1 be compared with Pl. XLI. fig. 3, illustrating the foetal *Dasyure*, there is not a single feature of importance in which any difference can be detected. The organ opens similarly, the cartilage of Jacobson is similar, the palatine processes exactly agree, and further bear the same relations to the cartilages. Pl. XLVIII. fig. 2, which apparently is a section through the posterior part of the

organ, shows some of the Diprotodont characters, *e.g.*, the cartilages being considerably apart, and the organ having a large gland duct entering it from above.

Phascolomys mitchelli, Owen, (half grown specimen). In this specimen, which may be taken as the adult type, we have a great similarity in many ways to the condition in *Phascolaretus*. Here there is, however, but a very feeble development of the outer nasal-floor cartilage, and in this resembling *Macropus*.

In Pl. XLVIII. fig. 3 we have a section through the posterior part of the very large papilla—a portion of the papillary cartilage being still seen. At this plane the septum dips considerably below the level of the nasal floor, and has by the side of the deep portion a descending plate from the nasal-floor cartilage, or possibly rather an enormously thickened inner end of the cartilage. In fig. 4 this large inner part of the nasal-floor cartilage becomes still more developed and extends down into the hollow formed between the premaxillary and its palatine process, about to become detached in section. Below the bony isthmus is seen the very long and oblique naso-palatine canal. In fig. 5 the palatine process is detached from the premaxilla, and in the gap between is a distinct descending plate which almost meets the naso-palatine canal and rests on the palatine process. The cartilage is excavated in the middle for the anterior part of the organ, but its roof is entire and united with the feeble outer portion of the naso-palatine canal. Fig. 6 shows the anterior part of the organ situated in the hollow of Jacobson's cartilage and opening into the naso-palatine canal exactly as in *Macropus*. Here the outer part of the roof cartilage has become detached from the outer nasal-floor cartilage. A little behind this plane the lower part of Jacobson's cartilage passes up and forms a complete tube for the organ as in *Phascolaretus*. The palatine process is situated very much as in *Macropus*, but more inferiorly.

The organ is fairly developed, and more than half fills the cartilaginous tube. At its upper inner angle it receives a number of gland ducts, the glands lying at the inner side of the upper

end of the tube. Two large nerves lie at the upper end of the tube, and on the inner side are two or three moderately large veins. There is, however, no hilar plexus as in *Phascolarctus*.

COMPARATIVE OBSERVATIONS.

From the examination of Jacobson's organ in the various types of Marsupials, it will be noticed that although there are many variations of details, the same general plan is followed in all; though the habits of the different animals vary greatly and with the habits are very distinct differences of tooth structure; though some of the animals are nocturnal and others lovers of the light, some gregarious and others solitary; all possess moderately developed organs of Jacobson, and in all have we the one main type of structure followed. Studies in Eutherian forms lead to the same conclusions, viz., that the type of organ does not vary with the habits, but remains constant throughout large groups of apparently not very nearly related animals. For example, we have one type in such dissimilar forms as the Ox, Sheep, Horse, Dog, Cat, and Hedgehog, but quite a different type in the Rodents. From this constancy of type followed by the organ it is manifest that it must be a very valuable factor in the classification of groups—apparently of more importance than even the dentition.

Before considering the morphological importance of the different varieties in the Marsupialia, a few general observations may be well. In Mammals generally it would seem that the organ is best developed in small forms, and that in animals which have increased much in size from what may be considered the ancestral type, the organ is not found to have increased proportionally, and though still retaining the typical sensory character it is in a measure degenerate. Then, again, in all forms apparently there are mucous glands in connection with the organ and which discharge into it. In small forms, *e.g.*, *Mus*, *Petaurus*, *Miniopterus*, &c., the glands are few and mostly situated at the posterior end of the organ; while in relatively larger forms as *Lepus*, *Trichosurus*, &c., the glands are numerous and open into the organ along nearly

its whole extent. This peculiarity is well seen in the two species of *Dasyurus*; in the small *D. viverrinus* the glands are few, while in the large *D. maculatus* they are very numerous. I am not aware that sex has anything to do with the peculiarities of this remarkable organ, concerning the function of which we know so little.

In the three Polyprotodont genera the nasal-floor cartilage and its inner division or Jacobson's cartilage are very simple in structure and, as already pointed out, bear considerable resemblance to the simple Monotreme type of *Echidna*. In *Echidna*, however, the organ is much better developed, as is also the cartilage. By comparing the series of sections of the anterior region of Jacobson's organ in *Echidna*, given in my paper on the organ of Jacobson in the Monotremes, with the similar series from *Dasyurus* (Pl. XLI.) there will be found no difficulty in tracing the homology of the parts. In fig. 5 of the *Echidna* sections Jacobson's cartilage is found on section to be C-shaped, with the upper outer end much thickened. By comparing this with Pl. XLI. figs. 2, 8 and 11 from *Dasyurus* and *Phascogale*, it will be seen that it is this thickened outer rim of the cartilage in *Echidna* that becomes the outer bar of Jacobson's cartilage in *Dasyurus*. In *Echidna*, on passing backwards, the lower part of the C joins the upper outer thickened bar (fig. 6), and a complete capsule is formed; and on tracing the outer thickened bar still further back it is found to be continuous with the turbinal plate, and represents probably the rudiment of a turbinal which once extended right to the front of the organ, as is still seen in *Ornithorhynchus*. In *Dasyurus* and other Polyprotodonts the main differences are due apparently to the feebler cartilaginous development. The outer bar is present at first in connection with the upper part of Jacobson's cartilage as in *Echidna*, and almost immediately behind the opening of the organ the lower border of Jacobson's cartilage sweeps round and becomes attached to it, but there is the difference in Marsupials that as a rule before the lower connection is established the upper has given way, so that there is usually for a short distance a detached bar, which on section is apparently

neither attached to upper or lower borders. In *Echidna*, at the posterior part of the organ, the upper connection gives way and we have the irregular U-shaped appearance as in Marsupials. We may thus conclude that we have in the simple Marsupials a somewhat degenerate Monotreme type, the outer bar being the rudimentary remains of a primitive turbinal.

In *Didelphys* and *Perameles* we have a short almost vertical naso-palatine canal; while in *Dasyurus* it is rather long and oblique. In *Perameles* there is a small yet distinct downward process of Jacobson's cartilage in the notch between the pre-maxillary and its palatine process, a process which is more or less developed in all the Diprotodonts, and apparently the forerunner of the long anterior process which supports Jacobson's duct in the higher mammals of the Cat or Sheep type. In *Didelphys* there is only a slight indication of this process; and in *Dasyurus* it is absent. From this we may consider that *Dasyurus* is the more primitive. As regards the portion of Jacobson's cartilage supported by the palatine process all three genera differ. In *Dasyurus* the support is on the lower edge and lower inner third; in *Didelphys* on the lower inner half; while in *Perameles* the whole inner side of the cartilage is supported by the palatine process. In neither of the latter two genera, however, is the lower edge of the cartilage completely supported by bone as in *Dasyurus*. In all three genera there is but a single hilar vessel; and as a rule the supply of mucous gland is scanty. *Perameles* is peculiar in having a small anterior prolongation of the organ in advance of the opening, as well as in the extreme shallowness of the secondary palate.

In the Phalangers we enter on a well differentiated type. The most remarkable points of difference from the previous forms are to be found in the complex nature of Jacobson's cartilage in the anterior region. There is a well developed inferior septal ridge into which is sent a cartilaginous process from the ascending inner part of the nasal-floor cartilage, and which is unquestionably homologous with the similar process in the Polyprotodonts. In addition, however, there is an ascending process, only rudimentary

in the carnivorous Marsupials and but feebly indicated in *Perameles*, and there is also a very marked descending process by the side of the naso-palatine canal in the notch. The ascending and descending processes are well seen in their adult condition in Pl. XLIV. fig. 4, representing the condition in the adult *Pseudochirus*, while their mode of development is well seen in Plate XLV. representing the different stages of the young *Trichosurus*. By comparing Pl. XLIV. fig. 4. with, say Pl. XLIII. fig. 1,—the condition in the young *Perameles*, and fixing the two unquestionably homologous parts—the processes passing into the inferior septal ridges—the two additional processes will be readily seen. In the primitive condition of the palatine processes there is also a marked difference from that of any of the Polyprotodonts. In those latter it is always apparently developed as a small curved splint, supporting a considerable area of the cartilage. In the Phalangiers it is developed as a rod along the middle of the inner side of Jacobson's cartilage. This would lead one to assume that the middle region of Jacobson's cartilage in the Phalanger is probably homologous with the lower third of the cartilage in *Dasyurus*, which is the region where the palatine process first developed. If this be so the downward process in the Phalangiers would become the more manifestly an additional development.

In its posterior parts Jacobson's cartilage follows much the same lines as in the Polyprotodonts. The outer part of the ridge process very early becomes separated into the outer bar of Jacobson's cartilage, which, after being isolated for a short distance, becomes attached to the under part of Jacobson's cartilage, and the condition differs little from that of the Polyprotodonts. The organ itself is very similar to that in *Dasyurus* or *Didelphys*; there is, however, one very constant difference in that while in the Polyprotodonts there is only a single blood vessel running along the hilus, in the Phalangiers there is a distinct plexus. At the extreme anterior end there is usually one or two large veins, and these on passing backwards divide into four or five large subequal branches which run parallel along the hilus. This is a character met with in the Monotremes, but it is probably not of

any very deep significance, as in the Mouse there is but a single hilar vessel, while in the allied Guinea-pig there is a regular plexus. Still it is interesting to note that the plexus is constant among the Phalangers, so far as known. The arrangement of mucous glands is very variable anteriorly; in *Petaurus*, *Pseudochirus* and *Petauroides* they are absent or scanty, while in *Trichosurus* they are abundant. As already observed, this is a point of little importance.

In *Phascolaretus*, not having examined the early conditions of the parts, it would be rash to say much on the relationships of the organ. Apparently the adult organ and cartilage differ very considerably from those in the Phalangers. Its most interesting points are – (1) the large proportional development of the nasal-floor cartilage; (2) the low position relative to the cartilage of Jacobson occupied by the palatine process; (3) the anterior development of the vomer; (4) the persistence of the cartilaginous roof; (5) the complete tube formed by Jacobson's cartilage; and (6) the presence of a plexus on the outer side of the organ. Whether as a parallel development or as indicating an affinity it is difficult to say, but there is a very decided resemblance in many ways to the condition in the Wombat.

In the Macropods, though there are features of resemblance to the Phalangers, both the ascending and descending processes of the inner parts of the nasal-floor cartilage are less marked. In *Macropus* the descending process is due more to a bending down of the nasal-floor cartilage than to a distinct downgrowth, though in *Æpyprymnus* the downgrowth though short is quite distinct, at least in the foetus. In *Macropus* the relations of the naso-palatine canal to the opening of the organ and the nasal cavity follow the usual type. In *Æpyprymnus*, however, there is, with practically no difference in other details, the remarkable and, so far as my studies go, unique condition of the organ opening out to the anterior nasal floor, and not into the naso-palatine canal. This is practically the condition which we find in an extreme degree in the Rodentia. If the section (Pl. XLVII. fig. 11) illustrating the condition in the Rat-Kangaroo be compared with the similar

section in *Didelphys* (Pl. XLII. fig. 7) it will be seen that the peculiarity is only due to a slight difference in the relative position of the naso-palatine canal. In the low position occupied by the palatine process and the simple condition of the nasal-floor cartilage the Rat-Kangaroo comes considerably nearer the Polyprotodonts than does *Macropus*.

The Wombat in its early condition shows a very marked agreement with *Dasyurus*, and also considerable agreement with *Æpyprymnus*, though the organ opens in the usual way. In the adult the cartilaginous development is on the type of the Macropods, though the perfect cartilaginous tube formed by Jacobson's cartilage gives it more of the appearance of *Phascolarctus*.

CONCLUSION.

From the study of this limited region in the snout of the Marsupials we get a number of interesting suggestions in the way of apparent affinities. In the first place there can be little doubt in placing *Perameles* with *Dasyurus* and *Didelphys* and away from the Phalangers, and though it is more differentiated than either it seems to retain certain primitive characters lost in the others. The Phalangers are all closely allied, though it would seem that *Trichosurus* is a little further differentiated than *Pseudochirus* and *Petaurus*. *Phascolarctus* is a much modified and aberrant form, and it seems probable that a study of the foetus will reveal that it is not so near the Phalangers as has been supposed. The Kangaroo group though allied to the Phalangers is, as regards the region under consideration, nearer the Polyprotodonts; and the Rat-Kangaroo, though slightly aberrant, helps to bridge over the gap. The Wombat is a very near ally of the primitive or ancestral Macropods apparently, though it has become much modified along an independent line.

I must acknowledge my indebtedness to Sir William Flower for the specimens of *Didelphys* examined; to Mr. A. G. Hamilton, of Mt. Kembla, N.S.W., for the young and adult *Perameles*; and to Prof. Wilson for the permission to examine his sections of the

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PRINCIPAL BIBLIOGRAPHY ON THE LOWER MAMMALIAN ORGAN
AND RELATED STRUCTURES.

1. BALOGH, C. ... "Das Jacobson'sche Organ des Schafes." Sitz. Akad. Wien. 1862.
2. BROOM, R. ... "On the homology of the palatine process of the Mammalian premaxillary." Proc. Linn. Soc. N.S.W. 1895.
3. ——— ... "On the Organ of Jacobson in the Monotremata." Journ. Anat. and Phys. 1895.
4. ——— ... "On the Organ of Jacobson in an Australian Bat (*Miniopterus*)." Proc. Linn. Soc. N.S.W. 1895.
5. ——— ... "Observations on the relations of the Organ of Jacobson in the Horse." Proc. Linn. Soc. N.S.W. 1896.
6. FLEISCHER, E. "Beitr. zu der Entwickl. des Jacobson'sche Organs, &c." Sitzungsber. Phys.-Med. Soc. Erlangen. 1878.
7. GRATIOLET ... "Recherches sur l'Organe de Jacobson." Paris. 1845.
8. HARVEY, R. ... "Note on the Organ of Jacobson." Q.J.M.S. 1882.
9. HERZFELD, P. "Ueber das Jacobson'sche Organ des Menschen und der Säugethiere." Zool. Jahrb. Bd. 3. 1888.
10. HOWES, G. B. "On the probable existence of a Jacobson's organ among the Crocodilia, &c." P.Z.S. 1891.

11. JACOBSON ... "Rapport de M. Cuvier sur un Mémoire de M. Jacobson." Ann. du Mus. d'Hist. Nat. 1811.
12. KLEIN, E. ... "Contrib. to the Minute Anat. of the Nasal Mucous Membrane." Q.J.M.S. 1881.
13. ——— ... "A further Contrib. to the Minute Anatomy of the Organ of Jacobson in the Guinea-Pig." Q.J.M.S. 1881.
14. ——— ... "The Organ of Jacobson in the Rabbit." Q.J.M.S. 1881.
15. ——— ... "The Organ of Jacobson in the Dog." Q.J.M.S. 1882.
16. LEGAL, E. ... "Die Nasenhöhlen und der Thranennasengang der Amnioten Wirbelthiere." Morph. Jahrb. Bd. 8. 1883.
17. PARKER, W. N. "On some Points in the Structure of the young *Echidna aculeata*." P.Z.S. 1894.
18. RANGE, P. ... "Le canal incisif et l'organe de Jacobson." Arch. Internat. de Laryngolog. 1894.
19. RÖSE, C. ... "Ueber das Jacobson'sche Organ von Wombat und Opossum." Anat. Anz. 1893.
20. SCHWINK, F. ... "Ueber den Zwischenkiefer und seine Nachbarorg. bei Säugethiere." München. 1888.
21. SMITH, G. ELLIOT "Jacobson's Organ and the Olfactory Bulb in *Ornithorhynchus*." Anat. Anz. xi. Band, Nr. 6, 1895, p. 161.
22. SYMINGTON, J. "On the Nose, the Organ of Jacobson, &c., in *Ornithorhynchus*." P.Z.S. 1891.
23. ——— ... "On the Organ of Jacobson in the Kangaroo and Rock Wallaby." Journ. of Anat. and Phys. 1891.

24. SYMINGTON, J. "On the homology of the dumb-bell-shaped bone in *Ornithorhynchus*." Journ. of Anat. and Phys. 1896.
25. ZUCKERKANDL, E. "Das peripherische Geruchsg. der Säugthiere." Stuttgart. 1887.

REFERENCES TO PLATES.

a.J.o., anterior prolongation of Jacobson's organ; *a.n.*, alinasal; *gl.*, gland; *J.c.*, Jacobson's cartilage; *J.o.*, Jacobson's organ; *l. d.*, lachrymal duct; *Mx.*, maxilla; *n.*, nerve; *n.f.c.*, nasal-floor cartilage; *n.g.d.*, nasal gland duct; *n.p.c.*, naso-palatine canal; *n.s.*, nasal septum; *o.b.J.c.*, outer bar of Jacobson's cartilage; *o.n.f.s.*, outer nasal-floor cartilage; *p.c.*, papillary cartilage; *Pmx.*, premaxilla; *p.Pmx.*, palatine process of premaxilla; *r.p.*, ridge process of Jacobson's cartilage; *v.*, vein; *Vo.*, vomer.

PLATE XLI.

Dasyurus and *Phascologale*.

- Figs. 1 - 4.—Transverse vertical section of Jacobson's organ and relations in *D. viverrinus* (mam. foet., head length 15 mm.), $\times 27$.
- Figs. 5 - 9.—The same in *D. viverrinus* (two-thirds grown), $\times 12$.
- Figs. 10-12.—The same in *Phascologale penicillata* (mam. foet., head length 9 mm.), $\times 36$.

PLATE XLII.

Didelphys.

- Figs. 1 - 3.—Transverse section of region of Jacobson's organ in *Didelphys murina* (mam. foet., head length 14 mm.), $\times 34$.
- Figs. 4 - 8.—The same in *D. marsupialis* (mam. foet., head length 37 mm.), $\times 14$.
- Fig. 9.—Transverse section of Jacobson's organ in *D. marsupialis* (mam. foet.), $\times 33$.

PLATE XLIII.

Perameles.

- Figs. 1 - 3.—Transverse vertical section of region of Jacobson's organ in *Perameles nasuta* (mam. foet., head length 21 mm.), $\times 30$.
- Figs. 4 - 7.—The same in *P. nasuta* (two-thirds grown), $\times 17$.

Fig. 8.—Transverse section of Jacobson's organ in *P. nasuta* (two-thirds grown), $\times 27$.

Figs. 9-11.—Transverse section of region of Jacobson's organ in *P. nasuta* (adult), $\times 14$.

PLATE XLIV.

Pseudochirus, Petauroides, and Petaurus.

Figs. 1-3.—Transverse section of region of Jacobson's organ in *Pseudochirus peregrinus* (mam. foet., head length 8.5 mm.), $\times 40$.

Figs. 4-7.—The same in *P. peregrinus* (adult), $\times 11$.

Figs. 8-9.—The same in *Petauroides volans* (adult), $\times 10$.

Figs. 10-12.—The same in *Petaurus breviceps* (adult), $\times 16$.

PLATE XLV.

Trichosurus.

Figs. 1-3.—Transverse section of region of Jacobson's organ in *Trichosurus vulpecula* (mam. foet., head length 7.5 mm.), $\times 36$.

Figs. 4-6.—The same in *T. vulpecula* (mam. foet., head length 10.5 mm.), $\times 42$.

Figs. 7-9.—The same in *T. vulpecula* (mam. foet., head length 20 mm.), $\times 18$.

PLATE XLVI.

Trichosurus and Phascolarctus.

Figs. 1-6.—Transverse section of region of Jacobson's organ in *Trichosurus vulpecula* (adult), $\times 10$.

Figs. 7-9.—The same in *Phascolarctus cinereus* (half grown), $\times 7$.

PLATE XLVII.

Macropus and Aepyprymnus.

Figs. 1-3.—Transverse section of region of Jacobson's organ in *Macropus* sp? (early foetus, body length 29 mm.)

Figs. 4-9.—The same in *M. ualabatus* (mam. foet., head length 50 mm.), $\times 10$.

Figs. 10-12.—The same in *Aepyprymnus rufescens* (mam. foet., head length 15.5 mm.), $\times 25$.

PLATE XLVIII.

Phascolomys.

Figs. 1-2.—Transverse section of region of Jacobson's organ in *Phascolomys wombat* (foetus, body length 19 mm.), after Röse, $\times 37$.

Figs. 3-7.—The same in *P. mitchelli* (half grown), $\times 6$.

Figs. 8.—The same in *P. mitchelli* (half grown), $\times 18$.

Broom, Robert. 1897. "On the comparative anatomy of the organ of Jacobson in marsupials." *Proceedings of the Linnean Society of New South Wales* 21, 591–623. <https://doi.org/10.5962/bhl.part.8486>.

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