tions of the body in Lucanidæ in general. He then pointed out that most of the *Lucanissi* and *Dorcini*, unlike the *Odontolabini*, differed comparatively little except in size, whereas the latter subfamily must be regarded as polymorphic. The variability and plasticity of many *Odontolabini* was so great, that it was practically impossible to separate them into sharply distinct species. The chitinous portions of the male sexual organ were valueless as specific characters in this group.

In the second, or systematic part of his paper, Dr. Leuthner monographed the three genera *Neolucanus*, Thoms., *Heterochthes*, Westw., and *Odontolabis*, Hope, which form the subfamily Odontolabini, giving full synonymy, and carefully describing the female and the various forms of the male in each species.

This memoir will be published entire in the Society's 'Transactions.'

The following papers were read :—

1. On the Tongues of the Marsupialia.

By Edward B. Poulton, M.A., F.Z.S.

[Received December 18, 1883.]

(Plates LIV., LV.)

I am greatly indebted to the kindness of our Secretary for supplying me from the Society's collection with a great part of the materials upon which this paper is written. I have received from him spirit specimens of the tongues of *Macropus*, *Belideus*, and *Didelphys*, and fresh specimens of those of *Petrogale* and *Dasyurus*.

Professor Moseley also very kindly gave me excellently prepared tongues of *Halmaturus*, *Phalangista*, and *Perameles*, and a spirit specimen of *Acrobates*. These specimens were obtained in 1874, and are described in the 'Notes by a Naturalist on the Challenger.' I was also fortunate enough to procure a living specimen of *Phalangista vulpina*.

In a previous paper ("The Tongue of *Perameles nasuta*") in the 'Quarterly Journal of Microscopical Science' for January 1883, I described a new type of compound filiform papilla, which I then thought to be peculiar to that animal and modified for the capture of insects. I now find that it is characteristic of the Marsupial tongue, and I propose for it the name "coronate papilla." During my work upon this organ I find it absolutely necessary to use new terms in addition to the old ones (which I retain as far as possible), as these latter do not cover the ground. I therefore add a provisional list of the technical terms used in such descriptions as are contained in the present paper. New terms are printed in italics.

Circumvallate papillæ.—Used in its old sense for the large bulb-bearing papillæ (or in some cases ridges) at the back of the upper

surface of the tongue, always sheltered by a trench, and sometimes very completely protected. Gustatory.

Posterior angle.—The angle made by the posterior circumvallate papilla with the two anterior papillæ, when only three are present, arranged in an isosceles triangle (universal in Marsupials).

Lateral gustatory organ or lateral organ.—Used in its old sense. The term foliate organ or papilla foliata is misleading in directing the attention to the ridges instead of to the grooves (which are primary). Gustatory.

Fungiform papilla.—In its old sense, except that it should not be used for the circumvallate papilla. The latter is primarily gustatory, the former primarily, and perhaps ultimately, tactile.

Filiform papilla.—The old sense. It may be either mechanical or tactile. Its papillary process bears secondary processes.

Hair-like papilla.—A very fine filiform papilla of which the papillary process does not bear secondary processes. Mechanical.

Coronate papilla.—A compound filiform papilla; the summit being crowned by a ring of recurved hair-like papillæ. Mechanical. Characteristic of Marsupials.

Fasciculate papilla.—A convenient term for the compound filiform papilla in which the secondary papillæ are not arranged in a circle, but brush-like. Mechanical.

I will now proceed to describe the tongues, beginning with those that least resemble this organ in higher mammals, and gradually working upwards.

The Tongue of *Halmaturus ualabatus*.

The material consisted of the back part of one tongue, the lateral gustatory organs of others, and the part containing a circumvallate papilla. All these had been hardened in chromic acid and were in excellent condition.

General description.—The smaller tongue was 27·5 mm. in width posteriorly (although there was some distortion due to cuts permitting the entrance of the hardening fluids); the other dimensions are shown in fig. 1. Plate LIV., and from this also the size of the complete organ is suggested. The upper surface is densely crowded with large coronate papillæ, between which, just above the smooth lateral surface, a few fungiform papillæ of normal appearance are scattered. The lateral gustatory organ is in the form of a series of mound-like elevations (about six in number), placed just below the posterior part of the side of the papillate surface (see figs. 1., 11., 111. Plate LIV.). At the summit of each elevation an elongated (sometimes circular) depression is situated like a crater. The whole appearance suggests a series of gland-ducts; and this view of the origin of the lateral gustatory organ is confirmed by a study of the minute structure. Below these elevations there is a less regular, longer row of smaller depressions sometimes situated upon mounds, but in some cases only surrounded by slightly raised rings. These structures extend for some distance in front of the former (and often to some extent

posteriorly also). The resemblance between the larger and smaller mounds is very complete, and the latter are true gland-ducts and apparently nothing more. Above the lateral organ the densely papillate surface is limited by an irregular row of filiform papillæ extending posteriorly and superiorly beyond the lateral organ. These papillæ are probably tactile, and their position is constant in Marsupials (as far as I have observed), even in the absence of a lateral organ. The two anterior circumvallate papillæ are situated (11 mm. apart) at the level of the posterior end of the lateral organ. The posterior papilla is set very far forward in this species, so that the three are nearly in one straight line, the posterior angle being very obtuse. All that can be seen of the papillæ from the surface is a funnel-shaped depression (about 1 mm. across at the widest part), at the bottom of which the apex of the papilla can generally be detected, directed forwards (see fig. IV. Plate LIV. taken from the larger tongue). The opening leading into the involution containing the central papilla was entirely invisible from the surface, and the papilla was only discovered accidentally. The opening may be surrounded by a sphincter of smooth muscle; and it is probable that the central opening is not really smaller than the others, since the papillæ and the involutions are quite similar. A further proof of its contracted state was found in the folded condition of the inner surface. The coronate papillæ crowd closely upon the openings in the smaller tongue, but in the larger separate opening (fig. IV. Plate LIV.) they become less conspicuous posteriorly. Immediately round the openings there is an irregular ring of short simple papillæ (fig. XIX. Plate LIV., which also indicates the very constricted passage leading into the involution for the posterior papilla of the smaller tongue).

Minute Structure.—I. *Gustatory Structures.*

A. *The Circumvallate Papillæ.*—The remarkable shape and extreme protection of the papillæ is shown in fig. XIV. Plate LIV. The taste-bulbs are seen to be very numerous; there are over 30 tiers, and those round the central thickest part contain 80–90 in a single tier (see fig. XXI. Plate LV.). They are closely packed round the circumference, but there are generally one or two places in each section where they are absent, and they cover the whole surface of the papilla except a small part below the apex, which is the only unprotected region (see fig. XIV. Plate LIV.). There is I believe no doubt that the mouth of the depression can be closed upon the apex of the papilla, and that thus the delicate end-organs are completely protected. The mechanism for opening and closing is, however, very uncertain: smooth muscle-cells may be present in the mucosa parallel with and just outside the involution; such fibres would act as a dilating agency, aided by the contraction of other bands, which may also contain smooth muscle, and which radiate horizontally outwards from the thickened mucosa round the mouth. The closure of the mouth may be effected by a sphincter of smooth muscle-fibres, but in all these cases I cannot be certain as to the existence of the smooth muscle. By a different mechanism the papilla can

be drawn downwards from below, and this action alone would tend to close the mouth. The dense mucosa (perhaps containing smooth muscle-cells) which lies outside the epithelium of the involution is invaginated into the papilla from below, forming a distinct layer in it (to be described). Inside the papilla smooth muscle-cells may exist in the invaginated mucosa. At the point where the mucosa bends round to enter the papilla many striated muscle-fibres terminate in it, their direction being vertical to the surface of the tongue. Any contraction of these fibres must draw down the papilla, and produce a tendency to close the mouth. It is possible, however, that the tension produced by contraction acts also upon the mucosa outside the involution, and thus tends to open the mouth. If this is the case it is probable that closure of the mouth is rendered a specially effective protection by the apex of the papilla being tightly clasped by the contracting orifice (the papilla being raised valve-like against the descending mouth by relaxation of the muscular contraction). Conversely the papilla may be drawn downwards from below, and the mouth opened by the same mechanism. It is only possible to decide by experiment as to which action really takes place. It is in favour of this view, that lateral compression of the fresh tongue causes a descent of the papilla and an opening of the mouth in the similar anterior papillæ of *Phalangista.* Glands of serous type are extremely abundant round these structures, and their ducts open into the space between the involution and the papilla, at all heights, and not especially round the base of the papilla (the rule in higher types).

The taste-bulbs are of the normal Marsupial type (as described in a paper upon "The Tongue of *Perameles nasuta*" by the present writer, in the 'Quarterly Journal of Microscopical Science' for January 1883), showing traces of their origin from the epithelial cells of an interpapillary process, in the indications of papillæ between the bulbs, and in the fact that the cells do not converge into a distinct basal pole. I was never able to detect indications of the protrusion of any structures through the gustatory pores. In order to be *certain* of the absence of such delicate processes (described in the higher mammals) the fresh tissue should be examined; but upon the whole I am inclined to think that such structures are absent from the bulbs of Marsupials, which are less specialized than those of the higher forms in the above-mentioned points. I have examined so many hundreds of distinct pores and bulbs with the cells apparently perfect, in so many species, that I believe some trace of these structures would have been detected if they were present. The gustatory pores are very short, only penetrating a thin superficial corneous lamina of the epithelium, which easily splits away from the rest. Very often the epithelial cells below the thin lamina split away with the latter, thus rendering the dome-like coverings of the taste-bulbs very distinct. The same layers tend to split away from the wall of the involution in which the papilla is contained. It is probable that the bulbs present a less marked separation than is met with in higher mammals, into peripheral protective cells and central cells which are nervous end-organs. But there is

some indication of such a separation in the presence of two kinds of nuclei in the bulbs—the one spherical or oval, and the other greatly elongated. The latter must belong to the central cells. To be sure of this point, or indeed of anything in minute structure, the fresh tissue should be examined. Considering, however, that these structures in *Halmaturus* were not fresh, it would be hardly possible to have obtained tissues in better condition for minute examination. The question of the termination of nerves is better considered after the description of the layers within the papilla. These are shown in fig. XXI. Plate LV., which represents a transverse section through the thickest part of a papilla. In the axis are the nonmedullated nerves, which enter from below. They do not form any distinct ganglion in the papilla (as in *Perameles* and *Phalangista*). In a few cases isolated ganglion-cells were seen in the axis of the papilla, in one instance at some considerable height. It is probable that the ganglion-cells, which are always connected with the nerves of special sense, form small ganglia on the nerve-branches near the base of the papilla. The axial nerves are supported by trabeculæ from the next layer, and large blood-vessels are present, entering with the nerves. The next layer, already mentioned, is derived from the dense mucosa, and is composed of fibrous and possibly smooth muscular elements. Blood-vessels are present in it; and nerve-branches passing from the axial nerves to the subepithelial layer may be seen streaming outward through it. The next subepithelial layer is characteristic, not occurring elsewhere. It represents the unravelled elements of the two other layers united into interpenetrating networks. The importance of the layer is well seen by looking at the tissues underlying the ordinary epithelium, after looking at that beneath the bulbs. Below the limits of the taste-bulbs the subepithelial layer thins away abruptly, but its connective-tissue elements are probably continuous with a delicate layer which lies between the deeper denser part of the mucosa and the lowest layer of the epithelium on the outside of the involution. The subepithelial layer disappears less rapidly above the limits of the bulbs, and in some places its fine fibrils end against the lowest epithelial cells. This is seen with especial clearness in the cells of interpapillary processes; and it may be that bulbs are arising directly in this region, or (as is more probable) that these masses of epithelial cells with the appearance of nerve-terminations in them represent bulbs that have degenerated into the structures from which they originally arose. This, however, is merely a suggestion. Capillaries are present in this layer. At certain places the subepithelial layer is converted into a tissue resembling adenoid tissue, which may also invade the layer last described, sometimes even reaching the axial nerves. A similar tissue has been described in a corresponding position in the tongue of *Ornithorhynchus* (see paper on this subject by the present writer in the 'Quarterly Journal of Microscopical Science' for July 1883). When the subepithelial layer is studied under high powers ($\frac{1}{18}$ oil-immersion of Zeiss), fine fibrils are seen to terminate abruptly against the contour of the convex lower surface of the bulb, separated only from the cells by the linear

(even under this power) basement membrane. The fibrils often expand at their termination, becoming funnel-shaped. Such appearances are observed over the whole proximal surface of the bulb and not merely at its centre. It was really impossible to be certain in the identification of these fibrils as nervous, and yet there are some fibrils which can be considered nervous with a very high degree of probability. These are distinct under comparatively low powers as sharply defined dark fibrils that pass straight through this layer from the fibrous layer towards the taste-bulbs. These fibrils confer a radiate appearance upon the subepithelial layer (see fig. XXI. Plate LV.). Round or oval, deeply-staining nuclei are very characteristic of this layer, and are obviously related to the nervous elements, as they are almost completely limited to the region of the end-organs. These nuclei belong to small multipolar cells continuous with some strands of the network; but it seems more probable that they belong to a special supporting connective tissue (such as the neuroglia) than that they are nervous. This subepithelial layer bears a strong resemblance to certain retinal layers, and is probably identical in structure (both consisting essentially of the unravelled elements of supporting and nervous tissues arranged in fine interpenetrating networks, as has been mentioned).

These layers and their relation are better seen in longitudinal than in transverse sections of the papilla (see fig. XX. Plate LIV., which shows the same arrangement in *Phalangista*).

B. *The Lateral Gustatory Organs.*—When a section is taken at right angles to the long axis of one of the depressions (upon one of the elevations previously described), the latter is seen to be the mouth of a narrow chink which is obviously the duct of a gland (see fig. XXXI. Plate LV.), in the epithelial walls of which a few taste-bulbs have been developed. The lateral ducts sometimes open into the chink above the taste-bulbs, and below the points where the latter occur the main duct breaks up into smaller tubes. Horizontal sections show that the narrow ducts into which the depressions open are always slit-like, although the latter may appear to be circular, and the long axis of the slit is always at right angles to the inferior limit of the papillate surface above. In this respect the primitive lateral structures of *Halmaturus* are similar to the furrows of the lateral organ in higher animals. Although the bulbs are scattered irregularly in vertical sections, their arrangement is much more even in sections taken horizontally. It is therefore probable that the real arrangement is in regular tiers, but that the tiers themselves do not follow one another regularly. The subepithelial layer is not strongly developed beneath these bulbs, but traces of it can be distinguished. The nerves approach the bulbs from the sides, running horizontally beneath the epithelium for a considerable distance. Ganglion-cells are very numerous in little groups on the nerves. The cells are enclosed in distinct nucleated capsules. The glands into which the ducts of the lateral organs lead are of course serous. The smaller gland-ducts which open below and in front of the lateral organs (see fig. I. &c. Plate LIV.) lead down deeply into

mucous glands, although some of the lobules appear to be serous. No bulbs are present in the walls of these ducts. The epithelium round the lateral organs (and that of all the non-papillate surface I examined) is of the dense complex kind, similar to that described in the tongue of *Ornithorhynchus* (in the paper previously referred to). In such an epithelium four distinct layers can be made out. By far the thickest of these is the lowest layer, which presents all the characters of the rete Malpighii, staining deeply below, slightly above; over this is a thin layer of cells that stain deeply in most reagents, and possess very long thin nuclei (in vertical sections): above this is a layer of about equal thickness, behaving toward reagents in the same manner as corneous cells; this again is followed by a thicker, deeply staining layer of fusiform cells with distinct elongated nuclei. The remarkable thing about this epithelium (as was pointed out in describing the tongue of *Ornithorhynchus*) is that, in upward succession, cells presenting the characters of a corneous layer should again come to present the characters of non-corneous epithelium (see fig. XXXI. Plate LV.). A hair was seen in one section of a lateral organ; and probably due to the irritation caused by it, the mucosa beneath was crowded with large deeply staining cells.

C. *Fungiform Papillæ.*—The same imperfect type of bulb is seen on the summit of these papillæ that has been described in the same situation in *Perameles* (paper previously mentioned). Such bulbs show more distinct traces of their origin from interpapillary epithelial cells than those in any other part of the tongue. Their appearance upon these papillæ is probably very recent, and it is noteworthy that this is the only instance of their occurrence without the immediate proximity of serous glands. Large non-medullated nerves are found in the axis of the papilla. Beneath the bulbs the subepithelial layer is distinct. Gustatory pores are present, and as many as six bulbs can be seen in a single section of one papilla. It is not unlikely that these papillæ are tactile (they are tactile in *Ornithorhynchus*, and if gustatory here, the change is recent).

II. *Mechanical and Tactile Structures.*

A. *The Coronate Papillæ.*—These are of the usual Marsupial type, much resembling the same papillæ in *Perameles* (described in the paper alluded to). Horizontal sections at successively higher levels show that the main papillary upgrowth is at first irregular in shape, then horseshoe-shaped (the concavity anterior) with the arms gradually breaking up into the separate papillary upgrowths for the secondary papillæ. Hence the posterior side of any such section can be known at a glance, because here the secondary processes arise at a higher level, and therefore some of them have not yet separated from the main upgrowth. (See fig. XXVIII. Plate LV.) If the section is taken sufficiently high to show a complete ring of secondary papillary processes, it is still easy to know the posterior side, because posteriorly the processes are cut through at a lower level. (This is rendered clear by fig. XXVI. Plate LV., which shows a single coronate papilla of *Macropus* in perspective.)

The ring of secondary papillæ is less regular in *Halmaturus* than in *Perameles* &c., and it is common to find single papillæ *within* the ring (*i.h.p.*, fig. XXVIII. Plate LV.). Between the coronate papillæ isolated hair-like papillæ are common, rising singly from the epithelium. In all respects these resemble the hair-like papillæ of the coronate rings. (They are shown in fig. XXVIII. Plate LV., *s.h.p.*, and in vertical section in fig. XXVII. Plate LV., *s.h.p.*) These isolated slender papillæ with no tendency to coalesce into rings are very characteristic in tongues which in other respects also show traces of more primitive affinities than those of other Marsupials. (The posterior part of the tongue of *Ornithorhynchus* is covered with closely set single hair-like papillæ, very much resembling the papillæ here described, and agreeing in the important point that each hair-like papilla possesses but a simple papillary upgrowth.) The coronate papillæ are of large size, and there are only about 10 to the square millimetre close to the posterior circumvallate papilla. A little anteriorly (by the anterior circumvallate papillæ) they become rather smaller, and I counted 12 to the square millimetre.

In ascending from the smooth to the papillate surface, the long papillary processes of the former first bear simple papillæ; these form an irregular row (one or two deep, and sometimes absent) and then coalesce into the coronate papillæ. There are a few of these simple papillæ, bent upwards so as to be almost parallel with the surface of the tongue, below the lateral organ in some sections. The coronate secondary papillæ curve upwards from the sides towards the middle of the tongue (see fig. XXIX. Plate LV.); but this is not so marked as in *Phalangista*, at any rate in the posterior part of the tongue. The secondary papillæ of the upper surface are curved backwards; but this is very slightly marked posteriorly, where the coronate papillæ are tall and slender; while anteriorly (in the piece of tongue in my possession) they become shorter, stouter, and the hair-like secondary papillæ much recurved (see fig. XXVII. Plate LV.). The epithelium is immensely thickened in passing from the smooth into the papillate region (see fig. XXXI. Plate LV., *s.e.*, where the transition is taking place, and compare the thickness with the less magnified fig. XXVII. Plate LV., which is taken in the middle line of the papillate surface). Although the epithelium changes in thickness, the four layers of the complex epithelium can be detected in it and enter into the coronate papillæ. This is best shown near the transition. (See fig. XXIX. Plate LV., which represents diagrammatically the arrangement of the four layers in a single coronate papilla close to and above the lateral organ. The section is of course vertical and transverse, and the curve of the secondary papillary processes is upwards. The layers correspond to those in fig. XXXI. Plate LV. In other parts of the papillate surface the distribution of the corneous layer (2) would be more symmetrical upon the secondary papillæ.) We thus have a proof that the layer (2) previously described is truly corneous, inasmuch as in these fine processes, of mechanical use, it rises to the surface and is confined to the effective side, or both sides where both are effective. The very

granular cells which in many other Marsupial tongues (*Perameles* &c.) form the transition into the upper corneous layer are slightly marked here. It is very likely that the transition described through the complex layers takes the place of the other method. There are, however, some finely granular cells in layer (4). The complex epithelium ends at the entrance into the involution for the circumvallate papillæ in the same way as at the mouths of the lateral organ (see fig. XXXI. Plate LV.).

B. *The Filiform Papillæ*, forming the limits of the papillate surface above and behind the lateral organ, are probably tactile in function. They are of small size for so large a tongue. They are similar to those described in *Phalangista*.

Thus in many points connected with the tongue, *Halmaturus* is the most primitive Marsupial yet examined—in the very primitive lateral organ, in the extremely protected circumvallate papillæ with bulbs nearly covering them, and in the irregular coronate papillæ and the existence of scattered hair-like papillæ between the latter, with no apparent tendency towards coalescence into rings.

The Tongue of *Macropus melanops*.

This tongue had been kept in spirit, and the tissues were not in a condition for minute examination; but many points of interest could be ascertained. The pieces of the tongue from which I intended to make sections I placed in spirit, gradually increasing the strength until they were finally placed in absolute alcohol, and were cut after remaining some little time in this fluid.

General description.—The appearance of the tongue from above is shown in fig. VI. Plate LIV. (half natural size). This organ is evidently closely related to that of *Halmaturus*. The circumvallate papillæ are arranged as usual, the posterior angle being exceptionally obtuse, although not to the same extent as in *Halmaturus*. As in the latter animal, the depressions leading into the cavities containing the papillæ are alone visible from the surface and are very inconspicuous. The lateral organ (fig. VII. Plate LIV., natural size) also resembles that of *Halmaturus*; but the mound-like elevations are arranged in a regular curve, and the depressions have more of the normal appearance. Independent mucous glands cannot be seen in this specimen, but they may be present; filiform papillæ are arranged above the lateral organ. The fungiform papillæ are very abundant all along and just above the edge where the papillate joins the non-papillate surface. At the tip the junction is beneath the tongue and forms a line parallel with the contour (see fig. V. Plate LIV., natural size). On this papillate surface beneath the tip fungiform papillæ are extremely abundant, and many of them are unusually large. There is little doubt that papillæ in this position are tactile. The free part of the tongue is about 60 mm. long, and there is a raphe detectable for about 80 mm. from the tip backwards. The inferior median ridge is low and wide, and the lateral grooves shallow (see fig. V. Plate LIV.).

Minute Structure.—I. *Gustatory Structures.*

A. *The Circumvallate Papillæ.*—All three are probably similar in structure, and seem to be intermediate between the *Halmaturus* type (fig. XIV. Plate LIV.) and the higher form approaching radial symmetry. The symmetry here is, I believe, decidedly bilateral, the papillæ distinctly directed forwards, and the protection extreme; but in none of these points do the papillæ equal those of *Halmaturus*. There were some indications that the posterior papilla is less inclined than the anterior, but I am not certain that the appearance is genuine. The posterior involution is also surrounded by a prominent rim with papillæ upon it. Nothing could be ascertained as to nerve-cells in the papillæ. I could not decide as to the height to which the bulbs extend on the papillæ—probably up to the point at which the sides begin to slope sharply inwards to form the summit, which seems to end in a simply pointed apex. The base of the papillæ seems to be invaded by glandular tissue.

B. *The Lateral Gustatory Organs.*—These are much the same as in *Halmaturus*, but are more advanced; they do not obviously represent gland-ducts, but suggest depressions into which the latter enter. The mounds on which the furrows open are more prominent than in *Halmaturus*.

C. *The Fungiform Papillæ.*—These papillæ contain bulbs and are richly supplied with nerves. The epithelium below the tip is smooth, but probably tactile from the abundance of nerves beneath it. I could not distinguish any difference between the large and small papillæ of the tip, or between the papillæ of the tip and those situated posteriorly. I should like to work at this point again with specially prepared material.

II. *Mechanical and Tactile Structures.*

A. *The Coronate Papillæ.*—On the upper surface of the tip horizontal sections prove that there are generally 9–12 secondary papillæ forming an anterior horseshoe, and a single large posterior papilla, indicating the beginning of that peculiar modification of the coronate type which reaches its culmination in *Didelphys*. This posterior papilla is especially cornified, and its base tends to pass forward as two horns; it is broad at the base, pointed above, and it must be concave from side to side anteriorly. Its papillary upgrowth is very large and triangular, the angles tending to pass anteriorly with the horns. The coronate papillæ of this part of the tongue very much resemble the transitional forms that pass into the strongly marked region of *Didelphys*. The coronate papillæ are oval antero-posteriorly. In the anterior horseshoe there are occasional irregularities, but isolated hair-like papillæ are absent in this part of the organ. Vertical longitudinal sections confirm the conclusion derived from a study of horizontal sections. There are about eleven papillæ to the square millimetre.

Midway between the tip of the tongue and the anterior circumvallate papillæ, the isolated hair-like papillæ are very abundant.

The coronate papillæ are generally circular and very large (about five to the square millimetre); they are not closely packed as in the region to be next described. The posterior side can be recognized by the same character that it presents in the papillæ of the tip. There are generally 6–8 secondary papillæ in the anterior horse-shoe; the arrangement is occasionally irregular.

Between the anterior circumvallate papillæ there are no isolated hair-like papillæ. The coronate papillæ possess very complete rings of secondary papillæ (13–17 are the common numbers, and 17 is not at all uncommon). The rings are very symmetrical, and the posterior side is not much marked, though generally recognizable by the higher level at which the secondary papillæ arise.

The coronate papillæ are generally circular and are very closely packed (about seven to the square millimetre). In one section the papillæ were about ·375 mm. in diameter, and the spaces between them from ·075–·025 in width, and most frequently the latter. Longitudinal vertical sections show that the coronate papillæ in this region are beautiful and tall, with their hair-like papillæ slightly recurved at the tip (see fig. XXVI. × 14·5, Plate LV., which shows one of these papillæ in perspective). They are over 2 mm. in height (from the top of a perfect secondary papilla to the surface of the superficial epithelium of the tongue). The upper cells of the main papilla stain deeply like those of *Perameles* and many other Marsupials.

B. *The Filiform Papillæ.*—Probably normal in structure, but no minute investigation was possible.

Thus this tongue decidedly follows the type of *Halmaturus*, but it shows an advance in all the points which the two have in common.

The Tongue of *Petrogale xanthopus.*

I have recently received a fresh specimen of this tongue, so that I am able to add a general description. The whole tongue is strikingly similar to *Macropus*, and, like it, follows the type of *Halmaturus*. The circumvallate papillæ are arranged in a similar triangle (the posterior angle being very obtuse), and nothing can be seen from the surface except the orifices of the involutions. The posterior papilla appears to be rather different from the anterior, the entrance being extremely small (probably contracted), and lies in the centre of a raised subcircular area, of which the surface is smooth. The anterior openings are larger (probably less contracted), and the raised area is less distinct. The fungiform papillæ are arranged as in *Macropus*, along the sides and tip, where some of them are larger; a few are scattered on the upper surface, and these may also be present in *Macropus* in the fresh state. The lateral organ is not arranged in the segment of a circle (as in *Macropus*), but apparently forms an irregular line of openings which are not raised upon elevations. The line is of considerable length, and the depressions are separated by more than the usual interval. The openings were very contracted, and could hardly be made out on the left side. No

gland-ducts were visible. The raphe, inferior median ridge and grooves, and the arrangement of the coronate papillæ are all exactly as in *Macropus*.

Obviously this organ is very close to that of *Macropus*.

The Tongue of *Dasyurus maugæi*.

Quite recently I received a fresh tongue of this species; and I am very glad to be able to add the general description, because until now I have not had the opportunity of investigating this organ in any of the Marsupialia Sarcophaga, and I felt uncertain as to whether the previous observations (such as the existence of coronate papillæ) would hold. I was also much interested in ascertaining whether the organ was much modified by the very distinct change of habits, and in determining the relative resemblance of this organ to the other various types.

The shape was not remarkable, the tip being simply rounded as seen from above and forming a rather sharp edge. The junction between the papillate and non-papillate surfaces was sharp and even; the ridge and grooves as usual. There is a slight trace of a median raphe. The circumvallate papillæ form the usual triangle, which is here fairly equilateral, but the sides are a little shorter than the base. The papillæ seem to be bilaterally symmetrical, and their tall pointed apices are *directed backwards*. If this is the condition in the living state, it is unique as far as I have yet observed. The posterior papilla seems to be a little larger than the others. They are all studded with small protuberances (secondary papillæ) on the anterior side of the lowest part visible. The upper recurved part exactly resembles a large filiform papilla, and as these are common round the circumvallate papillæ, the suggestion arises that the available (otherwise unused) surface of the latter has been modified into the former. There seems to be no trace of a lateral organ. The fungiform papillæ are distributed as usual, extending round the tip and scattered over the whole upper surface in considerable abundance. The filiform papillæ are long and also flap-like; they are continued backwards and upwards from the usual position on to the area of the circumvallate papillæ, as has been previously described in *Perameles*. Posteriorly the coronate papillæ seem to be transitional into the filiform papillæ by a relative increase in the posterior secondary papilla and a gradual disappearance of the rest of the ring (also noticed in *Perameles* and the same general tendency in many forms). The coronate papillæ seem to be well developed and of normal structure over the whole of the upper surface. Of course this can only be rendered certain by sections. Posteriorly in the middle line, just in front of the anterior circumvallate papillæ, it appears that the secondary papillæ are much shortened, but traces of them can be made out.

Thus upon the whole this tongue comes nearest to the *Halmaturus* type, in the possession of three bilaterally symmetrical circumvallate papillæ. But this conclusion is not certain, and may

be much modified by sections. The tongue is typically Marsupial in the possession of coronate papillæ, &c.

The Tongue of *Phalangista vulpina*.

I was fortunate enough to obtain two specimens of this organ—the back part of one (given me by Professor Moseley) and a fresh and complete tongue taken from an animal which I procured last Easter (1883). The back part of the tongue had been hardened in chromic acid and afterwards in spirit, while the whole tongue was hardened in a gradually strengthened mixture of chromic acid and spirit, the hardening being completed in spirit.

General description.—The back part of the tongue (Professor Moseley's) as seen from above is shown in fig. VIII. Plate LIV. (natural size), and from the right side in fig. IX. Plate LIV. (natural size). The posterior circumvallate papilla is seen to be large and radially symmetrical; it is not highly protected (as in *Halmaturus* &c.), and exposes a large circular disk (its summit) to a surface view, as in the higher mammals; it is situated far back from the anterior papillæ so that the posterior angle is acute. The anterior papillæ are smaller, concealed from view (except their apices), bilaterally symmetrical, and directed forwards as in *Halmaturus* &c. There is a well-developed lateral organ visible from above and from the sides (shown in both figures); it presents a great advance upon the same structure in *Halmaturus*, and yet even here the attention is solely directed to the slit-like depressions as the only essential organ. In the highest form of lateral organ (as in some Rodents) the surface between and around the slits undergoes modification, producing a foliate papilla in which the attention is directed to the lamellæ or ridges with bulbs on their sides, the intervening furrows appearing quite subordinate as merely the necessary spaces between the ridges. However, in such a tongue as that of *Phalangista* it is seen that the furrows are primary and the development of the ridges quite secondary. Many of the higher animals have the same simple type of lateral organ. The fungiform papillæ occur along the sides and probably on the upper surface. The filiform papillæ have the usual distribution; they are pointed, and very frequently of the triangular flap-like shape. Sometimes a papilla of the latter shape divides into two or three secondary papillæ. The whole surface is densely covered with coronate papillæ. The complete tongue enabled me to ascertain the true size:—length 63 mm. from the tip to the epiglottis; width at the level of the anterior circumvallate papillæ 18·25 mm. The tip had a rounded margin; the median ridge and grooves as usual. The free part of the tongue was 21·5 mm. in length.

Minute Structure.—I. *Gustatory Structures.*

A. *The Circumvallate Papillæ.*—The posterior papillæ were radially symmetrical and the anterior bilaterally symmetrical. The posterior and anterior papillæ of the complete tongue are shown in figs. XX. and

xvi. (Plate LIV.) respectively. Glands are very numerous (as they seem to be in connection with the circumvallate papillæ of all Marsupials), as many as seven ducts being seen in one vertical section (of an anterior papilla); they open at all levels into the involution (see figs. xvi. and xx. Plate LIV.). Peripherally the serous glands are replaced by mucous glands, although the latter are very abundant and sometimes even enter the papillary body. The mucous glands open upon the surface of the organ. In the larger posterior papilla the central nervous mass is ganglion-like (as in *Perameles*, though not to an equal extent), and nerve-cells occur high up in the papilla, and in still greater abundance in an axial downward extension of the central nervous tissues (see fig. xx. Plate LIV.). This conditior was not equally well marked (although present) in the incomplete tongue; and nerve-cells were not detected in any of the anterior papillæ, although they occur in nerves at the base and the downward extensions are present. In all the papillæ of both tongues the dense mucosa beneath the epithelium of the involution is reflected upwards into the papilla, and there forms a protective layer encircling the axial nervous mass (see fig. xx. Plate LIV.). In fact this arrangement is exactly as in *Halmaturus*, with the same subepithelial layer &c. (compare fig. xxi. Plate LV.). Striated muscles terminate in the dense mucosa at the point at which it curves round to enter the papilla (fig. xx. Plate LIV.). The various possibilities as to the action of these muscles have been discussed (*Halmaturus*). Here also it is possible that smooth muscle-fibres exist.

The arguments apply with greater force to the anterior papillæ, for their shape at once suggests that the mouth of the involution can be closed.

There appear to be 1100–1200 bulbs to the square millimetre on these papillæ and the grooves of the lateral organ.

The space between the papilla and its involution and the gland-ducts were often filled with a deeply-staining coagulum in the incomplete tongue; it was probably a constituent of the secretion of the serous glands acted upon by the hardening reagents. There had also been a distinct discharge of a fluid substance from the gustatory pores into this coagulum, in the form of small globules often still connected with the pore by a narrow neck; the globules were distinct from the coagulum, as they remained unstained.

The inferior convexities of the taste-bulbs are prominent and distinct, without any of the filling-in between the bulbs that occurs in higher animals. The bulbs still resemble interpapillary processes. The pores are very short.

B. *The Lateral Gustatory Organ.*—Vertical sections show that the downward direction of the furrows is as irregular as their surface view (see fig. xxxii. Plate LV.). The serous glands are very abundant, opening at the bottom of the trenches. In one vertical section three ducts were seen. At the sides the serous glands are replaced by mucous glands which open freely on the surface, but never, as far as I observed, into the furrows. Nerves are abundant, and commonly contain nerve-cells collected in small ganglia; they

approach the organs as in *Halmaturus* (running beneath the epithelium of the general surface). The bulbs are found on the sides of the furrows in about 7–10 tiers, extending right up to the lips of the opening. Beneath the bulbs there is also the same delicate subepithelial layer that exists in the circumvallate papillæ; there is also the same dense mucosa with striated muscle-fibres terminating in it. (This is a character of the whole organ, and the possible significance suggested above is a result of its greater relative predominance in that particular region.)

C. *The Fungiform Papillæ.*—As described above, I include these structures under the present head because of the existence of bulbs in them; but I believe that they are essentially tactile, and it has to be proved that they are gustatory in any case. The bulbs are of the same primitive type described in this position in *Perameles*. The bulbs are evidently a very recent development in the fungiform papillæ of Marsupials.

II. *Mechanical and Tactile Structures.*

A. *The Coronate Papillæ.*—Over much of the surface of the organ there is no very distinct backward sweep of the secondary papillæ, but a very decided curve inwards and upwards, even carried to the middle line. Anteriorly the backward curve is followed. The coronate papillæ do not seem to give way (by transition) to any other type at the limit of the area on which they occur; they simply become less distinct, their rings of papillæ becoming isolated as a few scattered points. There are about 31 coronate papillæ to the square millimetre just in front of the anterior circumvallate papillæ. There are 8–15 papillæ in the rings. The coronate papillæ are circular. Occasionally a secondary papilla is placed within the ring, but such irregularity is not common. The shape of these papillæ is exactly like those described as the anterior type of *Perameles*, the succession of cells being very similar (see paper referred to, p. 599). Just above the tip, and on the tip itself, there appear to be 11–12 papillæ in the rings, and here there are only 20 main papillæ to the square millimetre. They are oval in shape, and ·275 mm. in length and ·175 mm. in breadth. The posterior secondary papillæ are much developed (fig. xxx. Plate LV.). The upward succession of cells is very complicated in these papillæ, even more so than that of *Perameles*. The succession is shown in fig. xxx. (Plate LV.).

B. *The Filiform Papillæ.*—These are probably tactile, as nerve-fibres are very abundant close to and in them (with many nerve-cells in the nerves about their bases). The epithelium is not cornified, and (in common with the papillæ in this position in all Marsupials) their function cannot be mechanical. It is probable that the nerve-endings are of the most delicate intraepithelial kind, and therefore invisible except by special treatment of the fresh specimen. Mucous glands are very abundant near these papillæ, the ducts often opening beneath them.

Thus this tongue commences a new type, chiefly characterized by

the possession of two anterior circumvallate papillæ, following *Halmaturus*, and a posterior papilla much resembling that of higher animals.

The Tongue of *Belideus breviceps*.

This specimen had been preserved in spirit, and although unsuitable for minute work I was able to make out a great many interesting points. The hardening was conducted as in *Macropus*.

General description.—The size and shape of the organ, as seen from above, are shown in fig. x. Plate LIV. (natural size). The tip of the tongue had been injured by the teeth of the animal and was bent down so as to be invisible from above; but I think that this is accidental, and have taken this view in the drawing. The contour of the tip of the tongue in *Acrobates* bears out this view. The posterior circumvallate papilla is large and radially symmetrical, showing a large circular area on the surface; the two anterior papillæ are not radially symmetrical, and are nearly hidden from view in narrow, slit-like, oblique depressions. Thus the arrangement is an exaggeration of that met with in *Phalangista* (compare figs. viii. and x. Plate LIV.). The filiform papillæ are normal in appearance and position. There is a lateral organ just below the bases of the anterior filiform papillæ, invisible from above. Four or five grooves are present, which are very small and recognizable with difficulty. The free part of the tongue appears to be about 11 mm. long. There is a sharp inferior median ridge with the two grooves.

Minute Structure.—I. *Gustatory Structures*.

A. *Circumvallate Papillæ*.—The posterior papilla resembles that of *Perameles* in possessing a ganglion within it, which is not prolonged into the base as in *Phalangista*. Nerve-cells are very numerous in the axis of the base, extending upwards for half the height of the papilla. The summit of the papilla is beset with small secondary papillæ, thus resembling *Phalangista* rather than *Perameles*, but the whole shape more resembles the latter (compare figs. xvii. and xviii. Plate LIV.). The papilla is certainly radially symmetrical, and the irregularity shown in fig. xvii. is due to contraction. There are traces of a raised ridge round the papilla as in *Perameles*. Striated muscle-fibres terminate beneath the papillæ, as has been described in *Phalangista* and *Halmaturus*. This is also true of the anterior papillæ, which bend inwards and probably forwards as well (see fig. xv. Plate LIV., and compare with fig. xviii.), so that they are bilaterally symmetrical taken together, but not singly. They are extremely different from the posterior papilla. There appear to be 5–8 tiers of bulbs. Nerve-cells can sometimes be detected in the nerves at the base of the papillæ. The relations of the striated muscle and the supporting framework of the papilla are as in *Phalangista*.

B. *Lateral Gustatory Organ*.—The appearance, position, and ap-

parently the structure are as in *Phalangista*. There are the same serous glands connected with the grooves, and the same distal mucous glands. The grooves are similar in being less regular than in higher mammals. Sometimes there are patches of adenoid tissue close beneath the bulbs. Sometimes, even here, there is a slight rising to the lips of an opening, just suggesting the mouth of a gland. There are the usual nerve-cells in the nerves going to the bulbs. The bulbs seemed few and irregularly placed in the furrows, but this may be due to change in the tissue.

C. *The Fungiform Papillæ.*—Nothing could be made of their structure, but they are almost certainly similar to those of other marsupials (e. g. *Phalangista*).

II. *Mechanical and Tactile Structures.*

A. *The Coronate Papillæ.*—These papillæ are often oval just above the tip, the long axis being directed antero-posteriorly. It is common to find 8–10 secondary papillæ in the rings. I calculated that there are rather under 40 papillæ to the square millimetre. I could not find any isolated hair-like papillæ in the tongue. The papillæ are much recurved anteriorly, especially at the tip, where vertical sections seem to indicate a modification of the usual structure; but this part was much altered. Horizontal sections, taken posteriorly just in front of the anterior circumvallate papillæ in the middle line, show rather irregular rings of secondary papillæ, as in *Phalangista*; the common number in a ring seems to be 8–10. When crowding or irregularity occurs, it is at the anterior side of a ring. There are about 37 papillæ to the square millimetre. The upper cells of the main papillæ stain deeply, exactly as described in *Perameles* (see paper above noticed). The curvature of the secondary papillæ becomes less posteriorly, and over a large region only the tips are recurved, the papillæ being tall and slender and very beautiful. Again posteriorly they become recurved. (See fig. xxvi. Plate LV., which represents a similar papilla of *Macropus*.) The non-papillate epithelium at the side of the organ is smooth and without papillary upgrowths; it appears to be simple. The transition into the coronate papillæ is sudden, and the latter curve inwards as well as backwards, the inward curve being especially marked towards the middle line, but outside this rather irregularly. Behind the limits of the coronate papillæ on the upper surface the epithelium becomes smooth, and there are some indications of complexity.

B. *The Filiform Papillæ.*—Nothing could be made out certainly, but their shape and position indicate that they are normal in other respects.

This tongue is very close to *Phalangista*.

The Tongue of *Acrobates pygmæus*.

I am only able to give a general description of this interesting little tongue (the species is the "Opossum Mouse," the smallest marsupial). There is the most remarkable difference in size be-

tween the anterior and posterior circumvallate papillæ. The posterior is very large and shows perfect radial symmetry, exactly resembling the ordinary papillæ of higher mammals as seen from the surface; it is placed some distance behind the anterior papillæ, as in *Belideus* &c. The anterior papillæ are small, but quite distinguishable from above; they seem to retain very little (if any) bilateral symmetry and forward direction. To be certain on this point, sections are necessary. The great development of the posterior papillæ in Marsupials, where there is any difference between the three, compares in an interesting manner with the condition of many higher mammals. In these latter it is quite common (*e. g.* in many Insectivora &c., &c.) for the posterior papilla of the triangle to be altogether lost, and for the tongue only to possess two papillæ on the same level; these two obviously represent the anterior papillæ, for in allied species (*e. g.* the Hedgehog among Insectivora) the triangle is complete. The three circumvallate papillæ of *Acrobates* are placed on a depressed smooth area at the back of the tongue. Immediately anterior to the two foremost papillæ the coronate surface begins with a sudden transverse rise right across the tongue, thus sheltering the circumvallate structures. There is a distinct normally placed lateral organ beneath the filiform papillæ, which is interesting in its possession of only two furrows (as far as I can tell from surface examination); these are distinct and well developed, and surrounded by prominent lips. The coronate papillæ are as abundant as usual and have the ordinary arrangement. Fungiform papillæ are very common on the upper surface as well as on the sides.

On the underside of the free part the ridge and grooves are normal. The pointed tip of the organ is not turned down, suggesting that the figure of *Belideus* (fig. x. Plate LIV.) is correct. It is extremely interesting that (as in the young marsupials and in Cetacea) the epiglottis can be made to protrude through a notch in the soft palate, so that breathing can go on uninterruptedly during the time that the animal is drinking the sweet juices of the flowers of *Eucalypti*, which constitute its food. The epiglottis is long and tubular, and its opening is prolonged into a slit posteriorly, so that it must be a great protection at all times, and a perfect protection when it is thrust through the notch, as I found it in this specimen.

The soft palate is continuous with the pharynx laterally for a long distance backwards; its free edge is a deep mesial notch, of which the anterior convex edge is just over the tubular epiglottis, and of a size and shape that the latter fits completely. The fluids (as in other cases) must pass on each side of the epiglottis.

This tongue obviously belongs to the *Phalangista* and *Belideus* type, and is a more complete specialization in the same direction than is met with in these latter.

The Tongue of *Perameles nasuta*.

I have already described the general appearance and histological details of this tongue in the 'Quarterly Journal of Microscopical

Science' for January 1883. I will shortly recapitulate the main features to show the relations to the other tongues described in this paper. I received from Professor Moseley the back part of the organ. The three circumvallate papillæ (see fig. XVIII. Plate LIV.) are very large (for so small a tongue) and resemble one another; they are radially symmetrical, only differing from those of higher mammals in their constricted bases and in the primitive type of bulb always present in Marsupials. They present a large circular area to a surface view (as in *Didelphys*, the posterior papilla of *Phalangista* &c., and in higher mammals). There is no lateral organ. The fungiform papillæ are scattered over the surface, but especially distributed along the sides; they contain more primitive bulbs than the circumvallate papillæ. The filiform papillæ are generally long and pointed, and they extend from the usual position, upwards and backwards, to the circumvallate papillary region. The coronate papillæ are normal.

Thus the tongue comes nearest to that of *Didelphys* (as far as this form could be investigated), and with the latter is the nearest approach to the structure of this organ in the higher mammals. It again begins a new type, characterized chiefly by the possession of three similar radially symmetrical circumvallate papillæ.

The Tongue of *Didelphys quica*.

The specimen had been preserved in spirit and the minute structures could not be made out; but some important points were ascertained, especially concerning the coronate papillæ, which were not much altered. The general description of the organ is also probably accurate in nearly all points. I used the same methods of hardening that were adopted with *Macropus*. I was extremely interested to observe how far the American form would follow the marsupial type as regards the coronate papillæ.

General description.—The size and appearance of the tongue, as seen from above, are shown in fig. XI. Plate LIV. (natural size). The transverse grooves crossing the organ in front of the circumvallate papillæ are probably due to contraction. The tip was injured, and I am not certain that it possessed an even contour as it is drawn. There were some indications of a division into lobe-like papillæ or processes, but I cannot be sure of this. The three similar circumvallate papillæ are round and large, resembling those of *Perameles* (see paper above referred to), but not so large in comparison with the size of the tongue. As seen from above they (together with those of *Perameles*) resemble the circumvallate papillæ in higher animals, in their radial symmetry and the size of the circular area exposed. There is a very even (though short) row of large upward and inward curving filiform papillæ in the usual position, but I could detect no traces of a lateral organ. The fungiform papillæ were not well preserved, but a few large ones are seen in the usual place. The junction of the papillate and non-papillate surfaces is sharp, but the latter is slightly rough. The coronate papillæ, covering a patch

some little distance behind the tip, are very strongly developed and of a remarkable structure. The powerful horny hooks characteristic of this region are distinct to the naked eye. The free part of the tongue is 19 mm. long (nearly half the total length), and the median ridge below is sharp and the grooves deep.

Minute Structure.—I. *Gustatory Structures.*

A. *The Circumvallate Papillæ.*—The transverse sections show that the circumvallate papillæ resemble those of *Perameles* (see fig. XVIII. Plate LIV.) in their constricted bases. Nerve-cells are abundant in the nerves at the base and probably within the papilla also. The minute structure could not be made out, but I saw some indications of peculiarity in the bulbs and their arrangement. There was an appearance of terminal organs in the papillary processes above the usual limits of the bulbs. The bulbs also seemed to be papillary in position, and were very unusual in appearance. I did not see gustatory pores, but it is most likely that they are present. The above suggestions of peculiarity may be entirely dissipated by the examination of a specimen prepared for histological work. Comparison with the state of the bulbs in *Belideus* leads me to believe that the peculiarities are not genuine structures, except perhaps the terminal organs outside the region of bulbs. I give no figure because the papillæ were much shrunk. Provisionally these papillæ may be regarded as close to those of *Perameles*, from their general shape.

B. *The Fungiform Papillæ.*—Nothing could be made of the minute structure. The shape, size, and position being normal, it is likely that the structure is also normal.

II. *Mechanical and Tactile Structures.*

A. *The Coronate Papillæ.*—The strongly developed papillæ (fig. XI. *s.c.p.*, Plate LIV.) of the patch behind the tip were shown by horizontal sections to be remarkably modified forms of the normal coronate papilla (see fig. XXIII. Plate LV.). The posterior secondary papillæ seem to be fused into a single strong recurved horny hook. In other parts of the circle, the secondary papillæ are normal and generally regularly arranged, except for an occasional one or two within the circle. These secondary papillæ are numerous (12–19). Isolated hair-like papillæ also occur abundantly in this region. These modified coronate papillæ are large and not very closely placed, so that there are only about 5·5 to the square millimetre. The shape of the posterior hooks, as shown in horizontal sections, is very remarkable. The thick corneous layer is only developed (except where the hook rises above the main papilla) posteriorly to the crescentic papillary upgrowth for the hook (with its concavity directed posteriorly). Posteriorly to the (in section) crescentic upgrowth the epithelial cells become cornified in a thick mass, which anteriorly presents a convexity approximately parallel with the concavity of the crescent. Laterally the thickened corneous mass is

continued into two horns which pass anteriorly round the papilla outside the ring of secondary hair-like papillæ. As the section is taken at successively higher levels, these horns are prolonged further and further anteriorly until they seem to meet and enclose the whole papilla. (Thus fig. XXIII. Plate LV. represents a section taken rather low.) The cornified cells of the hooks are remarkably hard, so that the razor cuts them with a very audible sound and with much detriment to its edge; they remain bright yellow after treatment with logwood. A vertical longitudinal section through one of these papillæ is drawn in fig. XXII. Plate LV., and it shows the great size and strength and the curvature of the posterior hook; it also shows the thin anterior corneous layer first appearing where the hook becomes clear of the main papilla. Both these figures alluded to are semi-diagrammatic, and are in some points the probable interpretation of very doubtful appearances due to changes in the tissues. This region is very interesting, for it shows how the slender elements of the coronate papillæ have been modified to perform the tough work of the horny filiform papillæ of higher animals. It is obvious that the strong posterior hooks would first meet any object, and would be obliged to do practically all the work, when the tongue was drawn backwards in licking.

The coronate papillæ above the tip, in front of this peculiar region, are of more regular form; but the posterior secondary papilla (and occasionally one beside it) is more strongly cornified and larger than the others. The cornification also tends to pass anteriorly round the outside of the other secondary papillæ as two horns. In these points there is a transition towards the modified papillæ described above, but the characters increase very suddenly at the limits (posteriorly also) of the peculiar region. The secondary papillæ in the rings are not numerous, 6–8 being common; they are much recurved: the papillæ are small and numerous, *i. e.* about 72 to the square millimetre. There are no isolated hair-like papillæ. The coronate papillæ just in front of the anterior circumvallate papillæ are rather small and closely packed (about 60 to the square millimetre); they are round or oval, and some irregular in shape. A few are remarkably elongated antero-posteriorly (see fig. XXIV. Plate LV., in which the effect may be increased by a slight obliquity of section, but is remarkable anyhow): such elongated papillæ are doubtless formed by longitudinal coalescence, as I have seen traces of a central constriction, and the number of secondary papillæ is about twice the usual number (8–10). There is no special size or cornification in the posterior secondary papillæ. Isolated hair-like papillæ are not present. The upper cells of the papillæ stain deeply, as has been described in *Perameles*; in fact these posterior coronate papillæ are very similar to those of *Perameles*. They are recurved, but less than the anterior papillæ; they are not of the tall slender type like the posterior coronate papillæ of *Belideus*, but are more like the posterior type of *Perameles*, differing from these in the greater symmetry of the ring of secondary papillæ when cut horizontally. The modified papillæ described above are transitional

into these by a lessening of the posterior cornified part until it ceases to differ from the rest of the ring.

B. *The Filiform Papillæ* are probably normal in structure, as they are in shape and position.

Thus this tongue comes nearest to *Perameles* in the circumvallate papillæ, but is very peculiar in the coronate papillæ, and primitive in the possession of isolated hair-like papillæ.

General Conclusions.

The above observations may be shortly recapitulated, and the tongues of all the Marsupials yet examined may be classified as follows (the types are printed in italics):—

I. A. *Circumvallate papillæ* approximately identical, bilaterally symmetrical; much protected (the mouth of the involution probably capable of closure), and the pointed apex directed forward (exc.). The taste-bulbs ascend high up the papillary sides in the most typical instances. Posterior angle very obtuse (exc.).

B. *Lateral organ* very primitive, and showing its origin as a row of gland-ducts.

C. *Coronate papillæ* with irregular circles of secondary papillæ (in some places). Intercalated single hair-like papillæ present.

Halmaturus; Macropus; Petrogale; Dasyurus (?).

II. A. *Circumvallate papillæ.*—The two anterior are smaller and of the type described above, although sometimes presenting the characters to a less degree; the posterior larger, and radially symmetrical; the summit is a circular disk which can be seen from the surface; the whole papilla resembles that of the higher mammals (except for the constricted base). Posterior angle acute.

B. *Lateral organ.*—Less primitive; an irregular row of slit-like furrows; gland-ducts distinctly open at the *bottom* of the furrows.

C. *Coronate papillæ* less irregular; no intercalated hair-like papillæ.

Phalangista; *Belideus*; Acrobates.

III. A. *Circumvallate papillæ* approximately identical and of the same type as the posterior papillæ of Division II. Posterior angle varies.

B. *Lateral organ* absent.

C. *Coronate papillæ* very regular; no intercalated hair-like papillæ.

Perameles; Didelphys? (does not follow C).

It is very interesting (and I venture to think significant) that the structural features which combine together to make one of the above divisions show considerable correlation with one another.

Thus in I., the lateral organ is certainly primitive, the circumvallate papillæ come nearest to those of *Ornithorhynchus*, and the scattered hair-like papillæ perhaps show an approximation to the same animal, in which all the back part of the tongue is thickly covered with papillæ of this description; and so also with divisions II. and III. Even the fact that *Didelphys*, following a different development in another area, should combine some of the characters of two divisions, is exactly what might be expected. The fact that *Didelphys* retains a distinctly marsupial tongue is a proof of the great persistence in this organ of characters which at first sight appear to be transient, and merely related to food and habits.

In a paper on "The Tongue of *Ornithorhynchus*" in the 'Quarterly Journal' for July 1883, I suggested that we found in this animal a structure intermediate between the circumvallate papillæ and the lateral organ. In this I was wrong; it is only related to the former, and the latter develops independently in Marsupials, with the appearance of bulbs in the walls of a row of lateral gland-ducts. But my argument that such a structure might represent an ancestral form of a circumvallate papilla—then based on few data—can now be supported by a long series of intermediate forms.

Looking at this latter question in the light of the observations recorded, the evolution of the circumvallate papillæ and their taste-bulbs is as follows:—Subepithelial tactile end-organs were at first the only means by which food could cause a nervous stimulus. These became more sensitive by the upward growth of the papillary processes (in which they were contained), so that the end-organs were separated from the stimulus by a lessening thickness of epithelium. At the same time sapid substances gained a greater power of penetration by the development of serous glands out of those of the wide-spread mucous type. Probably the gland-ducts surrounded a circular or oval surface in which the end-organs existed. Finally the upgrowth of the end-organ reached a climax in the perforation of the epithelium. At the same time the end-organ must have become gradually modified in a gustatory direction, losing its tactile functions. But at the perforation of the epithelium, the delicate subepithelial end-organ became exposed to the various agencies at work upon the surface of the epithelium. Hence the folding down of the sides of the area, and the opening of ducts into the furrow thus formed, and the protection of nearly all the end-organs (*Ornithorhynchus*, fig. XII. Plate LIV.). In an exposed part of the tongue of the same animal the protective change was carried much further (fig. XIII. Plate LIV.). Then comes a great gap, during which the papillary subepithelial end-organs disappear (due to their delicacy and their need of protection to such an extent as to cause slight usefulness), and new end-organs are developed from the epithelium of the interpapillary processes. These new terminal organs (taste-bulbs) are met with in Marsupials, with distinct indications of their interpapillary origin. Being thus comparatively recent, traces are retained of the old protection necessary for a more delicate end-

organ, and hence the series (figs. XIV—XVIII. Plate LIV.) in which the most protected forms show *independent evidence* of their primitive condition. With the most perfect protection, there is also the presence of bulbs over the whole of the papillary surface; and as the papilla becomes less protected, the bulbs gradually sink into their normal position of a zone round the papillary base. Even in the highest marsupial papillæ there is some trace of the original protection in the presence of a much constricted base. In some marsupial tongues both conditions coexist, and the less protected, radially symmetrical form is the posterior (*i. e.* the papilla most sheltered by its position, and thus able most quickly to abandon the old excessive protection). It has been much in favour of this theory that I have been able—in more than one part of the subject—to confirm previous suggestions by subsequent work.

As to the primitive triangle of circumvallate papillæ, I have no doubt that we have here the ancestral form of the inverted **V** arrangement in many higher animals (*e. g.* man). It is possible that, the above being the history of the primitive circumvallate papillæ, in some cases their number may be added to by *direct* development from fungiform papillæ; but this is only a suggestion founded on a superficial examination.

EXPLANATION OF PLATES LIV. & LV.

Fig. I. Natural size. The back part of the tongue of *Halmaturus ualabatus* seen from the right side. The upper surface is seen to be densely papillate, the papillæ being of the coronate type (*i. e.* papillæ surmounted by a circle of fine, hair-like, generally recurved, secondary papillæ, the whole of mechanical function, and as far as is yet known peculiar to and always present in Marsupials; see fig. XXVIII, Plate LV.). *f. p.* Fungiform papillæ of the normal structure; few in number and scattered irregularly among the coronate papillæ above the lateral line of junction with the non-papillate surface. *l. f. p.* Lateral filiform papillæ, forming the limits of the papillate surface at the posterior part of the junction with the non-papillate surface. These large and probably tactile papillæ are very constant in this position in the tongues of Marsupials and probably of other Mammalia. The lateral gustatory organ, when present, is to be found (as in this tongue) in the non-papillate surface just below the anterior part of the row of filiform papillæ. *l. g. o.* Lateral gustatory organ, here presenting the appearance of a row of circular elevations with a crater-like depression (generally somewhat elongated) on the summit of each; beneath these elevations is a longer, less regular row of smaller but otherwise apparently similar elevations, *gld. d*; the depressions on the summits of these latter are gland-ducts leading from glands of mucous type. No taste-bulbs are to be found in the walls of the ducts, but they are present in small numbers in those of the larger elevations (*l. g. o.*). But in other respects these last depressions are precisely similar to the former; they lead into glands of serous type, and all their relations are those of gland-ducts (see fig. XXXI. Plate LV.). We therefore have here the simplest form of lateral organ—a row of simple gland-ducts, in the walls of which scattered bulbs are developed. From this type we can pass by gradual stages to the complex lateral organ of Rodents, in which there is but little indication of the true origin, except when looked at in the light derived from the study of such a tongue as that of *Halmaturus*. The arrow (⟶) in all cases points

toward that part of the figure which represents the anterior end of the object depicted.

Fig. II. Natural size. The right lateral organ and the adjacent structures of a larger tongue of the same species (*Halmaturus ualabatus*), seen from the side. The references are the same as those of the last figure.

Fig. III. Natural size. The posterior part of the left lateral organ, and the adjacent structures of the tongue of the same species (*Halmaturus ualabatus*), seen from the side. In this specimen two of the smaller elevations (*gld. d.*) are placed higher than the others, and thus come to be situated between the two posterior elevations of the lateral organ. The same references.

Fig. IV. Natural size. One of the three circumvallate papillæ (*c. v. p.*) of the tongue of *Halmaturus ualabatus*, seen from above. The arrangement of these three papillæ is perfectly uniform in Marsupials as far as I have observed; *i. e.* at the angles of an isosceles triangle with the base directed anteriorly. In this species the posterior papilla is situated so far forward that it is placed between the other two, and the three papillæ are very nearly in the same straight line. The reference mark points to the circular funnel-shaped depression leading to the expanded cavity in which the large papilla is situated (see fig. XIV. for vertical section of this structure). The sharp anteriorly directed apex of the papilla is seen in the depression. Coronate papillæ cover the surface round the depression, but they are less marked posteriorly.

Fig. V. Natural size. The tip of the tongue of *Macropus melanops*, seen from beneath. The papillate surface is seen to be continued on to the inferior aspect of the tip, and there ends in an abrupt line against the smooth epithelium. This line of demarcation is parallel with the lateral and anterior contours of the organ. The fungiform papillæ (*f. p.*) are unusually abundant and very variable in size: they are in the usual situation, *i. e.* on the papillate side of the above-mentioned line of demarcation. Their function is probably tactile, and they are scattered among the coronate papillæ. *r.* Ridge in the middle line of the inferior surface of the anterior part of the organ: very constant in Marsupials; it is bordered on each side by a groove (*gr.*). The ridge is usually sharper and the grooves deeper than in this specimen.

Fig. VI. Half natural size. The tongue of *Macropus melanops*, seen from above. *Ep.* Epiglottis. The walls of the cavity have been held open by a needle, shown in the drawing. The reference mark (*c. v. p.*) points to the depression leading into the left anterior circumvallate papilla. The structure is very similar to that of *Halmaturus*. The lateral filiform papillæ (*l. f. p.*) and the lateral organ (*l. g. o.*) occupy very nearly the same position that they have in *Halmaturus*. Only the posterior parts can be seen from this point of view. They are better shown in the next figure. *r'* Median raphe, well marked anteriorly, disappearing posteriorly at about the middle of the length of the organ. Almost the whole of the surface represented is covered with coronate papillæ.

Fig. VII. Natural size. The left lateral organ and adjacent structures of the tongue of *Macropus melanops*, seen from the side. The filiform papillæ have the usual structure and arrangement; anteriorly and superiorly to them the surface is covered with coronate papillæ. The lateral organ (*l. g. o.*) still takes the form of a series of slight elevations with slit-like depressions on their summits. The series forms a very perfect arc, and the regular arrangement (together with the whole structure) shows a decided advance upon the condition of this organ in *Halmaturus*, although a close relation with the latter is obvious. It forms the first transition towards the more complex lateral organ.

Fig. VIII. Natural size. The back part of the tongue of *Phalangista vulpina*, seen from above. The lateral gustatory organ (*l. g. o.*) shows a great advance upon that represented in the last figure. (For other aspects of the lateral organ of *Phalangista* see the next figure and fig. XXXII.

Plate LV.). It now takes the form of a series of slit-like depressions in the smooth epithelium beneath the papillate surface. There are no mound-like elevations, and the whole appearance more resembles that of the well-marked organ of certain higher mammals. Corresponding with this, the sides of the depressions are crowded with closely packed taste-bulbs, and the gland-ducts seem to begin where the taste-bulbs end. Without the knowledge derived from the preceeding species, there would be no suggestion that the gustatory part of the depression is itself a gland-duct (see fig. XXXII. Plate LV.). This well-marked organ is still behind the most complex organ of Rodents in that there is no indication of a lateral area upon which the depressions are arranged, and no elevation of the ridges between the depressions; in fact the attention is merely directed to the slits, while in the more complex organ the ridges also attract notice. Further the slits are less uniform in size and less regular in arrangement than in the well-marked organs of Rodents, &c. The filiform papillæ (*l. f. p.*) have the usual arrangement; many of them have the shape of a triangular flap attached along the base. The circumvallate papillæ (*c. v. p.*) are arranged in the normal manner; the two anterior papillæ are smaller than the posterior and of a different shape (compare figs. XVI. and XX.), the former following the type of *Halmaturus* and *Macropus*, the latter resembling the papillæ of higher mammals. The upper surface of the organ is, as usual, covered with coronate papillæ. This is also true of the other tongues figured (and probably of all Marsupials).

Fig. IX. Natural size. The same tongue (of *Phalangista vulpina*), seen from the right side. The references are the same as those previously used.

Fig. X. Natural size. The tongue of *Belideus breviceps*, seen from above. There is a lateral organ present (hardly visible from above) in the same situation as that of *Phalangista* and of similar structure. The relation of the anterior circumvallate papillæ (*c. v. p.*) to the posterior papilla is also similar to that described in *Phalangista* (compare figs. XV. and XVII.). The anterior contour of the tongue may not be correct. The drawing was made from a spirit specimen in which the tongue was bitten through at the tip, and the anterior narrower part was bent down abruptly. In the figure I have assumed that this was accidental, and this was probably the case.

Fig. XI. Natural size. The tongue of *Didelphys quica* seen from above. The cavity around the epiglottis (*Ep.*) has been widened by separating the walls with a needle (drawn in the figure). The normally arranged circumvallate papillæ (*c. v. p.*) appear to resemble one another, and to follow the higher type. It was impossible to be certain of this, because there had been considerable alteration in the spirit specimen. There appears to be no lateral organ. The transverse ridges in front of the circumvallate papillæ may be accidental. The anterior contour of the tongue may not be quite correct. The coronate papillæ covering a well-marked patch behind the tip (*s. c. p.*) are peculiarly modified, a change being very distinct to the naked eye. The posterior part of the ring of secondary papillæ is occupied by a single, very strong, cornified, recurved hook (see fig. XXII. Plate LV.).

The seven succeeding figures (XII. to XVIII.) illustrate a gradual transition from the circumvallate papillæ of *Ornithorhynchus* to those met with in the higher mammals. This transition is from a bilaterally symmetrical structure, with taste-bulbs developed over its entire surface, to a radially symmetrical structure with the taste-bulbs confined to a belt round the base of the papilla. At first the papilla is but slightly withdrawn from the surface (fig. XII.); then it is deeply placed at the bottom of a narrow cleft (fig. XIII.); it then gradually emerges through a long series into the usual type of higher mammals (figs. XIV. to XVIII.).

Fig. XII. ×14·5. Transverse section of the posterior bulb-bearing ridge of *Ornithorhynchus*. It is probable that taste-bulbs were first developed

upon an oval area surrounded by gland-ducts. Owing to the delicacy of these terminal organs the area became protected by a fold round its circumference in which all the bulbs except those of the central line were sheltered. This is the stage represented in the figure, and has not proceeded further because the whole structure is additionally protected by its position in the tongue. *t. b.* taste-bulbs. *f. h. p.* Fine hair-like papillæ covering the posterior part of the organ. *f. h'. p'.* Fine hair-like papillæ posterior to the bulb-bearing organ and of different form from the others. *gld. d.* Gland-duct of serous gland.

Fig. XIII. ×14·5. Transverse section of the obliquely directed anterior bulb-bearing ridge of *Ornithorhynchus*. *gld. d.* Duct of serous gland opening into the narrow space between the ridge and the cavity in which it is placed. The ridge is placed upon a very exposed part of the tongue, and is therefore most exceptionally protected, being only reached from the surface through a narrow chink (probably closed by a sphincter muscle). The necessity for this extreme protection is probably to be found in the structure of the bulbs, which is very different from that of higher mammals.

Fig. XIV. ×14·5. Vertical longitudinal section through the left anterior circumvallate papilla of *Halmaturus ualabatus*. *c. p.* Coronate papilla. The taste-bulbs (*t. b.*) are now of the normal marsupial type (leading up to those of the higher mammals, but showing traces of development from the cells of an interpapillary process), and are probably less sensitive than those of *Ornithorhynchus*, which are essentially sub-epithelial. The apex of the papilla emerges from the cavity in which most of it is placed, but the part thus exposed is not covered by taste-bulbs, which are present over all the protected part (nearly the whole). The apex is directed forwards and the symmetry is bilateral. It is very likely that the mouth of the depression can be closed.

Fig. XV. ×14·5. Vertical section through one of the anterior circumvallate papillæ of *Belideus breviceps*. The apex is directed inwards rather than forwards, but the two papillæ are bilaterally symmetrical together, if not so individually.

Fig. XVI. ×14·5. Vertical longitudinal section through one of the anterior circumvallate papillæ of *Phalangista vulpina*. The apex is directed forwards. *gld.* Gland of which the ducts (*gld. d.*) are seen opening into the space between the papilla and its cavity.

Fig. XVII. ×14·5. Vertical section through the posterior circumvallate papilla of *Belideus breviceps*. It is likely that this papilla is radially symmetrical, for the difference between the two sides is probably accidental. The overhanging surface which bears the bulbs is a trace of the structure shown in the preceding figures. Otherwise the shape resembles that of the higher mammals. It is very interesting that the anterior and posterior papillæ of the same tongue should belong to such different types (figs. XV. & XVII.).

Fig. XVIII. ×14·5. Vertical section through a circumvallate papilla of *Perameles nasuta*. Very similar to the last, but symmetry decidedly radial. All the three papillæ in this species are of the same type.

Fig. XIX. ×40. Horizontal section through the depression (*c. v. p. o.*) leading into the cavity containing the posterior circumvallate papilla of *Halmaturus ualabatus*. The opening is surrounded by an irregular ring of fine papillæ (*r. f. p.*) (not aggregated into coronate papillæ). This section indicates the extreme narrowness of the opening into the cavity. It is very probable that the mouth can be closed by a sphincter, and that it is contracted in this instance.

Fig. XX. ×40. Vertical section through the posterior circumvallate papilla of *Phalangista vulpina*. This papilla also belongs to the higher type, while the anterior papilla of the same tongue is shown in fig. XVI. Most of the references have been previously explained. *gn. c.* Ganglion-cells arranged in groups at the lower part of a mass of nervous

tissue prolonged downwards from that in the axis of the papilla. A few cells are also present in the upper part of the same mass. *n.* Nerve leaving the mass in the axis of the papilla. *t. m.* Dense mucosa prolonged into the papilla, where it becomes unravelled and supports the nervous structures. *st. m.* Striated muscle-fibres terminating in the dense mucosa at the point where the latter is bending upwards to enter the papilla. It would seem that contraction of these fibres must retract the papilla, and may protect it by causing the mouth of the cavity to close tightly round its upper part; but another and opposite interpretation is possible.

Fig. XXI. ×71·5. Section transverse to the long axis of a circumvallate papilla of *Halmaturus ualabatus* at about the thickest part (see fig. XIV. Plate LIV.). *s. l.* Superficial lamina of cornified epithelium, through which the short gustatory pores pass vertically. *s. ep.* Stratified epithelium between the outer parts of the bulbs (the remains of that from which the bulbs were developed). *t. b.* Taste-bulbs. *s. e. l.* Subepithelial layer, probably consisting of elements of the nervous and fibrous tissues (of the next layer), arranged in extremely fine interpenetrating networks. In addition to this arrangement straight radial fibrils are seen passing from the next layer towards the bulbs. It is evident that the nerve-fibres are reduced to their ultimate structural elements in this layer before ending in the cells of the bulbs. *f. l.* Fibrous layer supporting the nervous tissues and the whole papilla, continued into the papilla from the dense mucosa round it (see fig. XX. Plate LIV.). Nerves are seen passing through this layer to that last described (*s.e.l.*). *c. n.* The nerves in the axis of the papilla, gradually passing outwards through the last layer (*f. l.*).

Fig. XXII. ×40. Vertical longitudinal section through one of the strongly developed and modified coronate papillæ from the patch behind the tip of the tongue of *Didelphys quica* (see fig. XI. *s.c.p.*, Plate LIV.). *s. e.* Superficial epithelium. *p. h. p.* Strongly cornified (*c. e.*) recurved hook taking the place of the normal posterior hair-like papillæ. *p. p. p.* Posterior papillary process entering the base of the latter. In this section a line of cells continued from the apex of the papillary upgrowth can be distinguished from the cornified cells of this hook-like structure. *a. h. p.* Anterior hair-like papilla of normal structure. *a. p. p.* Its papillary process. This section is taken along the line A–B of the next figure.

Fig. XXIII. ×50. Horizontal section through a similar papilla (of *Didelphys quica*), taken along the line A–B of the preceding figure. *p. h. p.* The posterior cornified hook is seen to possess a very singular outline. The two arms of the crescent arise outside the normal secondary papillæ, indicating that the structure does not entirely correspond to the latter, but probably belongs in great part to the sides of the primary papilla. *p. p. p.* The crescentic papillary upgrowth for the hook, of very remarkable outline and relation to the papillary processes of the normal secondary papillæ. *a. h. p.* Anterior hair-like secondary papilla (normal). *s. h. p.* Single hair-like papillæ scattered between the coronate papillæ as in some other Marsupials, and similar to the normal secondary papillæ of the coronate structures.

Fig. XXIV. ×50. Horizontal section through a coronate papilla just in front of the anterior circumvallate papillæ of *Didelphys quica.* *h. p.* Hair-like secondary papilla, of which there is a very unusual number. The shape of the coronate papilla is very remarkable, and probably arises from longitudinal coalescence.

Fig. XXV. ×14·5. Horizontal section through the coronate papillæ (*c. p.*) of the region halfway between the tip and the anterior circumvallate papillæ of *Macropus melanops.* Posteriorly the section is deepest, and shows the single main papillary upgrowth for the whole coronate papilla (*c. p. p.*). A little higher the secondary papillary processes for the anterior hair-like papillæ are distinct (*a. p. p.*), while the posterior

processes are still fused into a single upgrowth, crescentic in section (*p. p. p.*). At a higher level than is shown in this section the complete ring of secondary processes would be distinct. Hence the posterior papillary processes are given off at a higher level (compare fig. XXVI.). *s. h. p.* Single hair-like papillæ, as in fig. XXIII. This section shows that the upgrowths for the isolated hair-like papillæ are very distinct from those of the coronate papillæ even at the lowest levels.

Fig XXVI. × 14·5. A single coronate papilla from the region between the two anterior circumvallate papillæ of *Macropus melanops*, shown in perspective from the left side. The secondary papillæ are probably finer than in reality.

Fig. XXVII. × 10. Vertical longitudinal section along the middle line of the papillate surface in front of the anterior circumvallate papillæ of *Halmaturus ualabatus*. The section shows the relation of the isolated fine papillæ (*s. h. p.*) to the coronate papillæ (*c. p.*).

Fig. XXVIII. × 40. Horizontal section through the coronate papillæ of *Halmaturus ualabatus*, taken in the middle line just anterior to the posterior circumvallate papilla. This also shows the relation of the isolated (*s. h. p.*) to the coronate papillæ (*c. p.*), and also indicates that the secondary papillæ on the latter are not always regularly arranged in the ring. The posterior side of a coronate papilla can sometimes be detected by the fact that some of the posterior secondary processes remain still coalesced, although they are distinct at other points of the circumference. *i. h. p.* Single hair-like papillæ within the ring of some of the coronate papillæ.

Fig. XXIX. × 40. Vertical longitudinal section through a coronate papilla (vertical transverse through the organ), just above the lateral organ of *Halmaturus ualabatus*. The figure shows the relations of the four layers of a complex epithelium to the papillary structure. The layers are:—1, staining moderately, the cells fusiform and nucleated; 2, a thin layer, behaving with reagents as if the cells were cornified; 3, deeply staining, elongated cells with long thin nuclei; 4, a layer presenting all the characters of normal *rete Malpighii*. The distribution of layer (2) in the secondary papillæ (*p. h. p.* and *a. h. p.*) also indicates that it is cornified. The same layers are met with in the smooth epithelium beneath the papillate surface (see fig. XXXI.). The shading is diagrammatic. In other parts of the organ, the distribution of layer (2) is more symmetrical in the secondary papillæ.

Fig. XXX. × 50. Vertical longitudinal section through a coronate papilla from the surface above the tip of the tongue of *Phalangista vulpina*. The figure shows the arrangement of the cells much resembling that described in *Perameles*, but more complex. The normal lower layer (*n. l.*) graduates into attenuated granular cells (*a. c.*), passing through a mass of similar cells of which the nuclei stain deeply (*n. c.*), into the very attenuated cells of the posterior process (*p. c.*), in which hardly any nucleus can be detected. Above, in the centre of the main papilla, the cells are still granular, but swollen and non-staining (*s. c.*), while remnants of the nucleus can be often detected. Higher still, and towards the posterior secondary papilla, the cells again become attenuated, rarely nucleated, and deeply staining (*a'. c'.*), and they are continued on to the posterior papillæ. The swollen cells pass directly into the attenuated cells of the anterior papilla without forming a layer in the main coronate papilla. All the secondary papillæ also derive cells from their own papillary upgrowths, and also from the superficial epithelium surrounding them. The latter is simple and of the usual structure.

Fig. XXXI. × 14·5. Vertical transverse section through one of the elongated depressions of the lateral organ of *Halmaturus ualabatus*. The depression (*g. d.*) is seen to present all the characters of a gland-duct, and a secondary duct opens into it above the region of the taste-bulbs (*t. b.*). In the epithelium the four layers described in fig. XXIX. are shown.

The layers are thicker on the left because that side leads towards the thicker epithelium of the papillate surface.

Fig. XXXII. × 145. Transverse vertical section through four of the furrows of the larval organ of *Phalangista vulpina*. The drawing is in outline only, and the bulbs are not indicated. The irregular direction of the trenches makes it impossible to obtain a true transverse section of them all, and therefore the epithelium in places appears thicker than it really is (being cut obliquely). Owing to the same cause two or three rows of bulbs are sometimes seen in one thickness of epithelium. *s. e.* Superficial epithelium with papillary processes below. *g. d.* Gustatory depressions with smooth epithelium. *gld.* Serous glands with their ducts (*gld. d.*) opening into the bottom of the furrows.

2. A Contribution to our Knowledge of the *Embiidæ*, a Family of Orthopterous Insects. By J. Wood-Mason, Deputy Superintendent, Indian Museum, Calcutta.

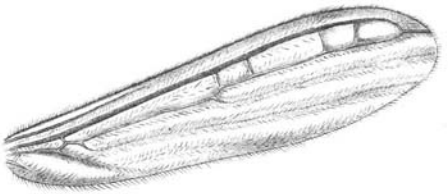
[Received November 28, 1883.]

(Plate LVI.)

Introduction.—While I was at home on furlough in 1877–79, Mr. R. M'Lachlan, F.R.S., drew my attention to this imperfectly known little group of insects, and begged me to attempt, on my return to India, to supply some of the deficiencies in our knowledge regarding it. I promised to do what I could in the matter; and, before leaving England, prepared myself for my task by examining the different collections of dried specimens and by reading up the literature of the subject; in particular Mr. M'Lachlan's[1] then recently published paper, containing (1) a *résumé* of the few and scattered items of additional information that had been placed on record by various naturalists during the forty years that had elapsed since the appearance of Westwood's[2] memoir in the year 1837; (2) descriptions of four new species; and (3) the record of the discovery, in an orchid-house near London, of the so-called nymph-stage of a species imported into England with plants from India—a valuable observation, which proves that in the Embiidæ we have to do with a group of insects whose members, like the true Orthoptera, the Earwigs, and the White Ants, and like the Psocidæ, the Physopoda, and the Rhynchota, attain to the adult condition without undergoing any metamorphosis in the entomological sense of the term.

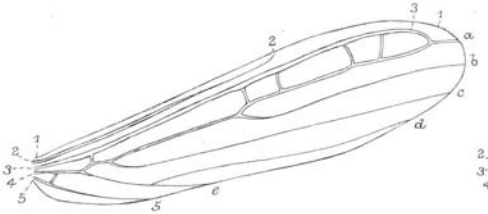
From the examination of specimens and the perusal of the literature I arrived at the conclusion that all the specimens of all the species

[1] Journal Linn. Soc. Lond., Zoology, vol. xiii. pp. 373–384, pl. xxi.
[2] Trans. Linn. Soc. Lond. vol. xxii. pp. 369–375, pl. xi.

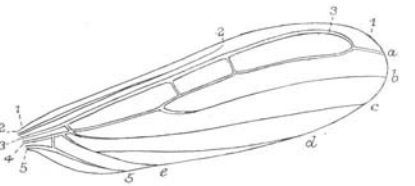


1 ×10

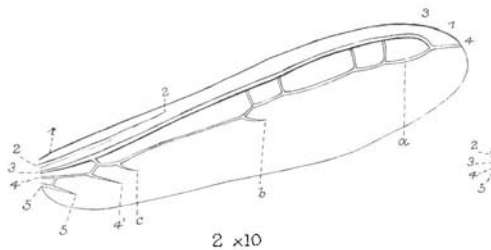
1α ×10



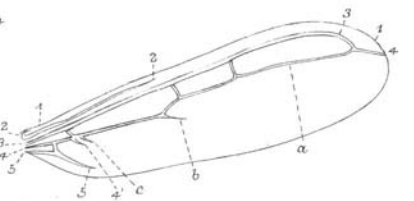
3 ×10



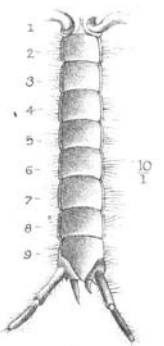
3α ×10



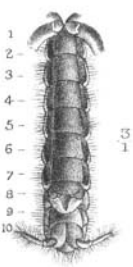
2 ×10



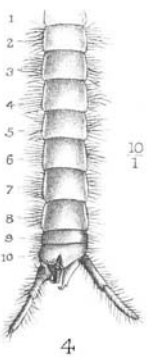
2α ×10



5



6



4

B.L.D. et J.W.M. del. Hanhart imp. J Smit lith.

MORPHOLOGY OF EMBIIDÆ.

that had up to that time fallen into the hands of entomologists were of the male sex, and that the females were consequently unknown; for in all the specimens examined by me the abdomen invariably presented a mesially imperforate series of nine sterna, the ninth and terminal of which was produced nearly to the extremity of the body so as to cover the tenth sternum and its contained genital aperture, just as in male Cockroaches, Earwigs, &c.; it exhibited a greater or less degree of asymmetry of its terminal somites or of their appendages or of both, as in many male Cockroaches, Phasmatidæ, Lepidoptera, Trichoptera[1], &c.; and, moreover, an asymmetrical system of highly indurated spines and hooks springing asymmetrically from its podical plates, and analogous to the similar, but usually more complicated, apparatus developed around the genital aperture in male Cockroaches and Mantodea, could generally be made out.

I also formed the opinion that the females when discovered would prove to be wingless, and probably larger in size.

Both conclusion and opinion have since been fully verified by the careful examination of living and spirit-specimens of indubitable males, and by the discovery of the larger and wingless female of one species; from which latter fact I have no hesitation in inferring greater size and winglessness in the females of all the species of the group.

Discovery of Larvæ of a Species apparently living in Society.—My first acquaintance with a living species of Embiidæ was made a few hours after landing in India, on the journey by rail from Bombay to Calcutta, in the end of July 1879, at Jubbulpore, where I was obliged to stay a night in order to break the journey. While strolling about in front of the hotel about noon on the following day I came upon a bare and sandy spot, over which larvæ of a species of Embiidæ were actively running by dozens; and I succeeded in capturing a number of specimens, both in the open and beneath the old bricks that lay scattered about and had evidently been used in the construction of rude fire-places for cooking their food by a party of coolies by whom the spot had a short time before been occupied as a

[1] I am indebted to Mr. M'Lachlan for the following information concerning the asymmetry of the male anal appendages in this order of insects. Inequality is not confined to any special portion or set of appendages, and occurs in all the four or five species of the genus *Glossosoma*, and is generic, affecting the ventral portion of the anal apparatus; in an undescribed species of *Leptocerus*, from Portugal, in a pair of inner processes, which in other most closely allied species are equal (a long series of specimens examined); in *Setodes interrupta*, in which one pair of appendages extends far beyond the extremity of the body, and is, as I can testify from having inspected Mr. M'Lachlan's drawings, tremendously unequal; and probably in other species. The last case is, as Mr. M'Lachlan writes, especially "remarkable, because there is another species (*S. similis*, M'L., represented by many individuals) from Turkestán so similar in all other respects that it did not occur to me [him] at first to consider it distinct; but I [he] thought I [he] might as well see if locality had caused any modification, and to my [his] astonishment found a purely symmetrical and utterly different (specific) condition (correlated with a very slight and unimportant difference in wing-markings)."

camping-ground. A violent thunder-storm which suddenly came on while I was searching for the nest or tunnels inhabited by the insects drove me indoors; and, having to resume my journey shortly afterwards, I had much against my will to forego an opportunity of ascertaining the habits of the Embiidæ that may not soon recur. Not expecting to meet with *Embiæ* in such a place, I should have passed them over without notice had it not been for their marked Thysanurous gait and shape; and I was much disappointed at finding, as I soon did, that instead of a new Thysanuran with two-jointed cerci and a living representative of the ancestors of the Staphylinidæ, I had got hold of an *Embia*.

Some of the specimens obtained on this occasion were forwarded to Mr. M'Lachlan[1], who has expressed the opinion that they probably belong to *Oligotoma saundersii* of Westwood, a species originally described from Calcutta specimens. In none of those which were retained by me for my own use are the slightest traces of wings to be detected, although the asymmetry of the caudal appendages, which I consider to be characteristic of and exclusively confined to the male sex, is already quite apparent. The asymmetry of the tergum of the terminal abdominal somite and of the cerci in the males of *Necrosia maculicollis*, one of the Phasmatidæ, appears at the corresponding early stage, and in nymphs is quite as strongly marked as in perfect insects.

Discovery of a Female.—In the following October, on the first zoological excursion I made after my return to Calcutta, I met with an insect possessing all the characters, including the peculiarly fashioned fore legs of the Embiidæ, but devoid of all traces of wings and abdominal asymmetry. I found it in the large plant-house in the Botanic Gardens, crawling over the leaves of a plant of the habit of *Fittonia*. It is a shining black insect with pale-tipped antennæ, and as it lay upon the leaves it bore a striking resemblance to a larva of some brachelytrous beetle or to an Earwig with a short forceps. It measured no less than three quarters of an inch in length from the front of the head to the end of the abdomen, and is consequently about thrice as large as the smallest, and twice as large as the largest, of the previously described specimens, compared with which it is further remarkable for its thick and firmly chitinized integument. It, in fact, answers exactly to the idea I had formed of what the female would be like, and it is, as I shall show, a female.

Description of the Female.—In its abdomen, counting the so-called "*segment médiaire*" as the first somite, as it unquestionably is, though here, as is often the case in other groups of insects, its tergum is firmly ankylosed to the metathorax in adults and its sternum appears to be undeveloped, ten terga, the full number of the typical insectean abdomen, are externally visible, the two penultimate ones (which in the Cockroach and in the Earwig are shortened and squeezed up out of sight between the last or tenth and the seventh) being equally well developed with the rest; the last or tenth tergum is entire, rounded, obtuse, and deflexed at the end, and, with the two-jointed

[1] Proc. Ent. Soc. 1879, p. xliii.

cerci attached to its huge and firmly chitinized podical plates, perfect in its symmetry.

Turning to the lower or ventral surface of the animal, and counting as before the "*segment médiaire*" as the first abdominal somite, we find a series of nine sterna, corresponding to the nine basal terga, all likewise visible without dissection, the eighth and ninth not being shortened any more than are their terga, nor concealed from view by any enlargement and production of the seventh, as they are in the Cockroach and in the Earwig, and the tenth alone being hidden by the overlapping posterior margin of the ninth. The abdomen, in fact, in this insect is, so far as its eighth and ninth somites are concerned, less modified than in either of these two forms, thus resembling that of *Campodea*. Between no two of the eight basal of these sterna is any aperture to be detected in the middle line, nor is there any between the ninth and tenth, the former of which is identical in shape and texture with the seven basal ones; but the eighth is shorter and differently shaped from those which precede it, its hinder angles being produced and rounded so as to form in its hinder border an emargination, to the bottom of which is movably articulated by its base a triangular plate, whose basal angles are divided off from it by sutural lines; between the eighth sternum with its triangular plate and the ninth lies a wide and membranous space conspicuous by its white colour, and in it an aperture, which is ordinarily concealed by the triangular plate. As no other median aperture save the anus exists, this must be a genital aperture, and since it is placed, as in the females of the Cockroach and the Earwig, between the eighth and ninth sterna, and since moreover the genital aperture of winged specimens is situated, as in the males of the same two insects, one somite further behind, it must be the female genital aperture, and the insect a female.

Capture of Males.—Several winged specimens were captured during 1880 in my dining-room, whither they had been attracted by the lights. After flying for a while round and round the lamp in the centre of the table, they settled and walked about the cloth with a most peculiar gait, by which they were always readily recognizable, and which appeared to be due to locomotion on all sixes over such a surface being rendered impossible or awkward for them by the peculiar structure of their fore legs.

These insects, which undoubtedly belong to *O. saundersii*, are all of the same uniform brown colour.

Later, a winged specimen of another species was brought to me by one of the Museum assistants, who had found it clinging to the mosquito-curtains of his bed, a position in which insects that have been attracted by the lights of the house over night are not unfrequently to be found in the morning. This specimen is black.

Description of the Male Sexual Characters.—All the winged specimens examined by me agree with the above described female insect in the number of their externally visible terga, differing from it in having an unbroken and mesially imperforate series of nine, instead of eight, sterna; their genital orifice must consequently lie behind the ninth

or last of these sterna, in the same somite, that is to say, as that of the male Cockroach, and one somite further back than in the female, in which, as we have seen, it is placed between the eighth and ninth sterna just as in female Cockroaches. All present a more or less marked asymmetry of the caudal appendages; and in some there project between these appendages the tips of one or more "slender spiniform processes," which Mr. M'Lachlan suggests may be an intromittent organ, but I consider to belong rather to a genital armature analogous to that of the common Cockroach.

In *Oligotoma saundersii*, the only species of which I have as yet examined spirit-specimens, the abdominal asymmetry is carried to an extreme, and the genital armature is well developed and readily seen. In this species not only are the caudal appendages unequal on the two sides, but the tenth tergum and the ninth sternum also depart widely from symmetry, especially the former, which, as will be seen from the accompanying figures, is incompletely divided by a deep angular notch into two unequal and greatly dissimilar parts; and each podical plate bears one or more processes forming an asymmetrical apparatus of spines and hooks, which are analogous to the incomparably more complex genital armature of most male Cockroaches, and doubtless serve, in the absence of an intromittent organ, to keep the aperture of the vas deferens closely applied to that of the oviduct during copulation.

On the Wings.—No one can look upon an Embia without being struck by the wide difference between it and such an insect as a fully winged Cockroach in the mode and place of attachment of the wings and in the condition of the wing-bearing somites. In the larvæ of all ametabolous insects the thoracic somites differ from those which follow only in their greater size, and their terga are distinct from, and overlap, each other just in the same manner as do those of the abdomen; they are, in fact, temporarily in the same condition they permanently have in the Thysanura, which never possess wings—young *Blattæ* and young Earwigs resembling adult *Campodea* and adult *Machilis*. The wings appear as expansions of the sides and hinder angles of the two posterior of these somites, the terga of which are in the perfect insect no longer freely movable upon one another, but on the contrary are firmly knit together and soft, and have the fully evolved wings attached to them along the whole length of their sides. But species which have lost their organs of flight retain the primitive characters of their wing-bearing somites throughout life.

We thus see that concentration of the two alary somites accompanied by flexibility of their terga is correlated with the fully-winged condition, and, conversely, that the absence of such concentration and flexibility, that is to say, the retention of the primitive characters of the thorax, is correlated with the wingless condition.

In winged Embiidæ, and especially in *Oligotoma michaeli*, the thorax retains much of the primitive (larval) character of its two posterior somites, and the wings, instead of articulating with the whole length, are attached along only very short portions, and those at the extreme anterior ends, of the sides of their elongated somites.

This remarkable position of the wings seems to be explained by their having been gradually reduced till they became so small as no longer to need a concentrated thorax such as is to be seen in fully winged insects, and by the thorax having as gradually reverted to its primitive condition in the larvæ, and come to retain it permanently. In fact, as little by little the wings decreased in breadth, and consequently in the breadth of their attachments, their two somites appear to have increased in length behind them. Of their having been reduced, and of their being probably in process of still further reduction, the wings of two of the species bear the evidence on the face of them in the shape of one or more rudimentary veinlets; and one of the species, namely *O. michaeli*, has, according to Mr. M'Lachlan's figure of it, narrower and more pedunculated wings, and a more primitive thorax than the other, namely *O. saundersii*, the wings of which are fully described and figured below.

The species of the subgenus *Embia* would also seem to differ amongst themselves in the breadth of the wings, some having been described as having these organs broad, others as having them narrow.

The coloration of the wings is also remarkable. It is usually described by systematists as "fuscous black" or "fuliginous," "with four" or "five whitish streaks," as the case may be; but for my purpose it will be better to describe it as hyaline with the [black or] brown veins all so broadly bordered on both sides with pale [black- or] brown-smoky as to leave only narrow streaks of the ground-colour visible. In addition to the microscopically minute setæ with which the whole wing-membrane is thickly and regularly studded, other and much longer setæ are present, having a definite arrangement along the edges and in rows on the disk of the wings, namely, one row on each vein, and one row on each side of each vein along the margins of the brown bands, or three rows to each vein. The advantage of describing the colour and clothing of the wings in the way I have done will at once become evident when I add that the brown bands with their triple lines of setæ remain to mark the original courses of veins which have long since disappeared, and are now only represented by minute tapering processes jutting out from existing veins a short distance into the wing-membrane.

There is yet another point of interest about the wings. Professor Westwood describes and figures the second or subcostal vein of both pairs of wings as long and as anastomosing with the third or radial vein near the extremity of the wing; and Mr. M'Lachlan speaks of the coalescent subcosta and radius; and both in dried and alcoholic specimens these veins under an ordinary lens really appear to have this arrangement and development; but when the wings are mounted in spirit and viewed under the microscope, it is readily seen that the subcosta is quite short, and that its inclination to the anterior margin is such that it would, if produced far enough, run into the costal vein at a point situated a little beyond the middle of the wing. The illusive appearance of the presence of two concomitantly and com-

mensurately developed veins in the anterior part of each wing is apparently due to a shadow of the radius being cast upon the margin of the brown border of the costa, so as to coincide with the remains of the subcosta; and Professor Westwood has been the victim of an optical illusion.

Affinities.—In anticipation of the full and detailed account of the numerous and important differences between them and the *Perlidæ* which is in preparation, and will be published as soon as the drawings needed to render my descriptions intelligible are ready, I may say that the *Embiidæ* undoubtedly belong to the true Orthoptera, that they are in my opinion in some respects the lowest term, and in others the lowest term but one, of a series formed by the families *Acridioidea, Locustidæ, Gryllidæ,* and *Phasmatidæ,* and that their resemblances to the much lower *Perlidæ,* which may well be direct descendants of a form closely related to *Campodea,* are due to their low position in the division of Orthopterous insects to which they belong, and do not imply any such close genetic relationship to them as has been suggested.

EXPLANATION OF PLATE LVI.

Fig. 1. The right anterior wing of a male of *Embia* (*Oligotoma*) *saundersii*, Westwood, × 10.

Fig. 1 *a*. The right posterior wing of the same, × 10.

Figs. 2, 2 *a*. The same wings with all the details omitted in order that the venation may be seen more distinctly:—1, 1, the first or costal vein; 2, 2, the second or subcostal vein; 3, 3, the third or radial vein; 4, 4′, 4, the forked fourth or discoidal vein, 4′ its rudimentary posterior prong; *c*, the rudimentary first branch; *b*, the rudimentary second branch; and *a*, the termination of its anterior prong (4, 4), which is apically anastomosed to the radius, and connected with it by five transverse veinlets in the anterior wings and by three in the posterior; and 5, 5, the rudimentary fifth or anal vein, which is simple and unbranched and connected with the root of the fourth by a transverse veinlet in both the nearly homonomous wings of this insect.

(N.B. All the lines in these figures represent veins, with the exception of that commencing at a point situated a short distance behind the apex of the anastomosed radial and discoidal veins, ending near the origin of the fifth vein, and representing the posterior margin, in which there is no vein.)

Figs. 3, 3 *a*. The same wings with the venation restored by the aid of the brown bands and triple lines of setæ: *e*, the lost posterior, and *d*, the lost anterior fork of the rudimentary posterior prong of the discoidal vein.

(N.B. All the lines in these figures represent veins.)

Fig. 4. The abdomen of *Embia* (*O.*) *saundersii* ♂, from above, × 10.

Fig. 5. The same from below, × 10.

Fig. 6. Abdomen of *Embia* (*O.*) *michaeli*, M'L., ♀, from below, × 3.

(N.B. The arabic numerals in the three preceding figures refer to the somites of the abdomen.)