THE JOURNAL

OF

THE LINNEAN SOCIETY.

On the Gastric Glands of the Marsupialia.

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[Read 1st December, 1898.]

(PLATE 1.)

W. A. FORBES in 1881, in an account of an investigation of the anatomy of a Koala, was led, by a consideration of many points of similarity between this animal and the Wombat, to deduce a closer degree of relationship between the two forms than was then generally admitted. The common possession of a "gastric gland," a structure which Forbes considered to be so peculiar as to render it highly improbable that it should have been independently acquired in two forms unrelated to each other, afforded him a "convincing token of their affinity." Whether or not a fuller knowledge of the nature of this structure than Forbes possessed materially strengthens his contention, does not seem certain, but this investigation into the minute structure of the gland,—an investigation suggested by reading Forbes' paper,—seems to disclose certain points worth noting.

The first mention of the presence of a gastric gland in the stomach of *Phascolomys* seems to be that made by Home (4) in 1808, who refers to it as closely resembling that of the Beaver, and "forming a very extraordinary peculiarity." Home gives a very correct figure of the external appearance of the gland, a figure which Owen (9) repeats. Owen knew of the existence of the gland in *Phascolarctus*, and described it as closely

resembling that found in both *Phascolomys* and the Beaver. Later references to the gastric gland of the Marsupials in the literature are those of Huxley, 1871 (6), Flower, 1872 (2), Forbes, 1881 (1), Fleischman, 1891 (3), and Oppel, 1896 (8). Forbes had the opportunity of examining the fresh stomach of a newly-dead Koala, and described the gastric gland as red and vascular, while the surrounding mucous membrane was pale; he suggested a histological comparison of the glands of *Phascolarctus* and *Phascolomys*, with a view to finding whether the resemblance was more than an external one.

Oppel, in his important work on the comparative microscopic anatomy of the stomach, gives a very short description of the stomach of the Koala (8. pp. 291–2) and a figure of the gastric gland in section. The glands of the greater curvature and of the gastric gland itself he describes as "Fundusdrüsen." There is no exact account of the limits of the gland regions, but a reference is given to a paper by Edelmann in which the absence of the peculiar "Cardiadrüsenregion" in the Koala is described. Oppel's work (8. p. 298) contains no account of the histology of the gastric gland in *Phascolomys*.

Fleischman has a criticism of Toepfer's work (11) on the comparative anatomy of the stomach in the Rodentia, and the author makes some interesting remarks on the parallelism in structure of the stomach in the Rodents and in the Diprotodont Marsupials, which lead him to a belief in a close genetic relationship of these two groups.

"Gastric glands" in the Mammalia outside Marsupials occur only in *Manis* among the Edentates, and in *Castor* among the Rodents. The glandular appendages on the stomach of *Manatus* evidently belong to a distinct category. The structure in the stomach of the Beaver (fig.1, I., p. 4), which seems to have been first mentioned by Schmidt (10) in 1805, was figured and described, so far as external characters are concerned, by Home (4), and its minute anatomy was more exactly described by Toepfer (11) in 1891. The stomach of *Castor* is a simple one, lined throughout by a glandular epithelium. The cuticular lining of the œsophagus ceases at the opening of that organ, and the gastric gland is situated to the pyloric side of it on the surface of the lesser curvature. Home gives a figure of a hand-section through one of the openings of the gland, which shows a number of short tubules opening into a short terminal duct, and forming a structure

more closely resembling the gastric gland of *Phascolomys* than the corresponding structure in *Phascolarctus*. But the gland differs from that in the Wombat and Koala in that the openings have a serial arrangement; though, from the accounts given by various authors, the number and precise disposition of these openings is irregular. Such variation also occurs in the two Marsupials.

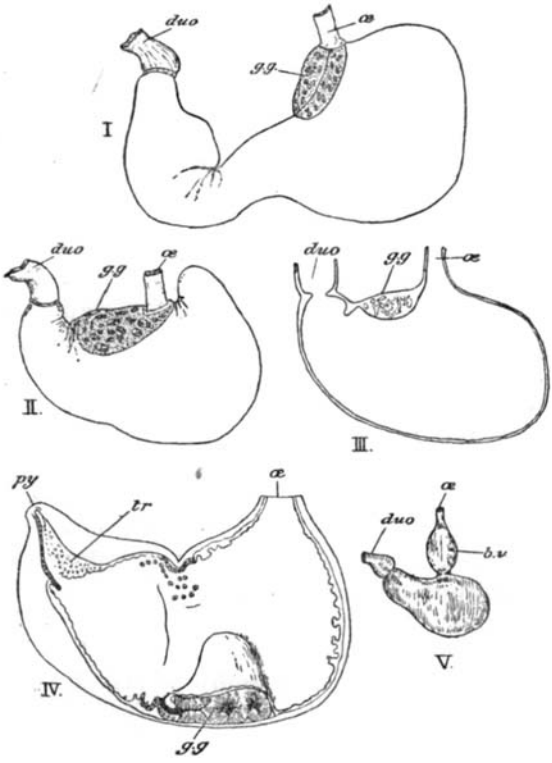
Manis javanica also possesses a complex glandular apparatus which may be termed a gastric gland, using the term in the same sense as in connection with the stomachs of *Castor* and the Marsupials. But the stomach of *Manis* (fig. 1, IV., p. 4), which was minutely described by Weber in 1891 (**12**), is a very specialized one; and the gastric gland is certainly morphologically a different structure from the "gastric glands" of other Mammalia. The epithelium of the stomach, with the exception of certain patches, is a non-glandular one, cuticular in nature. Three groups of openings, leading into much branched gland tubules, occur—one at the pyloric aperture, one on the lesser curvature, and one on the greater near the orifice of the gastric gland. The latter is a prominent pad on the region of greater curvature, projecting into the cavity of the stomach and opening into it by a single opening. Within there is a system of complex foldings, lined with an epithelium, which consists of closely set gland tubules possessing the characteristic central and parietal cells. At the opening of the gastric gland there is a portion of the cuticular epithelium covered over with small horny processes. A similar structure (Triturationsorgan) is found on the greater curvature at the opening of the gastric gland.

The "Vormagen" of *Myoxus avellanarius* (fig. 1, V., p. 4), and teh glandular appendage on the cardiac portion of the stomach of *Manatus australis*, which Leydig (**7**) compares with the gastric gland of the Beaver and the "Vormagen" of *Myoxus*, are evidently only analogous structures.

My material consisted of the stomachs of specimens of *Phascolomys* and *Phascolarctus*. The Wombat was a full-grown animal, and the area on the smaller curvature occupied by the glandular thickening measured 2·8 cm. along the longitudinal axis, and 3·4 cm. on the shorter axis of the stomach. The gland was situated closer to the œsophagus than in the case of the Koala, and its thickened rim partially embraced the latter, several of the

openings being situated laterally to the ostium of the œsophagus. The number of these openings was about thirty, but it was difficult to count them exactly, as occasionally several seemed to open out from the bottom of little gutters, and very short ducts frequently branched quite near to the surface into several smaller tubules. Their arrangement was an irregular one, but they occupied a central

Fig. 1.



Schematic representations of the stomachs of—I. *Castor* (after Home), II. *Phascolomys* (Home), III. *Phascolarctus* (Oppel), IV. *Manis* (Weber), V. *Myoxus* (Toepfer). I. and II. have their inner surfaces everted; III. and IV. are in sagittal section. All the figures reduced.—*b.v.*, bulbus ventriculi; *duo*, duodenum; *g.g.*, gastric gland; *œ*, œsophagus; *py*, pylorus; *tr*, "Triturationsorgan."

position on the thickened area, leaving an annular space free. The Koala was a young one, measuring about 26 cm. from the snout along the back to the root of the tail. The gland on the lesser curvature was almost circular in shape and measured about

10 mm. in diameter. Although it had not attained its greatest development in point of size, I have no reason to suspect that its anatomical details differed in any essential respects from those characteristic of the gland in the fully-grown Koala. The openings were much smaller than those in the Wombat, 25 in number, and occupied a central portion of the glandular thickening, round which was a part of the thickened area of mucous membrane free from openings. Unlike *Phascolomys*, the gland was situated nearly midway between the œsophagus and pylorus.

Phascolomys.

A section of the gland in the Wombat, taken parallel to the surface of the stomach, some little distance below the surface but before the bifurcation of the tubules has taken place, shows a number of tubules of varying diameter and of irregular distribution. The area of the gland is sharply bounded by a circularly running tract, which contains the cardiac glands of the surrounding epithelium of the stomach, and in which those glands are cut somewhat obliquely: this appearance is due to the plane of the section passing through the thickening of the gastric gland and surrounding epithelium. The gland itself is a somewhat lenticular shaped pad, due entirely to the complex folding which the mucous membrane has undergone. The surface of this thickening, facing the interior of the stomach, is slightly depressed. Towards the external surface the gland presents a convex border. In relation to each tubule there is a closely investing sheath of muscularis mucosæ, which accompanies it in its evagination outwards. This sheath consists mostly of a layer of plain muscle fibres, running transversely in relation to the long axis of the tubule, and, external to this transverse layer, of a very meagre, and in many places discontinuous, sheath of fibres running in the direction of the long axis of the tubule. Between these tubules is a space which is an extension of the submucosa of the general gastric epithelium, and which is occupied by areolar tissue containing blood vessels, lymph spaces, and muscle fibres. The latter are of two kinds—bundles of plain muscle fibres and of less abundant striated fibres. These are almost entirely derived from the muscular coats of the stomach, but probably also to some extent from the muscularis mucosæ. The primary tubules in the epithelium lining the evaginations which make up the gland are continuous with those in the cardiac region of the

stomach, and, like these, contain the typical central and parietal cells. In sections taken parellel to the surface of the gland, these tubules are for the most part cut longitudinally, though many are obliquely and even transversely cut.

In a nearly sagittal section (Pl. 1. fig. 1), taking in pyloric and œsophageal orifices, the extent of the gland exhibited is rather less than in one passing to one side of the œsophagus. This is due to the extension of the gastric gland laterally to the œsophageal opening. All the layers of the stomach-wall are present. The serosa (*ser.*) is scanty in the middle line, but can be recognized; the muscularis (*musc.l.*, *musc.t.*) is rather reduced; the submucosa (*sm.*) is largely encroached on by the folded mucosa and the presence of muscle bundles between these folds. The mucosa itself (*muc.*), to which the great thickness of the wall is due, is seen to have undergone an elaborate folding. At the pyloric extremity there is a gradual transition between tubules containing the parietal cells, which are present in the gland, and the epithelium immediately adjoining on the pylorus (*muc.py.*), in which the primary gland-tubules contain only central cells. At the œsophagus there is a sharp transition between those parietal-celled tubules which are present on the epithelium to the left of the former and the stratified œsophageal lining.

In any one section in such a plane (Pl. 1. fig. 1) one or more of the openings (*o*) of the gland are cut through. These are then seen to lead into a more or less complex system of cavities, into which the mucosa is prolonged. There appear, also, isolated portions of the mucosa often containing a lumen, and in which the primary gland tubules are cut in all possible planes. Accompanying each of the secondary tubules making up the gastric gland is a sheet of muscularis mucosæ (Pl. 1. fig. 3, *mm.*). As stated above, this consists of a tunic containing fibres mostly running transversely to the long axis of the tubule.

The muscularis is present over the whole surface of the gland. Passing from the pyloric to the cardiac extremity, the strongly developed layer of transversely running fibres forming the pyloric sphincter (*m.py.*) thins out with the commencement of the gland-thickening, and is almost entirely replaced by a layer of striated muscle fibres (Pl. 1. fig. 1, *musc.t.*). The course of these is both transverse and longitudinal to the long axis of the stomach; and the arrangement is such that the

longitudinal bundles (fig. 1, *musc.l.*) are external and the transverse ones (*musc.t.*) internal. But many are cut obliquely, and over the area occupied by the gastric gland (*i. e.* almost the whole of the lesser curvature) the oblique and longitudinal bundles form the greater part of the muscularis. Mixed with these striated muscle bundles there are strands of plain muscle fibres (Pl. 1. fig. 3, *mp.*), the number and masses of which diminish towards the œsophagus. Striated muscle fibres are found over the region of the pyloric glands, and indeed form the musculature of the gastric-gland thickening. Delicate strands of both plain and striated (Pl. 1. fig. 3, *m.int.*) muscle fibres penetrate into the submucosa, between the secondary tubules of the gland, although most of these are unstriated fibres, and are derived probably both from muscularis and muscularis mucosæ.

The course taken by the secondary tubules or involution of the gastric gland is, in *Phascolomys*, a comparatively simple one. Many openings on the surface of the gland lead into simple pits, but others are more complex, and a single tubule divides into a small number (2–6) of branches. But the length of these side tubules relatively to their diameter is much less than in *Phascolarctus*. The lumen is always a narrow one; and the thickness of the epithelium lining these tubules is generally greater than that on the free surface of the stomach.

Phascolarctus.

The most striking differences in the structure of the gastric gland of the Koala and that just described for the Wombat, lie in the greater compactness of the former and greater complexity in the ramifications of the tubules, and in the nature of the muscular coat. The latter is arranged in an external longitudinal (Pl. 1. fig. 2, *musc.l.*) and an internal circular layer (*musc.t.*). But the musculature over the gastric gland, which in *Phascolomys* was composed predominantly of striated fibres, is here made up entirely of nonstriated fibres (Pl. 1. fig. 4, *musc.l.*, *musc.t.*). The muscularis is less strongly developed than in *Phascolomys*, and the transverse bundles are the more numerous. At the œsophagus striated muscle fibres (Pl. 1. fig. 2, *m.œ.*) are present; and the transition from these to plain fibres is, on the pyloric side of the œsophageal opening, a sharp one. On the cardiac side, however, the longitudinal musculature of the œsophagus extends for a short distance unmixed with nonstriated fibres over the surface of

the stomach. The striated, transverse œsophageal musculature is gradually replaced by the nonstriated musculature of the stomach. On the pyloric side, the distribution of striated muscle fibres is coterminous with that of the œsophageal epithelium. On the cardiac side this double line of demarcation between œsophagus and stomach is not so clear, but exists to a large extent.

The primary gland tubules, as in the case of *Phascolomys*, are made up of central and parietal cells. But the tubules which in the Wombat are straight and unbranched, are here more complex. A single tubule (Pl. 1. fig. 6) is lined at its opening on the surface of the stomach with columnar cells (*cn.*), which in the neck are replaced by clear cubical cells. At the first bifurcation the parietal cells (*cp.*) appear. In the tubule figured a group of eight lesser tubules is brought about by a triple bifurcation. Other of the glands are simpler or more complex, but this type seems to be the more general.

Each opening (*o*) on the surface of the gastric gland leads into a relatively wide tubule which, after remaining undivided for a length equal to twice or more than twice its own diameter, branches into two or more divisions, from which other branches are given off, either laterally or terminally. These branches end blindly; in diameter they are about 0·5 mm. There are no anastomoses. In the end a very complex cluster of short tubules is produced. The course of these branch tubules is generally transverse to the long axis of the stomach, so that in sections taken through the pylorus and œsophagus they are mostly cut transversely. In sections in the same plane, passing through the more peripheral portion of the glandular thickening, where there are no openings on to the internal surface of the stomach, the whole gland-pad consists of a closely packed mass of these branched tubules bound together by muscular and connective tissue. I have counted as many as 35 of them cut transversely in a section passing through the peripheral portion of the gland.

As might have been expected from their external form and situation, the gastric glands of *Phascolomys*, *Phascolarctus*, and of *Castor* do not exhibit any essential points of difference in their minute anatomy. From Toepfer's account (11), the gland in the

Beaver, except in the arrangement of its openings on the internal surface of the stomach, is not dissimilar from the structures I have described in the Koala and Wombat. In each case the cavity of the stomach is prolonged by means of a variable number of evaginations into short tubular extensions which, branching frequently, end in series of tubules which do not anastomose but end blindly. The mucous membrane covering the general surface of the stomach is prolonged without interruption into, and forms the walls of, these systems of branching cavities. But whereas in *Phascolomys* the ramifications of the proximal portions of the evaginations are comparatively simple, the terminal portions short, the branches few, and the lumen a contracted one, in *Phascolarctus* each separate evagination forms a very complex system of tubules communicating with the stomach, which simulate the form of a true racemose gland. The terminal portions are relatively long and their lumina conspicuous. The primary gland tubules making up the gastric epithelium of the gland in both cases are cardiac glands similar to those found on the cardiac portion of the stomach and contain parietal cells. In *Phascolomys* these glands (Pl. 1. fig. 5) form a close-set series of straight unbranched tubules, in length about 0·56 mm., in which parietal cells extend from near the neck to the base of the gland, although they are rather concentrated at the middle of the tubule; while in *Phascolarctus* each gland (Pl. 1. fig. 6), which is about 0·3 mm. in length, consists of a terminal neck portion, lined with columnar or cubical cells (*cn.*), which branches several times, forming a series of long tubules opening through a common orifice at the lumen of the gastric-gland involution. As in *Phascolomys* and the Beaver, the gland contains both central (*cn.*) and parietal (*cp.*) cells.

Only the mucosa and muscularis mucosæ of the various coats of the stomach take part in the formation of the gastric gland. Submucosa and muscularis are only passively affected. In *Phascolarctus* the musculature over the thickened area is the layer consisting of outer longitudinally and inner transversely disposed fibres, which is characteristic of the other parts of the stomach. But in *Phascolomys* the musculature consists almost entirely of bundles of striated fibres; and the division of these into external longitudinal and internal transverse layers is not so evident as in the case of *Phascolarctus*, most of the bundles pursuing a more or less oblique course.

The great development of striated muscle fibres over the gastric gland seems remarkable, but since the posterior limit of the striated musculature characteristic of the upper part of the œsophagus seems to vary in different animals, this extension into the region of lesser curvature of the stomach is probably without any special significance. But it suggests a comparison with the glandular "bulbus ventriculi" of *Myoxus avellanarius*—an organ which, though not strictly homologous with, probably belongs to the same category of structures as, the gastric glands of the other mammals mentioned, and in which the musculature is a striated one. This organ was first described by Home (5), who compared it with the gastric gland of the Beaver, with which he found it to correspond "very minutely in its internal structure." It appears as a bulb-like enlargement of the lower portion of the œsophagus resting on the stomach, from which it is separated by a deep constriction. The cuticular lining of the œsophagus ceases at its anterior extremity, and is replaced by a very thick layer of glandular epithelium containing glands made up of central and parietal cells. Home describes these glands as having an arrangement similar to those in the glandular pad of the Beaver's stomach. "Each orifice," he says, "exposes three small openings, these again lead to smaller processes, as has been described and delineated in the glandular structure of the Beaver." Leydig (7), speaking of the glandular appendage on the cardiac part of the stomach of *Manatus*, where a compound tubular gland is found, refers to the "Vormagen" of *Myoxus* as something similar. Meckel regarded it as a truly avian structure. Toepfer (11), who investigated the structure of this organ, found it to be provided with a thick layer of striated muscle-bundles which are a direct continuation of those found in the upper part of the œsophagus; and, in a discussion as to its morphological nature, he regards the presence of the epithelium rich in glands as affording a more reliable test of the morphological nature of the organ than the presence of an œsophageal musculature. If the bulbus is gastric and not œsophageal in origin, then the whole stomach of *Myoxus*—*i. e.* the true stomach and bulbus ventriculi—is homologous with the simple stomach of *Castor* provided with a concentration of cardiac glands on the region of its smaller curvature, since in *Myoxus* such a concentration occurs round the entrance of the œsophagus.

In the Beaver, as in *Phascolomys* and *Phascolarctus*, there is the

important difference in the disposition of the gland regions of the stomach as compared with *Myoxus*, that the cardiac glands of the latter, that is the glands composed of parietal and central cells, are restricted to the bulbus ventriculi, and the rest of the stomach contains only pyloric glands; while in the three first mentioned forms the whole stomach is glandular, and cardiac glands, although predominantly crowded together in the gastric-gland thickening, are not wholly restricted to it as they are to the bulbus of *Myoxus*, but are found to a certain extent over the region of the fundus. The area on the stomach of the Beaver occupied by cardiac glands is therefore to be regarded (on Toepfer's view) as homologous with the "Vormagen" of *Myoxus*. The extent to which these glands extend over the lateral walls and region of greater curvature of the stomach has not been investigated, nor have the precise limits of the pyloric glands been determined, either for *Castor* or for the Marsupials referred to.

In *Manis*, although the gastric gland on the greater curvature of the stomach cannot be regarded as homologous with those in other mammals, it is more comparable to the bulbus ventriculi of *Myoxus* than to any of the others, for here there is a definite restriction of the cardiac glands to a portion of the stomach-wall, where they are arranged as a complex glandular organ, the rest of the stomach being non-glandular, with the exception of certain patches which contain glands probably homologous with the pyloric glands of the other mammalia. Here, too, it seems that a direct correlation with the nature of the food and the other parts of the alimentary canal and disposition of the mucous membrane of the stomach exists; a proposition that can hardly be made with regard to the gastric glands of either the Marsupialia or the Rodentia. There are simple stomachs unprovided with any complex glandular apparatus in the Phalangers, as in the *Myoxidæ* other than *M. avellanarius*.

The formation of the "gastric gland" as we find it in the Marsupials seems to be explicable in one of two ways. First, as the result of a tendency to localization of the gland regions,—a tendency which finds its expression alike in the structures I have described, in the glandular cardiac appendage of *Manatus*, and more completely in the "gastric gland" of *Manis* and the bulbus ventriculi of *Myoxus*. But we may also with Oppel (8. pp. 402–3) in the case of the Beaver and the Marsupials, regard it as due to the necessity for increase in the area of the gastric

epithelium containing cardiac glands ("progressive development"), and in *Manis* as due to the restriction of that area ("retrogressive development"). In the first case it is related to the necessity of digestion of an exceeding large amount of food-material; and in the second to the digestion of a small quantity of easily assimilated food.

The terms "gastric gland" of English authors and "grosse Magendrüse" employed by the Germans, are alike misnomers. The organ, as both Oppel and Toepfer have pointed out, is not a gland in the sense in which that term is legitimately employed, but a complex evagination of the gastric wall, bearing, in common with the rest of the stomach, true glands; and as such it does not seem as if its value can be very great as affording any trustworthy indication of the phylogenetic history of the animal in which it occurs. In the case of two forms like *Phascolarctus* and *Phascolomys*, known, from other considerations, to be nearly related to each other, the common presence of a "gastric gland" may indeed afford reason for their closer approximation; and in these animals the organ does seem to be homologous, although in the Koala its structure is more specialized than in the case of the Wombat. But statements as to an organ in the Rodentia resembling the "gastric gland" of Marsupialia, and conclusions as to a closer degree of genetic relationship of these two groups, deducible therefrom, in view of the great specialization of the stomach occurring in some Rodents, must, I think, be received with hesitation.

I am indebted to Prof. G. B. Howes for supplying me with the material reported on, and for kindly furnishing me with many of the works cited. Part of this investigation was done while I was still a student under him in the Research Laboratory of the Royal College of Science, London.

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EXPLANATION OF PLATE 1.

Fig. 1. Vertical section through the gastric gland of *Phascolomys* parallel to the long axis of the stomach, but passing to one side of the œsophageal and pyloric apertures. × 6 diameters.

Neither in this nor in figs. 2, 3, & 4 has any attempt been made to represent the histological details of the mucous epithelium. But broken lines and circles are employed to indicate the direction in which the primary gland-tubules are cut.

Fig. 2. Vertical section through the gastric gland of *Phascolarctus* parallel to long axis of the stomach but passing to one side of the œsophagus. × 8 diameters.

Fig. 3. Portions of three contiguous tubules of the gastric gland in *Phascolomys* from its pyloric extremity. Vertical section, parallel to longitudinal axis of stomach. × 20 diameters.

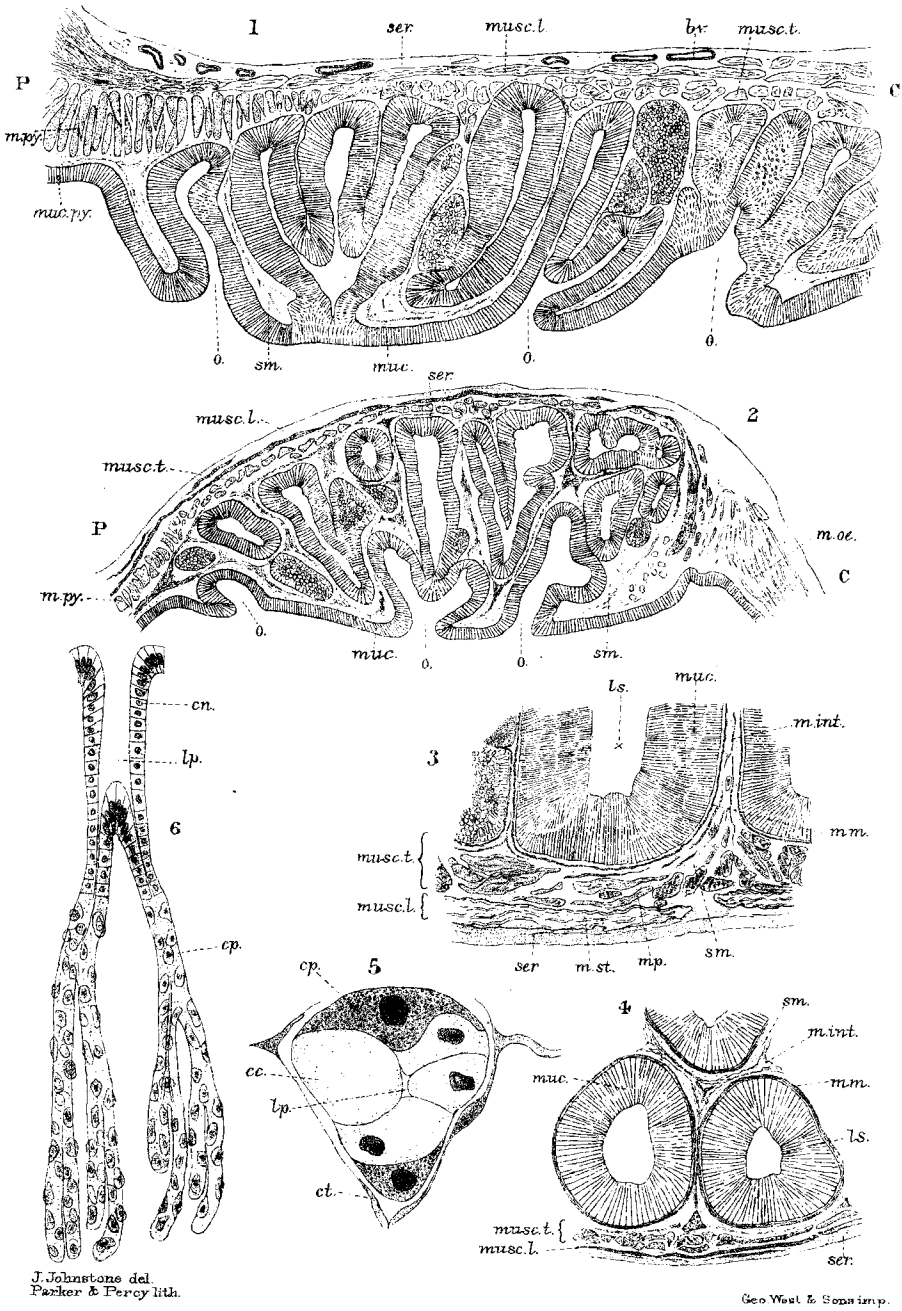
Fig. 4. Three contiguous tubules of the gastric gland of *Phascolarctus*. Vertical section, parallel to longitudinal axis of stomach. × 30 diameters.

Fig. 5. Transverse section of a primary gland-tubule from the gastric gland of *Phascolomys*. × 694 diameters.

Fig. 6. A primary tubule from the gastric gland of *Phascolarctus*, seen in optical section. × 266 diameters.

Reference Letters.

bv. Blood-vessels.
cn. Neck-cell in primary gland tubule.
cp. Parietal cell.
cc. Central cell.
ct. Connective tissue between primary gland tubules.
lp. Lumen of primary gland tubule.
ls. Lumen of gastric-gland tubule.
musc.l. Longitudinal layer of muscularis.
musc.t. Transverse layer of muscularis.
m.int. Nonstriated muscle fibre between gastric-gland tubules.
mp. Nonstriated muscle fibres.
mst. Striated muscle fibres.
mm. Muscularis mucosæ.
m.œ. Œsophageal musculature.
m.py. Pyloric sphincter.
muc. Mucosa.
muc.p. Pyloric mucosa.
o. Opening of the gastric-gland evaginations into the stomach.
ser. Serosa.
sm. Submucosa.
C. Cardiac extremity of gastric gland.
P. Pyloric extremity of gastric gland.



J. Johnstone del.
Parker & Percy lith.

Geo West & Sons imp.

GASTRIC GLANDS OF MARSUPIALIA.