











THE

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### TRANSACTIONS

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OF

### THE LINNEAN SOCIETY.

I. A Contribution towards our Knowledge of the Morphology of the Owls. Part II.—OSTEOLOGY. By W. P. PYCRAFT, A.L.S., F.Z.S.

### (Plates 1 & 2.)

Read 19th June, 1902.

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### I. INTRODUCTORY.

THE present paper is the result of a careful study of the skeletons of the STRIGES in the Collection of the British Museum (Natural History). Although probably one of the largest collections extant, unfortunately there are many gaps yet to be filled, and consequently I have been unable to make my work as complete as could be wished. A large number of genera are still wanting, among the most important of which are :---

Scotopelia.	Gisella.
Sceloglaux.	Micropallas.
Scotiapex.	Heliodilus.

Besides, nestling skeletons of all ages are greatly needed. Many gaps in this direction could be filled, I am sure, by members of this Society, who, residing in the country, must have many opportunities of procuring nestlings of the Long- and Short-eared Owls, Tawny and Barn-Owls. Knowing the persecution which besets these most useful and

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#### MR. W. P. PYCRAFT ON THE

harmless birds at the hands of ignorant and thoughtless people, it is with the greatest reluctance that I make this request; yet in the interest of Science, I feel justified in doing so. Those who may feel as much reluctance in helping to furnish these desiderata as I feel in making the request therefor, will, I hope, find consolation in the reflection that my demands entail upon the species mentioned a tax which must be quite imperceptible. Say thirty young, all told, drawn from an area probably of hundreds of miles, and spread over a period of several years perhaps, can certainly not seriously injure the species called upon to furnish these victims! Of course, it would be well, if possible, to procure nestlings of various ages of at least one species in every genus, or at any rate of all the more important genera. The skulls of the nestling *Nyctala* and *Photodilus*, for example, would be extremely valuable.

For the only skeleton of *Photodilus* which the Museum yet possesses we are indebted to Dr. Charles Hose, resident magistrate of Borneo. It has only recently come to hand, so recently that at the moment of writing this, the skull only has been prepared; the rest of the body awaits dissection before the skeleton of the trunk can be set up.

The nestling skeletons of *Syrnium* we owe to Mr. W. Storrs Fox, who spared himself no pains to procure the young at the ages I requested. The nestling skeletons of *Scops* and *Speotyto* have been prepared from downy young sent me by my late and ever lamented friend, Daniel Meinertzhagen, who looked forward with keen delight to the prospect of making drawings of the skeletons thereof for me when this should be written. I regret, as we all must, that he was not spared to fulfil his hopes, for his loss to the ranks of Ornithology is very great.

### II. THE SKULL OF THE ADULT.

The skull of the Striges is desmognathous and holorhinal, and bears a strong superficial resemblance to that of the Falconiformes, as well as a general likeness to the skulls of the Caprimulgi.

It may be distinguished, however, from both Falconiform and Caprimulgine skulls by the extreme shortness of the parasphenoidal rostrum, the thick spongy lachrymal, which lacks a supraorbital process, the large and functional basipterygoid processes (not universal in the Falconiformes or Caprimulgi), and by the fact that the palatines are separated one from another posteriorly by the vomer. Other distinctive characters will be enumerated as they arise in the course of the following remarks.

The Occipital Region.—The occipital condyle is sessile, and the plane of the occipital foramen looks directly downwards, forming only a very oblique angle with the basicranial axis. The supra-foraminal border is extremely thin, and passes on either side into a swollen ridge doing duty for the base of a paroccipital process. A barely perceptible cerebellar prominence forms a broad occipital crest passing upwards into the *lambdoidal ridge* which, in the *Buboninæ*, may almost be said to terminate at the apex of the temporal fossa. In some species of *Bubo* (e. g. *B. magellanica*) the crest is folded back upon itself into a narrow loop, the lower limb of which may be traced outwards and

downwards along the free border of the tympanic wing of the exoccipital. The lambdoidal ridge can best be traced in the Asionidæ and Strigidæ, wherein temporal fossæ are wanting.

The *paroccipital processes*, so conspicuous a feature in *Rhea*, for example, and slightly developed in the Falconiformes, are practically wanting in the Striges, the exoccipital tympanic wings from which these processes are developed being very thin, and curving forwards to complete the *recessus tympanicus anterior*.

The Roof of the Cranium.-In the Asionidæ (including Photodilus) the interorbital region stands out in strong contrast to the portion forming the cerebral roof, by reason of the narrowness of the former and the great width of the latter, which often nearly equals the whole length of the skull. The free edge of this interorbital region is generally much thickened over the anterior region of the orbit, and furthermore this thickened area is produced caudad into a pair of supraorbital spinous processes, recalling the supraorbital process of the lachrymal. That portion of the interorbital region lying between the thickened lateral borders just referred to, is also much thickened by pneumatic tissue, developed, apparently, by the inflation of anterior ends of the frontal and the immediately overlapping portion of the nasals. The result, in the adult skull, is peculiar, in that the base of the culmen of the beak-formed by the nasals and premaxillary-looks as though it had been wedged into a spongy mound of bone. In this way an imperfect nasal hinge has been formed. The cerebral portion of the roof, as we have already remarked, is of great width, expanding behind the orbits into a broad tongue-shaped postorbital process, which may extend downwards to within a short distance of the quadrato-jugal bar. The outline of the cerebral region, traced from the supra-foraminal border upwards and forwards into the interorbital region, may be fairly described as ⊃-shaped, so that the crown of the head is nearly flat. Very shallow tongue-shaped temporal depressions are always traceable in the Buboning, but are widely separated one from another in the median line.

The roof of the skull in the Strigidæ differs conspicuously from that of the Asionidæ by reason, partly, of the excessive development of spongy, pneumatic tissue; and partly, because the width across the skull at the postorbital processes is much less. The width across the interorbital region is relatively somewhat greater than in the Asionidæ; the relations between the beak and the skull also resemble those of the Asionidæ, the former having the appearance of being wedged into the latter when in a plastic state, but the resulting nasal hinge is still more imperfect. The cerebral portion of the dome rises up into a blunt cone culminating at the interorbital region, and marked along the middle line by a deep furrow which extends forwards to the base of the beak, and laterally by a shallow depression above the orbits. This depression is crescentic in shape, and extends from the base of the postorbital process upwards and forwards, terminating above the middle of the orbit. A row of pits along the arc of this depression marks the position of the larger disc-feathers. Partly on account of the relatively smaller brain-case, which causes the occipital foramen to appear to lie further backwards, and partly because of the great development of spongy tissue, the outline of the cerebral portion of the skull differs markedly from that of the Asionidæ. The post-

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orbital processes stand out conspicuously from the skull, and extend downwards so as nearly to touch the quadrato-jugal bar.

Seen in section, the cranial roof presents some interesting features. As already stated, this region of the skull is considerably thickened by the development of spongy tissue which attains its maximum over the interorbital region. In *Asio* and *Bubo*, for example, the *tabula externa* and *tabula vitrea* are of extreme thinness, and separated by a mass of diploë to which has been added, in the interorbital region, a mass of pneumatic tissue. Between the layer of diploë, and, anteriorly, between the diploë and the pneumatic tissue, there runs, from the parietal region forwards, a distinct pneumatic canal, which, however, is lost in the region above the olfactory fossa. The great development of the pneumatic tissue has caused the anterior end of the frontal to fold over upon itself so as to overlap the base of the nasals and the proximal end of the nasal process of the premaxilla. The pneumatic tissue, it is to be noticed, does not extend downwards between the interorbital septum, save only along its anterior border where it runs downwards and backwards to terminate at the great air-sinus, the anterior tympanic recess.

Syrnium differs conspicuously from *Bubo* in that the diploë and pneumatic tissue alike present a regular cellular arrangement of superimposed layers—a series of separate plates of bone supported by delicate bony pillars. This laminate arrangement, however, terminates near the anterior end of the frontal, giving place to the normal irregular spongy tissue.

Strix agrees with Asio and Bubo in that the diploë and pneumatic tissue are of the ordinary spongy type, having no regular arrangement; but the skull differs both from Asio and Syrnium in that the spongy mass descends downwards from the frontal to inflate the whole of the interorbital septum. To such an extent has this development proceeded, that the groove into which the olfactory nerve passes in its passage from the skull along the roof of the orbit to the olfactory cavity has now become entirely surrounded by the pneumatic tissue, the tabula externa having been driven outwards, leaving the groove, now converted into a tube, completely invested. In Eurystopus, one of the Caprimulgi, we have a stage halfway between the normal arrangement and that in Strix, the nerve running in a deep trough of pneumatic tissue the edges of which nearly meet to form a tube as in Strix.

The Base of the Skull.—The basitemporal platform is roughly triangular in form, having a very broad base, and its apex lying in the middle line between the basipterygoid processes. Above the apex lie the Eustachian apertures. The anterior lateral borders of the plate, save at the apex, have fused partly with the base of the parasphenoidal rostrum and partly, on either side of the rostrum, with the wall of the recessus tympanicus anterior, so that the Eustachian grooves are converted into canals, which open into the floor of the mouth of the recess. The paroccipital notch, which is deep in many Falconiformes, in the Striges is wanting, having been obliterated by the great development of the meatus externus and the recessus tympanicus anterior. It is to this same great development of the tympanic cavity that the loss of distinct paroccipital processes is due, since the bony tissue used in their formation appears to have been utilized to complete the mouth of the *meatus* by joining with the tympanic recess and closing the notch in question.

The position of the obliterated paroccipital notch is indicated by a foramen, for the passage of a branch of the sinus venosus, which can be traced upwards and forwards to its mouth on the inner side of the articulation for the quadrate. Midway between this foramen and the occipital condyle lies the vagus foramen, and mesiad of the vagus lie the condyloid foramina.

The basipterygoid processes are represented by two very short stout pillars rising from the base of the parasphenoidal rostrum, which is of considerable breadth. In the Strigidæ these processes are much reduced in length, so as to be little more than prominences.

The pre-condylar fossa is well marked.

The parasphenoidal rostrum of the Striges presents some interesting modifications. Apart from its great breadth at the base, which appears to be characteristic of the Owls, the parasphenoid, in the majority of the Asionidæ, has undergone a very considerable shortening, terminating at the level of the palato-pterygoid articulation, instead of running forward to terminate just above the hinder end of the maxillo-palatine processes, as in the Falconiformes, for example. This abbreviation of the rostrum is also noticeable in the Caprimulgi.

Among the Owls, however, *Surnia* has a relatively long rostrum, since it terminates midway between the pterygo-palatine articulation and the hinder border of the maxillopalatine processes. The Strigidæ appear also to have an abbreviated rostrum, but until I have an opportunity of examining nestlings I cannot settle this point, owing to the extraordinary inflation of the tissues of this part of the skull.

The Lateral Surface of the Cranium.—The tympanic cavity is unusually large in the Striges, and presents some interesting modifications. Studied in its least specialized condition, the increased size of this cavity is found to be due to the great development of the tympanic wing of the exoccipital and the external border of the squamosal, the outgrowths from these two bones forming a conspicuous outstanding wing of varying shape, according to the genera examined. The squamosal portion of the wing it is to be noted is borne by the region corresponding to the squamosal prominence of the Falconiform skull, a prominence generally more conspicuous among the Owls, in the nestling skull; its presence in the adult skull is marked by the great thickening of the skull-walls by the development of pneumatic tissue, a thickening which causes the quadrate in the adult Striges to appear to be set much nearer the middle line than in the nestling.

Not only is the tympanic cavity proper actually increased in size by the development of the lateral wings above described, but a more or less perfect chamber is added thereto by the outward extension of that portion of the wing which arises from the region of the squamosal prominence. This additional chamber is especially well developed in a few genera to be described presently.

It may be studied in its simplest form perhaps in *Syrnium aluco* or *Surnia funerea*. Here it forms a vestibule, opening forwards into a deep trough formed by the large postorbital process, a trough which is, however, non-existent in the living bird, inasmuch as it is filled up by the temporal muscles. During life, then, the tympanic cavity forms a spacious chamber, which, traced inwards, leads to other and smaller chambers. The latter, three in number, are approached through a common and well-defined elliptical mouth, whose long axis slopes obliquely backwards. The hinder border of this mouth is formed by the free edge of the tympanic wing of the exoccipital, and the free edge of the inferior border of the squamosal, but this can only be made out in the nestling: the anterior border is formed by the *processus articularis squamosi*. This last, arising immediately behind the squamosal head of the quadrate, is continued, not infrequently, downwards and backwards to meet the inferior external angle of the exoccipital wing. In the Falconiformes this process is represented by a downwardly projecting spine, serving, as in the Owls, to hold the quadrate in position.

Within this mouth we distinguish two apertures, one above the other, and divided by a bony bar formed by the otic head of the quadrate. The upper aperture is the mouth of the *recessus tympanicus superior*, a large pneumatic cavity hollowed out between the pro-otic and the squamosal and further extended by the absorption of the spongy tissue of the parietal, leaving only the inner wall of the bone to protect the brain. The position of the aperture of this recess is interesting, inasmuch as it varies considerably in different groups. Thus in the Steganopodes, for example, it opens in front of the articular surface for the quadrate, whilst in the Falconiformes, e. g. *Circaëtus*, its aperture divides the articular surface into two portions, the quadrate thus serving as a bar across the aperture. Furthermore, the position of the aperture in the Steganopodes is, as in *Circaëtus*, occupied by a deep fossa. In the Striges, as in the Falconiformes, the mouth of the recess divides the articular surface for the quadrate for the quadrate into two portions, but having apparently shifted further backwards, the aperture lies almost wholly behind the quadrate. The Caprimulgi agree with the Owls in this respect.

The lower of the two apertures now under discussion is often smaller than the upper, and lying well within its mouth will be found a vertical bony column dividing two tunnel-like openings, one in front of the other. The anterior opening leads to the *recessus tympanicus anterior*, which is very spacious, running forwards and inwards to meet its fellow of the opposite side in the middle line. In the formation of the anterior end of this space the whole of the spongy tissue of the basisphenoid and parasphenoidal rostrum has been absorbed, so that the pituitary pit, and the tunnels for the internal carotids which open into it, are completely isolated, the pit appearing as a delicate thin-walled cup, supplied from below by two converging tubes. The hinder of the two openings of this lower tympanic aperture lodges the foramen ovale and the foramen rotundum.

The great size of the aperture of the *recessus tympanicus superior*, as well as the surprising size of the cavity itself, can be fully realized if the quadrate be removed. The aperture is then seen to lie between the squamosal and otic articular surfaces for the quadrate, which are on this account widely separated one from another.

The tympanic cavity in the typical, less specialized skulls of the Asionidæ is overshadowed by a conspicuous squamosal prominence, e. g. *Bubo*, from which arises, be it noted, the squamosal wing of the tympanic cavity just described. Above this prominence lies a broad, shallow, linguiform temporal fossa, which, in some forms, to be presently described, may be absent.

Regarding the tympanic cavity of Syrnium as representing, at least approximately, the archecentric (cf. P. C. Mitchell, Trans. Linn. Soc., ser. 2, Zool. viii. (1901) p. 181) condition, let us turn now to a consideration of the more important apocentricities which may be traced therefrom. These are of two kinds: (a) symmetrical, and (b) asymmetrical. Amongst the symmetrical forms the departure from the archecentric type begins by the formation of large bullæ derived by an increase in the size of the squamosal wing which forms the posterior tympanic wall, and which may, as in Scops asio, S. rutilus, and S. semitorques, fuse by its superior external angle immediately behind the base of the postorbital process, thus bridging the temporal fossa. By this inflation of the tympanic wing a very spacious cavern is formed, bounded posteriorly and superiorly by the squamosal and exoccipital wings, anteriorly by the postorbital process. It is divided into two more or less well-marked chambers, an outer and an inner, one leading directly into the other, the division being bounded by the quadrate. In Gymnasio and Spectyto, by the way, the squamosal wing joins the postorbital process directly, and thus not only bridges the temporal fossa but also roofs in the tympanic cavity. The size of this wing not being increased, however, the resulting outer chamber is very small.

The form of the tympanic cavity in Asio is still further modified. It appears to be a further specialization of the type seen in *Photodilus* and *Strix* (see p. 9). The squamosal and exoccipital moieties of the tympanic wing are here combined to form an outstanding wing of bone extending upwards and forwards to terminate above the base of the postorbital process, from which it is divided, however, by a low, saddle-shaped ridge. The exoccipital moiety of the wing curves downwards and forwards so as to form a spacious antechamber leading directly to the apertures of the recessus tympanicus superior and the meatus externus. The tympanic cavity in front is bounded by the postorbital process, of which more anon. Above, the cavity is bounded only by a low ridge connecting the angles of the postorbital and squamosal wings of the tympanic cavity just described. The deep cavity enclosed by these wings corresponds to the "posterior division of the cavernum" of the first section of this memoir. For brevity's sake it may be called the post-cavernum. The post-cavernum of Asio differs from that of Spectyto, for example, mainly in its greater upward extent, in its relatively greater width, and in that it is less perfectly closed above. But whilst the tympanic wing of Speotyto forms a conspicuous laterally expanded bulla, the wing in Asio forms rather a vertical flattened plate, the inferior portion of which, however, is bullate. This change in the form of the tympanic wing has resulted in an interesting modification-to wit, the suppression of the temporal fossæ-and fresh attachments for the first portion of the temporalis muscle. The temporal fossa is in consequence obliterated in Asio.

In Spectyto, Scops asio, Scops rutilus, and Scops semitorques, it must be remembered, the tympanic wing has also extended upwards; but in these cases the temporal fossa is not suppressed, the wing being perforated to allow of the passage of the muscle.

We must turn now to a consideration of the asymmetrical tympanic cavity as exhibited in the skull of *Nyctala Tengmalmi*. This appears to be a modification of the type seen in *Speotyto*, the squamoso-occipital tympanic wings forming large bullæ.

On the left side of the skull (Pl. 2. fig. 1 a) the tympanic wing has grown upwards and forwards to join the postorbital process, bridging the temporal fossa as in Spectyto. But with this difference, the fossa is reduced to a mere vestige in the shape of a narrow groove deep enough perhaps to lay a horse-hair in; this groove passes between the junction of the tympanic wing and the postorbital process through a minute hole into the tympanic cavity. I have not been able to dissect out the muscles of the head, but when this is done it will probably be found that not more than a vestige of the first portion of the temporal muscle remains; possibly even this has disappeared. The cavity enclosed by the squamoso-parietal wing and the postorbital process corresponds to the postcavernum of Asio. It is considerably larger than the corresponding cavity in Spectyto, and curves downwards and forwards, so as to form at the same time a shield for, and a spacious antechamber leading to, the apertures of the recessus tympanicus superior and the meatus externus. In the nature and function of the exoccipital moiety of the tympanic wing, Nyctala, it should be remarked, agrees also with Asio and Speotyto, for example. But the tympanic wing of the left side in Nyctala differs from that of any other of the forms with which it has been compared in the development of a large tongue-shaped plate of bone which projects from the middle of the tympanic wing, forwards and downwards, to terminate just below and outside the articulation of the quadrato-jugal bar with the quadrate.

The tympanic cavity of the right side of the skull in *Nyctala* differs conspicuously from the left, in that the squamosal portion of the tympanic wing extends upwards to within a short distance of the crown of the head, and lies far behind the base of the postorbital process. Near the middle, the free border of this wing, as on the left side, is drawn out into a tongue-shaped process, which curves inwards at its tip to join the inferior end of the postorbital process. Thus, on this side the articulation of the quadrato-jugal with the quadrate is fully exposed.

If the *post-cavernum* of the right and left sides be compared, it will be found that that of the right side has a very large oval aperture, the inferior border of the rim of which lies considerably above the level of the orbital process of the quadrate. The cavity itself may be likened to a deep pocket, which runs directly backward. The aperture of the left side is incomplete, a large gap being present in its lower border, owing to the failure of the tongue-shaped process of the tympanic wing to reach the postorbital process. Furthermore, the aperture is narrower, crescentic in shape, and terminates superiorly at the level of a line passing forwards from the upper limb of the crescent to the base of the beak. Thus its upward extent is very considerably less than on the right side. A comparison of the figures (Pl. 2. fig. 1, 1 a) will make this plain.

The mesial wall of the *post-cavernum* of the right side, it may be mentioned, is marked by a shallow groove which, traced upwards, is found to lead to a minute aperture, corresponding to the point of union of the tympanic wing with the base of the postorbital process of the left side. But here, the tympanic wing having shifted backwards, the aperture in question lies considerably behind this process. From the aperture there runs, backwards and downwards, a vestigial temporal fossa, also corresponding to that of the left side.

The tympanic cavity of *Photodilus* and the Strigidæ is of the same type as that found in Asio. Indeed this cavity in the latter appears to be a further modification of that seen in the two subfamilies above mentioned.

That of Strix is the least specialized of all; that portion of the cavity which lies above the head of the quadrate, and between the squamosal wing and postorbital process, is of comparatively slight extent, consisting merely of a small depression. In Asio, it will be remembered, it forms a large, oblong, and concave fossa. Photodilus is intermediate in some respects between the two. In the skull of this form the fossa is nearly as long as in Asio, but very narrow from side to side. In the great size of the postorbital process Photodilus differs both from Asio and Strix. In the development of the squamosal wing it is also peculiar. This is larger than in Strix, smaller than in Asio. Asio, Strix, and Photodilus all agree in the absence of the horizontal temporal fossa so conspicuous, for example, in Bubo.

The orbits in the Asionidæ are large, and their capacity is still further increased by the lateral expansion of the postorbital processes. They are overarched by the frontals, and bounded in front by the lachrymals, whilst the antorbital processes (prefrontals) and the orbital process of the quadrates form an imperfect floor. Feeble supra-orbital processes are commonly, but not invariably, present. These, it is to be noted, are furnished by the frontals themselves, and not, as in the Falconiformes, by the lachrymals. The interorbital septum forming the partition wall between the two orbits is imperforate, save in Surnia, Spectyto, and some species of Scops. The orbitosphenoid is completely ossified.

The optic foramina are widely separated one from the other, and lie on a level with a line drawn forward from the bottom of the rim of the recessus tympanicus superior.

The trigeminal foramina open above the roof of the recessus tympanicus anterior on a level with a line drawn downwards and forwards from the anterior zygomatic process to the basipterygoids.

Immediately external and posterior to the optic foramen lie the foramina of the third, fourth, and sixth nerves.

The orbit in the Strigidæ differs conspicuously from that of the Asionidæ and Photodilidæ in that it is extremely small. Its horizontal axis scarcely, or not at all, exceeds that of the horizontal axis of the lachrymal, though it must be remarked this last-named bone is relatively very much larger than that of the two suborders with which it is contrasted. Even, however, where the lachrymal of the two suborders is relatively as large as that of the Strigidæ, the greater size of the orbit with regard to the lachrymal would still remain the same.

The Strigidæ are furthermore peculiar in having the interorbital septum, which is very short antero-posteriorly, enormously inflated by the development of spongy tissue.

The Ethmoidal Region .- The mesethmoid, which by its posterior extension forms the interorbital septum, agrees more nearly with the mesethmoid of the Caprimulgi than  $\mathbf{2}$ 

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with that of the Falconiformes, being relatively very short antero-posteriorly, and in some genera enormously thickened by the development of spongy tissue. It is relatively largest in Surnia and Spectyto: a fact which can best be realized by comparing the mesethmoid of either of these genera with that of, say, Bubo, Asio, or Syrnium. In the last-named genera the anterior free border is sharply truncated, sloping obliquely backwards to pass into a remarkably abbreviated parasphenoidal rostrum (p. 5) immediately above the pterygoidal articulation. In Surnia the parasphenoid extends considerably further forwards, passing insensibly into the anterior border of the mesethmoid at a point corresponding with the level of a line passing behind the lachrymals. The horizontal plate of the supero-anterior angle of the mesethmoid is not much developed, in consequence of the slight development of the olfactory cavity. The antorbital plate (prefrontal) in Surnia and Spectyto is short and strap-shaped and projects from the inferior angle of the mesethmoid. In Bubo it appears to arise rather below the middle of the anterior border, an appearance which is due to the fact that the anterior border of the mesethmoid by its greater obliquity projects further downwards. In Asio the antorbital plates are very long, nearly touching the lachrymals and quadrato-jugal bar.

The Strigidæ differ conspicuously from the Asionidæ in the form of the mesethmoid. One of its most conspicuous features in the adult skull is its enormous thickness, due to the great development of spongy, pneumatic tissue. The interorbital region, in addition to its great thickness, is relatively shorter than in the Asionidæ, whilst the olfactory region is relatively longer, and is furthermore peculiar in that its inferior border lies almost horizontally rather than obliquely. The antorbital plate is also much swollen, so much so as to become club-shaped. The interorbital septa, however, of *Asio* and *Photodilus* are exceptional, being swollen by pneumatic tissue as in *Strix*, though to a slighter extent.

The olfactory cavity is fairly spacious, but contains no turbinal ossifications. Bounded posteriorly by the ali-ethmoidal antorbital plates, it passes forwards into the anterior narial aperture, which is divided from its fellow of the opposite side by an imperforate nasal septum. A certain amount of ossification has taken place in the ali-ethmoidal walls of the anterior region of the olfactory chamber, the nature and extent of which appear to be best displayed in *Surnia*, where the cartilaginous portions of the wall, removed by maceration, have left a free edge of bone lying immediately within the anterior narial aperture. Traced inwards, this ossification is found to have formed a cup-shaped cavity forming the floor of this region of the chamber, and rising upwards, passes into the nasal septum. Posteriorly the wall of the cup is broken down, thus placing the anterior and posterior moieties of the chamber in communication with one another. The external alinasal wall is somewhat more extensively ossified in *Asio* and *Bubo*, thus rendering the contour of the nasal aperture formed by the premaxillary limb of the nasal somewhat irregular.

The floor of the anterior nasal cavity undergoes certain limited changes. Thus in *Ninox* it is arched instead of hollow, lying above the level of the rim of the narial aperture: in *Bubo* it is flat; in *Strix* it is perforated. The *septum nasi* is separated from the mesethmoid by the *cranio-facial fissure*, which is deep. Furthermore, in some Owls, as in Bubo, it is perforated near its superior border, so as to place the hinder division of the olfactory cavity in communication with its fellow, at least in the dried skull. In *Strix* the perforation, by its extension backwards, is converted into a deep notch. It is interesting to note that owing to the ect-ethmoidal ossifications above described, the nasal septum is not visible from the ventral aspect of the palate, as in the schizognathous palates of certain Falconiformes. That is to say, in the middle of the anterior palatal vacuity of the schizognathous Falconiform palate the nasal septum is plainly visible, the roof of the cavity being formed by the premaxilla; whilst in the Strigine palate the roof of this cavity is formed almost entirely by the ossified ali-ethmoids, only the extreme anterior end of this vaulted chamber being formed by the premaxilla.

The *lachrymal* differs conspicuously from that of the Falconiformes, and agrees closely with that of the Caprimulgi. As in the last-mentioned group, there is no supraorbital process, and the descending limb, which extends downwards to the quadrato-jugal bar, is greatly inflated by spongy tissue, and is attached to the under surface of the fronto-nasal region of the skull, instead of the external border thereof as in the Falconiformes. It varies somewhat in form in the different genera, but typically, in the Asionidæ, it may be described as columnar, and marked by a deep groove on its external face, near its upper third, the groove passing forward into the lachrymo-nasal fossa. The latter, by the way, is extremely small, having been practically obliterated by the great development of the maxillo-palatine processes, which rise upwards to cover almost the entire anterior border of the lachrymal. In *Bubo* it is almost crescentic, the horns of the crescent being directed outwards. In some species of *Scops* it is very small, tapering from above downwards. In *Syrnium, Surnia*, and *Asio* it is perhaps most nearly columnar, and in the two latter the lachrymo-nasal groove is especially deep.

The lachrymal is largest in *Strix*, where it is subconical in form, with the apex pointing forwards into the lachrymo-nasal fossa, and the base hollowed to accommodate the eye. It is grooved across the middle of its outer surface, deeply in some, slightly in others, according to the species. Again, in some species, the lachrymal extends so far forwards as to leave only a small hole representing the lachrymo-nasal fossa, whilst in others, *e.g. S. poensis*, a comparatively large fossa is left, which is open below down to the quadrato-jugal bar. These differences in the form of the lachrymal, it should be noted, are correlated with others in other parts of the skull.

The Cranial Cavity.—The metencephalic fossa in the Asionidæ very closely resembles that of the Falconiformes, being both moderately wide and fairly deep. The *ragus* foramen lies very near the exoccipital border. The *internal auditory meatus* is deep, and separated from the vagus foramen by a swollen ridge. About midway along the anterior lateral border of the fossa, mesiad of the mouth of the trigeminal foramen, lies the small abducent foramen. The oculo-motor lies behind and below the optic foramen on a level with the external angle of the sella turcica.

In the Strigidæ the vagus foramen is reniform, and the internal auditory meatus is in a very shallow pit into which the foramina for the facial and auditory nerves open. The foramen for the oculo-motor is minute, and lies on the extreme external angle of the sella turcica between the optic and trigeminal foramina : passing through the wall.

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it emerges immediately beneath the foramen for the first branch of the trigeminal. The foramina for the 1st and 2nd-3rd branches of the trigeminal in the Strigidæ, by the way, pass out from a horizontal slit-like foramen on the superior lateral border of the fossa. The *abducent foramen*, like the oculo-motor, is minute, and lies mesiad and below the inner angle of the fossa for the trigeminal branches 1 and 2-3. It opens into a fossa, immediately behind the optic foramen, which contains besides the apertures of the first portion of the trigeminal and the oculo-motor. Thus, as in the Asionidæ, all three open into a common pit.

The *cerebellar fossa* presents no characters of any importance. It appears to be slightly larger, relatively, in the Strigidæ. The floccular fossa is well-marked.

The mesencephalic fossa appears to be relatively largest in Syrnium, and smallest in Strix. In Syrnium and Bubo the boundaries of the fossa are extremely welldefined.

The *pituitary fossa* is relatively much wider in transverse diameter than in the Falconiformes, and differs furthermore therefrom in that its anterior wall rises upwards into a steep wall to pass into a wide but ill-developed optic platform (*prepituitary ridge*). The preoptic ridge is rounded, swollen and prominent in the Asionidæ, ledge-shaped in the Strigidæ, and less prominent. At its outer angle this ridge plunges sharply downwards to join the tentorial ridge.

The *optic foramina* are widely separated one from another, owing to the enormous size of the anterior tympanic recess, the anterior end of this great pneumatic chamber lying immediately under these foramina.

The cerebral fossæ have encroached upon the cerebellar fossa, appreciably reducing the size of its upper portion. The tentorial ridge, where it leaves the preoptic platform, plunges sharply downwards to the level of or below the sella turcica, when it sweeps downwards and upwards over the pro-otic, meeting its fellow of the opposite side immediately over the cerebellar fossa. From the point of this union there runs forwards in the middle line a prominent swollen ridge, the bony falx, which is continued forward to form the roof of the olfactory fossa. In the Strigidæ the middle region of this ridge is produced into a sharp edge. A more or less prominent ridge corresponding to the Sylvian fissure in the cerebrum is present in all the Striges.

The olfactory fossæ appear to be largest in Bubo, and are never very large.

### The Premaxilla.

The *premaxilla* of the Striges is almost indistinguishable from that of the Falconiformes. It appears, indeed, to differ therefrom only in the greater share which it takes in the formation of the anterior narial aperture, in the nature of the anterior palatine vacuity (which in the Owls is roofed by the ossified alinasal floor, thus concealing the nasal septum), and in that the inner surface of the curved tip is not provided with a median ridge. Seen from the ventral surface, this bone recalls that of the Cathartæ. But in the latter both nasal septum and ect-ethmoidal ossifications are wanting, thus revealing the nasal process of the premaxilla, bounded by very long anterior narial apertures—features which in the Striges are conspicuous by their absence.

### The Maxillo-jugal Arch.

The *maxilla* is indistinguishably fused with the premaxilla, and is indeed entirely covered by that bone externally.

The maxillo-palatine processes in the Asionidæ are of considerable size, highly pneumatic, being composed entirely of spongy tissue, and project backwards in the form of large bullæ, rising on each side above the quadrato-jugal bar so as partly to obliterate the lachrymo-nasal fossa, which is reduced in some cases to the vanishing point, in Gymnasio, for example, only a minute hole being left. This lateral and upward growth of the process forms in Bubo, Gymnasio, and Ninox a quadrate mass at the inferoposterior angle of the beak. In Asio, Scops, and Surnia this lateral mass is less developed, and it is wanting altogether in other forms, such as Surnia and Speotyto, for example, where the upward growth of the bullate process may be seen filling up the lower portion of the lachrymo-nasal cavity. The lachrymal, it should be remarked, fits very closely on the hinder end of this lateral maxillo-palatine mass. Compared with the maxillo-palatines of the Falconiformes, it is interesting to notice that the lachrymo-nasal orifice of the antrum is incomplete above, inasmuch as the inner border of the dorsal surface does not rise upwards to join the descending process of the nasal. The palatal vacuity in the floor of the antrum, which lies in the triangle formed by the palatine, premaxilla, and maxilla (Pl. 1. fig. 8), is large, as in the Falconiformes, and this traced forwards will be found to lead into the spacious anterior palatal vacuity.

The maxillo-palatine processes of *Photodilus* differ from those of the remaining Asionidæ merely in their somewhat smaller size, their lateral extension being less. That is to say, they do not extend outwards to fuse with the descending maxillary process of the nasal. They may best be described perhaps as intermediate in character between those of the Asionidæ and Strigidæ.

In the Strigidæ the maxillo-palatine processes are relatively much longer than in the Bubonidæ, and differ from them in shape, forming delicate backwardly-directed and somewhat spindle-shaped processes. Viewed laterally, they are seen to lie near the middle line and to leave a large cavity between themselves and the descending (maxillary) process of the nasal. The lachrymo-nasal aperture of the antrum is wanting altogether, but the palatal aperture is large.

The palate of the Owls appears at first sight to be schizognathous; in reality, however, it is desmognathous, for although the bullate portions of the maxillo-palatines are widely separated in the middle line, the palate is nevertheless bridged by the ect-ethmoid ossifications extending from the nasal septum outwards and downwards on either side to join, posteriorly, the maxilla.

### The Vomer, Palatine, Pterygoid, and Quadrate.

The *vomer* is short and blade-shaped, but generally more or less inflated in appearance, so much so, in *Asio* and *Strix*, for example, as to become fusiform. In *Asio* it is pneumatic. In *Surnia* it is vestigial. In *Speotyto*, *Ninox*, and some other genera it appears to be wanting. It is supported by a pair of small spurs projecting inwards from the dorsal border of the palatines, which effectually prevent the latter from meeting one another in the middle line, the space between them being equal to the width of the parasphenoidal rostrum. This peculiar feature appears to be found only among the Owls.

In *Photodilus* the vomer is extremely reduced, most nearly resembling that of *Ketupa*. In this respect *Photodilus* differs conspicuously from the Strigidæ.

In *Strix* the vomer, seen from below, appears as a fusiform body, highly pneumatic and of extreme delicacy, the surface being converted into a delicate filagree work. Its pointed end runs forward for some considerable distance between the maxillo-palatine processes. Seen from above, the vomer presents the appearance of the bow-end of a canoe, the sides of which are kept apart by a most delicate lattice-work of bone. Posteriorly, the vomer fuses with the quadrato-palatine plate described below.

The *palatines* take the form of flattened rods, in the Asionidæ and Photodilidæ having a strong outward curve. In the larger skulls the mesial borders of the posterior ends on either side of the vomer—send down a sharp keel. In *Surnia* the palatines are relatively very short and broad.

In the Strigidæ the palatines are straighter and relatively longer than in the Bubonidæ, and, moreover, they are not separated one from another as in the Bubonidæ.

The separation of the palatines in the Asionidæ one from another by the development of lateral spurs is an extremely interesting feature, and becomes still more so when contrasted with the conditions which obtain in the Strigidæ. Here the palatines, viewed from above, appear to have fused one with another, posteriorly, and with the vomer, presenting, in front of the pterygoid articulation, a broad quadrate wall sloping upwards and forwards, and having a doubly notched free dorsal border.

The *pterygoids* are long, and, near the middle, send inwards a thick spur to articulate with the basipterygoid processes. In some forms they are nearly straight, *e.g. Bubo*, *Scops*; in others they are sigmoidally curved, *e.g. Surnia*, *Strix*. In all they are blade-like rather than rod-shaped. They are sharply truncated anteriorly, and articulated with the extreme postero-external angle of the palatine. Proximally they articulate with the shaft of the quadrate, the articular end in some species expanding to encroach upon the orbital process, *e.g. Ninox*.

It is interesting to note that the angle formed by the pterygoids with the long axis of the skull is a much wider one in the Striges than in the Falconiformes. This appears to be due to the very decided antero-posterior shortening of the skull, brought about by the reduction of the interorbital region. The shortening is even more marked in the parasphenoidal rostrum, which in Bubo, for example, is extremely reduced. As a consequence of this abbreviation, the posterior ends of the palatines lie relatively much further back than in the Falconiformes. This same shortening, as we have elsewhere pointed out, has also brought the antorbital plate almost directly over the pterygo-palatine articulation.

In the great length of the pterygoids the Striges resemble the Caprimulgi more nearly than the Falconiformes, the orbital process and squamosal head being subequal in length.

• The quadrate is Falconiform in its general shape. It differs from that of the Falconiformes chiefly in the greater length and distinctness of the otic process, and in the more backward and downward position of this, and in its greater separation from the squamosal head. Furthermore, the pneumatic apertures in the Striges do not extend below the base of the otic head, whilst in the Falconiformes they extend downwards to the base of the orbital process. In the Asionidæ the pneumatic apertures are two in number, and open, one on either side of the base of the otic head, into a deep groove. In the Strigidæ there is but a single aperture; this is large and opens beneath the otic head.

The form of the quadrate in *Strix* is markedly different from that of any of the Asionidæ, the orbital process being reduced to a short spine, seated rather below the middle of the body of the quadrate, which is bent sharply backwards forming a **Y**-shaped angle with the process in question. Furthermore, the internal mandibular condyle in the Strigidæ is comparatively feebly developed, whilst in the Asionidæ it is nearly as large as the external condyle, and in *Bubo*, for example, projects downwards far below the articulation of the hinder end of the pterygoid.

The squamosal head of the quadrate is bounded in front by a zygomatic process, which is longest in *Asio*, and especially so in *A. madagascariensis*, in which the maximum length appears to be reached, and behind by the *processus articularis squamosi*. This last often extends downwards and inwards to join the pretemporal wing of the basitemporal.

### The Mandible.

The most conspicuous feature of the mandible in the Asionidæ and Protodilidæ is the wide angle formed by the rami, and the great length of the internal angular process. The angular is sharply truncated. A ramal vacuity is generally present. The only suture that can be cut is the dentary, and this is often obliterated. The coronoid ends in a free point partly closing the ramal vacuity.

In the Strigidæ the angle of the rami is less open; the coronoid is less degenerate than in the Asionidæ, but has fused more completely with the jaw, reducing the size of the lateral vacuity.

### The Hyoid.

The hyoid resembles that of the Accipitres among the Falconiformes. The basihyal is triangular in form, deeply notched in front, and has the posterior angle drawn out into a small pair of cerato-hyals. The basibranchial is more or less 'rod-shaped and produced backwards between the cerato-branchials. The cerato-branchials are long and slender, and surmounted by a pair of slender, ossified epi-branchials.

### III. THE SKULL OF THE NESTLING.

The sutures of the skull appear to remain distinct, at least until the young is nearly half-grown. The changes which take place between the skull of the nestling and that of the adult are at once striking and instructive.

It is to be regretted that the Museum Collection contains no nestling skulls of the Strigidæ. The following description is based on skulls of Syrnium aluco and Speotyto cunicularia.

### The Cartilage-bones.

The *basioccipital*, seen ventrally, is more or less linguiform in shape, and has a straight anterior border overlapped by the basitemporal plate. Its lateral borders are convex, and approach one another towards the middle line, reducing the posterior border to a small segment forming the centre of the occipital condyle, and forcing its way between the exoccipitals to bound the occipital foramen. Its lateral boundaries are formed by the pro-otic and exoccipital; the former occupying the anterior and the latter the posterior half of the border.

The *exoccipital* is large and irregular in shape. Ventrally its mesial border, which is concave, bounds the basiccipital; its anterior border is convex and overlapped by the wings of the basitemporal plate, whilst its external lateral border bounds the tympanic cavity, the posterior half of the border being produced to form the floor of the trumpet-shaped mouth of that cavity. Its posterior border is more or less triangular in shape, the outer face of the triangle being bounded by the squamosal and the inner face by the supraoccipital. Dorsally, the exoccipital is entirely concealed by the pro- and epiand opisthotic bones, only a small portion of its mesial border being visible.

The exoccipital seen ventrally is of considerable size, yet of smaller extent than in the Mesially, of course, it bounds the basioccipital and lateral portions of the adult. foramen magnum; the increase in size which takes place as growth proceeds is due to additions to the external lateral border forming the tympanic wing. In the nestling one-quarter grown this external border is divided into two regions, an anterior and a posterior, by a deep notch. The anterior segment is represented by an almost quadrate plate bounding the basioccipital and forming the floor of the pro-otic; the posterior segment belongs to that portion of the plate which bounds the foramen magnum. The external border of this plate extends outwards to form the lower portion of the trumpet-shaped mouth of the tympanic cavity. This posterior segment is bounded superiorly by deep grooves filled by cartilage, covering the pro-otic, the groove being bounded on the other side by the squamosal. In the adult this groove is completely obliterated, the exoccipital passing insensibly into the tympanic wing of the squamosal, to be described presently. Within the cranial cavity the exoccipital is almost entirely concealed by the pro-otic and opisthotic, only an extremely small portion being visible, mesiad of the opisthotic.

The *supraoccipital* is a relatively small bone, deeply cleft in the median line from the crest of its superior border downwards to the middle of the bone. On either side of the median cleft lies a long crescentic groove, which later becomes closed by the meeting of the edges of the groove and converted into the channel for the *vena cephalica posterior*. Between the supraoccipital and the squamosal is a large space filled by cartilage, which, in the dried skin, shrinks and reveals the pro-otic. In the adult this space becomes filled in by the approximation of the edges of the squamosal and supraoccipital.

The *pro-otic* appears externally as an oblong mass of cartilage, of small extent, between the supraoccipital, squamosal, parietal, and exoccipital bones. Internally it is

of relatively large size, and is bounded superiorly by the parietal, anteriorly by the alisphenoid, and mesially by the basioccipital, inferiorly by the opisthotic, and posteriorly by the epiotic. The floccular fossa, which is deep and pit-shaped, lies wholly within the pro-otic, but is closed posteriorly by the epiotic. The *meatus internus* is very shallow. The pro-otic is concealed from view externally entirely by the squamosal, but is widely separated from contact with the latter by a great air-space—the *recessus tympanicus superior*.

The *epiotic* in the skulls now under description is completely ossified, and anchylosed with the supraoccipital. Its relations to the pro-otic are made manifest through fine sutures passing through into the floccular fossa.

The *opisthotic* has completely fused with the pro-otic and basioccipital, only a trace of a suture remaining visible below the floccular fossa to mark the separation of the two otic bones. Fusion with the basioccipital is complete. A well-defined suture remains, however, to divide the opisthotic from the epiotic and supraoccipital bones.

The basisphenoid, seen from the cranial cavity is still distinct; seen in section, the suture between itself and the basioccipital is also distinct. Only the inner table of the basisphenoid is, however, represented; all the rest of this bone has been absorbed to contribute towards the formation of the huge *recessus tympanicus anterior*. The pituitary fossa forms a basin-shaped pit, which is externally completely surrounded by the air-sinus just described. There is no indication of the ossification of the basisphenoid from separate centres, such as is seen in the Pygopodes, for example.

The presphenoid, if present, is still represented only by cartilage.

The alisphenoid proves to be an exceptionally interesting bone in the Strigidæ. In the young skull of *Syrnium*, this bone is partly concealed externally by the squamosal, which overlaps its infero-external border. So much as is visible is roughly oblong in form, its long axis extending from the interorbital septum outwards.

Besides being overlapped by the squamosal, it is embraced above by the orbital process of the frontal, and below by the basisphenoid. Its precise form can best be studied from the inside of the skull. Viewed from this aspect, it will be found somewhat linguiform in outline, and to send inwards from its anterior border a long arm-like process which arises from a swollen base. But little change takes place in the form of this bone in later development; the space which is left above this arm-like process is filled in by the orbital process of the frontal and the orbito-sphenoid.

The relations which obtain between the alisphenoid, parietal, squamosal, and frontal are discussed on p. 18. They are especially worthy of note, seeing that they differ completely from those which obtain in *Spectyto*, for example.

The orbito- and pre-sphenoids have not yet begun to ossify.

The mesethmoid (Pl. 2. fig. 7 a) is yet only partly ossified. In the skulls in the Museum Collection it forms a linguiform plate projecting downwards from the skullroof to the parasphenoid. Its anterior border is straight, its posterior border convex. The dorsal border is expanded into an oval horizontal plate visible, in the youngest skulls, on the surface of the skull, where it appears wedged in between the frontals, and overlapped on either side by the nasals and nasal processes of the premaxilla.

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The *quadrate* has not yet assumed its fully adult form, the orbital process being still cartilaginous.

The *columella* in the older skulls has completely ossified, but stapedial rays are not traceable.

The articular is still separately distinguishable.

### Membrane-bones.

The *parietal* presents two distinct forms. In *Syrnium* it may be described as oblong in form, but having the infero-lateral angles obliquely truncated by the overlapping of the squamosal. It extends outwards and forwards to the alisphenoid, and divides the frontal from the squamosal. In a half-grown skull of *Syrnium aluco* the frontal sends down, immediately behind the alisphenoid, a tongue-shaped process to overlap the supero-external angle of the parietal, and thus appears to diminish the distance between itself and the squamosal.

Bubo, Scops, Ketupa, Gymnoscops, Syrnium, and Strix have this parieto-alisphenoid articulation. In Scops, however, the skull appears to be undergoing a change in the matter of the relations of the bones of this region, inasmuch as the oblique external lateral border has been cut back so as to cause it to fail to meet the alisphenoid, and allow the squamosal and frontal to meet.

Spectyto differs markedly from the type seen in Syrnium in the form of the parietal, and in the relations of this to the neighbouring bones—alisphenoid, frontal, and squamosal. In Spectyto the superior border of the parietal, instead of being straight, rises upwards and forwards for a considerable distance and is sinuous in outline. Its external lateral border is deep, but separated from the alisphenoid by the whole width of the squamosal. Finally, by the considerable backward extension of the squamosal, the inferior parietal border is restricted to the supraoccipital region, instead of extending outwards above the exoccipitals also.

The *frontal*, save in the differences in the relations between itself and the neighbouring bones in the two types just described, differs but little in form in either. Its general conformation can be seen in Pl. 2. figs. 7, 8.

The squamosal, like the parietal, differs considerably in form and its relation to the alisphenoid, frontal, and parietal bones. In Syrnium it undergoes considerable changes in course of growth: in the quarter-grown skull it is pentagonal in form, and bent upon itself so as to present two distinct faces, an external lateral and a posterior; in the half-grown skull it has become oblong in form and quadrangular. Both stages, however, differ from the squamosal of Speotyto; for whilst in Syrnium the superior border of the squamosal is gently arched and runs forward beneath the parietal to the alisphenoid, in Speotyto this border suddenly rises, near its middle, to form a large quadrate plate, articulating by a long horizontal suture with the frontal, and widely separating the parietal from the alisphenoid (Pl. 2. figs. 7, 8).

The mesial border of the squamosal, as may be seen when this bone is dissected from the skull, turns sharply inwards, forwards, and downwards, the resulting flattened face articulating and ultimately fusing with a similar flattened area on the parietal and alisphenoid. As a consequence of this inturning of the convex squamosal, a spacious chamber is formed—the *recessus tympanicus superior*.

A comparison between the skull of the adult and nestling of *Syrnium* and *Speotyto* reveals yet other characters of considerable interest; these concern the morphology of the postorbital process and the tympanic wing, and the formation of the temporal fossa. All three points may conveniently be discussed here.

Commencing with the postorbital process, we may remark that this, in *Syrnium* and other forms with a similar type of skull, is formed by the alisphenoid, whilst in *Speotyto* it is formed by the antero-inferior angle of the squamosal.

The tympanic wing in both types of skull is formed by the free edges, exoccipital and squamosal.

The temporal fossa in the young skulls is wanting. It is formed, in *Syrnium*, by a depression which has for its centre the sutures of the alisphenoid, squamosal, and parietal bones, and later becomes more sharply defined by the excessive development of the postorbital processes and tympanic wing (compare Pl. 2. figs. 4, 6).

From the cranial cavity the squamosal in *Syrnium* is only visible as a small hourglass-shaped tract of bone lying between the alisphenoid and parietal and laterad of the pro-otic; but in *Spectyto* it forms a large quadrangular plate bounded above by the frontal, below by the pro-otic, behind by the parietal, and in front by the alisphenoid, thus contributing to a very considerable extent to the formation of the brain-case.

This upward growth of the squamosal externally, accompanied by the gradual absorption of the underlying frontal and parietal elements and the usurpation of their function in the protection of the brain, is an extremely interesting feature, and marks an advance in the evolution of the skull. Proof of this advance we may derive from the fact that the arrangement seen in *Syrnium* is a primitive one, agreeing almost exactly with that seen in *Dromæus* for example. In the latter, it is furthermore interesting to note, the squamosal has not yet succeeded in absorbing the parietal wall, and so is entirely excluded from participation in the formation of the cranial cavity.

I propose to deal with this question shortly in another communication, in which I hope also to be able to show that, in the evolution of the Avian skull, a gradual increase in the length of the frontal has taken place, accompanied by a shifting backwards of the parietal and supraoccipital, the last two moving backwards through a quarter of a circle.

The *nasal* is truncated posteriorly, and does not extend backwards quite so far as the posterior border of the horizontal plate of the mesethmoid. Mesially the nasals meet one another in *Syrnium*, and almost conceal the mesethmoid; but in *Speotyto* they only overlap the mesethmoid, leaving the centre of that plate fully exposed. The form of the nasal cleft is holorhinal. The maxillary process of the nasal is truncated inferiorly; the premaxillary process is long and slender.

The *lachrymal* is placed rather far forwards, and lies entirely underneath the nasal. It differs but little from that of the adult stage in form.

The premaxilla has the nasal processes strongly arched, and terminating at the

anterior end of the mesethmoid plate. The palatal processes are vestigial, the maxillary processes relatively large.

The maxilla extends backwards, from the level of the maxillary process of the nasal to the level of the tip of the orbital process of the quadrate, in the form of a long slender rod constituting the outer sheath of the quadrato-jugal bar, and forwards as far as the level of the anterior angle of the anterior nares. Its maxillo-palatine process is very large and swollen, so much so as nearly to obliterate the lachrymo-nasal fossa. The antrum of Highmore opens far forwards on its floor, and leads forwards by an extremely short channel into a vault in the premaxilla roofed by ossified alinasals.

The *jugal* has the usual elongated and splint-like form, and overlaps the quadratojugal posteriorly and the maxilla anteriorly.

The quadrato-jugal is long, extending forwards along the inside of the bar to beyond the middle of it.

The parasphenoid appears to present the usual elements-a basitemporal plate, a pair of pretemporals, or alisphenoidal wings, and a rostrum. It seems to me a point of some significance that the basitemporal plate is quite separate from the rostrum in the youngest skulls in the Museum Collection, a sharply defined suture-line being visible when the skull is seen in section. It suggests, however improbable it may seem on reflection, that what appears to be the middle region of the parasphenoidal rostrum may really be the floor of the basisphenoid; the parasphenoid in this case would be represented only by the basitemporal plate and the tip which projects beyond the basisphenoid in such a way as to look as if it had been thrust through the antero-ventral angle of that bone. So much of the bone as would underlie the basisphenoid is thus supposed to have become absorbed. Elsewhere (p. 17) I have interpreted the features observable in this region by supposing the basisphenoid floor to have become absorbed and the parasphenoidal rostrum to be persistent. The reverse may be the case, though it must be admitted the weight of probability is in favour of the earlier interpretation. Instances of the replacement of one bone by another by absorption, till the invading bone more or less completely establishes itself, are not unknown in the skull. The stages in the process may be studied in the casque of the Cassowary, and in the growth of the squamosal for example: both these elements were originally quite external, but are now slowly working their way inwards so as to take part in the formation of the cranial cavity. The point in question can only be determined by a careful examination of much younger skulls than we at present possess. The remarkable shortness of the rostrum in the Owls is a feature already commented upon.

The *vomer* is small, and quite divorced from the hemipterygoid segment of the pterygoid. Its support has now been transferred to the palatines, which send inwards, for this purpose, from their mesial edges a pair of quadrate spurs.

The *palatine* may be described as scimitar-shaped, increasing in breadth gradually from before backwards. It terminates anteriorly near the tip of the beak in a fine point, but the posterior extremity presents some features of interest. Viewed from the ventral surface, it will be seen that the movement towards the middle line has caused the articulation with the pterygoid, which takes place at about this time, to form on the extreme postero-external, instead of on the extreme posterior end of the rod. Viewed from above, it will be seen that a strap-shaped bar has been developed from the mesial border of the rod, and that this runs forwards and inwards to form a support for the vomer. Immediately behind this process will be found a degenerate hemipterygoid.

The *pterygoid* differs from that of the adult only in so far as the articulation with the palatine is concerned. In the young Owl, as in other Neognathæ, it is only very imperfectly formed. Viewed from above in a half-grown nestling of *Syrnium* (Brit. Mus. n. 99.7.19.1), the main shaft may be clearly distinguished from a hemipterygoid relatively large but which yet fails to reach the vomer. The hemipterygoid rests upon the mesial border of the palatine, and extends backwards to be received into an indistinct cleft in the main shaft. The palatine immediately behind the hemipterygoid extends backwards as far as the lower lip of the cleft. Ultimately a synovial joint is formed with the palatine and pterygoid shaft, whilst the hemipterygoid, by fusion with the palatine, disappears. The method of articulation recalls that of the Sphenisci.

The *dentary* resembles that of the adult skull.

The *splenial* is still distinct: in the youngest skulls it is of considerable size, terminating posteriorly on a level with the lateral vacuity, and anteriorly near the distal fifth of the ramus.

The *coronoid* overlaps the proximal end of the lateral vacuity, and posteriorly takes part in the formation of the internal angular process.

The *angular* forms the inferior border of the proximal end of the ramus, and extends forwards nearly as far as the distal extremity of the splenial, turning inwards on its way, so that whilst the proximal half of the ramus has the inferior border formed by the angular, this border for the anterior half is formed by the dentary.

The *supra-angulare* passes forwards between the dentary on the one side and the splenial on the other.

### IV. THE VERTEBRAL COLUMN, WITH REMARKS ON THE EXCALATION OF VERTEBRÆ.

All the presynsacral vertebræ are free; the thoracic are heteroccolous. In general shape they resemble those of the Falconiformes rather than those of the Caprimulgi, but they possess characters which distinguish them from both of those groups. These distinctions, however, are so slight that they only hold good when the vertebral column as a whole is compared, single vertebræ being frequently easily confounded either with the Falconiform or Caprimulgine vertebræ, according to the particular peculiarities. Generally speaking, the vertebræ of the Striges are rather less pneumatic than those of the two groups above mentioned. The pleurosteites, and the diapophyscal lamellæ with which they fuse, form in the Striges a narrow and well-defined outstanding projection on either side of the anterior end of the centrum, sharply contrasting with the Falconiformes. Hyperapophyses, so conspicuous in the cervicals of the larger Falconiformes, are wanting or only feebly developed in the Striges.

The neural arches of the atlas rise almost straight upwards above the centrum, and

arching over the neural canal form but a narrow bar. The odontoid ligament is unossified. The neural arches of the 2nd to 4th cervicals form, as in the Falconiformes and some Caprimulgi, a broad quadrate plate having the postero-external angle produced into more or less prominent hyperapophyses. From the 5th to the 9th vertebræ, the arch is deeply notched posteriorly, and the neural spine is either wanting or very feebly developed. From the 6th to the 9th the vertebræ bear prominent catapophyses, which at the 10th give place to hypapophyses, which are continued backwards to terminate with the 2nd or 3rd thoracic vertebra.

The thoracic vertebræ are all free save the last, which is fused with the synsacrum. The hypapophyses, which vary in length and slenderness, never extend beyond the 3rd vertebra. The neural spines (e. g. Asio, Strix) interlock by means of a pair of spinous processes, which projecting backwards from the postero-superior angle of the vertebra embrace the antero-superior angle of that next behind. This interlocking is further strengthened, in Asio for example, by long backwardly directed processes extending from the hyperapophyses of the 1st and 2nd thoracic vertebræ, and by similar processes formed by the production forwards and backwards of the external angles of the transverse processes of the 4th to 6th vertebræ. Conspicuous pneumatic apertures open beneath the transverse processes of the thoracic vertebræ.

The synsacrum includes from 13 to 14 vertebræ. Of these, two are thoracic, four may be lumbar, three lumbo-sacral, two sacral, and three caudal.

The parapophyseal processes of the lumbar vertebræ are short, the last abutting against the inferior border of the preacetabular ilium near its middle.

A planum coccygeum is generally present, and is especially distinct in certain forms, e. g. Syrnium, where it is isolated by a deep fovea pudendalis; whilst in Bubo, for example, its distinctness is masked by retention of the parapophyseal processes of the 1st and 2nd caudal vertebræ.

The transverse processes of the free caudal vertebræ appear to be relatively longest in *Asio* and *Strix*. Free intercentra are present in the most proximal vertebræ; posteriorly these elements fuse with the centra, forming blunt hypapophyses.

As in other groups of birds, there is evidence of a slow process of reduction in the length of the vertebral column, apparently brought about both by excalation and absorption of the vertebræ, the former method taking place in the presacral region, the latter in the postsacral region.

A secondary process of reduction, affecting the number of vertebræ in the different series, has caused the actual reduction in the total number of the series to be generally overlooked. The reduction in the numbers of the different series chiefly affects the thoracic and cervical series, and is largely due (1) to the backward shifting of the sternum, and (2) to the reduction of the sternal facet for the sternal segments of the ribs. The backward shifting has resulted in the divorce of certain sternal segments of ribs from their articulation with the sternum, and the consequent transference of the vertebra bearing the rib to the cervico-thoracic series. The degeneration and final disappearance of the sternal rib rapidly follows this divorce : later the vertebral segment of the rib likewise becomes reduced, finally disappearing also. At least this appears to be generally the case: sometimes, however, the capitulum and tuberculum and a remnant of the shaft remain, and fusing with the di- and par-apophyses of the vertebra form a bridge for the vertebral artery, thus converting the cervico-thoracic into a "true" cervical vertebra.

The sharp distinction maintained between the cervical and cervico-thoracic vertebræ, by reason of the fusion of the rib-element of the former with the centrum, is a point of some interest. This fusion may be ascribed, perhaps, to kinetogenesis; or, more vaguely, to the adaptation to the peculiar and characteristic movements of the neck in birds. Only in very young birds are the riblets of the cervical vertebræ free, but in *Archæopteryx* they appear to have been free throughout life. The number of these cervical vertebræ is, as we have already pointed out, being constantly augmented by additions from the cervico-thoracic series. The latter series is fed by the thoracic, as the sternum shifts further and further backwards.

The posterior thoracic vertebræ become severed from the sternum by the reduction of the articular surface for the sternal ribs, a reduction sometimes associated with a reduction of the sternal plate itself. Severance from the sternum brings about, as in the case of the anterior ribs, first a reduction of the sternal, and finally of the vertebral segments; the amount of the reduction being proportionate to the period of their isolation. The result of the final disappearance of the last vestiges of these ribs is to leave the vertebra to which they belonged indistinguishable in appearance from the vertebræ of the lumbar series, with which it is generally reckoned. Occasionally, small spicules of the sternal ribs remain after the complete disappearance of their vertebral segments.

The fate of this hindmost vertebra brings us to the consideration of the question of reduction by excalation.

Excalation appears to occur most frequently in the lumbar region, but also in the cervical, lumbo-sacral, and caudal regions.

In the cervical region the number of vertebræ is constantly 14. So far I have found only one exception to the rule, when the number was reduced to 13 (*Athene*, Brit. Mus. n. 1095 e). Of these 14 vertebræ the number bearing fused riblets varies between 11 and 13, the remainder being cervico-thoracies bearing free ribs or vestiges of them. Since in the skeleton of *Athene* the maximum number of thoracic and lumbar vertebræ are present, there can be no doubt but that the reduction in the cervical region is a real, not an apparent one.

In the lumbar region the maximum number of vertebræ is four (fig.  $\Lambda$ , p. 28). But for the correct determination of the vertebræ in this region it is necessary carefully to determine the number and limits of the thoracic series; inasmuch as the last thoracic, by the loss of the vertebral segments of the ribs, become indistinguishable from the lumbar series (\*7, fig. B, p. 28).

The number of thoracic vertebræ appears invariably to be 7, six of which may be attached to the sternum, though frequently only four succeed in effecting such an attachment. Earlier, in more primitive ancestral forms, as we have already pointed out, probably as many as ten vertebræ reached the sternum; severance from it has taken place at both ends of the sternal plate. The seventh pair of thoracic ribs are frequently found only in minute traces of their sternal segments (figs. B, C, s.r. 7, p. 28), at times even these are wanting. Sometimes traces may be found of vertebral as well as sternal segments, and still more rarely the whole rib may be found, though it fails to reach the sternum (fig. A, s.r. 7, p. 28). In three specimens in the Museum Collection the seventh rib is well preserved—*Bubo* magellanicus (s.r. 7, fig. A, p. 28), a Nyctala 98.22, and a Ninox 1332 a.

The constancy in the number of the cervical and thoracic vertebræ and the fixed point afforded by the sacral vertebræ enable one to determine, with some certainty, the number of the lumbar and lumbo-sacral series.

Only five skeletons in the National Collection have as many as four lumbar vertebræ. At first sight, two skeletons of this five appear to have five lumbars, indistinguishable one from another ; as a matter of fact, the first vertebra belongs to the thoracic series, as is proved by the vestiges of the 7th pair of sternal ribs. Thus, it is absolutely necessary to fix the last thoracic before attempting to count the lumbar vertebræ; and this fixation is often only possible through the presence of the sternal segments of the thoracic ribs just referred to.

The maximum number then of lumbar vertebræ is four, and this is now rarely attained; in all, save five, of the skeletons under my charge, only three are present. Since there is no suspicion whatever of the fusion or reduction by crowding of two contiguous vertebræ in this series, I gather that the loss of the vertebræ in the series is due to excalation. It is possible, in some instances, that the 4th lumbar has, by loss of its par- and di-apophyseal processes, become merged in the lumbo-sacral series; but in this case, it is still a fact that a vertebra has been lost, only it is a lumbo-sacral and not a lumbar that is missing.

The lumbo-sacral vertebræ are three in number, but in five cases they are reduced to two, as in fig. C, 1-2, p. 28. Instances of this can be seen in the annexed table. Excalation appears to have been at work here again, since there is no trace of the reduction and fusion of contiguous centra.

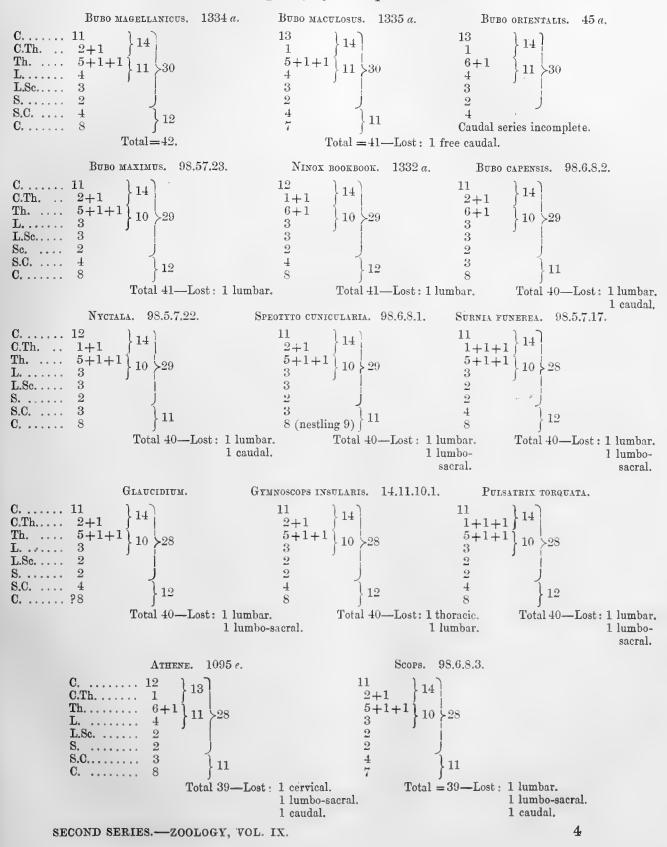
The primitive sacrals are two in number (s.v., figs. A, B, p. 28), but the ribs, either of the 1st or 2nd pair, are occasionally wanting.

The sacro-caudal are three or four in number (1-3, fig. C, p. 28). Occasionally the vertebra corresponding to the first free caudal fuses with the last sacro-caudal, so that the synsacrum actually projects beyond the limits of the mesial borders of the post-acetabular ilia.

The post-synsacral vertebræ or free caudal vertebræ are either 7 or 8 in number. In very young birds, *e. g. Spectyto*, there are 9 free caudals, the additional vertebra lying in front of the pygostyle. It is small and wedge-shaped, and gradually diminishing, partly by the mutual pressure of vertebræ on either side. Later in development all trace of this vertebra disappears, owing to its fusion with the pygostyle.

Proof of a reduction in the number of presacral vertebræ may be equally well demonstrated if the component numbers of the various series be disregarded and the total number of vertebræ be counted between two fixed points—the atlas and second sacral vertebræ. As is shown in the following table, the number counted in this manner varies between 28 and 30, whilst the variation in the total number ranges between 39 and 42.

# Table showing Variation in the Number of the Vertebræ, caused partly by Excalation and partly by Absorption.



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25

The component elements of the typical vertebral column may be expressed as follows:---

Cv. 11: Cv.Th. 3. Th. 
$$5+2$$
: Lb. 4. Lb.Sc. 3: Sc. 2: Cd.  $4+8=42$ .  
 $7$ 

It should be stated that the evidence for the excalation of vertebræ, which, it is contended has taken place, rests upon the fact that the presacral vertebræ show no trace whatever of fusion of elements, and the nerve-apertures are all perfectly normal. This is a point of some importance, since in the vertebral columns of Amphibia possessing fewer than the normal number of vertebræ, the reduction appears generally to have been brought about by the fusion or confluence of vertebræ, rather than by excalation. The reduction in the number of the caudal vertebræ among the Aves, however, is, as we have just indicated, undoubtedly brought about by the absorption of the vertebræ lying immediately in front of the pygostyle. This is well seen in Brit. Mus. 28.5.7.39, showing the remains of the 7th free caudal, which consists, now, of a small portion of the centrum only, and this forms a wedge between the 6th vertebra and the pygostyle. Later in life this wedge fuses with, and forms part of, the pygostyle itself.

It may be contended that the inconstancy in the number of presacral vertebræ is due to what Mr. Bateson calls "Meristic variation." It seems to me, however, that the facts submitted rather favour the view that a general and orderly reduction in the length of the vertebral column is taking place, rather than that which implies simply a series of sporadic variations of no apparent meaning. Before this matter can be settled satisfactorily, it will be necessary to examine a much larger series of individuals of the same species, and, if possible, of nestlings from the same nest.

### V. THE RIBS.

The cervical ribs are styloid and short. The heads of the ribs have the form of flattened band-like lamellæ and fuse above with the diapophysis, below with the catapophysis of each vertebra, thus forming a canal for the vertebral artery. The head and the short shaft are sharply contrasted one with another; so that, in a lateral view, the pleurapophyseal lamella stands out buttress-fashion against the centrum. The hindmost cervicals or cervico-thoracics, however, must be excepted. These are two or three in number. The 1st and 2nd are generally represented by vestiges, only the tuberculum being present : the third is generally long and styliform. From this we may gather that from two to three of the thoracic vertebræ have been transferred to the cervical series by the shifting backward of the sternum, the sternal ribs disappearing after their severance from the sternum.

The thoracic ribs are long and slender, and increase in length from before backwards: as a result the thoracic cavity is very spacious.

The number of thoracic ribs may reach a total of seven pairs, of which six pairs may articulate with the sternum, e.g. Ninox. But this is rare, the number in the majority

of forms varying between 5 and 6 pairs, the last of which fail to reach the sternum. Some species of *Strix* (e.g. S. delicatula), Asio, Carine, Surnia, Speotyto, Syrnium, have five pairs, which articulate with the sternum, the sternal segment of the 6th pair being generally bound by connective tissue with the lower fourth of the fifth corresponding segment. In one skeleton of Strix, however, in the Museum Collection (1223 a) the sixth pair articulates with an imperfect facet projecting from the lower one-third of the fifth segment. Frequently only four pairs of ribs articulate with the sternum, the fifth, or even fifth and sixth pairs having sternal segments too short to reach the sternum.

Various stages in the reduction of the number of the ribs are to be met with. Leaving out of consideration the anterior thoracic (cervico-thoracic), we may have as many as seven pairs of true thoracics. Of these not more than six pairs ever articulate with the sternum, the seventh in some cases being quite long, the sternal segment almost reaching the sternum, e. g. Athene (1095 e). In others vestiges of the vertebral segment only remain, e. g. Gymnoscops (94.11.10.1), or of the sternal segment only, e.g. Bubo capensis (98.6.8.2). The reduction of the 6th and 5th pairs proceeds in a similar way.

There is evidence to show that at least nine pairs of ribs recently articulated with the sternum. Of these the first and second pairs, by loss of their sternal segments, have become transferred to the cervico-thoracic series; whilst the last pair, by loss of their vertebral segments, have become transferred to the lumbar series. In many species the number of ribs has become, as we have already remarked, reduced to five pairs, of which four pairs only articulate with the sternum, the reduction taking place sometimes from the anterior, sometimes from the posterior members of the series.

The uncinate processes are well developed, but except rarely not more than five pairs are present. Occasionally the last cervico-thoracic rib bears an uncinate, but the last (7th) thoracic appears to have lost the appendages completely. They are long and slender in shape, sloping obliquely upwards and backwards. They are relatively longest in *Strix*, extending backwards on to the third rib from their base of attachment.

# VI. THE PECTORAL GIRDLE AND STERNUM.

The pectoral girdle of the Striges is extremely uniform in character throughout the group, and in certain characters bears a very close resemblance to that of the Falconiformes.

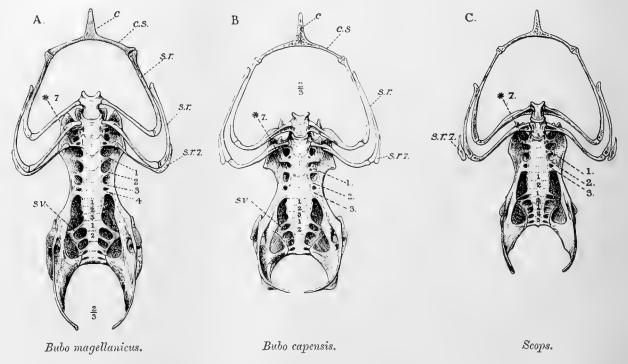
As a whole the girdle of the Striges can be distinguished from that of the Buteonine section of the Falconiformes by the presence of a prominent procoracoid process, and from the Falconine section, in which a procoracoid process is present, by the smaller relative size of the acrocoracoid, which in the Falconidæ is large, and by the form of the furcula. This, in the Striges, is relatively long and slender, only slightly curved dorsoventrally, and is furthermore frequently incomplete, the limbs failing to meet in the middle liné.

The pectoral girdle of the Striges can readily be distinguished from that of the Caprimulgi, in that in the latter group there is no procoracoid process, and the furcula is strongly curved dorso-ventrally.

The *coracoid* is long, being nearly or quite as long as the sternum; it has a prominent acrocoracoid and a large procoracoid process, broad at the base, and terminating in a downwardly directed hook-shaped process articulating with the furcula.

The coracoid of the Asionidæ may be distinguished from that of the Strigidæ in that in the former the acrocoracoid affords an articular surface for the furcula, which develops a corresponding articular facet by sending outwards from the distal end of each limb an oval plate. This articulation between these two bones is wanting in the Strigidæ.

The coracoid of the Striges bears a close resemblance to that of the Falconiformes, but it may be distinguished from all, except the Falconidæ, by the presence of the procoracoid process. With the Falconidæ, however, the case is different; and it becomes a matter of nice discrimination to tell the coracoid of the Falcones or Polybori from that



Synsacra showing the reduction of the vertebræ by excalation; cf. pp. 23, 24.

of one of the Striges. The Falcons may be distinguished by the absence of a supracoracoid foramen; but in the Polybori and Striges the foramen is present, and almost identical in size and position. In the Striges, however, it will be found to lie somewhat nearer the scapula. In the Striges the base of the coracoid is comparatively deeply grooved to fit the dorsal lip of the groove; whilst in the Polybori, what corresponds to the dorsal lip of the groove in the Owls is represented only by a low and incomplete ridge.

The scapula has a swollen acromion, with that portion of its surface which forms the roof of the foramen triosseum perforated by pneumatic foramina.

The *furcula* is long, slender, and but slightly arched dorso-ventrally, and wants a hypocleideum.

In the Asionidæ, its distal extremities are laterally compressed, and furnished with an oval facet for articulation with the coracoid. In some species, the two limbs fail to meet in the middle line, *e. g. Spectyto*, *Glaucidium*, *Surnia*, whilst in others the degeneration of this region has not proceeded quite so far, the limbs being still united, but by a very slender thread of bone. In the nestling *Spectyto* it is interesting to note that the furcula is still entire. The backward extent of the furcula varies considerably. In many of the Asionidæ the furcula reaches the inferior and anterior angle of the carina, and is held in position by strands of connective tissue, no articulation taking place. In others the furcula falls considerably short of the carina, *e. g.* some species of *Bubo*, *Syrnium*, *Asio*.

In some cases, *e.g. Bubo maximus*, the furcula is closely bound to the anterior border of the keel, the union taking place near the middle of the border. The furcula is pneumatic in all the Asionidæ.

In the Strigidæ the furcula articulates with the carina, which at the point of articulation has developed a lateral expansion. The furcula differs from that of the Asionidæ, not only in the fact of this articulation, but in that the distal ends lack the articular facet for the coracoid. Furthermore it is non-pneumatic.

The sternum is nearly as broad as long, and bears a well-developed carina. The spina externa is moderately large, but the spina interna is wanting.

The sternum of the Striges more nearly resembles that of the Falconiformes than any other group. This resemblance, it should be stated, is most marked where comparisons are made between Strigine sterna and those of Accipitres. The following characters will be found useful in determining between sterna belonging to these two very different groups. The posterior border of the sternum in the Striges is never entire, and never fenestrated, but always notched. With the exception of the sterna belonging to the Strigidæ, and the sternum of *Huhua nipalensis* (p. 37) of the Asionidæ, there are two pairs of notches. The single pair of notches of *Huhua* are of great size. They lie on either side of the metasternum, and extending forwards to beyond the level of the middle of the posterior lateral process, cause the sternum of this bird to resemble closely that of *Microhierax* among the Accipitres. The great difference in size, however, renders any possibility of confusion on account of this resemblance impossible.

The anterior lateral processes are small and form blunt-pointed projections from the antero-lateral angles of the sternal plate, which are deeply grooved for the origin of the sterno-coracoideus, the groove extending back as far as the last rib articulation.

The spina interna is wanting, a deep notch occupying its place. The spina externa is present only in the Asionidæ, and here it projects downwards rather than forwards.

The single pair of notches in the sternum of the Strigidæ resemble those of some Accipitres, e. g. Elanoides, in that they are very shallow, so that the posterior lateral processes pass almost insensibly into the metasternum, being divided therefrom only by a sinuous line. But the processes are relatively much longer in the Strigidæ than in the Accipitres, and the sternum is narrower.

## VII. THE PELVIC GIRDLE.

The pelvic girdle of the Striges bears a very close resemblance to that of the Accipitres, among the Falconiformes. As in the Accipitres, the innominate bones are never free in the adult, the preacetabular ilium is very long, and the pectineal process is wanting.

The Strigine may, however, be distinguished from the Accipitrine girdle by the following characters:—(1) The preacetabular ilium has the middle of its inferior border deeply emarginate, so that a line drawn from the cephalic end of the emargination inwards and forwards to the point where the superior border intersects the vertebral column, cuts off a large triangular segment of the innominate. (2) The dorsal plane of the postacetabular ilium is continued forwards and outwards to form a conspicuous shelf overhanging the acetabulum. (3) The ischium is continued backwards into a point along the publis. (4) The publis is always complete.

The preacetabular ilia never meet one another directly above the neural spines of the lumbar vertebra. In *Gymnoscops, e. g. G. insularis*, the two preacetabular ilia rise to the level of, and just succeed in touching, the crest of the neural spine of the 1st lumbar vertebra. By this a pair of conspicuous *canales ileo-lumbales* are formed. In the majority of the Striges the hinder openings of these canals are much restricted by the greater backward extension of contact between the neural spines of the vertebræ and the superior iliac crest. In many cases the ilia are really rather widely separated, the canal being roofed by lateral expansions of the crests of the neural spines which extend outwards to fuse with the ilia. In many genera, *e. g. Asio, Bubo, Nyctala, Strix*, the canals are closed posteriorly, and thus become converted into *cavæ ileo-lumbales dorsales*. The postacetabular ilium lodges a fairly large iliac pocket.

The pre- is about twice as long as the post-acetabular ilium, and the latter, it should be noted, is not sharply deflected as in the Accipitres. The *fovea lumbalis* differs from that of many Accipitres in that, owing, probably, to the relatively shorter neural spine, the vertebral column lies within the fossa. In the Accipitres, the vertebral column projects beyond the margin of the cavity, and is plainly visible when the skeleton is viewed from the side. The *fovea ischiadicus* is of considerable size, lofty, and strongly defined. Clearly defined limits are not so characteristic of the *fovea pudendalis*. This region can best be studied in *Syrnium*, where a lofty chamber divides the sacrum from a well-defined *planum coccygeum*. Generally this chamber is obscured by the close approximation of the sacral and caudal vertebræ, the ribs of the one, and the paraphyseal bars of the other, cutting the chamber up into a number of compartments. The *iliac recess* is well developed in all the Owls.

The pelvic girdle of the nestling is instructive. At this stage the preacetabular is more than twice the length of the postacetabular region, and the neural spines of the lumbar vertebræ are low and project above the innominate.

A feature of especial interest is the part played by the postacetabular ilium in the formation of the iliac recess. If the innominate be removed from the synsacrum, it will be seen that the mesial border of the postacetabular region curves inwards and downwards in the form of a strap-shaped plate, finally meeting the ischium; at this point it turns abruptly upwards and outwards to meet the postero-external angle of the dorsal plane, and at the same time closes the ilio-ischiadic foramen. This peculiar downgrowth, and its subsequent upgrowth, forms the recess in question. Seen from above, the downgrowth leaves an unfilled triangular space immediately behind the hinder border of the ilium which later becomes filled up. The above description is based on the innominate of a nestling *Speotyto*. In a slightly younger *Syrnium aluco* the mesial inturned border of *Speotyto* was here twisted so far outwards as to make it appear that the recess was formed rather by an extension backwards of the *inner half* of the *hinder*, and not the mesial border of the ilium. Furthermore, the downward extension of the plate, and its union with the ischium, was slightly different, inasmuch as, seen from below, it formed a scroll-shaped mass lying at right angles between the ischium and the long axis of the pelvis. In the adult, not the slightest clue is obtainable of the origin of this recess.

The *ischium* has the posterior extremity rounded, not pointed as in the adult, its anterior extremity presents a sharply truncated face to unite with the pubis, and sends upwards a long columnar spur to unite with the ilium, and close the acetabulum posteriorly. The *pubis* develops from the dorsal surface of its anterior extremity a cylindrical spur, truncated at both ends, which are wedged in between the ischium on the one side, and a descending bar from the preacetabular ilium on the other.

# VIII. THE PECTORAL LIMB.

The pectoral limb bears a strong resemblance to that of the Falconiformes. It may, however, be distinguished by the relatively smaller pectoral crest of the humerus, the deeply excised postaxial border of Ph. 1, Mc. II, and the fact that the proximal end of Mc. III fuses with Mc. II distad of the extremity of Mc. I. In the Falconiformes, excepting in the Cathartæ, the fusion of Mc. III takes place at a point corresponding to a line drawn across the shaft of Mc. II from the distal extremity of Mc. I. The Cathartæ agree with the Striges in the last particular.

The humerus in the Asionidæ has a well-developed pectoral crest, rounded in outline, the palmar surface of which, for the insertion of the *pectoralis*, is generally sharply cut off from the shaft by a well-defined *tinea aspera*. The *sulcus transversus* (coraco-humeral groove) is very shallow or wanting, and the *incisura capitis* is only moderately deep. The *tuberculum internus* is large, and the *tuberculum externus* distinct. The pneumatic foramen is large. The *crista inferior* is only moderately developed. The *linea aspera* marking the insertion of the *deltoideus major* extends a considerable distance down the shaft, terminating in a sharp point. The scar for the insertion of the *brachialis inferior* is linguiform and of considerable length. The shaft is nearly cylindrical, sigmoidally curved, and presents a conspicuously expanded palmar surface, owing to a large, rounded entepicondylar process. Both ulnar and radial trochleæ are well developed, and there is a small ectepicondylar process. The humerus of the Strigidæ differs from that of the Asionidæ mainly in its greater slenderness, and in the feeble development of the various crests and tuberosities.

The humerus, in the adult, is larger than the manus, but shorter than the forearm. The humerus of the Striges may be distinguished from that of the Caprimulgi by reason of the extremely well-defined radial tuberosity and the deep *incisura capitis* seen in the latter. In the Owls these are not conspicuously developed.

The forearm offers no characters of systematic importance.

The *ulna* has a well-developed olecranon process, feebly developed tubercles for the remiges and under tail-coverts, and affords a large articular surface for the radius. Two distinct glenoid surfaces are developed on the palmar surface for the articulation of the metacarpus.

The radius, which is much more slender than the ulna, is more or less sigmoidally curved, the distal half running parallel with the ulna, leaving but a narrow space between. The forwardly bowed portion of the shaft starts abruptly from the proximal moiety involved in the articulation with the humerus, giving the cotylus for the radial tuberosity of the humerus the appearance of being supported on a rather long neck. A large sesamoid, the os prominens, is generally found attached to the distal end of the radius, as in some Falconiformes, e. g. Elanus among the Accipitres. In Ninox connivens this os prominens is of relatively enormous size, and should be carefully examined in the living bird.

In a considerable number of Owls the second fifth of the radius develops from its postaxial surface a delicate arch of bone for the *extensor metacarpi radialis brevis*. Is this character to be regarded as due to kinetogenesis?

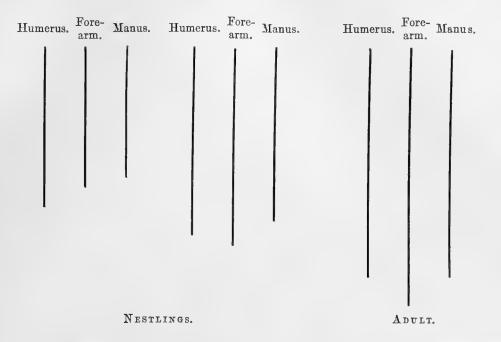
The *carpal bones* call for no special comment: the most interesting character which they present is a deep indentation on the radiale for the reception of the tubercular metacarpal I when the wing is fully extended.

The manus is long and slender. The carpo-metacarpus may be distinguished from that of the Accipitres by the fact that the Mc. III joins the shaft of Mc. II distad of the Mc. I. The trochlea for the ulnare lies on a level with the inferior border of Mc. III, and not in the middle line of this as in the Falconiformes. The intermetacarpal space is wide.

Phalanx 1 of Mc. II has a deeply emarginate postaxial border, the proximal end being cut away so as to leave a cylindrical shaft, whilst the distal end is expanded to form a broad plate for the support of the remiges. Ph. 1 of D. III presents a deeply emarginate postaxial border, the proximal end being broad, the distal end tapering.

The proportions of the various segments of the wing appear to vary considerably between the nestling and adult stages. The measurements afforded by a comparison of two nestlings of *Spectyto*, of different ages, and an adult illustrate this.

In the youngest nestling in the Museum Collection (98.5.7.39) the humerus is slightly longer than the forearm, whilst the latter and the manus are almost subequal. In a second specimen (98.5.7.38) the humerus is conspicuously shorter than the forearm, whilst the latter is now markedly longer than the manus. In the adult, the humerus is one-quarter shorter than the forearm, and the disproportion between the latter and the manus has become still greater. The accompanying diagram illustrates this. Similar variations in the rate of growth obtain also in the pelvic limb.



The pneumatic foramen, so conspicuous in the humerus of the adult, is wanting in the nestling.

## IX. THE PELVIC LIMB.

The pelvic limb of the Striges is not pneumatic, but otherwise bears a strong resemblance to that of the Falconiformes. It may be distinguished therefrom, however, apart from this character, by the fact that the tibio-tarsus lacks an extensor bridge.

The femur is relatively long and slender, with a cylindrical shaft. The *linea aspera* dividing the surfaces for the *crureus* and *vastus externus* runs the whole length of the shaft from the ant-trochanter to the base of the internal tibial condyle in the Strigidæ; in the Asionidæ it bifurcates near the distal third of the shaft. The popliteal fossa is shallow. The rotular channel in the Bubonidæ is relatively shallow, but broad and deep in the Strigidæ.

The tibio-tarsus may be at once distinguished from that of the Falconiformes in that the extensor bridge is conspicuously absent. Ecto- and ento-enemial crests are not markedly developed. The shaft, in the Asionidæ, is long, markedly inflected, and bowed slightly forwards. The internal projects downwards below the level of the external tibio-tarsal condyle, whilst the lateral borders of the posterior trochlear surface are produced backwards and upwards into a pair of prominent ridges, a feature which is especially marked in the Strigidæ. The tibial shaft immediately above these ridges is somewhat deeply hollowed, so much so in some genera, *e. g. Bubo, Speotyto*, as to be saved only by a thin plate of bone from perforating the extensor groove on the other side of the shaft. A small but prominent tubercle projects from the side of the

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lower fifth or sixth of the inner side of the distal end of the shaft. The *fibula* in *Ketupa*, and less distinctly in *Bubo*, *Nyctala*, and *Strix*, may be traced downwards as far as the proximal tarsal mass. In *Speotyto* it fuses indistinguishably with the tibial shaft rather below the middle of it; in *Scops* it reaches as far as the distal sixth of the shaft; in *Carine* it extends some distance beyond the middle of the shaft, but not so far as in *Scops*. The fibular ridge borne by the tibia is fairly strongly developed, but varies slightly in length. It is short and near the proximal end of the shaft in *Megascops*, *Nyctala*, and *Carine*, long and low in *Asio*, *Bubo*, *Ketupa*, and the Strigidæ; for example, *Scops* and *Speotyto* have this ridge only feebly developed.

The *tarso-metatarsus* is remarkably Falconiform in its general conformation; it may be distinguished, however, by the presence of an extensor bridge—which is rarely absent—and the disposition of the trochleæ.

The length of the shaft varies much, being in some shorter than the femur, e. g. Scops, Nyctala, Carine; and in others longer than the femur, e. g. Spectyto, Strix. In Bubo, Ketupa, and Gymnoscops these two segments are subequal.

The hypotarsus is simple, being formed by a prominent and more or less quadrate bony plate arising from the inner border of the proximal end of the shaft. A deep groove divides this from a much smaller, laterally compressed plate arising from the outer border of the shaft somewhat higher up, so that its superior border contributes towards the formation of the glenoid surface for the ectocondyle of the tibio-tarsus. Not seldom the inner calcaneal process takes part in the formation of the glenoid surface for the entocondyle of the tibio-tarsus.

The shaft is grooved both on its anterior and posterior surfaces. Anteriorly the groove is confined to the proximal end of the shaft, and is both wide and deep. This feature is especially noticeable in the larger species of Bubo. In these the groove takes the form of a deep and wide fossa lying at the proximal end of the inner border of the shaft, and is crossed by an extensor bridge.

Mesially this fossa is bounded by a flat wall forming one side of a triangle, the other side forming the outer border of the shaft. Within this fossa lies a long narrow scar, the impression for the *tibialis anticus*. The posterior surface of the shaft is deeply grooved throughout, and perforated just below the hypotarsus by a small oblong foramen. Seen in section the shaft, below the hypotarsus, is  $\boldsymbol{\omega}$ -shaped, but lower down  $\boldsymbol{\sigma}$ -shaped. In *Ketupa* and the smaller Owls, the anterior groove extends across the whole face of the shaft. The posterior groove agrees with that of *Bubo* just described.

The trochleæ differ from those of the Falconiformes in that they are disposed in a more strongly curved arch, and in that the third trochlea is much shorter than the first and second—which are on the same level one with another—and directed backwards. There is, it may be remarked, a passing resemblance in the form and disposition of the trochleæ between the Striges, and especially *Ketupa* and *Pandion* among the Accipitres; but whereas in *Pandion* the 2nd trochlea has its mesial border strongly raised above the level of the shaft, and sloping inwards to over-arch trochlea 1, in *Ketupa* the middle trochlea presents no strongly developed ridges and is widely separated from trochlea 1.

Further, the tarso-metatarsus of the Striges, as a whole, may be readily distinguished from that of *Pandion*, inasmuch as in the former the hypotarsus is simple, in the latter compound.

The metacarpal I is relatively smaller than in the Falconiformes.

The *phalanges* of the *Striges* differ from those of the Buteonine section of Accipitres among the Falconiformes only in the matter of their respective lengths in different digits.

Ph. 1 D. II is very short, being only about half as long as Ph. 2; Ph. 1 of D. III is also very short, so also is Ph. 2, though slightly longer than Ph. 1; Ph. 3 is long, about as long as Ph. 1–2 combined; Ph. 1, 2, 3 of D. IV are all extremely abbreviated, their combined length being less than that of Ph. 4. The ungual phalanges are all very large, and in the larger species have the base encircled by a broad raised collar.

The phalanges of the Strigidæ differ from those of the Bubonidæ in that Ph. 1, D. II is long, so also is Ph. 2 of D. III.

## X. Observations on Generic and Specific Characters.

I hoped, when I commenced the present section of the memoir, to be able to give diagnostic characters, not only for every genus, but also for the bulk of the species in each genus. Unfortunately, this Collection, though undoubtedly an exceptionally good one as compared with that of other Museums, is still far from complete—so much so, as to render it impossible to fulfil my anticipation.

Many genera are entirely wanting, and those we have are represented for the most part only very imperfectly. Thus the genus *Syrnium* is represented, according to Dr. Sharpe, in his 'Hand-list of Birds' (26), by 31 species. The Museum Collection contains but 3. *Ciccaba*, with 8 species, is represented only by 1. *Ninox*, with 44 species, by 2. *Scops*, with 80 species, by 3.

It is extremely unlikely that all the species in such large genera will prove specifically distinct, according to the skeletal characters; but I think it certain that a very considerable number will be found to be more or less easily distinguishable if the sum total of all the osteological characters be taken into account. At least three examples of each species of a genus are necessary before full reliance can be placed on the apparent specific characters, but the following analysis is intended to show what may be done.

The genus Asio is represented, according to the 'Hand-list of Birds,' by 14 species; of these, five are possessed by the Museum—A. otus, A. accipitrinus, A. madagascariensis, A. nisuella, A. major.

The skulls of A. accipitrinus and madagascariensis are readily picked out from the skulls of A. otus, nisuella, or major, by reason of the fact that the postorbital process on its outer border bears a prominent projecting tubercle for the attachment of the membranous valve dividing the cavernum from the diverticulum in the external asymmetrical ear. This tubercle is represented by a mere vestige in the remaining species. Further, the latter are characterized by the greater prominence of their supraorbital processes, and greater width of the "post-cavernum"—the uppermost limit of the tympanic cavity.

A. accipitrinus and A. madagascariensis are also distinguishable by their skeletons:

inasmuch as the latter, apart from its larger size, has a relatively deeper post-cavernum overshadowed by a prominent tubercular swelling, a relatively larger postorbital process, crescentic instead of spatular in form, and supporting a relatively larger post-orbital tubercle which lies nearer the middle of the process; besides the vomer and posterior ends of the palatines are fused as in the Strigidæ. The metasternum is broader and the external pair of notches wider than in A. accipitrinus; and in the pelvis, the dorsal plane is wider and projects further forwards, relatively. In the foot Ph. 1, 2 of D. II are indistinguishably fused, but free in A. accipitrinus; whilst the furcula has the limbs nearer together and the median apophysis marked by a distinct ventralward flexure, which is wanting in A. accipitrinus.

The skulls of *Strix*, *Asio*, and *Photodilus*, when compared with regard to the tympanic cavity, prove extremely interesting, forming a series increasing in complexity, from *Strix*, through *Photodilus*, to *Asio*. The nature of the modifications can be studied in the Pl. 2. figs. 2, 3, 5.

The skull of *Photodilus* is in many respects besides an interesting one. In the form of its maxillo-palatine it is intermediate in type between the Strigidæ and Asionidæ. It has the vestigial vomer of Ketupa; the swollen antorbital and interorbital septum of Strix; the lachrymal of the Asionidæ; the skull-roof of Syrnium, though less swollen by pneumatic tissue; a quite peculiar quadrate, inasmuch as its orbital process is vestigial and recalls that of the Caprimulgi.

The skeletons of the larger species of *Athene* and *Glaucidium* are very difficult to distinguish, so much so that it is probable that a comparison of a large series would make it necessary to include both genera under one head. The small *Glaucidium* ridgwayi—the only small member of the genus represented in our Collection—differs far more from the larger members of the genus than the latter does from species of *Athene* of similar size.

The species included in the genus Syrnium require very careful study, judging from the few skeletons in our collection. It is possible that besides Pulsatrix one or two other forms will have to be redistributed. With regard to Pulsatrix it is interesting to note that whilst in its pterylography it is distinctly Bubonine, in its skull and trunkskeleton it partakes of the characters which obtain in Syrnium, being indeed almost halfway between S. uralense on the one hand, and Bubo on the other. S. uralense undoubtedly belongs to the genus Syrnium, though its skull differs at first sight from that of S. aluco. These differences, however, when examined, are only due to the exaggeration of the characters seen in S. aluco. Syrnium seloputo is another peculiar form, inasmuch as in its skull Bubonine characters are unmistakable, nevertheless Syrniine features predominate. The skull of Ciccaba is truly Syrniine, but I have not had an opportunity of examining Scotiapex in this particular. From the variability which obtains in the skulls of Syrnium it would seem that the group was but recently derived from the Buboninæ, and that but few of the connecting-links have yet disappeared. This subfamily will evidently repay much further research.

The parieto-alisphenoid articulation which obtains in *Ketupa*, *Bubo*, *Scops*, *Gymnoscops*, *Syrnium*, and apparently *Strix* also, may likewise be found in other genera when

nestling skulls are available. It will be interesting to see how many genera have the types of squamosal seen in *Speotyto*. I imagine it will be found in *Gymnasio*, *Nyctala*, *Surnia*, *Carine*, and *Glaucidium*, perhaps in others.

Genera and species are founded generally by ornithologists upon external characters only, and not seldom upon apparently slender foundations. In doubtful cases of this kind, an appeal to osteology will sometimes afford unexpected help. Thus Hodgson (14) founded the genus *Huhua* to include certain Owls hitherto regarded as belonging to the genus *Bubo*. Sharpe, in his Catalogue of Birds (25), suppressed Hodgson's genus, but has revived it in his Hand-list (26) and includes therein five species. Of these, but one is represented in the Museum Collection skeletons, in the shape of a trunk of *H. nipalensis*. The sternum of this is remarkable in that it differs not only from that of all the genus *Bubo*, but from that of all the Asionidæ, in possessing but a single pair of notches. It will be interesting to see whether this character is common to all the species included in the genus *Huhua*.

In the genus *Strix* specific differences are very small. Out of a total of 26 species recognized by Dr. Sharpe, only six are represented in the Collection. Of these six, strangely enough, that with perhaps the more distinctly marked skull, *S. poensis*, is regarded by Sharpe, on the evidence of external characters, as indistinguishable from *S. flammeus*.

Remembering the paucity of material at my command, it is well to be cautious in attaching importance to the distinctions which can be made out in these skeletons, but I give the following diagnoses as a foundation for further work.

A. Size larger, not less than 3 inches long.	
a. Pterygoids relatively thick, shaft with strongly curved anterior extremity ; supra-	
orbital process feeble; frontal not constricted in front of supraorbital process;	
sternum longer than coracoid	S. pratincola.
b. Pterygoid relatively slender, not much curved anteriorly; supraorbital processes	
large, triangular, frontal constricted in front of them; sternum and coracoid	
	S. delicatulus.
B. Size smaller, not exceeding 2.8 inches.	
c. Palatines with a slightly emarginate posterior lateral border; vomer large, filling	
space between maxillo-palatine processes; width of interorbital region behind	
lachrymal equalling distance from nasal hinge to anterior extremity of external	
nasal fossa; proc. lat. basalis of coracoid small, with emarginate lateral border	
not extending forward as far as proc. lat. anterior of sternum; sternum shorter	
than coracoid	S. flammeus.
d. Palatines with deeply emarginate posterior lateral border; vomer small, not filling	
space between maxillo-palatine processes; lachrymal relatively small; interorbital	
region with frontal not greatly inflated ; width across interorbital region behind	
lachrymal falling far short of distance from nasal hinge to anterior end of	
nostril; cerebral dome large and with a deep median furrow; sternum longer	
than coracoid; antero-ventral angles of preacetabular ilium produced forwards	
into long spikes	S. poensis.

$e_{*}$	Palatines with posterior lateral border convex ; vomer large, filling space between			
	maxillo-palatines; interorbital region behind lachrymal less in breadth than the			
	distance from nasal hinge to anterior angle of anterior nares; processus lateralis			
	basalis of coracoid straight, and extending beyond level of anterior lateral process			
	of sternum	S. perlatus.		
$f_{\cdot}$	Palatine with posterior lateral border nearly straight; vomer large; pterygoid of			
	great breadth distad of basipterygoid facet; lachrymal large and with very			
	shallow lachrymal groove	S. javanicus.		

## XI. SUMMARY.

It is doubtful whether, on the evidence of the skeleton alone, the Striges would ever have been separated from the Falconiformes, their resemblance osteologically to the Accipitres being most striking. The anatomy of the soft parts, however, shows conclusively that there is no real affinity between these two groups. The hind limbs of the Accipitres and the Striges, as Dr. Gadow has pointed out (12), are almost indistinguishable, yet the former has an ambiens muscle, the latter has not. Again, he reminds us, that though both Accipitres and Striges are carnivorous, yet the former have vestigial cæca and the latter extremely large cæca. In this absence of an ambiens, the form and size of the cæca, and in the convolutions of the intestines, according to Mitchell, we have a combination of characters agreeing more nearly with those of the Caprimulgi than with those of any other group. The pterylography also points to the same conclusion. Again, as in the Caprimulgi, the skull is often extremely pneumatic, e. g. Strix, Asio, Photodilus; whilst the peculiar form of the lachrymal of the Striges is met with elsewhere only among the Caprimulgi. The same may be said of the suppressed lachrymo-nasal fossa and the basipterygoid processes. The general character of the sternum is also Caprimulgine, though, strangely enough, the pelvis is most remarkably Accipitrine. The form of the anterior palatal fossa is peculiar to the Owls.

A comparison between the skull of a very young nestling *Syrnium* or *Bubo* with a skull of similar stage of development of *Steatornis* will reveal some striking similarities of structure which will still further aid in establishing the Caprimulgine theory of origin of the Striges.

It will be remembered that in the first part of this memoir, in which the pterylological characters were dealt with, this group seemed to fall naturally into two families, the first containing the Barn-Owls only, the second all the remaining forms; these were further divisible into two sub-families—the Asioninæ and the Nyctalinæ.

Judging by osteological characters alone, the main division into families still holds good, but it would appear to be necessary to recognize about six sub-families belonging to the Asionidæ, instead of two. This subdivision, it should be remarked, would be founded on the characters of the skull only, the axial and appendicular skeletons being remarkably alike in all the members of the family.

The six sub-families would be :---

1. Asioninæ.

2. Photodilinæ.

- 3. Buboninæ.
- 4. Syrniinæ=Syrnium, Scotiapex, Ciccaba.
- 5. Nyctalinæ=Speotyto, Gymnasio, Nyctala.
- 6. Surniinæ=Surnia, Athene, Glaucidium.

I do not, however, propose to supersede the classification I originally suggested by the above. It is set down here merely for the purpose of contrasting the results given by the two systems. It is almost certain that the outcome of a study of the myology, convolutions of the intestines, and other characters will suggest yet other combinations. Obviously, therefore, it is best to wait until a survey can be made of all the factors, before really sound results can be obtained.

## XII. KEY TO THE FAMILIES AND SPECIES.

#### A. SKULL. (Plates 1 and 2.)

Upper jaw markedly hooked; nostrils holorhinal and impervious; with functional basipterygoid processes; lachrymal without supraorbital process and placed far forwards so as to encroach upon the lachrymo-nasal fossa; lachrymo-nasal fossa greatly reduced, partly by the encroachment of the lachrymal, and partly by the great upward development of the maxillo-palatine processes; palate with a large anterior palatine vacuity; desmognathous, the bridge being formed by ossification of the alinasal cartilages forming the floor of the anterior olfactory chamber; maxillo-palatine processes not meeting in the mid-ventral line; parasphenoidal rostrum very short.

A. Orbit very small; interorbital septum of great thickness; vomer large, inflated, fusiform, and fused with palatines; maxillo-palatines relatively small; lachrymal of great size, subconical or subquadrate, thrust far into the lachrymo-nasal fossa, and leaving only a small passage for the lachrymo-nasal duct; roof of skull domeshaped, with a deep median groove, and highly pneumatic ; palatines fused one with another in the middle line behind the vomer; nasal septum deeply notched along its postero-dorsal border, the notch leading into the cranio-facial fissure; floor of anterior nasal cavity perforated; palatines fused with one another in the middle line behind the vomer STRIGIDÆ. B. Orbit moderately or very large; lachrymal columnar; interorbital septum thin \*; antorbital plates thin †; nasal septum without a notch posteriorly . . . . ASIONIDÆ. a. Orbit relatively small; tympanic cavity large, well-defined, the "postcavernum" rising upwards to level of supraorbital process; postorbital processes small, projecting obliquely from orbit, and arising in front of and below level of squamoso-parietal tympanic wing; conspicuous supraorbital processes; frontal between supraorbital process and base of squamoso-parietal wing with strongly bevelled free edges forming a shelving supraorbital plane; nostrils very long, and with irregular inferior border; vomer relatively large; antorbital plate very long, nearly reaching quadrato-jugal bar; interorbital

<sup>\*</sup> Asio and Photodilus only among the Asionida have a thick interorbital septum, but the peculiar form of the tympanic cavity and of the supraorbital region render the skulls of these two genera perfectly distinguishable from that of Strix.

<sup>†</sup> In Photodilus the antorbital plate is thick, and resembles that of Strix.

<ul> <li>b. Orbit very large ; interorbital septum thick ; antorbital plate spongy ; roof of skull arched with supraorbital processes ; postorbital processes of great size, projecting far outwards ; tympanic cavity extending upwards as a narrow gorge between the postorbital and squamoso-tympanic process (= post-cavernum); temporal fossæ wanting ; vomer vestigial</li></ul>	Photodilus.
<ul> <li>a'. Remains of vomer blade-shaped; palatines with mesial borders of posterior ends straight and meeting in middle line; pterygoids sharply truncated, expanded distally and touching the parasphenoidal rostrum; maxillo-palatines rising upwards so as nearly to obliterate the lachrymo-nasal fossa; lachrymal small, not reaching the quadrato-jugal bar</li></ul>	Ketupa.
<ul> <li>pterygoids; with large triangular supraorbital processes; lachrymonasal fossa extremely reduced.</li> <li>b". Palatines with strap-shaped processes on mesial border, keeping articular orde aport</li> </ul>	Pulsatrix.
<ul> <li>ends apart.</li> <li>a<sup>m</sup>. Fronto-nasal region of interorbital roof widest; lachrymal very large; temporal fossa never bridged</li></ul>	Bubo.
of tympanic	Scops.
<ul> <li>b<sup>4</sup>. Quadrato-jugal with a triangular process below postorbital process.</li> <li>c'. With prominent, blunt, supraorbital processes overarching middle of orbit; frontal laterally constricted behind supraorbital processes so as to cause postorbital processes to stand out prominently; palatines with large space caudad of vomer; vomer vestigial</li></ul>	^ Ninox. - Sceloglaux. { Syrnium. L Ciccaba.
<ul> <li>d'. Tympanic cavity closed above by junction of squamoso-tympanic wing with postorbital process.</li> <li>a". Tympanic chamber symmetrical.</li> <li>a". Temporal fossa large.</li> </ul>	Circcuou.
<ul> <li>a<sup>s</sup>. Supraorbital processes long and pointed; nostrils nearly circular.</li> <li>b<sup>t</sup>. Supraorbital processes vestigial; nostrils oblong.</li> <li>b". Tympanic cavity markedly unsymmetrical; temporal fossæ vestigial.</li> <li>e'. Supraorbital processes long and slender; quadrato-jugal with a triangular process below postorbital process; tympanic cavity open above; ramal</li> </ul>	~ •
<ul> <li>vacuity of mandible large.</li> <li>a". Squamosal wing of tympanic with broad, squarely truncated outer border, not projecting beyond postorbital process; pterygoid long, slender, and straight; tympanic cavity comparatively shallow, not rising to the level of the floor of the temporal fossa; palatines wide apart caudad</li> </ul>	Surnia.

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$b^{\prime\prime}.$	Squamosal wing of tympanic with broad rounded lateral border, projecting	
	considerably beyond base of postorbital processes; pterygoid sigmoidally	
	curved; tympanic cavity very large and bullate, extending upwards	
	and backwards to underlie the floor of the temporal fossa; palatines	
	nearly touching caudad	Carine.
$c''_*$	Squamosal wing of tympanic projecting but slightly or not at all beyond	
	base of postorbital process.	Glaucidium *.

#### B. VERTEBRÆ.

All the presynsacral vertebræ are free and heterocœlous; the last thoracic is included in the synsacrum. Innominates fused with synsacrum. The centra of the thoracic bear more or less conspicuous pneumatic apertures opening beneath the transverse processes. Only the 2nd to 5th and the 14th bear neural spines. The cervical ribs of all save the 13th and 14th vertebræ are very short or vestigial; the 13th and 14th ribs are free, and the 14th may bear uncinates; the catapophyses never meet to form a caual. The *fovea lumbalis ischiadica* and *pudendalis* are all well defined, and thereby the vertebral column may be readily distinguished from that of the Caprimulgi; but there seems to be no character of universal application by which the vertebral column of the Striges may be distinguished from that of the Falconiformes, when birds of a similar size are being compared. The distinctions between the vertebræ of the two families of the Striges and the various genera thereof are very slight.

a. Neural spines high, sloping forwards and interlocking.

a'. Transverse processes of thoracic vertebræ with anterior and posterior angles	
produced into lateral spinous processes; hypapophyses long, not extending	
beyond 2nd thoracic.	
a". Preacetabular ilium with dorsal border nearly straight; ventral border deeply emarginate; preacetabular width nearly equal to width across anti-	
trochanter	Asio.
b''. Preacetabular ilium with dorsal border nearly straight; ventral border gently hollowed; preacetabular width much less than width at anti-	
trochanter	Bubo.
c''. Preacetabular ilium with strongly arched dorsal crest; ventral border	
deeply hollowed; preacetabular width equal to width across anti-	
trochanter	Ketupa.
b'. Transverse processes without spinous lateral angles; hypapophyses long,	*
extending to 3rd thoracic; lumbar vertebra 4; lumbar parapophyses 1-2	
vestigial; planum coccygeum wanting	Carine.
b. Neural spines high, nearly vertical and feebly interlocking.	
Hypapophyses short, not extending beyond the 2nd thoracie; 4 lumbar vertebræ;	
roof of <i>fovea pudendalis</i> not obstructed by parapophyseal processes; a con-	
	Sumium
spicnous <i>planum coccygeum</i>	syrniam.
c. Neural spines high, not interlocking; hypapophyses short, not extending beyond	3.7*
1st thoracic; 3 lumbar vertebræ	Ninox.
d. Neural spines low, interlocking.	
a'. Hypapophyses long, spine-like, extending back to 3rd thoracic; planum coccy-	

geum indistinct.

\* For remarks on Glaucidium, see p. 36.

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	a''. 4 lumbar vertebræ	Glaucidium.
	a". 4 lumbar vertebræ	Megascops.
	$b^{\prime\prime}$ . 3 ,, ,,	Nyctala.
	b'. Hypapophyses obsolete, or 1-2 only; lumbar vertebræ 4; fovea pudendalis with	
	intervertebral perforations	Strix.
e.	Neural spines low, not interlocking ; hypapophyses long, spine-like, extending	
	back to 2nd thoracic.	
	a'. 4 lumbar vertebræ; canales ileo-lumbales opening near the middle of the strongly	
	arched fovea	Surnia.
	Canales ileo-lumbales opening near the anterior end of the crest of the pre-	
	acetabular ilium	Speotyto.
	b' 3 lumbar vertebræ.	Scops.

## C. STERNUM AND PECTORAL GIRDLE.

Corpus sterni large, with the hinder border always notched; carina well developed, extending backwards to the extreme end of the sternum; anterior lateral processes small; antero-lateral border of sternum marked by a deep scar for the sterno-coracoideus, which extends backwards to the level of the last sternal rib; coracoid grooves but slightly overlapping; coracoid with a large *processus procoracoideus*; furcula **U**-shaped, and lacking a hypocleideum.

A	. Sternal plate with a single pair of notches posteriorly; furcula non-pneumatic, articulating with antero-ventral angle of carina by a broad facet; distal end not	
	articulating with acrocoracoid by a special facet	STRIGIDÆ.
В	. Sternal plate with a pair of notches posteriorly; furcula pneumatic, not articulating with the antero-ventral angle of the carina by a facet; distal end articulating	
	with the acrocoracoid by a special facet	
	a. Outer pair of notches relatively small, but exceeding the depth of the keel	Asio.
	b. Outer pair of notches obsolete	Huhua.
	c. Length of coracoid equals length of sternum from its anterior border to the base of the inner notch.	
		Bubo.
	a'. Coracoid with large processus lateralis basalis	Ketupa.
	b'. Coracoid with a small processus lateralis basalis	Speotyto.
		Scops. Ninox.
	b'. Coracoid with a small processus lateralis basalis	Pulsatrix. Athene.
		Glaucidium. Syrnium.
	e. Spina externa of sternum wanting.	
	a'. Ventral lip of coracoid groove entire $\ldots$ $\ldots$ $\ldots$ $\ldots$	Nyctala.
	b'. Site of spina externa marked by notch	Gymnasio.

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#### D. PELVIC GIRDLE \*.

Innominate fused with synsacrum ; preacetabular ilium very long ; pectineal process wanting ; the preacetabular ilium with a deeply emarginate inferior border ; the dorsal plane of the postacetabular ilium continued forwards and outwards to form a conspicuous shelf overhanging the acetabulum ; ischium continued backwards into a point along the pubis; pubis always complete ; an iliac recess always present.

#### E. PECTORAL LIMB.

Humerus with a moderately large, rounded, pectoral crest, a small ectepicondylar, and large, swollen entepicondylar tuberosities, a deep linguiform impression for the *brachialis inferior*; the *sulcus transversus* obsolete, the impression for the pectoralis occupying nearly the whole of the pectoral crest, and the impression of the *deltoideus major* extending for a considerable distance down the shaft.

Forearm and hand non-pneumatic. Radius bearing a slender bony arch or traces of it, on the second fifth of the postaxial border, and a sesamoid at its distal end.

Manus with the proximal end of Mc. III joining Mc. II distad of the articulation of the pollex with its metacarpal; Ph. 1 of D. II with a deeply emarginate postaxial border.

#### F. Pelvic Limb.

All the bones non-pneumatic; ecto- and ento-cnemial crests not feebly developed; a tibio-tarsal extensor bridge wanting; hypotarsus simple; Mc. I very short.

A. Phalanx 1 of D. II short; Ph. 2 of D. III short; tarso-metatarsus with a strong	
extensor bridge	SIONID.E.
B. Phalanx 1 of D. II long; Ph. 2 of D. III long; tarso-metatarsal extensor bridge	
wanting	STRIGID.E.

# LIST OF THE MORE IMPORTANT WORKS AND PAPERS REFERRED TO OR CONSULTED.

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- 3. BEDDARD, F. E.-Structure and Classification of Birds. 1898.
- 4. BEDDARD, F. E.-" On Photodilus badius," Ibis, 1890.
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- 6. COLLETT, C.--" On the Asymmetry of the Skull in Strix Tengmalmi," P. Z. S., 1870.
- 7. COLE, F. J.—" Some Variations in the Spinal Nerves of the Frog, with a Note on an Abnormal Vertebral Column," Trans. Liverpool Biol. Soc., vol. xv. (1901).
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- 9. D'ALTON.- De Strigum Musculis Commentatis. Halis, 1837.
- 10. EVANS, A. H.-Birds. 1899.
- 11. GADOW, H.—"On the Evolution of the Vertebral Column of Amphibia and Amniota," Phil. Trans. Roy. Soc., B. vol. clxxxvii. (1896).
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- 13. GADOW, H.-Bronn's Thierreich, Syst. Theil. 1893.

\* The variation of the pelvis among the Striges is so slight that workable characters for distinguishing the Families and Genera cannot be found.

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- 19. MILNE-EDWARDS, A.—" Observations sur les Affinités zoologiques du Genus Photodilus," Nouv. Arch. Mus., 2<sup>e</sup> sér. t. i. (1878).
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- 22. PECK.—" Variation of Spinal Nerves in Caudal Region of Pigeon," Journ. Morphol., vol. iii. (1893).
- 23. RIDEWOOD, W. G.—"On the Development of the Vertebral Column in *Pipa* and *Xenopus*," Anatom. Anzeig., Bd. xiii. (1897).
- 24. SHARPE, R. B.-A Review of Recent Attempts to Classify Birds. 1891.
- 25. SHARPE, R. B.-Cat. Striges Brit. Mus., vol. i. (1875).
- 26. SHARPE, R. B.-Hand-list of Birds, vol. i. (1899).

с.,

n = nasal.

# EXPLANATION OF PLATES 1 AND 2.

Explanation of letters.

a.s. = alisphenoid.	no.p. = (error for a.op.).
ao.p. = antorbital plate.	n.s. = nasal septum.
a.p.v.=anterior palatal vacuity.	p. = parietal.
b.pt. = basipterygoid process.	pa. = palatine.
b.s. = basisphenoid.	po.p. = postorbital process.
col. = columella.	pmx. = premaxilla.
or cor.=coronoid.	pro. = pro-otic.
d. = dentary.	pt. = pterygoid.
e.g. = eustachian groove.	q. = quadrate.
exo. = exoccipital.	q.j.=quadrato-jugal.
f = frontal.	r.t.a. = recessus tympanicus anterior.
f.f. = floccular fossa.	r.t.p.= ,, ,, posterior.
h.pt. = hemipterygoid.	s.a. = supra-angular.
io.s. = interorbital septum.	s.o. = supraoccipital.
l. = lachrymal.	so.p.=supraorbital process.
l.pt. = (error for b.pt.)	sq. = squamosal.
mxp. = maxillo-palatine.	sq.o.w. = squamoso-occipital wing.
m.int. = meatus internus.	t.f. = temporal fossa.
mes. = mesethmoid.	v.=vomer.

## PLATE 1.

Figs. 1-7, dorsal aspect of adult skulls; 8-14, palatal aspects of adult skulls; 15 and 16, of young skulls.

- Fig. 1. Skull of *Bubo capensis*, showing the forward position of the vestigial supraorbital processes of the frontal.
  - 2. Skull of Bubo perspicillatum, to show the large size of the supraorbital processes.
  - 3. Skull of Nyctala Tengmalmi, showing the marked asymmetry of the skull in the position of the postorbital processes.
  - 4. Skull of Spectyto cunicularia, showing large postorbital processes and the temporal fossa bridged by the superior angle of the squamoso-occipital wing of the tympanic fossa.
  - 5. Skull of *Photodilus badius*, showing the great size of the postorbital processes and the backward position of the supraorbital processes.
  - 6. Skull of *Strix flammea*, showing the absence of supraorbital processes, and the peculiar "domeshaped" roof.
  - 7. Skull of Asio accipitrinus, showing an incipient supraorbital groove and peculiar postorbital processes, to see which properly a comparison must be made with Pl. 2. fig. 2. The interest about the supraorbital processes lies in the fact that they are developed by the

frontal bone, and not formed by the horizontal process of the lachrymal as in birds generally.

- 8. Palate of *Bubo capensis*, showing large maxillo-palatines and a small vomer. The palatines do not quite meet in the middle line.
- 9. Palate of *Bubo perspicillatum*, the vomer has become suppressed; and the palatines meet in the middle line.
- 10. Palate of Nyctala Tengmalmi, showing reduced maxillo-palatines; a vomer; and the great width of the base of the parasphenoidal rostrum.
- 11. Palate of *Photodilus badius*, showing great width of parasphenoidal rostrum; vestigial vomer; and large maxillo-palatines, and lachrymal.
- 12. Palate of *Strix flammea*, showing peculiar shape of vomer; great width of parasphenoidal rostrum at base; and the peculiar shape of the maxillo-palatines.
- 13. Palate of Asio accipitrinus, showing swollen parasphenoidal rostrum; the palatines separated one from another posteriorly; and large maxillo-palatines.
- 14. Palate of Spectyto cunicularia, showing maxillo-palatines and absence of vomer.
- 15. Dorsal aspect of skull of Syrnium aluco, showing sutures.
- 16. Dorsal aspect of skull of *Speotyto cunicularia*, showing sutures.—Note the great difference in the form of the squamosal in the two skulls.

## PLATE 2.

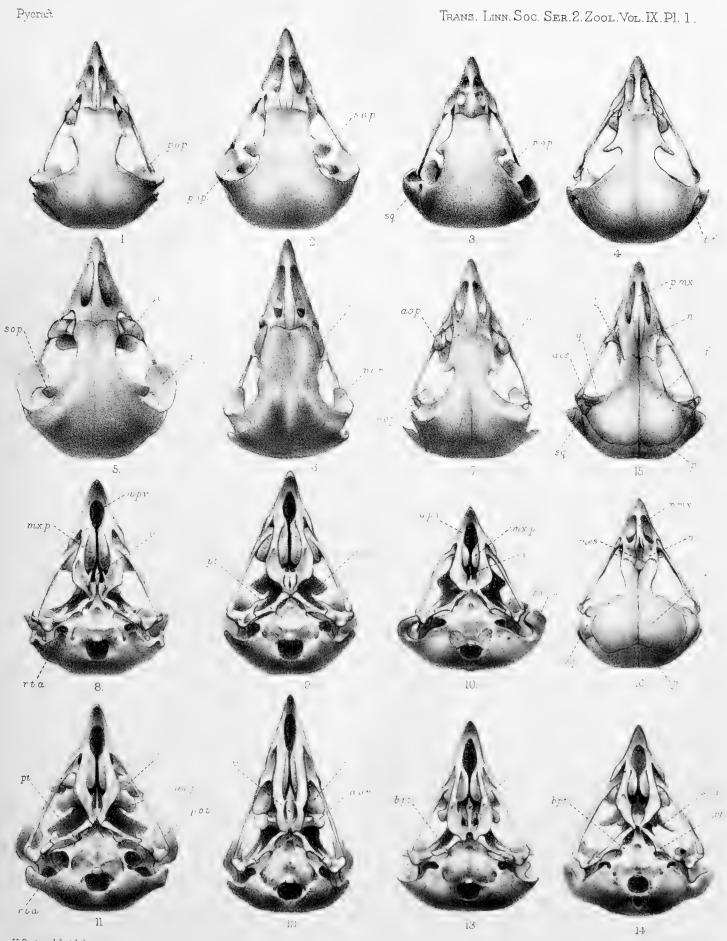
#### Lateral aspect of the skull.

- Fig. 1. Left side of Nyctala Tengmalmi, to show form of tympanic cavity.—Note the form of the squamoso-parietal wing and contrast with that of right side. For the sake of convenience in comparison the left side has been reversed.
  - 1 a. Right side view of same specimen.—Note the form of the squamoso-parietal wing and its relation to postorbital process, and contrast with fig. 1.
  - 2. Skull of Asio accipitrinus, showing the enlarged tympanic cavity or "cavernum" and the peculiar postorbital process.
  - 3. Skull of *Strix flammea*, showing the reduced size of the orbit, large lachrymal, and the high dome-shaped cranial roof.

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- Fig. 4. Skull of *Bubo capensis*, showing the large postorbital process and a well-marked temporal fossa; the only skull in this series, it is to be noted, in which this is normally developed.
  - 5. Skull of Photodilus badius, for comparison with Asio and Strix.
  - 6. Skull of *Speotyto cunicularia*, showing the large postorbital process; a large triangular plate on the jugal; and the temporal fossa bridged by the squamoso-parietal tympanic wing.
  - 7. Skull of nestling Syrnium aluco, showing sutures. Compare the form of the squamosal, and its relations to the parietal and frontal, with that of Speotyto, fig. 8.
  - 7 a. Inner view of the same.-Note the position of the squamosal.
  - 8. Skull of nestling *Speotyto cunicularia*, showing sutures.—Note the form and size of the squamosal, and its relation to the frontal, and compare with fig. 7.
  - 8 a. Inner view of the same.—Note the great amount of the squamosal surface visible from the inside of the skull.



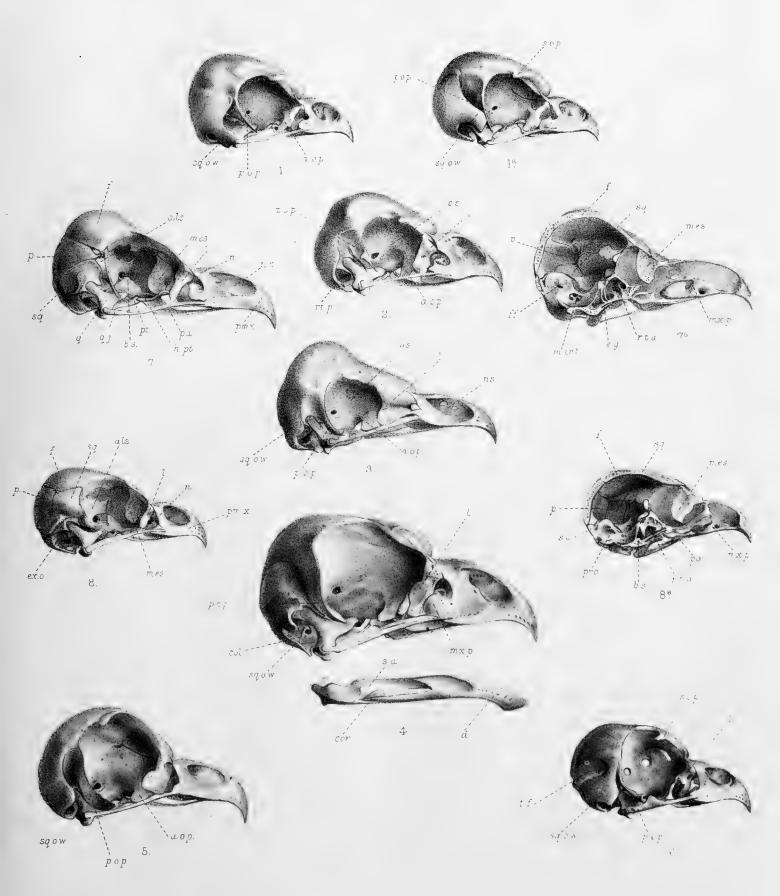
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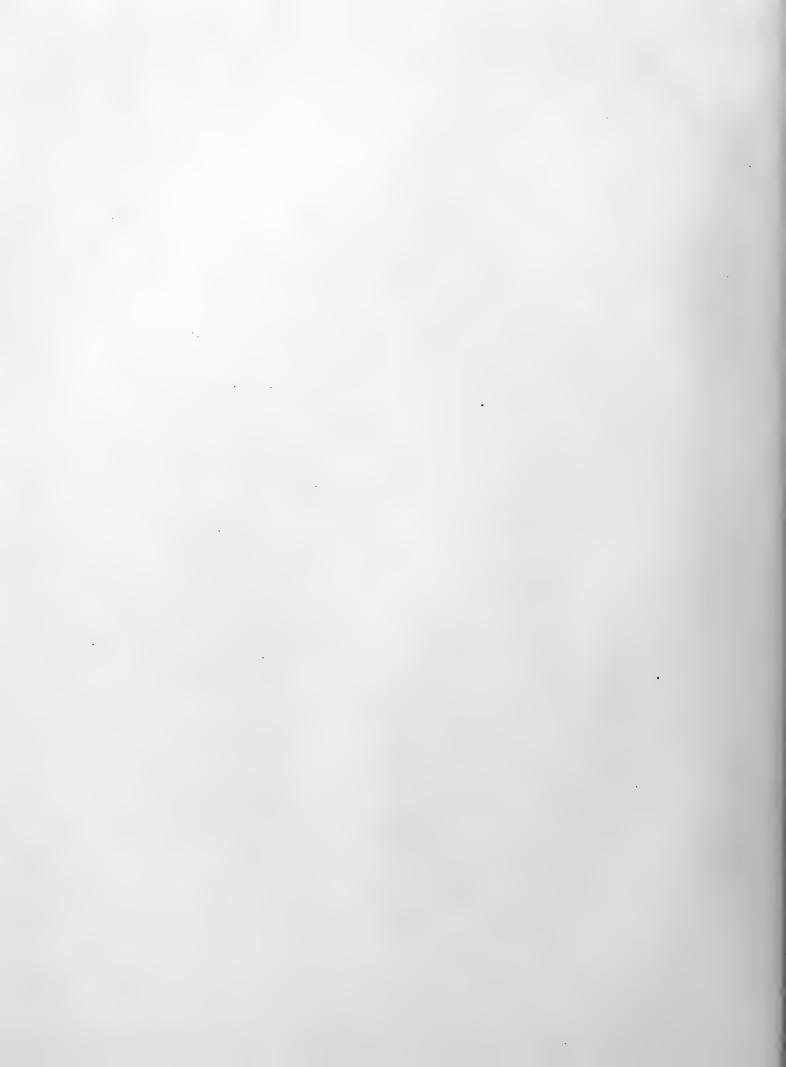


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West, Newman imp



# II. On some Points in the Visceral Anatomy of the Characinidæ, with an Enquiry into the Relations of the Ductus Pneumaticus in the Physostomi generally. By WALTER S. ROWNTREE, B.Sc., F.L.S.

# (Plates **3** & **4**.)

Read 5th March, 1903.

#### SYNOPSIS.

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# INTRODUCTORY.

THE notes here embodied represent an investigation, begun two years ago, in the course of which I have had under examination a considerable number of spirit-specimens and skeletons, representing some 55 species and 33 genera of the Characinidæ. Access to these has been permitted me by G. A. Boulenger, Esq., F.R.S., of the British Museum of Natural History, of whose sympathetic assistance I cannot speak too gratefully. For purposes of comparison I have also had under examination certain Cyprinoids, Siluroids, Gymnotids, and other Physostomes, together with *Polypterus, Protopterus, Acipenser, Amia*, and *Lepidosteus*, for the two latter of which I am indebted to the kindness of Professor Bashford Dean, of Columbia University, New York. The investigation owes its initiation to Professor G. B. Howes, F.R.S., whose encouragement and helpful criticism have been of the greatest value to me throughout.

Further, I gladly avail myself of this opportunity of expressing my indebtedness to other friends for assistance rendered: to C. E. Stansfield, Esq., M.A., and to Fraülein Stöy, for facilitating at various times the labour involved in searching the literature of the subject; and to the Rev. T. R. R. Stebbing, F.R.S., for kindly identifying for me a rare parasitical crustacean mentioned in the text. The starting-point of my work has been Sagemehl's masterly papers on the skull of the Characinidæ, and on the accessory branchial organ of *Citharinus*, published in the 'Morphologisches Jahrbuch' for 1885 and for 1886-7. I have also made large use of Boulenger's ' Les Poissons du Bassin du Congo ' and ' Matériaux pour la Faune du Congo '; of Günther's ' Catalogue of the Fishes in the British Museum,' vol. v.; of Cuvier and Valenciennes's ' Histoire Naturelle des Poissons,' vols. xix. and xxii.; of Stannius's 'Anatomje der Wirbelthiere,' and of several other works.

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The Characinidæ constitute a well defined yet widely diversified family of Teleostean fishes, falling under the division Physostomi. They are entirely restricted to the fresh waters of Tropical Africa and America, a distribution in itself sufficiently curious. The greater number of the five hundred odd species known are denizens of the Neotropical region. No genus is represented on both sides of the Atlantic.

Amongst the more obvious and generally recognized characteristic features of the family are :---

The fusion and modification of the first four vertebræ, in relation to the Weberian mechanism; a physostomous air-bladder, transversely constricted, as in the Carps, into an anterior and a posterior chamber; usually an adipose second dorsal fin; a non-protrusible mouth, the upper margin of which is commonly formed by both premaxilla and maxilla; usually teeth on the premaxilla and the dentary, sometimes also on the maxilla and the palatine; pelvic fins abdominal; pectoral fins set low on the body and folding like the pelvic fins; body covered with scales, cycloid or ctenoid; head without scales; parietals separated by a longitudinal fissure, or united by a sagittal suture; opercular bones complete; symplectic present; a supraoccipital spine, often long; suborbitals usually large; pyloric appendages present; barbels absent.

By the earlier writers on the subject the majority of the then known forms comprised in this family were classed as Salunonoids, others as Clupeids. Johannes Müller \* (1843-4) was the first to separate these and to include them in the Characinidæ, basing this change on the possession by these forms of the Weberian apparatus. It was, however, reserved for Sagemehl † (1884) to attach full weight to this character and to unite together the families possessing it—the Cyprinidæ, Siluridæ, Characinidæ, and Gymnotidæ—into one group, the "Ostariophyses."

The general effect of Sagemehl's paper is the establishment of three main propositions :—

- (1) That the parts of the Weberian mechanism in the families named are homologous, implying community of origin, not simply analogous, as previously held. This conclusion he supports by arguments deduced from comparison of the shouldergirdle, the interparietal fissure and other cranial characters, the opercular apparatus, and other structures.
- (2) That the Characinidæ fall naturally into three distinct subfamilies, no one of which can be regarded as being derived from another, but which have all branched off from a common ancestral line. These he designates the Erythrinoids, the Herbivorous True Characinidæ, and the Carnivorous True Characinidæ.
- (3) That the Characinidæ, and more especially the Erythrinoids, in numerous cranial and other features, recall the conditions found in *Amia calva* and, in a less degree, in other Ganoids.

<sup>\*</sup> Joh. Müller, "Über den Bau und die Grenzen der Ganoiden," Abhandl. der Berl. Akad. d. Wissensch., 1844.

<sup>†</sup> M. Sagemehl, "Das Cranium der Characiniden," Morph. Jahrb., Bd. x. 1884.

Sagemehl's conclusions appear to have been drawn in the main from the examination of the following twelve species :---

						Macroaon iranira.
Erythrinoids						Erythrinus unitæniatus.
						Lebiasina bimaculata.
Herbivorous True Characinids .				•		Citharinus Geoffroyi.
						( Alestes dentex.
						Tetragonopterus fasciatus.
						,, melanurus.
Carnivorous True Characinids .						,, maculatas.
Carmitorous 11de Charaennus .	•	•	Anacyrtus gibbosus.	Anacyrtus gibbosus.		
						Hydrocyon Forskalii.
						,, brevis.
						Sarcodaces odoë.

The Amioid characters insisted on so strongly in the paper in question, some only of which I can claim to have verified, I will attempt to summarize. They apply with especial force to the Erythrinoids, but some more generally. Most have reference to the skull. They are as follows :—

The angle of inclination between the posterior face of the skull and the skull-roof.

The whole exterior form of the skull, its solid roof, its bony surface, its naked and sculptured bone, its lateral shielding by the extended suborbital bones.

The naked dentigerous palatines, and the almost identical formation of the border of the mouth.

Certain relations of the labyrinth and the recess in which it lies.

The relations of the suspensorium.

The presence of a median cartilage situated between the hypopharyngeal bones, partially ossified and dentigerous in *Amia*, rudimentary in *Erythrinus*, further reduced and fused in *Macrodon*, absent in the other Characinidæ and apparently in all other Teleosts.

The relations of the nasal bones with the premaxillæ and the ethmoid.

The form of the parietals and of the squamosals.

The relations of the mucous canals of the cranial bones.

The relations of the intercalare.

Certain relations of the occipital region of the skull and the associated nerves.

The development of a canal for insertion of the eye-muscles.

In all these characters the conditions existing in at least some Characinidæ, usually the Erythrinoids, are such, according to Sagemehl, as suggest a connection with those found in  $\Delta mia$ . The differences are, indeed, often obviously such as have been conditioned by the development in the former of the Weberian apparatus. Nevertheless, apart from the skull region, there appears to be but little in the comparative anatomy of the two types to suggest close relationship; and in the skull itself there is at least the supraoccipital to be reckoned with as having no counterpart in  $\Delta mia$ .

In any case, the hypothesis of a direct genetic relationship between Amia and the

 $\mathbf{S}^*$ 

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Characinidæ seems to be rendered untenable by the fact that, whereas the resemblance is closest in the case of the Erythrinoids, the actually most primitive conditions in certain particulars are to be found in the highly modified herbivorous forms—conditions, indeed, the homologues of which have to be sought not amongst the Ganoids, but amongst the more lowly Selachians. This fact appears also to negative the hypothesis which suggests itself, that the Amia-like Erythrinoids represent the ancestral stock from which the other two groups have diverged.

- (1) The greater extension of the cranial cavity towards the nasal region, and the associated possession of long olfactory tracts.
- (2) The less advanced ossification of the primordial skull, especially in the ethmoid region.
- (3) The simple undifferentiated socket for the hyomandibular.
- (4) The possession (in *Citharinus* at least) of two "submaxillaries," ossifications which the author homologizes with the upper labial cartilages of Selachians. These are not found in the other Characinid groups, nor in *Amia*, though they exist in certain other Teleosts (*Gymnotus*, *Perca*, some Cyprinoids).
- (5) The persistence, in *Citharinus* and other herbivorous forms, of the epibranchial of the fifth arch, standing in connection with the fourth epibranchial, and serving to support the accessory respiratory organ. A similar vestige has been described in a Clupeid. In the other Characinids, and in *Amia*, it is unknown.

With regard to the Carnivorous Characinidæ (other than the Erythrinoids), Sagemehl considers that the cranial conditions are entirely such as might conceivably have been derived from the Citharinoid skull, but that the jaw-apparatus and the relations of the hyomandibular suggest rather a connection with the Erythrinoids.

On the whole evidence, therefore, so far as the skull region is concerned, the conclusion to be drawn seems to be that the carnivorous (non-Erythrinoid) forms present the most advanced conditions of development, whilst the Erythrinoids and Citharinoids are more primitive, but that these two latter groups do not show any nearer approach to one another; in fact, that the three groups must have branched out independently from a common stock.

The African form *Sarcodaces*, however, classed with the non-Erythrinoid carnivorous group, presents, as Sagemehl insists, most striking detailed resemblances to the Erythrinoids in its cranial and facial characters, though separated from them by the possession of an adipose second dorsal fin, and by the absence of teeth on the palatine.

Moreover, the assumption that all the herbivorous forms are to be classed together that is, that the herbivorous habit has only originated once within the limits of the family—would appear to be scarcely warranted by the examination of the single genus (*Citharinus*) described by Sagemehl, though, it is true, he refers at times to others.

The three groups or subfamilies marked out by that writer can, therefore, it seems to me, be only accepted as, at most, a provisional basis of classification.

My own observations upon this most interesting and perplexing family of fishes have

been, in the first instance, mainly directed towards the comparative examination of the viscera. No detailed description of these organs throughout any considerable section of the family at present, I believe, exists; and it is perhaps hardly to be expected that such plastic and adaptive structures should materially contribute to the elucidation of the affinities of the group. Nevertheless, it has seemed to me that such an investigation might not be altogether valueless; and amongst the results which I now make known, pending the conclusion of further work, are some hitherto unrecorded relations which seem to be of some interest and importance.

The following is a list of the species of Characinidæ examined by me. Except in a few instances, in which the skeleton only was available, they were represented by spirit-specimens, for the most part fairly well preserved. With certain specimens it has only been permitted me to make an abdominal incision, but with many a more complete dissection has been possible.

For convenience the list has been arranged on the basis of Sagemehl's classification, but it should be pointed out, in using the terms "carnivora" and "herbivora," that some forms under the former head ( $\Delta lestes$  for example) are clearly onnivorous in habit.

ERYTHRINOIDS: no adipose fin.

(Tropical America.)

- 1. Erythrinus unitaniatus.
- 2. Macrodon trahira.
- 3. Lebiasina bimaculata.
- 4. Pyrrhulina unifasciata.

#### TRUE CHARACINIDÆ: CARNIVORA.

(Tropical Africa.)	(Tropical America.)
5. Sarcodaces odoë.	26. Tetragonopterus abramis.
6. Hydrocyon brevis.	27. ", multiradiatus
7. ", Forskalii.	28. ,, fasciatus.
8. ,, goliath.	29. ", argentatus.
9. Bryconaethiops microstoma.	30. Brycon falcatus.
10. Alestes nurse.	31. Chalcinus brachypomus.
11. " Kotschyi.	32. Chalcinopsis dentex.
12. " longipinnis.	33. Myletes brachypomus.
13. ,, dentex.	34. Anostomus fasciatus.
14. ,, macrolepidotus.	35. Leporinus Frederici.
15. Micralestes acutidens.	36. Nannostomus lateralis.
16. ", altus.	37. Salminus maxillosus.
17. ,, Stormsi.	38. Serrasalmo piraya.
18. Petersius Leopoldianus.	39. " humeralis.
19. Eugnathichthys Eetveldii.	40. Anacyrtus microlepis.
20. " macroterolepis.	41. " guatemalensis.
21. Phago Boulengeri.	
22. " loricatus.	
23. Paraphago rostratus.	
24. Neoborus ornatus.	
25. Ichthyoborus niloticus (besse).	

(Tropical Africa.)	(Tropical America.)			
42. Distichodus niloticus.	49. Prochilodus lineatus.			
43. " Antonii.	50. Curimatus dobula.			
44. Nannocharax niloticus.	51. ,, albula.			
45. Xenocharax spilurus.	52. ", Gilberti.			
46. Citharinus Geoffroyi.	53. ,, cyprinoides.			
47. ,, latus.				
48. ,, congicus.				
48 a. ,, macrolepis.				
48 b. Citharidium Ansorgii.				

TRUE CHARACINIDÆ: HERBIVORA.

## THE ALIMENTARY CANAL AND ITS APPENDAGES.

#### The Stomach.

In Characinids the short gullet passes often insensibly into the stomach, but in some cases the transition is marked by a sudden change of calibre or of wall-thickness. This latter condition I have observed more particularly in *Distichodus*, *Serrasalmo*, *Lebiasina*, *Alestes nurse*, and *Leporinus*.

The stomach has the form of a more or less expanded sac, of variable size, bent sharply on itself at the pyloric region. This flexure is usually ventrally directed (Pl. 3. fig. 1). But I have found numerous exceptions. In *Sarcodaces* the flexure was dorsal in every one of the nine specimens examined (fig. 2). In *Macrodon* and *Erythrinus* also the flexure was dorsal or laevo-dorsal (fig. 3). In all the sixty-three specimens of *Ichthyoborus*, which happened to be examined for a special purpose, the flexure was directed to the left side. In *Hydrocyon Forskalii* (several specimens) the stomach was flexed towards the right side. In *Nannocharax, Eugnathichthys*, and *Phago* the flexure was dorsal. The regularity with which these conditions were found was somewhat striking, although one can scarcely attribute any great significance to them.

The anterior or cardiac chamber of the stomach is usually much more capacious than the ascending or pyloric limb. It is, moreover, at least in some forms, highly distensible; the lining membrane, which is often deeply rugose when the stomach is empty and contracted, becoming quite smooth when the organ is distended with food. At the same time the stomach-wall, which may in the contracted state appear quite thick and fleshy, thins out and becomes so transparent that the contents become visible even in detail. Thus in one instance (*Sarcodaces*), where an entire *Anabas* was found in the stomach, the species of the ingested fish could be easily identified without opening the organ. The distension takes place longitudinally as well as transversely. The organ may indeed stretch to the full limit of the body-cavity, although in its contracted state not exceeding half that length. In the instance above referred to the length of the distended stomach, drawn tightly over the contained fish, was 11 cms., the *Sarcodaces* itself being only 25 cms. long. It is obvious, in view of the narrow and acutely reflected pyloric limb, that the stomach must possess great digestive activity. Fig. 2 shows the stomach of *Sarcodaces* contracted; fig. 3, that of *Macrodon* distended; both are represented as having been opened.

The cardiac chamber is often prolonged beyond the pyloric flexure into a more or less pronounced blind sac. This prolongation is large in *Hydrocyon* (fig. 1), still larger in *Salminus*, and yet further exaggerated in *Serrasalmo*. It is large also in *Macrodon* (fig. 3) and *Erythrinus*, in *Bryconaethiops*, and in *Tetragonopterus abramis*. In *Sarcodaces* (fig. 2), *Petersius*, and at least some species of *Alestes* it is smaller. In the other forms examined by me this sac can hardly be said to exist. This is most decidedly the case with the herbivorous forms, the stomach and entire alimentary canal of which, however, are altogether peculiar. The cardiac chamber is perforated near its anterior end by the opening of the ductus pneumaticus, to which I shall refer later. I merely wish at this stage to point out that in at least some cases the orifice of the duct seems to be actually in the wall of the stomach, rather than the œsophagus, if one may judge from the extension in front of it of the rugose folds. Such is the condition, for example, in *Erythrinus* and *Macrodon*, in *Sarcodaces*, *Hydrocyon*, *Salminus*, *Ichthyoborus*, and many of the forms I have examined.

In other cases, however, in which a sudden transition is apparent from cosophagus to stomach, the opening of the duct appears to be just at or behind the junction of the two. This I have observed in *Distichodus*, *Serrasalmo*, *Micralestes*, *Eugnathichthys*, and *Xenocharax*. In certain other cases—*Citharinus*, *Lebiasina*, *Alestes nurse*, and *Leporinus*—the orifice is in the narrower and thicker part of the tract, which one is inclined to regard as the cosophagus.

The ascending pyloric limb of the stomach is usually firmer and thicker-walled than the cardiac chamber. This condition becomes greatly exaggerated in *Citharinus* and the other herbivorous Characinidæ; so much indeed that whilst the cardiac chamber is extremely thin and delicate, the pyloric limb assumes the character of a veritable gizzard. The contents of the canal—vegetable matter and mud—are reduced after passing through this gizzard to the condition of an extremely soft pulp. *Citharinus, Distichodus, Xenocharax, Prochilodus,* and *Curimatus* agree in this particular, as also in others to be mentioned later. *Xenocharax,* however, in this as in other points presents a lower stage of differentiation than the other forms just named, the difference between cardiac and pyloric regions being less marked.

In the newly discovered form *Citharidium* \*, which may be described, as regards its external characters, as a *Citharinus* with ctenoid instead of cycloid scales, I have not yet had the opportunity of observing these relations.

## The Pyloric Cæca.

The stomach is marked off from the intestine, sometimes by a slight constriction, especially in Citharinoids, but also by the pyloric appendages, which are constantly present in considerable number in the Characinidæ.

\* Boulenger, G. A., "Description of a new Characinid Fish discovered by Dr. W. J. Ansorge in Southern Nigeria." Ann. & Mag. of Nat. Hist., Ser. 7, vol. ix. 1902, p. 144. The conditions in my specimens have rarely permitted of accurate counting, and there is reason to think that there is considerable variation even in individuals; but, supplementing my own observations with those of previous writers, I may make the following statement regarding the number of appendages commonly found in different forms :—

Erythrinus	٠	30	Cuvier & Valenciennes.
Macrodon		60 (+) in 2 rows	,,
Lebiasina	•	5 or 6	27
Pyrrhulina	•	6 (5 right, 1 left)	59
Other Characinids .	•	10 to 25, rising in Hydro- cyon and Citharinus	Boulenger.
		to 35 or 40.	

The appendages vary not only in number, but also in length and thickness, and in their arrangement. Thus, according to my observations, those of *Hydrocyon* are large and fall into three groups, two opposing one another at the pylorus, the third posterior to these and forming a sort of fringe to the intestine for about one-sixth of its entire length (2.5 cms. in 14 cms.). In *Sarcodaces* the appendages are short and numerous, and form a fringe to the intestine for about the first ninth of its course (1.5 cms. in 14 cms.). In *Sarcodaces* the appendages are short and numerous, and form a fringe to the intestine for about the first ninth of its course (1.5 cms. in 14 cms.). In *Ichthyoborus* they are numerous and long, but fine, and fringe the intestine for nearly one-sixth of its length (1.5 to 2 cms. in 12 cms.). In *Macrodon* they are continued for about one-fourth or one-fifth of the length of the intestine (3-4 cms. in about 13 cms.). In *Distichodus* the extension of the excel fringe is at its maximum amongst the forms I have examined. In this fish, the appendages at the pylorus are long, numerous, and fine, and are thence continued in an abbreviated condition as a fringe or sacculated border for about 9 cms., which, however, is only about one-seventh of the length of the intestine—very long in this and other herbivorous forms. In *Salminus* they are large and numerous, extending about 2 cms. along the intestine. In *Anacytus, Tetragonopterus*, and *Alestes* I have noted that the appendages were large. In *Alestes macrolepidotus* 12 and 14 respectively were counted in two specimes. They apparently formed a single row, fringing the intestine for 2 cms. In *Leporinus* they are long and set in two rows of 7 each. In *Bryconaethiops* I made out two rows of rather long appendages—about 5 in each row. In *Xenocharax* they appear to be much reduced in number, size, and area, being in fact quite inconspicuous. In *Anostomus* they are rather long but not numerous; in *Citharinus* numerous, long, fine, and restricte

Looking at the foregoing observations as a whole, I find myself unable to do more than simply state the facts which have come under my notice. I may here, however, point out the curious circumstance that  $\Delta mia$  on the one hand, and the Cyprinidæ and Siluridæ on the other—families to which we are especially led to look for affinities with the Characinidæ—are entirely devoid of pyloric appendages, whilst the Gymnotidæ, as I have verified, possess them.

## The Liver.

The liver in the Characinidæ presents much variation in form and size. Usually three lobes are more or less distinct, but in some the middle lobe is not developed except as a mere band embracing the œsophagus ventrally and connecting the right and left lobes. In others, again, one of the two lateral lobes may be comparatively little developed; and in one form at least it is the middle lobe which is developed at the expense of the others. These conditions, though apparently specifically fairly constant, I regard as being mere adaptations to the exigencies of space and pressure in the abdominal cavity, and therefore of but slight significance. The gall-bladder, in every instance in which I have been able to identify it, was situated at the extremity of the right lobe, being thus sometimes in quite the posterior region of the body-cavity. Its duct could in some cases be traced along the right lobe to the middle liver, and thence to the duodenum, where it became lost amongst the pyloric appendages.

The following are the chief variations I have observed in the form of the liver :-

- Macrodon.-No middle lobe. Lateral lobes subequal and slender, extending to behind pelvic fins. Left lobe rather the longer, and somewhat expanded at its extremity.
- Lebiasina.—All three lobes long and slender, and nearly of equal length.
- Sarcodaces.—Lateral lobes slender, subequal, and extending beyond stomach. Middle lobe short and conical. Left lobe slightly expanded at its extremity.
- Hydrocyon.—Lateral lobes wide, ending bluntly, and of equal length, terminating just short of the pyloric flexure. Middle lobe rather large, triangular, and extending to near the middle of the stomach.
- Salminus.—Right lobe extends beyond stomach. Left lobe pointed and only half length of right lobe. Middle lobe little more then a bridge between the two, but somewhat drawn out to a point at its left border.
- Leporinus.—Liver small. Right lobe slender and rather shorter than stomach. Left lobe rather shorter, tapering to a filament. Middle lobe short, triangular, also tapering to a filament.
- Anostomus.—Liver small. Left lobe two-thirds length of stomach. Right lobe slightly shorter. Middle lobe short and triangular. All pointed.
- Serrasalmo .- Three lobes of moderate length. Lateral lobes subequal. Middle lobe shorter.
- Bryconaethiops.—Body of liver a mere narrow band, drawn out into three long and very slender lobes. Middle lobe very long, extending to end of body-cavity. Right lobe almost thread-like, extending beyond stomach. Both slightly expanded at extremity. Left lobe the stoutest and shorter than stomach.
- Ichthyoborus and Neoborus.—Liver very small, consisting mainly of the somewhat thick left lobe which ends about the middle of the stomach. Right lobe pointed, but very short. Middle lobe a narrow bridge connecting the two.

Eugnathichthys.-Lobes short, especially the right, which is broad and obtuse. Others subequal.

Phago.-All three lobes short.

Tetragonopterus argentatus.—All three lobes subequal and slightly longer than stomach. Right lobe the shortest.

Tetragonopterus fasciatus .-- Lateral lobes very long, extending almost to end of body-cavity.

- Alestes Kotschyi.—Lateral lobes subequal, about length of stomach and moderately stout. Middle lobe about half that length and triangular.
- Alestes nurse.—Three lobes slender, subequal, and extending slightly beyond stomach. SECOND SERIES.—ZOOLOGY, VOL. IX.

Alestes macrolepidotus.—All the lobes very long, and subequal. Middle lobe the longest. Left lobe the shortest.

Citharinus .- Liver very small. Three lobes short, triangular, and subequal.

- Distichodus.—Lateral lobes very short, but thick. Middle lobe drawn out as a narrow attenuated ribbon, ending in a small bulbous mass quite in the posterior part of the body-cavity.
- Xenocharax.—Liver small. Left lobe long and thread-like, extending nearly the length of the bodycavity. Right lobe short, broad, ending bluntly. Middle lobe short.
- Nannocharax.-Left lobe broad, blunt, and longer than stomach. Right lobe short and triangular, and occupying usual position of middle lobe. Middle lobe small, triangular, and displaced to the left.
- Prochilodus.--Right lobe moderately long. Left lobe shorter and thread-like. Middle lobe reduced to a bridge so narrow as not to be definitely traceable across the intervening space.

Curimatus.-Liver apparently very small.

# The Intestine.

The intestine of Characinids is, in the carnivorous forms, including Erythrinoids, short, simple, and comparatively uniform. From the pylorus it first runs backwards, then at a point more or less short of the end of the body-cavity turns and runs directly forward to about the level of the pyloric cæca, usually to the right of the stomach, and finally proceeds straight back, parallel to its former course, thus forming a single elongated loop. Its walls are usually thin-in spirit-specimens often fragile-but in Hydrocyon apparently stouter. The terminal portion sometimes appears to be wider than the rest of the course, but in other cases no difference is perceptible. The appearance naturally depends much on the distension due to contained material. In the specimens of Bryconaethiops examined by me the terminal segment appeared distinctly narrower than the preceding part, which was unusually wide. The length of the intestine, reckoned from the first pyloric appendages, is in these carnivorous forms approximately from twothirds to four-fifths that of the entire fish, including the tail. In four forms only-Lebiasina, Leporinus, Anostomus, and Alestes macrolepidotus-out of the twelve for which I have recorded both measurements has the intestine equalled the fish in length. In the last-named the intestine was longer than the fish in the proportion of about 7 to 5. But this fish appears to be mainly vegetarian. The others were Macrodon, Sarcodaces, Hydrocyon, Alestes Kotschyi, Alestes nurse, Ichthyoborus, Tetragonopterus abramis, and Tetragonopterus fasciatus. Very precise measurement of the intestine was often difficult; and it seems therefore better not to give the exact figures, especially as those obtained from different specimens of the same species were not always in close agreement. All, however, fell within about the limits stated, and for a general comparison the measurements were sufficiently accurate.

Turning to the herbivorous forms—Citharinoids—very different intestinal conditions from those above described are found to obtain. The intestine is long, sometimes enormously so, and is packed into the form of a flattened spiral, consisting, it may be, of several coils. The following are the measurements which I have thus far been able to make in this subfamily :—

#### VISCERAL ANATOMY OF THE CHARACINIDÆ.

Citharinus latus.—16 cms. Intestine 80 cms. Ratio of intestine to fish 5:1.
Distichodus niloticus.—23 cms. Intestine 60 (+) cms. Ratio of intestine to fish 3:1 approximately.
Prochilodus lineatus.—16 cms. Intestine 45 cms. Ratio of intestine to fish 3:1 nearly.
Xenocharax spilurus.—16.7 cms. Intestine 28 cms. Ratio of intestine to fish 2:1 roughly; or more nearly, 5:3.

In *Curimatus dobula* the intestine forms a beautiful and evidently very long coil, almost mathematical in the precision of its concentric circles, and constitutes a most striking object when the body-cavity is opened, looking like a small coil of cord. But it is so fine—at any rate in the small specimens (8 cms.) on which my observations were chiefly made—that I have not attempted measurement.

As in the stomach, so in the length of the intestine, Xenocharax evidences a lower stage of specialization for the herbivorous habit than either Citharinus or Distichodus. In this fish, moreover, the intestine does not exhibit the uniformity of calibre which characterizes the Characinids generally. Thus, in the specimen on which my observation was made, the first 16 cms. were narrow, the next 6 or 7 cms. rather wider, and the terminal 5 or 6 cms. very wide, resembling a second stomach in capacity. This latter condition was something more than mere distension due to enclosed material. In Distichodus also I have noted similar but less marked variations: the intestine being rather wide for 3 or 4 cms.; then narrow, and fringed as above mentioned, for about 9 cms.; then narrow and plain for some 10 or 12 cms.; then apparently wider for a long segment, which is intricately coiled; the terminal 8 cms. the widest of all. For Citharinus my notes are less precise, but here too I have recorded a variation of width in different parts of the intestine, the terminal 5 cms. being the widest. In Prochilodus the intestine was of uniform width, as also in Curimatus, so far as could be seen without minute dissection.

In these forms the intestine was found to be full of very fine soft mud, said to consist largely of diatoms, though this I cannot assert from observation. The intestine is thus of a dark brown colour. In *Citharinus* and *Distichodus*, possibly as a result of the action of the spirit, the whole lining membrane of the body-cavity was infiltrated with brown material which had apparently oozed through the intestinal wall. In a radiograph of *Citharinus*, taken under my direction, a curious effect is observable, the intestine having been rendered opaque to the rays by the mud contained in it. In the carnivorous forms subjected to the same treatment nothing of the kind resulted.

## The Air-Bladder.

The air-bladder in this family of fishes is well developed, and resembles externally that of the Carps. It is constricted into anterior and posterior chambers, the cavities of which remain in communication through a narrow and extremely short tube. The bladder lies immediately beneath the vertebral column, and extends usually from the diaphragm to the posterior end of the body-cavity, where it often tapers to a point. It may, however, be considerably shorter than the body-cavity; and, on the contrary, in one instance, to be referred to later, it is continued between the caudal muscles to the very root of the tail-fin. The posterior chamber, usually much the larger, communicates with the alimentary tract through the ductus pneumaticus, which is often of considerable length and stoutness. These more obvious characters are to be seen in Pl. 3. fig. 1.

The air-bladder consists of two coats : the outer stout, fibrous, and more or less opaque; the inner thin, delicate, glossy, and transparent. In the anterior chamber the two coats are non-adherent and easily separable. In the posterior chamber they are not separately distinguishable. The inner coat in the anterior chamber is thickened ventrally by what has the appearance of a narrow sheet of muscular tissue running longitudinally. In front the air-bladder abuts against a stout transverse membrane which passes backwards ventrally to the bladder as far as the constriction, where it merges into the outer tunic itself, and ends. This membrane is secured dorsally at two points, to the centra of two successive vertebræ, the first attachment taking the form of a stout peduncle; also laterally to the body-wall at two points about one-third of the distance from the middorsal to the mid-ventral line. At the second median attachment this membrane is confluent with the true outer coat of the bladder, which is also attached to the body of the next vertebra. Thus there are, in all, three median attachments, the last two only of which involve the true coat of the bladder. The first of the two coincides with the insertion of the hindermost of the series of ossicles constituting the Weberian mechanism. The description above given refers to Macrodon, in which my examination of these relations went into greatest detail. But I have not noted essential differences in these particulars in other forms.

The air-bladder lies outside the peritoneum, and thus in reality outside the bodycavity. In the herbivorous forms *Citharinus*, *Distichodus*, and *Prochilodus*, and in these only, this membranous partition, shutting off the bladder and kidneys from the other viscera, has become tough and fibrous to such a degree as to be quite resistant to the knife. It is also opaque, causing the illusion that the air-bladder is entirely wanting. In the other herbivorous forms examined, *Xenocharax* and *Curimatus*, the membranous partition is much more delicate, but still an advance on the condition met with in the other Characinidæ. Here, again, it is noticeable that *Xenocharax* presents a lower stage of differentiation than its allies *Citharinus* and *Distichodus*. What significance this particular modification can have is not clear to me. It is suggestive, however, of an adaptation in some way either to the herbivorous or mud-eating habit as such, or else to the ground-habit. It may be, and I am inclined to take this view, that it serves to protect the air-bladder from pressure arising from the distension of the large mass of coiled intestine. It is obvious that such variations of internal pressure on the air-bladder would interfere with its bathymetric sensibility.

Possibly to be connected with this feature is Boulenger's \* discovery that in these three genera, and these alone so far as is known, the dorsal and ventral lateral muscles diverge opposite the anterior chamber of the bladder, so bringing the organ into close contact at that point with the external skin. This condition is suggestive of the "lateral cutaneous areas" found in many Siluroids, and stated by Bridge and Haddon to

<sup>\* &#</sup>x27;Les Poissons du Bassin du Congo,' p. 199.

be restricted to that family \*, though by Boulenger apparently recognized also in certain Cyprinoids. Whether this character has any physiological significance as a means of increasing the sensibility of the bladder to external influences, or has simply arisen as a consequence of certain lines of growth, appears to be doubtful. But, in any case, it is worthy of notice as a further suggestion of affinity between the three herbivorous genera *Citharinus, Xenocharax*, and *Distichodus*.

The posterior chamber of the bladder usually exceeds the anterior chamber in length, in a ratio varying from about  $\frac{3}{2}$  to  $\frac{5}{1}$ . A notable exception occurs in the case of *Serrasalmo*, as will be shown later. The following figures represent approximately the ratios in the forms in which I have recorded measurements :—

Macrodon	•	3:2	Prochilodus 3:1	L
Curimatus		3:2	Anostomus 3:1	L
Alestes nurse		3:2	Ichthyoborus 4:1	L
Nannostomus		3:2	Neoborus	L
Sarcodaces		2:1	Eugnathichthys 4:1	L
Lebiasina		2:1	Phago 4:1	L
Leporinus		2:1	Xenocharax	L
Bryconaethiops		2:1	Alestes Kotschyi 4:	L
Alestes macrolepidotus		2:1	Distichodus	L
Hydrocyon		3:1	Citharinus 5:1	L

These ratios represent length, not capacity. They do not appear to carry any great significance. Herbivorous forms, for example, are found at both ends of the scale. Even two species of the same genus, *Alestes*, are seen to be similarly separated; but *Alestes kotschyi* is altogether peculiar as regards its air-bladder, and should not perhaps have been included in the list given above. Perhaps the most that can be said is that in the Erythrinoids the ratio is small; that in the herbivorous forms *Xenocharax*, *Distichodus*, and *Citharinus* it is large; and that in the allied genera *Ichthyoborus*, *Neoborus*, *Phago*, and *Eugnathichthys* the ratio is a high one. Also it may be noted that in this, as in many other points, *Sarcodaces* stands near the Erythrinoids.

In *Alestes kotschyi* a peculiar condition exists: the air-bladder extends backwards far beyond the boundary of the body-cavity—as far, indeed, as the root of the caudal fin. In this region it is slender and tapering, and lies between the caudal muscles to the right of the interhæmals of the anal fin. Such was the position in the two specimens I examined, but it is said to lie sometimes on the left side  $\dagger$ . Other members of the genus are stated to present the same formation in different degrees.

In the genus *Serrasalmo*, in which the body-cavity is short and deep, the air-bladder presents some curious features. It is much shorter than the body-cavity, and is unique among Characinids, so far as my observations extend, in that the anterior chamber is not only longer, but altogether larger than the posterior chamber. In *Serrasalmo piraya*, indeed, the latter chamber is reduced so far as to appear like a mere conical cap on the end of the former, which is several times its capacity. In *Serrasalmo humeralis* the

<sup>\* &</sup>quot;The Air-bladder and Weberian Ossicles in the Siluroid Fishes," Phil. Trans. B. vol. 184, 1893, pp. 295-6.

<sup>†</sup> Boulenger, ' Les Poissons du Bassin du Congo,' pp. 148-9; also Cuvier & Valenciennes.

disparity in size is less marked, though still considerable. The tube connecting the two is not axial, as in most Characinidæ, but at the ventral border of the bladder. The ductus pneumaticus arises from this tube so obliquely that it appears to spring from the anterior chamber; in reality its communication is as usual with the posterior chamber. The condition in respect of the relations of these tubes is somewhat suggestive of that met with in the Gymnotidæ, where, however, the two chambers of the bladder are much farther apart. The posterior chamber in Serrasalmo is concave in front, fitting over the rounded oviform anterior chamber in the manner of a ball-and-socket joint. The margin of its concave front face is raised on each side into some five or six small cæcal appendages, corresponding to internal pouches. A thick sheet of muscle on each side of the anterior chamber connects the outer tunic with the dorsal body-wall. Some of these features are shown in Pl. 3. fig. 4, together with internal characters to be described later. This peculiar air-bladder has been briefly described by Valenciennes, but only as regards its most obvious external characters; its marginal appendages and its internal structure are not mentioned by this writer. It is shown partially dissected in fig. 4. In Anacyrtus also, in which the body-cavity is short and deep, the air-bladder is peculiarly shortened and rounded, its entire length being only one and a half times its depth. The posterior chamber is, however, as usual, much the larger. Internally, also, there are points of interest (Pl. 3. fig. 8).

In the diminutive Nannocharax niloticus the bladder is much reduced. It does not extend more than half the length of the body-cavity. There is the usual division into two chambers, of which the posterior is considerably the longer, but the cavities appear to be largely obliterated. The anterior chamber is globular, with hard tough walls; I believe, indeed, that it is partially ossified, but its diminutive size renders its condition doubtful. The posterior chamber is narrowed almost to a filament. The ductus pneumaticus, though fine, has its usual relations. In no other Characinid have I met with so rudimentary a condition.

Internally, the walls of the anterior chamber of the air-bladder are plain and smooth in all the Characinidæ. With the posterior chamber, however, it is otherwise : its walls are often ridged by longitudinal bands of a ligamentous nature, some of which may be of considerable depth, so as to appear like septa dividing the cavity peripherally into longitudinal furrows or pouches. Most of the septa are restricted to the anterior part of the chamber, becoming rapidly shallower backwards, and finally disappearing after a comparatively short course. There are, however, usually two, one dorsal and one ventral, which extend the entire length of the chamber so as to meet one another at its posterior extremity; but these also become shallower as they proceed backwards. The others are more or less symmetrically arranged laterally, but in varying numbers and varying degrees of development. In a few cases such bands as are visible are but slightly raised, the wall of the chamber appearing nearly smooth. In only about two cases, however, have I observed the dorsal and ventral median bands to be absent or much reduced in length: in the Ichthyoborinæ the two chief lateral septa extend the whole length of the chamber, exactly like the dorsal and ventral pair, excepting that they are somewhat less prominent.

It may well be that the structure above described serves to maintain this chamber of the bladder, which is comparatively thin-walled, in a state of due distension, and to guard against its collapse. Such, indeed, one cannot but suppose, must be its effect. But that it may also possess a vestigial significance is suggested by a further very curious modification, which is met with in the genera Lebiasina and Erythrinus. In these two forms, and in these only amongst the Characinidæ, the longitudinal septa are connected for a certain distance by transverse septa, in such a way as to constitute a true cellular air-bladder-a suggestion of Ganoid affinities which harmonizes with deductions from the cranial characters. This structure, which is found only in the anterior third or two-fifths of the chamber, has been described by Valenciennes for Erythrinus as follows \* :--- " La vessie postérieure est conique, pointue; sa tunique fibreuse est plus confondue avec la tunique interne, et on y remarque quatre brides longitudinales : une supérieure, une inférieure et deux latérales. Le tiers antérieur de cette seconde vessie offre des parois celluleuses; les cellules sont déterminées par des brides transversales nombreuses, serrées, parallèles entre elles, et perpendiculaires aux grandes brides tangentes à la surface du cône. Ces brides elles-mêmes sont réunies par d'autres plus petites, excessivement plus nombreuses et perpendiculaires aux transversales que nous venons d'indiquer. Entre ces mailles on aperçoit de nombreuses lamelles entrelacées, auxquelles est due la cellulosité des parois de la vessie."

Of the bladder of *Lebiasina* this writer simply says that it resembles that of *Erythrinus*. My own observations, however, lead me to state that the cellular structure is distinctly more pronounced in *Lebiasina* than in *Erythrinus*. Figs. 5 and 6 (Pl. 3.) show that in the former the cellular part of the wall is of some thickness, materially narrowing the lumen of the chamber, whilst in the latter the bands or septa are comparatively slightly raised, and do not appear to encroach appreciably on the central cavity. It is remarkable that in *Macrodon*, which otherwise so strongly resembles *Erythrinus*, and in *Pyrrhulina*, which seems rather to be related to *Lebiasina*, there are none but the longitudinal septa (fig. 7). But in *Macrodon*, at least, these latter are strongly suggestive of cellular structure.

Regarding the resemblance in detail presented by this type of air-bladder to that of *Amia*, I can express no opinion, and observers are at variance. Sagemehl + considers the similarity to be closer than in the case of any other Teleost; whilst, according to Valenciennes ‡, it is not so great as in some species of *Hemirhamphus*.

In all the other Characinids, so far as they have been examined, cellulation does not exist, transverse septa being entirely absent. Nevertheless, the longitudinal septa, constantly present but presenting varying stages of development or degeneration, are, as it seems to me, suggestive of a former cellular condition of the bladder. In the short statement given below, the order represents, according to my observations, the degree of development of the longitudinal septa.

- \* Cuvier & Valenciennes, 'Histoire Naturelle des Poissons,' vol. xix. p. 485.
- † Sagemehl, Morphol. Jahrb., Bd. x. 1884-5, p. 108.
- 1 Cuvier & Valenciennes, 'Hist. Nat. des Poissons,' vol. xix. p. 493.

In Serrasalmo, although, curiously and quite exceptionally, the dorsal and ventral septa appear to be absent, there are some six lateral septa on each side which are of considerable depth, and extend backwards quite to the middle of the chamber, dividing the side-walls into a corresponding number of deep channels, continued at the anterior margin into well-defined pockets or pouches which are conspicuous externally. Intercalated between these main septa are some nine much smaller septa on each side, causing a further subdivision of the lateral space. I have not found any previous record of this peculiar condition shown in fig. 4, though the external features of the bladder have been described by Valenciennes \*.

In *Macrodon* (Pl. 3. fig. 7) the dorsal and ventral septa are large, and there are two strong but shorter lateral septa with at least 30 smaller bands of very varying size intercalated. The existence of lateral septa is denied by Valenciennes \*, who only recognizes the two median bands. In addition to the definite bands, the whole internal surface of the anterior part of the chamber presents the appearance of closely-set but interrupted longitudinal striæ, apparently of the same character as the bands themselves.

In *Prochilodus* the dorsal septum is deep, standing out boldly; the ventral less so. Both extend to the extremity of the bladder. There are also some five lateral septa on each side, which are short and of moderate depth. The whole bladder is very large.

In *Sarcodaces* there are the two long median septa, one shorter lateral band on each side, all well developed, and some three subsidiary septa on each side.

In Ichthyoborus, Neoborus, Paraphago, and Eugnathichthys, very closely allied forms, the two lateral bands extend to the extremity of the bladder, like the median bands, than which, however, they are less prominent. There are traces of about two other very faint and short lateral bands. In their near relative—Phago—the two lateral bands present an appearance which suggests a degeneration from the condition just described; they are unusually long, and each is continued to the extremity of the bladder as a coloured streak, which is not the actual band itself, but which implies its former extension. In Alestes nurse and A. macrolepidotus the median bands are strong, especially the dorsal, and there are three or four short lateral septa on each side.

In Bryconaethiops and Salminus two entire median, and two shorter lateral, septa are present, all well developed and of fair depth. In Hydrocyon, Tetragonopterus, Micralestes, Anostomus, Xenocharax, Distichodus, and Citharinus the septa are as in the two forms just previously mentioned, but are less distinctly raised.

In Leporinus and Curimatus the dorsal band is strong, the ventral apparently absent; two short weak laterals are present in Leporinus; none in Curimatus.

In *Anacyrtus* (Pl. 3. fig. 8) the condition differs from that of any of the foregoing. The dorsal and ventral septa are almost obliterated, extending for only a short distance. Vestiges of about five lateral bands on each side are seen running parallel to one another for about half the length of the chamber, and scarcely perceptibly raised. The whole lateral wall also shows a delicate network of fine, closely-set lines at right angles to one another, which, however, are not perceptible to the touch, and do not appear to be

\* Cuvier & Valenciennes, 'Hist. Nat. des Poissons,' vol. xxii. p. 280.

superficial. In its first-mentioned characters this air-bladder faintly suggests that of *Serrasalmo*, which it also resembles in the somewhat unusual thickness of its walls.

Upon the question whether or no the internal features of the air-bladder summarized in the preceding pages possess any real significance bearing on the affinities or classification of this puzzling family of fishes, it is difficult to speak with confidence. Certain facts, however, seem to be in some degree suggestive. Thus, of the Erythrinoids, two forms—*Erythrinus* and *Lebiasina*—present a similar cellular structure, but in different stages of development or degeneration, whilst *Macrodon* appears to follow suit after a much greater interval. Of the fourth form—*Pyrrhulina*—I have no satisfactory observation. Again, the members of the group *Ichthyoborinæ* agree, so far as they have been examined, in a unique extension of the two main lateral septa. Also the allied African mud-eating fishes—*Distichodus, Xenocharax*, and *Citharinus*—present conditions similar to one another.

The resemblances above pointed out are sufficient to inspire some confidence in the persistence and constancy of the structural features of the air-bladder; and it seems not unlikely that the examination of that organ in a larger number of forms might here and there yield evidence of value as an assistance in classification. I do not, however, feel justified in proceeding further with any such deductions from the slender material before me. The groupings found in my description may be in some degree accidental. Perhaps the most noteworthy points are :--(1) the isolated and aberrant conditions in *Serrasalmo* (Pl. 3. fig. 4), and to a less degree in *Anacyrtus* (fig. 8); (2) the fact that, of the African forms, *Sarcodaces* seems to stand nearest to the archaic Erythrinoids; and (3) the agreement of the *Ichthyoborinæ* in possessing two more completely developed lateral septa than are found in any other forms.

In conclusion, it is worthy of mention that in Cyprinoids I have observed two longitudinal bands in the posterior air-bladder, which are visible as streaks, but not appreciable to the touch, the surface being quite smooth. This condition suggests a further stage of degeneration from a primitive cellular air-bladder. A still further step seems to be recognizable in the Gymnotidæ, in which these bands are absent.

# THE DUCTUS PNEUMATICUS AND ITS RELATIONS IN THE PHYSOSTOMI GENERALLY.

The ductus pneumaticus has already received a brief mention. There remain, however, certain points in connection therewith which merit consideration.

The duct takes its origin in all the Characinidæ from the posterior chamber of the air-bladder, which is thus placed in communication with the alimentary tract in the transitional region between the œsophagus and the stomach. In some cases the opening appears to be in the stomach, in others in the œsophagus, and in others on the border line between the two regions. This border, it is true, is sometimes difficult to define; but, on the other hand, there may be a sudden change of calibre or consistency which one cannot but interpret as marking the transition, and this may be variously situated in relation to the opening of the duct.

In Physostomes generally the duct opens dorsally, and I am not aware of anything in SECOND SERIES.—ZOOLOGY, VOL. IX. 10

the literature of the subject to suggest that the opening is not median. It has, however, long been known that in the Erythrinoids, or at any rate in the genera *Erythrinus*, *Macrodon* (Pl. 3. fig. 3), and *Lebiasina* (fig. 5), the duct opens not dorsally but laterally in fact, in the middle of the left side. Valenciennes does not seem to have been aware of this peculiarity, but it is referred to by Stannius \*, and has been discussed at some length by Sagemehl ‡. No observations recording anything unusual in the other Characinidæ seem to have been made. In fact it is stated that these forms do not present any features of interest in this connection. This I shall show to be incorrect; and it is somewhat remarkable that Sagemehl at least—who bases an argument of some importance upon the conditions found in Erythrinoids—should have overlooked the true relations existing in the other Characinids.

I have paid special attention to these relations in every form which has come under my notice, for a priori it appeared unlikely that the Erythrinoids should stand absolutely apart from their allies in this matter. The results are as follows :—In the Erythrinoids *Macrodon, Erythrinus*, and *Lebiasina* the ductus pneumaticus opens into the middle of the left side of the tract. This is seen in fig. 3, and equally distinctly in fig. 5. In the fourth member of the Erythrinoid group, *Pyrrhulina*, the opening is dorsal, but well to the left side. This condition I shall refer to as "lævo-dorsal." Amongst the other Characinids, out of 35 species examined by me with reference to this point, 25 were found to have the opening of the duct very decidedly to the left side; in three others the opening was only slightly on the left side of the mid-dorsal line; in the remaining seven, owing to the condition of the specimens, I was not able to satisfy myself absolutely, but in at least 5 of the number the opening appeared to be slightly to the left. In no instance was the orifice on the right side, and in only two did it appear to be median. It should be stated that in some instances only one specimen was available; in others, several.

In Sarcodaces the duct was found to open quite in the middle of the left side (fig. 2), much as in the three first-mentioned Erythrinoids. This observation was made on several specimens. Thus this character, if it possess any significance, serves to strengthen the suggestions yielded by the skull of affinity between these forms. In none of the other Characinids examined does the opening lie so far to the left. Ichthyoborus (fig. 9), of the internal anatomy of which no description exists, stands next to Sarcodaces in this relation; but the opening of the duct is more dorsal. Neoborus and Eugnathichthys are closely similar. It is also well to the left in Hydrocyon (brevis and forskalii); in Alestes (nurse, longipinnis, and macrolepidotus) (fig. 10); in Micralestes stormsi; in Tetragonopterus (fasciatus and argentatus); in Petersius, Bryconaethiops, Salminus (fig. 11), Anacyrtus, Anostomus, and Leporinus; in Prochilodus (fig. 12), Xenocharax, Distichodus (antonii and niloticus) (fig. 13), and Citharinus macrolepis (fig. 13 a); and in Serrasalmo (humeralis and piraya).

<sup>\*</sup> Stannius, 'Anatomie der Wirbelthiere,' 1854, p. 224.

<sup>†</sup> Sagemehl, "Das Cranium der Characiniden," p. 108.

In the following forms the duct opens, according to my observations, only slightly to the left of the median line :—Alestes Kotschyi, Citharinus (latus and Geoffroyi).

Finally, with regard to Tetragonopterus (abramis and multiradiatus), Curimatus, Nannocharax, and Phago, I can only state, with some hesitation, that the opening appeared to be slightly to the left; and with regard to Paraphago and Micralestes acutidens, that it appeared to be in the mid-dorsal line. In these latter instances, however, either the size or the condition of the specimen before me was always an obstacle to an accurate determination. Viewing these results as a whole, I can state with confidence that, in spite of some individual variations, the position of the duct is fairly constant specifically, and is normally on the left side throughout the Characinidæ, so far as my observations have extended. The meaning of this asymmetric structural condition has been discussed at length by Sagemehl, who, however, as already stated, only recognized its existence in the Erythrinoid division. According to the view set forth by that writer, this condition supports the argument for a primitively ventral air-bladder, and is inexplicable on the hypothesis advanced by Boas \* of the dorsal origin of that organ. The matter is of sufficient importance to warrant a summary here of the argument set forth by Sagemehl, and the fact that my own observations, as will be seen, have an important bearing upon the question must be my justification for venturing to restate it.

Discussing the homology of the air-bladder with the ventrally-lying lungs of higher vertebrates, Boas contended that the primitively dorsal and unpaired organ must have undergone longitudinal fission, together with its duct; and that the now separate ducts, with their orifices, must have travelled round the œsophagus until they merged in a common ventral opening, producing the condition existing in *Polypterus* and in air-breathing vertebrates.

Sagemehl objects to this hypothesis on the following grounds :---

- (1) The absence of any imaginable cause for the occurrence of the changes involved; whereas a wandering in the reverse sense would naturally result from the acquisition of a hydrostatic function by a ventrally situated bladder.
- (2) The absence of any satisfactory explanation of the conditions found in Erythrinoids and in the Dipneusti, in which the single duct passes to one side of the œsophagus.
- (3) The relations of the lung-arteries in *Ceratodus* †, which arise on each side from the fourth branchial arch, that from the left arch passing under the œsophagus and following the ductus pneumaticus, which in the Dipneusti winds round to the right. If the dorsal situation of the bladder were the primitive one, the arteries on each side would pass directly backwards to their distribution, as those on the right side actually do.

This last objection appears to be conclusive as regards the Dipneusti, and inferentially for all dorsal air-bladders, although in Teleosts the bladder receives a different blood-

<sup>\*</sup> Boas, "Über den Conus arteriosus und die Arterienbogen der Amphibien," Morph. Jahrb., Bd. vii. 1881, p. 566.

<sup>+</sup> Boas, "Herz und Arterienbogen bei Ceratodus und Protopterus," Morph. Jahrb., Bd. vi. 1880.

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supply. It follows then, if the air-bladder originated as a ventral structure, that in order to arrive at the Teleostean condition the bladder and its duct must have travelled round the alimentary canal, to one side or the other, until finally both attained a dorsal situation. On this hypothesis, the position of the duct in Erythrinoids—and, as I have shown, in Characinids generally—becomes endowed with a peculiar interest as representing an incomplete stage in the evolution of the Teleostean air-bladder; as indicating the path along which the bladder and duct have travelled; and as bearing witness to the primitive character of the family of fishes under consideration.

It would appear, then, according to Sagemehl, and so far as the discussion has yet proceeded, that the dorsal position of the air-bladder in Dipneusti and Teleostei must have been arrived at in the two cases along two different routes, lying to the right and to the left respectively, each of which may have had as its starting-point the condition which is still persistent in *Polypterus*. It would seem that the two cases are further distinguished, firstly by the fact that in the Dipneusti the actual orifice of the pneumatic duct has not travelled more than a short distance, and secondly by the fact that in Teleosts the bladder has changed its blood-supply from the branchial artery to the dorsal aorta.

It may be further pointed out that this interpretation of the more or less laterally situated opening of the ductus pneumaticus in the Characinidæ would involve the derivation of the entire family from forms more primitive than Amia or any of the existing Ganoids, in all the families of which I find the position of the duct to be middorsal. A point referred to by Sagemehl in support of his argument is the fact that in *Polypterus* the left sac of the air-bladder is decidedly the larger. Thus it only becomes necessary to assume the complete atrophy of the already dwindling right sac.

Against this argument, we have at the outset the facts of ontogeny, which seem, so far as at present known, to represent the air-bladder as a dorsal outgrowth from the œsophagus \*. But this, it must be admitted, may conceivably arise from the elision of antecedent stages.

The discussion of this question involves the consideration of the relations of the ductus pneumaticus in the other families of Ostariophyses, and even in the Physostomi generally. I have accordingly extended the investigation in that direction, with the following results.

Of the Cyprinidæ I have examined specimens from the five diversified genera :---

Leuciscus (L. rutilus & L. leuciscus) (Pl. 4. fig. 14), Carassius (C. auratus), Barbus (B. Bynni), Varicorhinus (V. beso), Catostomus (C. macrolepidotus) (fig. 15).

In all these forms the opening of the duct is lavo-dorsal, and, in some cases at least, even far to the left of the median line. In fact, excepting that its position is usually

<sup>\*</sup> Miklucho-Maclay, "Über ein Schwimmblasenrudiment bei Selachiern," Jenaische Zeitschr. f. Naturwiss., Bd. iii. 1868.

further forward, the condition is precisely that which is commonest amongst the Characinidæ.

Thus far, the facts are in accordance with Sagemehl's hypothesis.

In turning, then, my attention to the Siluridæ, I was prepared to find conditions similar to those above described. To my surprise, however, investigation revealed a precisely opposite state of things, for in these fishes the opening of the ductus pneumaticus is actually and unquestionably on the *right* side of the mid-dorsal line of the  $\alpha$ sophagus (Pl. 4. figs. 16 and 17)—as far, indeed, to the right as it is in most Characinids to the left.

There may possibly be some significance in the fact that, in all the Siluroids examined, the pyloric flexure of the stomach was found to be lateral and to the left side. But, after careful observation and consideration, I am unable to see that this modifies the relations of the ductus pneumaticus with the æsophagus as above stated.

This statement is based upon the examination of forms taken from the following eight widely divergent genera, more than one specimen in most cases having been under examination :--

Amiurus (A. nebulosus), Clarias (C. lazera) (fig. 16), Synodontis (S. gambiensis), Malapterurus (M. electricus) (fig. 17), Chrysichthys (C. auratus), Siluranodon (S. auritus), Schilbe (S. mystus), Auchenoglanis (A. biscutatus).

In seven out of the eight the opening of the duct was decidedly on the right side. In the eighth case—*Siluranodon*—it appeared to be median; but in this case, and in this case alone, it has to be stated that the condition of the viscera was unsatisfactory and precluded a positive verdict.

Bridge and Haddon \*, in their detailed study of the air-bladder in the Siluroid fishes, describe the median connection of the ductus pneumaticus with the bladder itself, but make no reference to its precise relation with the œsophagus.

Of the Gymnotidæ, the fourth family of those fishes which possess the Weberian apparatus, I have examined three species from two genera---

Carapus fasciatus (1 specimen), Sternopygus carapus (2 specimens) (fig. 18), Sternopygus virescens (3 specimens);

with the result that the pneumatic duct was found to open into the cosophagus in the median dorsal line in *Carapus* and on the left side in both species of *Sternopygus* (fig. 18). The duct may thus fairly be described as having a tendency towards the left side.

\* "Contributions to the Anatomy of Fishes: the Air-Bladder and Weberian Ossicles in the Siluroid Fishes," Phil. Trans., B. vol. 184, 1893. The following is a summary of my observations on the other Physostomi :---

1. SALMO. Salmo trutta (3 specimens) and Salmo fario (1 specimen).—Duct short; opens distinctly on the right side of the dorsal wall of the œsophagus (Pl. 4. fig. 19).

2. COREGONUS. *Coregonus albus* (4 specimens).—Duct of moderate length; opens nearly medially, doubtfully to the right side.

3. OSMERUS. Osmerus eperlanus (3 specimens).—Duct rather long; opening apparently median.

4. THYMALLUS. *Thymallus rulgaris* (2 specimens).—Duct rather short; opens slightly to the right side.

5. MORMYRIDÆ. Petrocephalus bane (2 specimens) and Gymnarchus niloticus (4 specimens).—In both these forms the short, wide duct opens into the æsophagus lævodorsally. In Petrocephalus (fig. 20), the connection of the duct with the air-bladder is also on the left side. In Gymnarchus (fig. 21), which, by the way, has been erroneously included in the Ostariophyses by Bridge and Haddon in the paper previously referred to, as also by Wiedersheim \*, this is not the case, and the connection with the æsophagus is more nearly median than in Petrocephalus.

6. NOTOPTERUS. Notopterus kapirat (2 specimens). — The duct opens into the  $\alpha$ sophagus far forward, and slightly but distinctly to the left side (fig. 22). It is short and wide, and opens also into the left side of the air-bladder itself, which is longitudinally divided in the abdominal region by a vertically complete median septum. This septum has a free edge anteriorly, not quite reaching the transverse membrane, which partially separates this part of the bladder from the unpaired anterior chamber, and it is just on a level with this free edge that the ductus pneumaticus opens. These relations, with others not now before us, agree with those described by Bridge  $\dagger$  as existing in *Notopterus borneensis*, with the exception that in that form the pneumatic duct is described as being connected with the  $\alpha$ sophagus in the mid-dorsal line.

7. ELOPS. *Elops saurus* (2 specimens).—The air-bladder opens by a wide orifice, rather than by a definite duct, into the stomach at about the middle of its length, just behind the pyloric flexure, and in the front part of the very long blind sac. In one specimen the opening was in the mid-dorsal line; in the other, the stomach was irregularly shaped, and it became a mere matter of opinion whether the connection ought to be regarded as median or lævo-dorsal. Setting aside this doubtful case, we must take the evidence of the other as pointing to a median position of the duct (fig. 23).

8. ALBULA. *Albula conorhynchus* (1 specimen).—In this fish, primitive in the possession of a valved conus, the duct is longer than in *Elops*, and opens into the stomach much farther back, quite near, but not at, the extremity of the blind sac. It is in the mid-dorsal line (fig. 24).

<sup>\* &#</sup>x27;Elements of Comp. Anat.,' translation by W. N. Parker, 2nd edition, 1897, p. 226.

<sup>+ &</sup>quot;The Air-bladder and its connection with the Auditory Apparatus in Notopterus borneensis," Journal of the Linnean Society, Zool. vol. xxvii. 1900, p. 507.

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9. CLUPEA. Clupea sprattus and Clupea harengus.—As is well known, the duct is fairly long and opens medially into the extreme posterior end of the blind sac (fig. 25).

10. CHIROCENTRUS. *Chirocentrus dorab* (1 specimen).—In this fish, marked out as primitive by its intestinal spiral valve, the wide ductus pncumaticus opens medially into the dorsal surface of the stomach rather behind the middle of the blind sac, which is of enormous length (fig. 26).

11. GALAXIAS. Galaxias truttaceus (3 specimens).—The long duct opens far back on the stomach, quite near the extremity of the short blind sac, much on the same level as in *Albula*; but it is not median, being in fact very markedly displaced to the right (fig. 27).

12. Esox. *Esox lucius* (5 specimens).—The short duct opens far forward into the dorsal wall of the œsophagus. It is nearly median, but in all the specimens examined was just appreciably to the left side (fig. 28).

13. CYPRINODONTIDE. Cyprinodon calaritanus, Orestias Oweni, Fundulus robustus, and Goodea atripinnis (2 or more specimens of each).—Diminutive size here presented an obstacle, in most cases, to satisfactory observation, but in Orestias the duct was clearly made out to be situated far to the right of the mid-dorsal line. Apparently this was also the condition existing in Fundulus and Cyprinodon. The specimens of Goodea were not in sufficiently good condition for a satisfactory observation.

14. PERCOPSIDE. *Percopsis guttatus* (2 specimens) and *Columbia transmontana* (1 specimen).—In both these forms the ductus pneumaticus opens into the coophagus far to the right side of the mid-dorsal line.

15. HYODON. Hyodon alosoides (3 specimens).—The short, wide duct opens far forward on the œsophagus, nearly mid-dorsally, but, somewhat doubtfully, a little to the right side.

16. ANGUILLIDÆ. Conger conger (2 specimens).—In both cases I found the duct so difficult to trace, that I cannot commit myself to any statement as regards its relations with the alimentary canal.

17. HALOSAURUS. *Halosaurus macrochira* (1 specimen).—The rudimentary air-bladder, situated in the posterior part of the body-cavity, narrows in front into a band which is continued as a thread-like ligament. This ligament, apparently solid, terminates in the mid-dorsal wall of the stomach quite near to its posterior end, *not*, as has been stated \*, in the œsophagus.

Finally, in the three Ganoids *Acipenser*, *Amia*, and *Lepidosteus*, as I have verified, the communication of the air-bladder with the coophagus is in the mid-dorsal line. In *Acipenser* the duct is of some length, but in *Amia* and *Lepidosteus* the bladder opens directly by a slit-like orifice into the coophagus.

\* Günther, in the Report on the Voyage of the 'Challenger,' " Deep-sea Fishes," vol. xxii. Zool. 1887, p. 232.

		VENTE	ALLY.	DORSALLY.				
		Opening median. Bladder ven- tral : its left sac the larger.	Bladder	Opening on left side.	Op Incline to left		y median. Inclined to right.	Opening on right side.
Fishes with air-bladder communi- cating with	Communicating with esophagus or the part of the stomach immediately behind it.		Dipneusti*.	Mormyridæ. Notopteridæ. Characinidæ. Gymnotidæ. Cyprinidæ.	Esox.	Acipenser. Amia. Lepidosteus. Osmerus.	Hyodon. Coregonus? Thymallus.	Salmo. Siluridæ. Cyprinodontidæ. Percopsidæ.
alimentary canal by a ductus pneumati- cus.	Communicating with the stomach in its middle or posterior region.				Albu Clup Chire	Elops. Albula, Clupea, Chirocentrus, Halosaurus,		Galaxiidæ.

The foregoing analysis may be thus tabulated :---

Now, what is the meaning of the facts shown in the above table?

The constancy of the conditions in the families most extensively examined is strong evidence that these relations are not without some significance—not a mere matter of chance. In no single genus, and indeed in no single family, have I found the duct varying between right and left. Within any one family it may be median or more or less displaced to the left side; or, on the other hand, it may be median or more or less displaced to the right side. Beyond these limits I have not found any variation. Throughout the whole series of observations I have endeavoured to guard against fallacy arising from a mere mechanical twisting of the stomach on its axis. Such a twisting, it is true, does sometimes appear to exist either as a normal or an occasional condition; but the torsion produced does not involve the œsophagus in such a way as to lead to erroneous observations, except perhaps in such a case as *Galaxias*, where the duct communicates with the stomach near its extremity, and on what appears in relation to the pylorus to be the right side, but in which the pylorus is itself directed to the right.

Looking now carefully at the table before us, we may, I think, note the following fairly obvious points :--

1. The position of the ductus pneumaticus in relation to the alimentary canal is a characteristic feature in at least some groups of fishes, and as such may have a certain diagnostic or taxonomic value.

- \* Günther, A.: "Description of Ceratodus," Phil. Trans., vol. 161, 1871.
  - Parker, W. N.: "On the Anatomy and Physiology of *Protopterus annectens*," Trans. Irish Acad., vol. xxx. pt. 3. Spencer, B.: "Contributions to our Knowledge of *Ceratodus*—Pt. I. The Blood-vessels," Macleay Memorial Vol., Linn. Soc. N.S.W.
  - Spencer, B.: "Der Bau der Lungen von Ceratodus und Protopterus," Zoolog. Forschungsreisen in Australia und dem Malayischen Archipel, Jena, 1898.

2. Even eliminating all doubtful cases, there remains a substantial minority of families in which the opening of the duct is situated on the right side, the majority, however, having the duct situated medially or to the left side.

3. Many of the most primitive or generalized forms, including the three Ganoids, have the duct in the mid-dorsal line.

4. Families regarded as being allied do not always present similar conditions in relation to the situation of the duct. For example, the Siluridæ and the other Ostario-physes; and, again, the Esocidæ and Galaxiidæ.

Whatever may be the interpretation of the facts, it seems clear that the conditions found to obtain in the Salmonidæ and Siluridæ, at least, cut away the ground from Sagemehl's argument, in so far as it was based upon the supposed transitional conditions presented by the Erythrinoids. His contention for a primitively ventral air-bladder, which in the Teleostei has travelled round the left side of the æsophagus, may indeed still be the correct view, but it can no longer be supported by reference to the Erythrinoid conditions, unless with the reservation that the evidence supplied by the Salmonidæ and Siluridæ points to a journey in precisely the opposite direction.

If the facts of organization before us stood alone, we might legitimately deduce two divergent lines of evolution for the two groups into which the Physostomi are thus made to fall, eliminating those families in which the duct is median and conceivably to be derived from either condition. The idea is not without a certain fascination. But its demands are surely such as cannot be conceded.

It demands, for example, for the highly-specialized Weberian apparatus either an independent origin in the Siluroids and the other Ostariophyses, respectively, or else an antiquity at least equal to that of the postulated ancestral Polypteroid air-bladder. The former supposition is incredible: the latter highly improbable. The association of the Salmonidæ with the Siluridæ is a less serious difficulty, kinship not being necessarily implied, but possibly only parallel development.

If we set aside this hypothesis, as I think we must do, and admit that the duct may in all cases have travelled in the same direction, we may perhaps conclude from the weight of evidence that the rotation has been on the left side. This, however, necessitates the assumption that in the Siluridæ and Salmonidæ the duct has crossed the median line and become definitely associated with the right side of the æsophagus—a proceeding for which I am able to suggest no conceivable cause. Moreover, the possibility is not absolutely excluded that the rotation may have been in the reverse direction, and that it may be in the Characinid group of families that the crossing of the median line has taken place.

There still remains another view: that the immediate ancestors of the higher Teleostomi had already evolved, the evidence does not show how, a dorsal air-bladder connected medially with the œsophagus, and that the pneumatic duct afterwards shifted to one side or the other as the several families branched out. This view, however, attempts no solution of the problem of the *origin* of the air-bladder : it merely suggests an explanation of the varying conditions observed within the limits of the Teleostomi. Like the preceding hypothesis, it is unsatisfactory in that no cause is apparent which

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could have determined a definitely-directed wandering of the duct away from the median line; and it is to be remembered that in some forms—notably the Erythrinoids—the deviation is very great.

Of the three hypotheses here advanced, the third is most in harmony with the condition met with in Amia and the other Ganoids, and, indeed, as it seems to me, with the facts generally. As regards, however, the testimony afforded by the Ganoids and other so-called "primitive" forms, it is sometimes necessary to remind oneself that they are themselves final terms, not mean terms, of series which have survived to the present day, and that, whilst retaining certain primitive characters, they are not on that account necessarily less likely to have acquired extreme modifications in other directions.

With reference to the possible causes which may have operated in determining the position of the duct, it may be pointed out that in some forms—notably perhaps in *Amia* and *Lepidosteus*—the ductus pneumaticus is so short that any asymmetry in its position would almost inevitably be attended by an asymmetry in the position of the air-bladder itself. One can thus see a determining cause for its median position. In many Physostomi, on the other hand, such as the Characinidæ, for example, the duct is of such length and laxity that its asymmetry would appear at the present day to be independent of the position of the bladder, whatever may at one time have been the case. Whilst, however, it is fairly obvious that in many cases the precise position of the set any light upon the cause, either of its uniform asymmetry throughout entire families of fishes, or of the two opposite phases of asymmetry which characterize different families.

The one clear outcome of the investigation which I wish to emphasize, is the demonstration that Sagemehl's interpretation of the Erythrinoid condition of the ductus pneumaticus is not justified by a more extended knowledge of the facts. That interpretation may, indeed, yet prove to be the true one—the asymmetric condition of the air-bladder in *Polypterus* suffices to lend colour to it; but it cannot be held to be established by Sagemehl's line of argument. For it must be remembered that the argument was to a large extent based on the improbability of a wandering of the duct from the mid-dorsal line having occurred; and it is abundantly evident from the facts set forth in this paper that exactly such a wandering must have taken place, to one side or to the other, or perhaps to both.

The view that the air-bladder originated as a ventral structure remains, however, untouched. The blood-supply of the bladder in the Dipneusti would appear to be conclusive on that point. But as to when and how the air-bladder became a dorsal structure in the evolution of the Teleostomi, evidence is as yet wanting.

In comparison with the considerations just discussed, observations on the relative length of the ductus pneumaticus carry but little interest. I may, however, state, as the result of careful measurements, that its length in Characinids is commonly about one-tenth or one-twelfth of the length of the body of the fish. Considerable divergences from these proportions occur in certain forms. Thus in *Macrodon* the length found was  $\frac{1}{6}$  that of the body; in Sarcodaces  $\frac{1}{8}$ ; in Citharinus and Bryconaethiops  $\frac{1}{9}$ ; in *Hydrocyon, Salminus, Alestes, Leporinus, and Xenocharax* from  $\frac{1}{10}$  to  $\frac{1}{12}$ ; in Anostomus and Eugnathichthys  $\frac{1}{13}$ ; in Prochilodus  $\frac{1}{16}$ ; and in Ichthyoborus  $\frac{1}{30}$ . In some forms, for example Macrodon, Lebiasina, Serrasalmo, Distichodus, Anacyrtus, and Xenocharax, the duct dilates at its orifice; this is especially noticeable in the Erythrinoids, in which it terminates on a large papilla. In Serrasalmo, according to Valenciennes, the opening is furnished with a valve.

Differences are also observable in the width or stoutness of the duct, but these are not readily susceptible of measurement or of expression in definite terms. In one case, *Macrodon*, as stated by Sagemehl\*, the ductus pneumaticus is beaded by alternating widenings and narrowings, in the manner of a rosary.

I ought to state that, through an error of judgment in the early stages of this investigation, all comparisons made with the length of the fish include the caudal fin.

This concludes the remarks I have at the present time to offer upon the alimentary canal and its appendages. Of the other abdominal viscera, the ovaries alone have yet claimed my special attention.

## OTHER ORGANS.

## The Ovaries.

On the question of the type of ovary represented amongst the Characinidæ, the literature of the subject contains contradictory statements. Thus Joh. Müller † states that the ovaries are closed sacs, shut off from the body-cavity, and opening together on the exterior of the body. Valenciennes ‡, on the other hand, states in the most explicit manner that the ovaries are of the Salmonoid type, and that the ova fall freely into the body-cavity. This statement he makes for each of the following forms: Erythrinus, Macrodon, Lebiasina, Curimatus, and Parodon. Of Myletes he states that the ovaries fill two-thirds of the body-cavity, without, however, speaking of their With reference to the two first-mentioned forms - Erythrinus and character. Macrodon-Valenciennes himself makes apparently contradictory statements : thus, in one place (vol. xix. p. 493), speaking of Erythrinus he says : "La nature a donné aux poissons dont nous traitons ici une organisation semblable à celle des Saumons; en ce qui concerne les organes génitaux, nous les voyons en effet constitués par deux rubans portant dans les femelles les œus sur des replis transverses; ces œufs tombent dans l'abdomen pour s'échapper par deux trous percés de chaque côté de l'anus." But on page 484 of the same volume, speaking of the same fishes, he says, "Les sacs ovariens n'ont point de communication avec l'intérieur de la cavité abdominale, de sorte que ces organes ne sont pas faits comme ceux de beaucoup de genres de la famille des Saumons ou des Auguilles."

\* Sagemehl, " Das Cranium der Characiniden," p. 108.

† Joh. Müller, "Untersuchungen über die Eingeweide der Fische," Abhandl. der Berl. Akad. d. Wissenschaften, 1843, p. 189.

‡ Cuvier et Valenciennes, 'Histoire Naturelle des Poissons,' vols. xix. & xxii.

Of *Macrodon*, he says on page 513, "J'ai trouvé à l'ouverture de corps, les deux sacs ovariques enveloppés dans leurs replis peritonéaux, et adhérant chacun à la paroi abdominale"; but on page 515, "Quant aux organes génitaux, ils ont, comme nous l'avons déjà dit, la disposition de ceux des Truites." The ovaries of the other Characinids are not mentioned by Valenciennes.

Sagemehl \* states that he has satisfied himself that the ovaries in these fishes are closed sacs, thus confirming Müller's description. He does not say in what forms he has made the observations.

I have up to the present time examined the ovaries in the following 14 forms: Alestes nurse, Tetragonopterus abramis, Petersius Leopoldianus, Micralestes altus, Alestes longipinnis, Micralestes Stormsi, Hydrocyon Forskalii, Sarcodaces odoë, Anacyrtus microlepis, Curimatus Gilberti, Macrodon trahira, Erythrinus unitæniatus, Lebiasina bimaculata, Pyrrhulina semifasciata. In some cases, it is true, the condition of the specimen was not such as to justify any statement about the ovaries, owing to the disappearance of the membranous parts. In other cases, however, the membranes were intact, and I was able to satisfy myself, by the use of the seeker and of the blowpipe under water, that no communication existed between the ovarian sacs and the general body-cavity; the sacs, through the medium of their membranous continuations, opening directly upon the exterior by a common post-anal orifice. In all, the ovaries of the two sides were equally developed, arising at the level of the anterior chamber of the air-bladder.

Nevertheless, it has seemed to me that two different ovarian conditions are distinguishable amongst the Characinids above mentioned: Surcodaces (Pl. 4. fig. 29) may be regarded as typical of the one, and *Alestes nurse* (fig. 30) of the other; but the difference is, I think, only a question of degree in the backward extension of the ovigerous tissue, and the reciprocally developed forward extension of the oviducal membranes. In Sarcodaces the ripe ovaries extend back to just behind the level of the anus, where they become closely approximated, but are not confluent. Their membranes there continue as a single, very short common duct to the exterior. Each ovary has the appearance of being, as it were, slung by its membranes, which invest it completely, except on the dorsal side, where a space or canal runs without interruption to the external opening.

Similar conditions appear to obtain in *Macrodon*. Of the other Erythrinoids I can speak with less confidence, but I believe their ovaries to have the relations just described.

In *Alestes* and *Hydrocyon*, on the other hand, according to my observations, the ovaries fall distinctly short of the anus, so that the common oviducal space enclosed by the backward continuation of their membranes is of considerable extent, instead of being exceedingly small as in *Sarcodaces*.

The two conditions I regard as being modifications in different degrees of the same ovarian type. Although differing considerably at first sight, they agree absolutely

\* Sagemehl, " Das Cranium der Characiniden," p. 115.

in the absence of any communication between the ovarian tract and the general bodycavity, and in the continuation of the ovarian membranes to form a common duct to the exterior.

In some of the other Characinids in which ovaries were found, these organs appeared to coalesce at a point anterior to the anus, and to continue to the exterior as a common mass of ripe ova. Some such appearance I observed in *Petersius* and *Micralestes*. This condition I interpret as being referable to the *Alestes*-type; for obviously, if in *Alestes* the common oviducal space were crammed with ripe ova in transit, the appearance of the whole apparatus would be suggestive of an early coalescence of the ovaries themselves. In the Erythrinoid form *Lebiasina*, also, there was the appearance of coalescence, but beginning further back, about the level of the anus; also, but still further restricted to the posterior portion, in *Tetragonopterus abramis*. In all these instances of apparently coalesced ovaries the investing membranes themselves were not recognizably present, but the indications seemed to me to demand their existence.

It will be observed that the ovarian relations above described present no resemblance to those existing in Amia, in which the ova fall freely into the body-cavity, and thence pass by wide orifices into the oviducal funnels.

The testes seem to be of the normal Teleostean type, presenting no features worthy of remark. They are seen as narrow bands, arising at the sides of the anterior chamber of the air-bladder, and passing back uniformly to their junction just before opening to the exterior.

### The Kidneys.

The kidneys in my specimens have not, generally speaking, been well preserved, and I have no minute observations to record. It may, however, be stated that these organs in the Characinidæ extend for the whole length of the body-cavity, from near the diaphragm backwards immediately under the vertebral column. In some cases there seemed to be an anterior enlargement ("head-kidney"?) in which the anterior end of the air-bladder was more or less imbedded. No enclosure in muscle was observed.

## The Heart.

I carefully examined the heart in one of my largest specimens, *Macrodon*, for signs of a valvular conus. No valves, however, were found to exist, beyond the two small pockets at the exit of the ventricle and that guarding the auriculo-ventricular aperture.

# The Respiratory Organs.

Concerning the respiratory organs, I have as yet no new observation to record. The gills themselves seem to present no special features. There is, however, in certain of the Characinidæ an accessory branchial organ, arising as a blind sac from the upper margin

of the last gill-cleft. This organ, which has been described briefly by Kner\* and in detail by Sagemehl +, appears to be peculiar to the herbivorous forms, having been recorded by these writers for Curimatus, Canotropus, Hemiodus, Citharinus, and Prochilodus; and more recently by Boulenger ‡ for Xenocharax. Discussing the morphology of this curious organ, Sagemehl expresses the view that we have here to do with a structure arising from the gill of the rudimentary fifth branchial arch or "inferior pharyngeal bone." If this conclusion be correct, the presence of the organ in the herbivorous Characinids, and in these only, becomes of great interest, in view of the fact that traces of a fifth gill have not been found in any living Ganoid, but only in fishes of yet lower organization-certain Selachians and Dipnoids. That this character was at one time widely diffused is shown, as Sagemehl points out, by its presence in forms so far separated as Notidanus and Protopterus. Two important conclusions seem to follow from the identification of the organ under consideration with the gill of the fifth arch : (1) that the herbivorous Characinids which possess it form a natural group; and (2) that this division of the family cannot be derived from either the Erythrinoids or the other carnivorous Characinids, but is at least as ancient as either of those groups. It should be mentioned that an organ showing a somewhat similar minute structure has been described by Hyrtl § and by Gegenbaur || in certain Clupeids.

Another structure—a rudimentary opercular pseudo-branch—is referred to by Sagemehl  $\P$  as being present in some Characinids, as also in *Amia*. The only forms in which he mentions having found it are *Citharinus* and the following carnivora—*Hydrocyon*, *Anacyrtus*, *Alestes*, and *Tetragonopterus*. The Erythrinoids show no trace of it, contrary to what might have been expected from the consideration of their markedly Amioid cranial characters.

#### A PARASITICAL CRUSTACEAN.

An Isopod crustacean, about 1.5 cm. in length, was found within the body-cavity of a specimen of *Anacyrtus microlepis* from Asuncion, Rio Paraguay. Mr. Stebbing, as I have already mentioned, kindly identified it for me as *Artystone trysibia* \*\*, family Cymothoidæ. I learn from him that the species is of some rarity, having been previously only twice recorded, once from La Plata, and also from Brazil. My specimen, now in the Biological Museum of the Royal College of Science, South Kensington, was enclosed in a thick-walled capsule adherent to the ventral body-wall of the fish, and entirely within the body-cavity. The rectum and adjacent parts were unfortunately cut before

<sup>\*</sup> Kner, "Die Kiemenanhange der Characiniden," Verhandl. d. zoolog.-botanischen Gesellsch. in Wien, Bd. xi. 1861.

+ Sagemehl, "On the Accessory Branchial Organ of Citharinus," Morph. Jahrb., 1886-7.

1 Bouleuger, ' Les Poissons du Bassin du Congo,' p. 199.

§ Hyrtl, "Ueber die accessorischen Kiemenorgane der Clupeaceen," Denkschr. d. k. Akad. zu Wien, Mathem.naturw. Klasse, Bd. x. 1855.

Gegenbaur, "Ueber das Kopfskelet v. Alepocephalus rostratus," Morphol. Jahrb., Bd. iv. 1878, Suppl.

¶ Sagemehl, 'Das Cranium der Characiniden,' p. 113.

\*\* Schiödte & Meinert, "Symbolæ ad Monographiam Cymothoarum: Pt. IV. Cymothoidæ," 1883. Stebbing, T. R. R., "History of the Crustacca," Intern. Sci. Ser., vol. lxxiv. Cymothoidæ, 1893. the discovery was made, and the precise relations of this capsule were difficult to determine, but it had every appearance of being completely closed, and no communication could be made out between it and the exterior, either directly or through the rectum or "bladder." Mr. Stebbing tells me that the situation was unusual for such parasites, but that it is difficult to assign any limits to the liberties taken by them with their hosts.

## SUMMARY AND CONCLUSIONS.

The main conclusions to which I have been led in the investigation detailed in this paper are the following :—

(1) The ductus pneumaticus has a more or less asymmetric connection with the alimentary canal, not only in the Erythrinoids, in which it has been long recognized, but also in the Characinidæ generally, in the Cyprinidæ, the Gymnotidæ, the Siluridæ, the Salmonidæ, the Esocidæ, the Mormyridæ, the Notopteridæ, the Galaxiidæ, the Percopsidæ, the Cyprinodontidæ, and perhaps other families.

(2) This asymmetry is to the left side in certain families of fishes, and to the right side in certain others.

(3) In many families, including some of the most primitive and generalized, no asymmetry exists, the duct being median.

(4) The evidence furnished by the whole series of observations seems to point to the derivation of the asymmetric condition from a pre-existing symmetric or mid-dorsal position of the duct, this being contrary to the view advanced by Sagemehl, who regarded the Erythrinoid condition as being archaic.

(5) In certain fishes—*Notopterus* and *Petrocephalus* (a Mormyroid)—the ductus pneumaticus has also an asymmetric connection with the air-bladder.

(6) The posterior sac of the air-bladder presents in the Characinidæ a characteristic arrangement of longitudinal ligaments or septa. The similarity of these septa amongst the members of some natural groups, such as the *Ichthyoborinæ*, suggests a certain constancy in this character, which may be found to be of systematic value. On the other hand, the part played by these septa in the formation of a cellular air-bladder in *Erythrinus*, and especially in *Lebiasina*, together with their existence in varying degrees of development, suggests that they possess a significance as a vestige of a formerly cellular bladder in the ancestors of the family.

(7) The ovaries in the Characinidæ are closed sacs, without communication with the body-cavity. This statement, which is, however, based upon the examination of a limited number of genera, is in accordance with the statements of Joh. Müller and of Sagemehl, but is at variance with some of the assertions made by Valenciennes.

(8) I have described two somewhat different ovarian conditions, of which *Sarcodaces* and *Alestes* respectively may be taken as typical, the difference lying in the degree of backward extension of the ovaries. Both cystoarian \*.

\* Huxley, T. H., "Contributions to Morphology—Ichthyopsida. No. 2: On the Oviduets of Osmerus, with Remarks on the Relations of the Teleostean with the Ganoid Fishes," Proc. Zool. Soc. Lond., 1883.—Howes, G. B., "On some Hermaphrodite Genitalia of the Codfish (*Gadus morrhua*), with Remarks upon the Morphology and Phylogeny of the Vertebrate Reproductive System," Journ. Linn. Soc., Zool., xxiii. 1891. (9) The Characinid stomach is with or without a blind sac. The cardiac and pyloric regions are well differentiated. In the herbivorous forms the pyloric portion is highly muscular and gizzard-like. The pyloric flexure is usually directed ventrally, but in some forms is fairly constantly turned in some other direction.

(10) Pyloric cæca are always present in the Characinidæ, but in very varying number and development. They sometimes fringe the intestine for a considerable distance.

(11) The length of the intestine in the carnivorous Characinids does not exceed the body-length, and is usually less. In the herbivorous and mud-eating forms it is very much longer, varying from about twice to five times the length of the fish. It may vary also in calibre in different regions. No trace of a spiral valve was observed.

(12) The liver in the Characinidæ is usually tri-lobed, the proportionate development of the three lobes being very variable. In some forms one or more of the lobes may be greatly elongated, or may be much reduced. The gall-bladder is usually attached to the right lobe.

(13) The African Characinid Sarcodaces strikingly resembles the Erythrinoid Characinids, not only in cranial characters, as shown by Sagemehl, but also in certain visceral characters, notably in the opening of the ductus pneumaticus far to the left on the alimentary canal, in the character of the ovaries, and in the features of the air-bladder.

(14) The herbivorous Characinids, more especially *Distichodus*, *Xenocharax*, and *Citharinus*, resemble one another in the marked thickening of the sheet of peritoneum which shuts off the air-bladder from the body-cavity. In all the distinguishing visceral characters of this group, *Xenocharax* seems to present a lower stage of specialization than the other two associated forms.

(15) In the structural features of the air-bladder, *Serrasalmo* and *Anacyrtus* seem to be separately and somewhat widely divergent from the other Characinids.

(16) If the ridging of the posterior air-bladder be regarded as having a vestigial significance, the Characinidæ, Cyprinidæ, and Gymnotidæ would seem to represent successive stages of air-bladder evolution.

(17) With the possible exception of the indications of a cellular air-bladder, there appears to be nothing in the visceral anatomy of the Characinidæ which strengthens the deductions made from the skull as to the Amioid affinities of the group. In opposition to such deductions are especially the cystoarian ovaries, the asymmetric ductus pneumaticus, the presence of pyloric appendages, and the absence of all trace of a valvular conus and of an intestinal spiral valve.

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# DESCRIPTION OF THE PLATES.

### PLATE 3.

- Fig. 1. Hydrocyon brevis. General view of air-bladder and stomach. Liver removed. Stomach flexed ventrally. Blind sac somewhat large.
  - 2. Sarcodaces odoë. General view of air-bladder and stomach. Liver removed. Stomach flexed dorsally. Ductus pneumaticus opens into left side of alimentary canal. Air-bladder opened to show ridging.
  - 3. Macrodon trahira. Stomach greatly distended and flexed dorsally. Large blind sac. Orifice of ductus pneumaticus on the left side.
  - 4. Serrasalmo humeralis. Air-bladder partly opened, showing ridging and pouching. Posterior sac the smaller.
  - 5. Lebiasina bimaculata. Cellular air-bladder. Ductus pneumaticus opening into left side of alimentary canal.
  - 6. Erythrinus unitaniatus. Posterior sac of air-bladder opened to show rudimentary cellular structure.
  - 7. Macrodon trahira. Posterior sac of air-bladder opened to show ridging of its walls.
  - 8. Anacyrtus microlepis. Air-bladder partly opened to show faint ridging of posterior sac.
  - Figs. 9-28 represent the dorsal aspect of the stomach in a series of forms, with the relative position of the opening of the ductus pneumaticus.
- Fig. 9. Ichthyoborus niloticus.
  - 10. Alestes nurse.
  - 11. Salminus maxillosus.

# PLATE 4.

Fig. 12. Prochilodus lineatus.

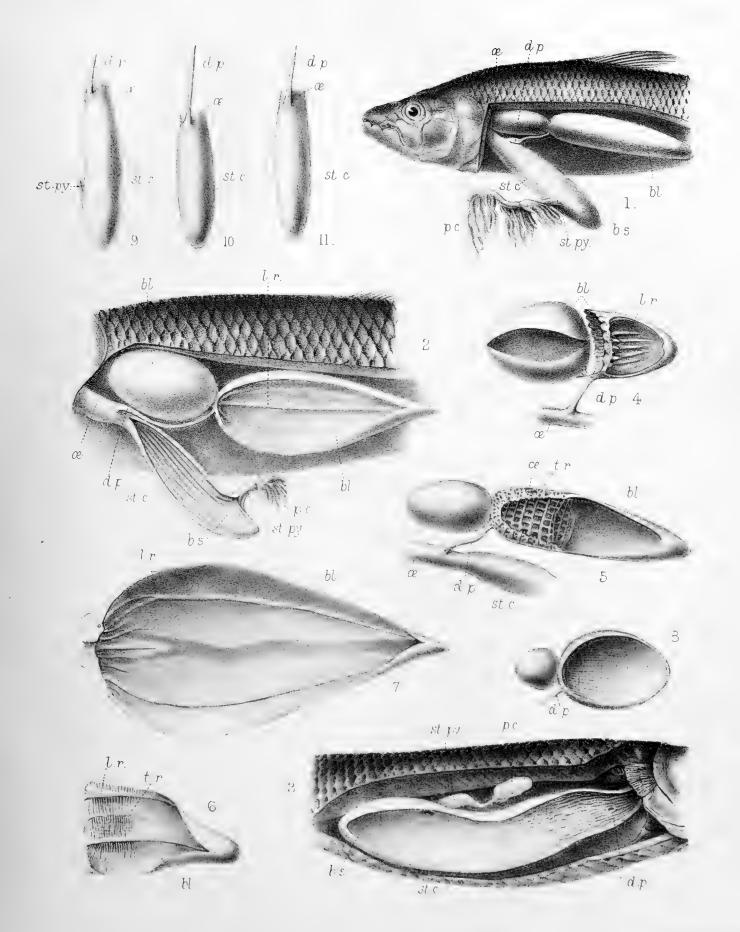
- 13. Distichodus Antonii.
- 13 a. Citharinus macrolepis.
- 14. Leuciscus rutilus.
- 15. Catostomus macrolepidotus.
- 16. Clarias lazera.
- 17. Malapterurus electricus.
- 18. Sternopygus carapus.
- 19. Salmo trutta.
- 20. Petrocephalus bane.
- 21. Gymnarchus niloticus.
- 22. Notopterus kapirat.
- 23. Elops saurus.
- 24. Albula conorhynchus.
- 25. Clupea sprattus.
- 26. Chirocentrus dorab.
- 27. Galaxias truttaceus.
- 28. Esox lucius.
- 29. Sarcodaces odoë. Ovaries form closed sacs, with investing membranes which continue as short ducts uniting just before their opening on the exterior. No communication with general body-cavity. Ova large.
- 30. Alestes nurse. Ovaries differ from the preceding in having a shorter backward extension, with a proportionally larger common oviducal space. No communication with general body-cavity.

REFERENCE LETTERS.

bl.,	air-bladder.	<i>@.</i> ,	æsophagus.
b.s.,	blind sac.	ov.,	ovaries.
се.,	cellular structure.	p.c.,	pyloric cæca.
C.O.S.,	common oviducal space.	st.c.,	cardiac stomach.
d.p.,	ductus pneumaticus.	st.py.,	pyloric stomach.
l.r.,	longitudinal ridges.	t.r.,	transverse ridges.
<i>m.s.</i> ,	membranous sac.		

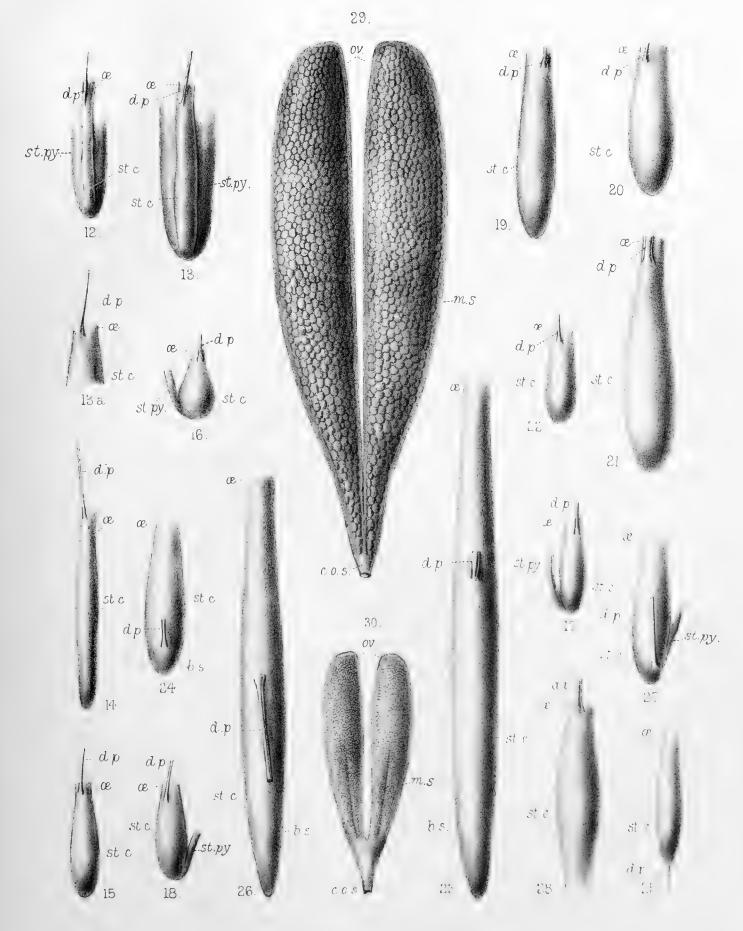
(Note by Author.)—The Plates are the work of Mr. James Green, to whom my thanks are due. The figures are from my own dissections and have been drawn under my direction. All are about natural size or slightly enlarged.—W. S. R.





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[ \$3 ]

III. On the Evolution of the Australian Marsupialia; with Remarks on the Relationships of the Marsupials in general. By B. ARTHUR BENSLEY, B.A. (Tor.), Ph.D. (Columbia), University of Toronto, Canada. (Communicated by Prof. G. B. Howes, D.Sc., LL.D., F.R.S., Sec.L.S.)

## (Plates 5–7.)

#### Read 7th May, 1903.

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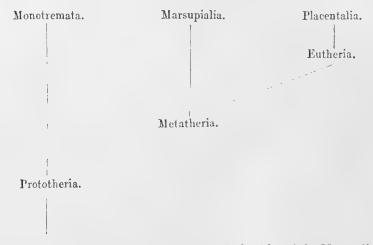
### INTRODUCTION.

ON reviewing the general progress of opinion in mammalian phylogeny, we note the fact that the discussions bearing on the affinities of the Marsupials have largely centred around the broader question of the relationships of these animals with the Placentals, and that in respect to the latter there has been a gradual change from an older view, by which the Marsupials were assigned an ancestral position, on the assumption that they represent a lower grade of organization, to a newer one, by which they are regarded as a collateral or even a derived group.

The three groups into which the existing Mammalia are divisible have been commonly recognized as representing, to a certain extent, three grades of organization—the Placentalia, mainly distinguished by their vascular nutritive allantois, standing highest in the scale; the Monotremata, in virtue of their sauropsidan characters, especially their oviparity, lowest; while the Marsupialia occupy a somewhat intermediate position, especially in respect to their combination of a non-vascular allantois, which they possess in common with lower oviparous forms, with the actual viviparity of the Placentalia. Following the evolutionary principle, the tendency has been to connect these groups

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into a line of descent, the lowest being associated with the Reptilia and indirectly with the Amphibia, or directly with the latter group. It has been found, however, that the Monotremata do not occupy a wholly prototypal position with reference to the Marsupialia, and that the latter are by no means wholly prototypal to the Placentalia; and the necessity has thus arisen for the recognition of hypothetical or ideal groups through which the evolutionary sequence might be assumed to have been established, and from which the existing groups might be supposed to have arisen by independent specialization. The clearest exposition of this principle is to be found in Huxley's essay of 1880, in which three type groups are characterized and designated as Prototheria, Metatheria, and Eutheria, these being assumed to have arisen in the order named, and to have given rise successively to the Monotremata, Marsupialia, and Placentalia.



A phylogenetic plan, showing the primary relationships of the Mammalia.

Naturally, the Eutheria, being a terminal group, are practically equivalent to Placentalia. Huxley remarks :—" It is a fact, curiously in accordance with what might be expected on evolutionary principles, that while the existing members of the Prototheria and the Metatheria are all extremely modified, there are certain forms of living Eutheria which depart but little from the general type. . . There is no known Monotreme which is not vastly more different from the Prototherian type, and no Marsupial which has not far more widely departed from the Metatherian type, than Gymnura or, indeed, Erinaceus have from the Eutherian type" \*.

\* Careful analysis shows that it is not absolutely necessary to recognize more than two primary mammalian groups, one including the stock-forms of the Monotremata, the other those of the Marsupialia and Placentalia. The question arises, How are these groups to be designated? and this leads to the further question, In fixing the designations, are we to rely on strict priority or on common usage? As early as 1872 Gill divided the Mammalia into two primary groups of Prototheria and Eutheria; and this division has been used by Cope (1889) and recently by Osborn (1899). Gill's Eutheria were not assigned a placental or aplacental character. Common usage has it that the Eutheria are placental, as specified by Huxley. It accordingly follows that if we revert to Gill's classification, we must characterize the Eutheria as fundamentally equivalent to Huxley's Metatheria and as aplacental like the majority of the Marsupialia, unless it is proved that the latter animals are of placental origin, as supposed by Wilson and Hill, and Dollo. Even in the latter event, it will be apparent that allowance must be made for a Metatherian stage in development, although not for a definite Metatherian group. The precise distinction of Huxley between the ancestral or metatherian characters of the Marsupialia and their special characters definitely removes the latter animals from an ancestral to a collateral position with reference to the Placentals. The principle is essentially one of reduction in number of the characters in which the Marsupials appear to occupy a prototypal position. For example, the single-tooth change of these animals was regarded by Flower (1867) and afterwards by Thomas (1887) as prophetic of the more complete tooth-change of Placentals, but was pointed out by Huxley as a special character of the Marsupials and as derivative of a former diphyodont condition common to the Metatherian ancestors of both Marsupial and Placental groups, but more completely retained in one of them than in the other. The correctness of this position has been amply confirmed through the embryological investigations of several zoologists, including Röse, Leche, Kükenthal, Woodward, Wilson and Hill, and Dependorf.

Recent research has, however, gone still further in the reduction of the recognized prototypal characters of Marsupials, and certain observers, namely, Wilson and Hill, and Dollo, are in favour of removing the most essential one, namely, the possession of a non-placental allantois, which they regard as a secondary feature of the Marsupials and as derivative of a former placental condition. This view is based on Hill's discovery of a placental connection in *Perameles*; and the reduction of the allantois in other Marsupials is supposed by Dollo to have been associated with premature birth and fundamentally with arboreal habit. In a former paper (1901 b), however, the present writer has pointed out the probability that the aplacental condition of most Marsupials is actually primitive, and that the placental connection in *Perameles*, like a multitude of other characters in which Marsupials resemble Placentals, has been independently acquired; in other words, that it represents a convergent or homoplastic \* development.

However this may be, we have the more definite fact that the Marsupials and Placentals are collateral and, in a certain sense, equivalent groups, of common parentage; and this conception may be welcomed as clearing the way for a better perception of the d tails of their secondary evolution or adaptive radiation. Especially is this true of the former: any attempt to explain their secondary differentiation on the basis of a Marsupial ancestry of the Placentals must naturally result in confusion, because of the lack of distinction between those of their adaptive characters which are, generally speaking, common to all of the members of the group and those distinctive of minor divisions, leading to the doubly erroneous conclusion that the evolution of the Marsupial group is not finite, and that characters of both kinds have been carried over from Marsupial to Placental stages. At the present time, while the evidence at our disposal may not be of sufficient extent to furnish a complete plan of the whole Marsupial radiation, we at least have the advantage of being able to form a clear conception as to what the problem involves. Referring to the plan above presented, the whole situation in Marsupial phylogeny may be summed up in three questions. In the first place, What are the characters of the ancestral Marsupio-placental or Metatherian forms? Some of these characters, as, for example, the narrow cranium and projecting zygomata,

<sup>\*</sup> Cf. recent paper on Homoplasy by Osborn (1902).

or the narrow iliac bones, we already know to have been carried over to the primitive forms (Didelphyidæ, Creodonta) of both of the derived groups, and reduced in the more specialized ones. Others, such as the double dentition and the normal pentadactyl pes, were carried over to the Placentals and lost in the Marsupials; while still others, such as the marsupial bones and the non-placental allantois, were carried over to the Marsupials and lost in the Placentals. Secondly we have to ask, What were the features of a divergent adaptation which, acting on the ancestral forms, brought about their division into Marsupial and Placental series, and gave to the former the characters which now distinguish them, namely, the reduced milk-dentition, the prehensile pes, and premature birth? The assumption by the ancestors of the Marsupial division of arboreal habit may be noted as a possible answer to this question. Given the primary differentiation of the Marsupials as a group, we have finally to ask, What is the sequence of events in their secondary adaptive radiation? This question involves the history of several faunas comprising the Jurassic series of the northern hemisphere (providing its members were actually related to the Marsupial division), the Oligocene Didelphyidæ of the same region, the Miocene series of South America, the existing didelphyid fauna of that country, and, finally, the Marsupial fauna of the continent of Australia and the adjacent islands.

Generally speaking, the history of a fauna can only be satisfactorily determined by reference to palæontology. In the Marsupial fauna of Australia we have the result of a radiation which we may be sure has proceeded along much the same general lines as that which has given rise to the existing Placentalia. Many members of each series present characters which have more or less perfect counterparts or parallels in the other. One has only to compare the dental characters of the Dasyuridæ, the Phalangeridæ, or the Phascolomyidæ with those of the Creodonta, the Primates, or the Rodentia to appreciate the intimate structural correspondences between the members of the two In attempting to define the details of the Australian radiation, however, groups. we are at once confronted with the difficulty that the fossil deposits of that country have not as yet furnished ancestral or collective types. The reason of this is rather obscure. There is still the possibility that older deposits may be found containing such types; and when we consider the progress of palæontological discovery in other countries, it seems difficult to believe that the finding of such forms in Australia is more than a matter of industrious exploration. There is a further possibility, however, that the ancestors of the Australian fauna passed the incipient phases of their evolution in another country, such as Asia or even South America. Again, the researches of Huxley and Dollo have shown that the ancestors of the existing Marsupials must have been arboreal animals; and this raises a suspicion that as such they may have been protected to a much greater extent than terrestrial animals living in caves, or upon the open plains, or frequenting the water-side, from those conditions which would result in the preservation of their remains by fossilization. However this may be, apart from a comparatively small number of arboreal forms (Petaurus, Dromicia) and some small terrestrial forms (Epyprymnus, Perameles), remains of which have been brought to light in cavedeposits \*, the extinct fauna is composed of large specialized terrestrial types showing no more approximation to theoretically prototypal forms than, if we may cite an analogous case, the members of the giant fauna of the mid-Tertiary portion of the placental radiation do in comparison with the actually ancestral Creodonta. It will be apparent, therefore, that beyond the limited although valuable evidence afforded by geographical distribution, or the occurrence of allied faunas living at different periods in other countries, we are dependent for the history of the Australian series on the sequence of adaptive characters as presented by living forms.

The results recorded in the present paper represent an attempt to construct a plan of the Australian radiation by tracing the sequence of adaptive modifications in the dentition and foot-structure of the various genera, in some cases of the species. The possibility of making such an arrangement with advantage was suggested to the writer some time ago by the perusal of the opinions expressed by Huxley and Dollo with reference to an arboreal ancestry of the Marsupials, as determined by the characters of the pes. The extensive observations of the latter writer in particular, although primarily designed to show the presence throughout the group of a prehensile type of pes, appeared to indicate further that most, if not all, of the progressive changes in foot-structure through which the Australian Marsupials have passed from the time of their origin are actually represented either in the existing Australian forms or in the American Didelphyidæ, and that it would accordingly be possible to explain in a measure the relationships of the various genera by simply arranging them on a basis of the sequence of adaptive modifications of the pes. The fact, however, that phylogenetic conceptions based on the adaptive characters of single structures have frequently been found to be misleading when applied to others, partly on account of the occurrence of convergent developments, and the presence of a conspicuous example of convergence in foot-structure between the Peramelidæ and Macropodidæ, indicated clearly the advisability of checking such an arrangement by reference to the adaptive changes of other organs. For this purpose the characters of the molar teeth were selected, the latter offering the advantage that the main features of their evolution have already been demonstrated in the parallel case of the Placentalia.

The results of this study were published in a preliminary paper (1901 a), but on account of many limitations both of material and literature they included only a general or family arrangement. The opportunity of examining the case in detail was afterwards afforded by a visit to London, where, through the kindness of the officials of the Geological and Zoological Departments of the British Museum, the writer was able to study the splendid collections both of fossil and existing Marsupials there preserved. The latter form the basis of the present paper.

Reference has been made above to the necessity of depending in the present case on

\* Cf. Broom (1896). The presence of these forms in cave-deposits will be noted as in all probability due to no efforts of their own, and therefore as throwing no light on the conditions affecting their ancestors before the differentiation of definite carnivorous forms.

the adaptive characters as presented by existing animals. Objection may be justly taken on general principles to basing phylogenetic conceptions on the characters of living forms, not only on account of the necessity it involves of selecting ancestral and derived characters from contemporaneous types, and thereby incurring a risk of mistaking the direction in which the evolution may be proceeding, but also on account of the necessity of recognizing hypothetical collective forms. Many instances might be cited in which the identification of such forms has not got beyond their original creation. While preferring to claim too little than to assert too much in favour of the stability of the present arrangement, the writer believes that such difficulties as those referred to are, in the case of the Australian radiation, more than compensated for by other advantages. It may be observed, in the first place, that in utilizing the characters of the dentition and foot-structure we are dealing with organs whose adaptive modifications are, to a much greater extent than those of others relating to the internal organization, of a definite and irreversible stamp. The Australian Marsupials represent, furthermore, a peculiarly homogeneous group. During their development they have been protected from competition with other animals. They have apparently been free from such disturbing conditions as result from the development of a large carnivorous clement. Their range of lateral radiation has been restricted by their geographical limitations; so that their progressive development has not been greatly disturbed by divergence. Finally, their evolution has not proceeded to the stage of over-population and the obliteration of less specialized intermediate types. Under these conditions we may expect to find—as, except in a few cases, we actually do—that the adaptive modifications follow one another with a precision which leaves no doubt as to the manner in which the evolution began and the direction in which it is proceeding.

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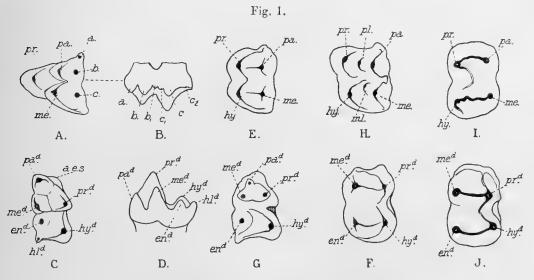
# THE ADAPTIVE MODIFICATIONS OF THE DENTITION IN THE AUSTRALIAN MARSUPIALS.

The following details of nomenclature may be noted :--

With reference to the cheek-teeth, it is a familiar fact that in the Marsupials the numbers of premolariform and molariform teeth are the reverse of those in the Placentals, being respectively 3:4 in the former and 4:3 in the latter. The question of their serial homologies is one which has given rise to considerable controversy; and several plans for the nomenclature of marsupial teeth have been proposed. A consideration of the

\* A paper on the general correlation of changes in the mammary apparatus is in course of preparation.

opinions expressed by Thomas (1887), Leche (1892, 1893, 1895), Woodward (1896), Wilson and Hill (1897), Dependorf (1898), and Lydekker (1899) leads to no definite conclusion; and it therefore appears inadvisable at the present time to adopt any system of nomenclature which will imply, intentionally or otherwise, definite homologies with the Placentals. Thomas (1895) has recently adopted the plan of designating the three premolariform teeth of Marsupials, in the order of their position from before backwards, as anterior, middle, and posterior; and this plan has been adopted throughout the present paper (with the substitution of the term median for middle), as presenting the advantage over numerical systems that it conveys the idea of homologies only within the limits of the Marsupial group. It may be observed that even these terms have some disadvantages, since, in order to express homologies, it has been necessary in several cases to disregard their descriptive applicability. In the advanced members of the Dasyurinæ, for example, where the posterior premolars have disappeared, the remaining teeth are still distinguished by the terms anterior and median.



Cusp-nomenclature of upper and lower molars.

A, B, crown and profile of upper, C, D, of lower molar of *Peratherium*; E, F, upper and lower molars of *Trichosurus*;
G, lower molar of *Perameles Bougainvillei*; H, upper molar of *Pseudochirus*; I, J, upper and lower molars of *Macropus*. Abbreviations: pr., protocone; pa., paracone; me., metacone; hy., hypocone; pl., protoconule; ml., metaconule; a, b, b<sub>1</sub>, c<sub>1</sub>, c, c<sub>2</sub>, external styles; pr<sup>d</sup>., protoconid; pa<sup>d</sup>., paraconid; me<sup>d</sup>., metaconid; hy<sup>d</sup>., hypoconid; en<sup>d</sup>., entoconid; hl<sup>d</sup>., hypoconulid; a.e.s., antero-external shelf.

The molariform teeth of the adult animals have been designated throughout as first, second, third, and fourth molars, the first tooth being regarded as a true molar rather than as a formerly deciduous premolar whose successor has been aborted (Lydekker, 1899).

The nomenclature used in describing the patterns of the molars is that proposed by Osborn (1891) in connection with the tritubercular theory of molar evolution. An exception has, however, been made in the case of the external cusps or "styles" in the upper teeth of polyprotodont forms. Certain of these elements, as they occur in the Cretaceous Mammalia and some of the Ungulata, have received special designations; and three of them, as they occur in Marsupials, have been shown by Winge (1882) to have definite homologies in the Placentals. Careful study, however, shows that in the Marsupials no less than six of them are represented, and all of these may occur together even in primitive forms (certain Didelphyidæ). It has therefore seemed preferable to express their homologies in the Marsupials by designating them alphabetically, rather than to extend the nomenclature without a reconsideration of their number and arrangement in the Placental series. The main points of cusp and style nomenclature are illustrated in the accompanying diagram (fig. 1, p. 89).

## DASYURIDÆ.

Viewing the dental characters of the Australian Marsupials from an adaptive rather than a taxonomic standpoint, the Dasyuridæ may be broadly distinguished from the remaining members of the series by the fact that they present a trend of evolution involving a progressive change from primitive insectivorous to specialized carnivorous modifications. The position of the family in the Australian radiation is approximately equivalent to that of the main insectivorous-carnivorous line represented by the Creodonta, the existing Talpidæ, and the Carnivora in the general placental radiation.

All of the Australian Marsupials—and the same appears to be true of mammals generally,—which are not at the present time in an insectivorous phase of dental development, have passed through that phase in the course of their evolution. We accordingly find in the smaller insectivorous members of the present family dental modifications which are prototypal not only to those of the more advanced carnivorous forms, but also, to a considerable extent, to those of the omnivorous Peramelidæ and Phalangeridæ, forms which are in turn prototypal in many respects to the members of the herbivorous section. The smaller Dasyuridæ would, no doubt, be wholly prototypal in dentition, were it not for the fact that the Peramelidæ present a more primitive arrangement of the external cusps of the upper molars and a more primitive condition of the upper incisor formula. In other words, the prototypal dental condition is nearly, but not quite, realized among the Australian Marsupials in the smaller forms of the Dasyuridæ. It is only in *Peratherium* and the existing Didelphyidæ of South America that all of the prototypal characters relating to the dental evolution of the Australian Marsupials may be found associated in a single form.

The dental evolution of the Dasyuridæ is not entirely homogeneous; two of the constituent genera—namely, *Thylacinus* and *Myrmecobius*—may easily be shown to have undergone independent development. *Thylacinus* has undergone a carnivorous evolution resembling so closely that of certain Neotropical forms (Sparassodonta of Ameghino), while differing from that of the typical Australian members of the Dasyuridæ, as to throw doubt on the propriety of its inclusion in the latter family. *Myrmecobius* has undergone a special development, characterized by incipient retrogression of the dentition, as a result of the adoption of the ant-eating habit.

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The various genera may be arranged on a basis of their molar and premolar characters as follows :—

А.	Protocone of upper molars well developed; external styles obsolete. Lower	
	molars with broad shelf-like talonid; no metaconid. Posterior premolars	
	well developed	Thylacininæ.
	Genus: Thylacinus.	
В.	Protocone of upper molars variable; external styles well developed. Lower	
	molars with basin-shaped talonid, which is well developed or reduced;	
	metaconid present, variable. Posterior premolars variable or absent.	
	a. Dentition normal; molar formula $\frac{4}{4}$	Dasyurinæ.
	Genera: Sminthopsis, Antechinomys, Phascoyale, Chætocercus,	
	Dasyuroides, Dasyurus, Sarcophilus.	
	<b>b.</b> Dentition retrogressive ; molar formula $\frac{5}{5-6}$	Myrmecobiinæ.
	Genus Murmerabius	

### DASYURIN.E.

From the standpoint of their dental sequence, the Dasyurinæ may be regarded as forming a continuous progressive series. Every gradation is presented between a primitive insectivorous condition and one indicative of high carnivorous specialization; there are no divergent developments of any significance, and the transformation takes place without reference to generic distinction. The evolution appears to be closely connected with increase in size of the body, and carnivorous characters are for the most part preceded by carnivorous habit \*.

The general relations of the various forms appear to be as follows :---The two genera Sminthopsis and Antechinomys in general represent the smallest and most primitive members of the series. Although differing in no essential characters of the dentition from the smaller species of *Phascogale*, they lack the range of modification which is characteristic of the latter genus, and which prevents it from being prototypal to the same extent. The larger species of *Phascogale* present specialized characters, such as the reduction of the posterior premolars, which make them transitional between the smaller species of the same genus and those of *Dasyurus*, to which they bear an ancestral relation. Of the species of Dasyurus, the form which approximates most closely to Phascogale is D. hallucatus, this animal almost repeating the dental characters of P. Wallacei or P. Thorbeckiana. Of the remaining species, D. viverrinus and D. Geoffroyi are intermediate, both in size and dental characters, between D. hallucatus and D. maculatus. The dental characters of the last-named form are exactly prophetic of those of Sarcophilus ursinus. The two genera Chætocercus and Dasyuroides are simply terrestrial modifications of Phascogale, and approximate closely in their dental characters to the larger species of that genus and to Dasyurus hallucatus.

<sup>\*</sup> The familiar accounts given by Gould (1863) and Lydekker (1894) of the habits of these and other Australian Marsupials have been extensively supplemented by Semon (1896).

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Sequence of Molar Patterns.—The molar characters are remarkably constant in the smaller species of the Dasyurinæ; so that, so far as these teeth are concerned, any one of them might be selected as representing the starting-point for the insectivorous-carnivorous evolution. The following description is based on Sminthopsis leucopus, the teeth of which are represented in Pls. 5 & 6 by figs. 2a, b of the second upper and third lower molars respectively.

The second upper molar presents the following characters :- The bitiug-surface is triangular in outline, with the apex of the triangle directed internally. The latter is separated from those of the neighbouring teeth in front and behind by triangular spaces, into which are inserted, when the jaws are closed, the anterior triangular pillars of the lower teeth. The longest axis of the crown is transverse, so that the tooth appears to be slightly compressed in an antero-posterior direction. The crown presents the trituberculate \* pattern in general common to the insectivorous Dasyuridæ and Didelphyidæ, and also to the placental Talpidæ, the primitive Creodonta, and the Cretaceous Mammalia. It bears three main cusps and an outer row of subsidiary Of the three main cusps, that placed internally, the protocone (pr., Pl. 5. styles. fig. 2a), is well developed and is supported on a separate root; its crown surface is placed slightly below that of the two remaining cusps of the triangle. Of the latter the anteriorly situate paracone (pa.) is comparatively small, while the posteriorly placed metacone (me.) is greatly enlarged and forms the most important element of the crown. Its posterior border is modified so as to form a trenchant spur, which shears against the antero-external border of the triangular pillar of the succeeding lower tooth. The shearing-edge is relatively short, and its direction is for the most part transverse. All three cusps are of a piercing or insectivorous type, their tips being triangular in section and sharply pointed.

The structures referred to as external styles are practically two in number, and are separated by a considerable space from the outermost of the main cusps. One of them (ab), placed opposite the paracone, shows indications of a composite structure. The remaining style (c) is much better developed; its tip projects almost to the same extent as that of the adjacent metacone.

\* Objection to this designation has been taken by Dr. Forsyth Major (1893, p. 199) on the grounds that so-called trituberculate teeth are often in reality polybunous. The justice of this view is obvious, such a tooth as that of *Sminthopsis leucopus* being no more actually trituberculate than (if one may be allowed to cite an analogous case of descriptive inapplicability) the Edentata are edentulous. The term is, however, of too great descriptive convenience to be easily dispensed with when employed to designate such teeth as those presenting three main cusps arranged in the form of a triangle, with or without a complement of intermediate conules or external styles.

Descriptive terms such as the present indicate definite states rather than progressions, and the evolutionist is hampered by the necessity either of extending their meaning to more than they literally signify, or of adopting a cumbrous nomenclature to designate minor modifications. As to how far a tooth may be modified away from its original type and still be designated as trituberculate is a question of individual opinion. The term can obviously not be applied to those teeth which have passed the tuberculate stage in the carnivorous evolution, and should not be applied to those which possess an incipient hypocone (cf. Pl. 5. fig. 8), indicative of an omnivorous evolution, in view of the fact that the latter element, in subsequent stages, comes to rank in importance with the three original cusps. Of the remaining upper molars, the first differs from the second in being less compressed antero-posteriorly, while the reverse is the case with the third. In the latter, also, the styles are not so well developed, this being especially the case with style c. The fourth tooth is greatly reduced through the lack of development of the metacone, there being no lower teeth situate behind it, against which it might shear. The cusps represented are the protocone, paracone, and style ab. The paracone is trenchant anteriorly.

The third lower molar (Pl. 6. fig. 2) shows the following characters:—The crown is relatively short and broad, and presents the tuberculo-sectorial pattern, being composed of an anterior triangular pillar (trigonid) and a posterior heel (talonid). The sectional area of the trigonid is slightly greater than that of the talonid. The former bears three cusps, of which the externally placed protoconid  $(pr^d.)$  is best developed, while of the two internally placed cusps the posterior metaconid  $(me^d.)$  is smaller and the anterior paraconid  $(pa^d.)$  still more so. The antero-external side of the trigonid, formed by the combined edges of the paraconid and protoconid, is trenchant and shears against the metacone-spur of the preceding upper molar. The trigonid also bears a small anteroexternal shelf (a.e.s.).

The talonid is basin-shaped, and its edge bears one outer and two inner cusps, representing respectively the hypoconid  $(hy^d)$ , hypoconulid  $(hl^d)$ , and entoconid  $(en^d)$ . The last-named cusp is, however, vestigial.

Of the remaining lower molars, the second repeats the characters of the third. The first tooth (cf. Pl. 6. fig. 6, Sminthopsis crassicaudata) presents the appearance of transverse compression, the paraconid and metaconid being partially reduced. As pointed out below, this tooth shows an interesting evolution connected with a gradual change to a premolariform condition, in which the condition in the present species represents the initial stage. The fourth molar shows a reduction of the talonid by lateral compression, the whole structure having the form of a spur attached to the posterior border of the trigonid.

Among the smaller Dasyurine the departures from the type just described are few and unimportant. There are certain minor variations in the characters of the external styles to which reference will be made in a subsequent section. The relative proportions of the sectional areas of trigonid and talonid differ slightly in different cases. The vestigial character of the entoconid seen in *Sminthopsis leucopus* is apparently common to all of the species of that genus except *S. crassicaudata*, in which this cusp is well developed. It is also found in *Phascogale minutissima* and in *Antechinomys laniger*. In the case of *Sminthopsis* and *Antechinomys* the apparently vestigial condition of the entoconid may in reality be due to mechanical wear, the animals being ground-feeding types. The cause of the reduction in the case of *Phascogale minutissima* is seen in the reduced character of the talonid, the latter structure being possibly in process of reduction in this form. The small size of the entoconid is, in any case, a secondary character, this element being well developed in all of the larger forms, as in *S. crassicaudata*, as it is in the primitive Peramelidæ and all of the Didelphyide.

On examining the molar modifications of the larger species of *Phascogale*, we find

that the only important change from the condition in Sminthopsis leucopus relates to increase in size\*. That this character is an essential feature of the carnivorous evolution is seen from the fact that it is only after passing through the successively larger species of *Phascogale* into the genus *Dasyurus* that we meet with animals of sufficient size to present carnivorous characters. Chætocercus cristicauda, Dasyuroides Byrnei, and Dasyurus hallucatus show no departure from the conditions in Phascogale; but, beginning with the still larger forms D. viverrinus and D. Geoffroyi, and passing through D. maculatus to Sarcophilus, we find the molar characters changing as follows :---Taking the second upper tooth as a basis of comparison of the upper molars (cf. Pl. 5. figs. 3 & 4, Dasyurus maculatus and Sarcophilus ursinus), there is (a) reduction of the protocone; (b) enlargement of the metacone, with lateral compression of its tip to form a trenchant blade, and encroachment of its base on the protoconeroot; (c) elongation of the trenchant metacone-spur and rotation inwards of its distal extremity, so that it comes to shear inwards rather than backwards, as in Sminthopsis; (d) lateral compression of the whole tooth, so that the external styles become approximated to their respective cusps.

Throughout the series the remaining upper molars differ from the second in exactly the same way as those of *Sminthopsis leucopus*. The first tooth always presents a condition of greater lateral compression. In *Sarcophilus* the external styles, which even in the second tooth are so closely approximated to their respective cusps that the tooth practically possesses a double cutting-edge, are in the first only separated from the latter by a narrow groove, style *ab* being almost indistinguishable from the paracone. The third tooth always presents a condition of less transverse compression, and style c, which was seen to be reduced in *Sminthopsis*, becomes quickly obliterated. The fourth molar becomes further reduced by the reduction of the protocone.

The extent of rotation of the metacone-spur, which forms such a conspicuous feature of the change, will be more apparent from the following data:—A line passing through the tip of the metacone and the distal extremity of its spur, or, in other words, along the shearing-edge, will pass through a tooth of the opposite side of the jaw—a posterior one in the case of the smaller primitive forms, and an anterior one in the case of the larger carnivorous ones. Such a line, drawn through the metacone-spur of the third molar of one side, will, in the case of *Sminthopsis leucopus*, *Phascogale Wallacei*, or *Dasyurus hallucatus*, pass through the second molar of the opposite side. In *D. viverrinus* it will pass between the first and second molars; in *D. maculatus* through the anterior part of the first molar, or between this tooth and the last (morphologically median) premolar. In *Sarcophilus* it will pass through the posterior portion of the canine.

Taking the third tooth as a basis of comparison, we find the following changes in the lower molars (cf. Pl. 6. figs. 3, 4, & 5, Dasyurus viverrinus, D. maculatus, and Sarcophilus ursinus):—There is (a) enlargement and lateral compression of the trigonid; (b) conversion of the tips of the paraconid and protoconid into trenchant blades; (c) rotation outwards of the shearing-edge formed by the adjacent edges of these cusps; (d) reduction of the metaconid; (e) reduction of the talonid.

\* Cf. general sequence in length of the tooth-rows given on p. 98.

In the first molar (cf. Pl. 6. figs. 7 & S, *Dasyurus Geoffroyi* and *Sarcophilus ursinus*) there is a further reduction and final obliteration of the paraconid and metaconid, the tooth assuming a premolar condition. In the fourth molar the talonid becomes reduced to a vestige.

That the above-mentioned modifications, with the partial exception of those of the first lower molar, represent the successive phases of an insectivorous-carnivorous evolution, can be readily shown by reference to their functions. The minute teeth of Sminthopsis leucopus serve three distinct purposes, adapting them for the comminution of insect-prey. A piercing action is performed by all of the cusps of the relatively broad crowns, a shearing one by the working of the metacone-spur of the upper molars against the paraconid and protoconid of the lower, and finally a crushing action is performed by the working of the protocone of the upper molars into the talonid of the In the extreme members of the series both the piercing and crushing actions lower. are abandoned, and the shearing action perfected. The lapse of the crushing function is indicated by the reduction of the protocone and talonid, while the lapse of the piercing action and the perfection of the shearing one is proclaimed by the lateral compression of the teeth and the conversion of the originally conical cusps into trenchant blades. The reduction of the metaconid is also attributable to the lapse of its piercing function, there being in the advanced stages no cusps against which it might shear. The rotation of the metacone-spur is no less a character of carnivorous adaptation than the trenchant modifications of the cusps: by means of it the teeth are made to shear together in a single longitudinal line instead of individually in parallel transverse lines, as is the case with Sminthopsis and its allies.

The changes which take place in the first lower molar, and result in the conversion of a typical tuberculo-sectorial tooth into one of premolariform character, are associated with the reduction of the posterior premolars shortly to be described, and are therefore only indirectly connected with the carnivorous evolution. In the smaller species of *Phascogale*, and in *Sminthopsis* and *Antechinomys*, where the upper posterior premolars are well developed, or at most only slightly reduced, the latter teeth shear against the protoconid and paraconid of the first lower molars in much the same manner that the metacone-spur does in the succeeding teeth. With the reduction of the posterior premolars in the larger forms this function is obliterated, and the protoconid loses its shearing character, while the paraconid disappears. The metaconid becomes reduced for the same reason as in the remaining teeth. In *Dasyurus* and *Sarcophilus*, where the posterior premolars are entirely absent, the first lower molars bite loosely against the median upper ones.

Incisors.—These teeth present a carnivorous evolution almost as marked as that just described for the molars. The change affects chiefly the relations of the median upper teeth and the length of the tooth-rows. Throughout the species of *Phascogale* the median upper incisors are sharply differentiated from the lateral teeth, being clongated, procumbent, and subcaniniform. They are separated at their bases and approximated at their tips. The lateral incisors are short and of the usual spatulate type, except that their tips are slightly pointed. In the species of *Sminthopsis* there is usually a more or less marked tendency for the median upper teeth to be separated at their tips as well as at their bases, and to project downwards rather than forwards. This condition is to be regarded as special rather than as primitive. *Dasyurus hallucatus* shows much the same condition as *Phascogale*, but following the remaining species of *Dasyurus* we find the median upper incisors undergoing a gradual reduction by which they come to resemble the lateral teeth. In *Sarcophilus* they are indistinguishable from the latter, except for their slightly more rounded section and their basal separation.

The differentiation of the median upper incisors in the smaller Dasyurinæ represents an insectivorous adaptation developed for the purpose of making the terminal teeth more serviccable in the capture of insect-prey, and their subsequent return to a normal spatulate condition, in the course of the carnivorous evolution, is due to the lapse of their original function. The reduction of these teeth is closely associated with a change in the relative length of the incisor rows. In the smaller Dasyurinæ the latter are relatively long, and meet in the middle line at an acute angle, so that the modified median teeth are placed in the most advantageous position. Passing through the species of *Dasyurus* in the order above mentioned we find a successive shortening of the incisor rows, until in *Sarcophilus* they form an almost straight line across the front of the muzzle. As mentioned below, there is also to be seen, in proceeding through the same series, an increase in the functional importance of the canines, indicating a gradual transference of the piercing and grasping functions from the median incisors to the latter teeth. The shortening of the incisor rows is in part connected with the thickening of the muzzle for the support of the enlarged canines, but is more cspecially developed for the purpose of placing the incisors in a position where they will least interfere with the action of the canines, namely as close as possible to the canine roots.

Many of the placental Insectivora present a close resemblance to the Dasyurinæ in respect to the differentiation of the median upper incisors. For example, in the Soricidæ, and in *Centetes* and *Chrysochloris*, the median upper incisors are much like those of *Phascogale*, and the more specialized modifications of *Sminthopsis* are repeated in the genera *Echinops*, *Ericulus*, and *Limnogale* (Centetidæ), and also in *Macroscelides* (Macroscelididæ). It is interesting to note that, with the partial exception of such forms as *Phascogale penicillata* and its prototypal relative *P. calura*, the insectivorous differentiation of the incisors in the Dasyurinæ is confined to the median upper teeth, but that in many of the Insectivora it extends to other of the incisors as well. More especially is this noticeable in the Soricidæ, where the median lower teeth are elongated in such a way that they work against the median upper teeth after the manner of the tips of a pair of forceps. This modification, while it is not indicated in the Dasyurinæ, is highly characteristic of the Phalangeridæ, and, as pointed out below, represents the starting-point for the whole diprotodont modification characteristic of the last-named family and its herbivorous derivatives. These facts taken together indicate that the differentiated condition of the incisors, and also that it represents a prototypal and

Canines.—These teeth are well developed in all of the Dasyurinæ, but are relatively weakest in Sminthopsis and Antechinomys. In the carnivorous evolution, as exemplified by Phascogale, Dasyurus, and Sarcophilus, they present a successive increase both in actual and relative size. The increase in relative size is not at first sight apparent, but is easily demonstrable by sketching to scale the profile aspect of the tooth-series in such representative forms as Sminthopsis murina, Phascogale flavipes, P. Wallacei, Dasyurus hallucatus, D. maculatus, and Sarcophilus ursinus.

**Premolars.**—In their general characters these teeth are of the simple piercing type common to the Didelphyidæ, Peramelidæ, and primitive Phalangeridæ (Acrobates and Distæchurus), as well as to the placental Insectivora and Carnivora. In their special characters they present a series of important modifications, which serve to support and extend the plan of dental evolution as determined by the molars, at the same time throwing light on the relations of the smaller forms with the remaining Marsupials, especially the existing Didelphyidæ and *Peratherium*.

The chief modifications are as follows:—(a) successive reduction of the posterior premolars, proceeding from a stage in which these teeth are the predominant elements of the series (*Sminthopsis* and *Antechinomys*) to one in which they are altogether absent (*Dasyurus*, *Sarcophilus*); (b) compensatory enlargement of the median premolars until the reduction of the posterior teeth is completed; (c) subsequent slight reduction of the anterior and median premolars in the final carnivorous stages.

Some of the features of the premolar evolution of this group have already been described by Thomas (1887), this writer having shown, by a carefully selected series of diagrams (pl. 27. figs. 1–5), that the two-premolared condition in *Dasyurus* is only the culminating stage of a process of reduction of the posterior premolars which is exemplified by the species of *Phascogale*. Thomas has further pointed out that the extent of reduction is always greater in the lower than in the upper teeth, so that in certain cases, such as *P. Thorbeckiana* and *P. apicalis*, where the upper teeth are vestigial, the lower may be entirely absent.

The modifications of the posterior premolars are of great interest, as showing much more clearly than those of the remaining teeth the primitive position of *Sminthopsis* and *Antechinomys* as regards dentition. In both of these genera the posterior upper premolars are always larger than the median teeth, and in some cases (*S. leucopus*, *A. laniger*) disproportionately so, while in *Phascogale*, with the exception of *P. minutissima*, in which they are again disproportionately larger, they are variable, being slightly larger than, or equal in size to, the median teeth, or in some cases wholly vestigial. As will be pointed out in greater detail in a subsequent section, *Sminthopsis* and *Antechinomys* make the closest approach to the prototypal condition found in *Peratherium*, where the posterior premolars are apparently always predominant, and, furthermore, they take up a position with reference to the latter genus approximately equivalent to that taken by certain of the existing Didelphyidæ (*Peramys*).

Relative size of upper posterior premolar.	Species.	Length of upper tooth-row.	No. of specimens measured.
I. Posterior premolar dispro portionately larger tha median	a Smininopsis hirripes	9.9 13 14 12.5	2 1 2 1
II. Posterior premolar slightl larger than or equal t the median	o K Phascogate flavipes	$12 \\ 12-13 \\ 13 \\ 14\cdot 5-15 \\ 15\cdot 5 \\ 16\cdot 5-17\cdot 5 \\ 16\cdot 17\cdot 5 \\ 22-25$	$2 \\ 4 \\ 1 \\ 3 \\ 2 \\ 3 \\ 2 \\ 3 \\ 3 \\ 3 \\ 3 \\ 3 \\ 3$
III. Posterior premolar smalle than median and be coming vestigial	- , Thorbeckiana	25 20 26 	1 2 1 
IV. Posterior premolar absent	Dasyurus hallucatus ,, Geoffroyi ,, viverrinus ,, maculatus Sarcophilus ursinus	$\begin{array}{c} 32 - 33 \\ 36 - 38 \\ 36 - 42 \\ 46 - 48 \\ 72 \end{array}$	3 5 7 2 2

Like the carnivorous evolution of the molars, the reduction of the posterior premolars is closely connected with increase in size of the animals, and the above table has been arranged to show this by a comparison of the relative sizes of the upper posterior premolars with reference to the median teeth, with the length of the upper tooth-rows. The various species are here arranged in four groups in order to avoid unnecessary description of the sizes of the premolars in each case. Within the different groups, however, the forms have been placed where possible in their natural order. The lengths of the tooth-rows have been measured in each case in a straight line from the bases of the median incisors to the ends of the fourth molars.

Two notable exceptions to this plan are found in *Phascogale apicalis* and in *Sminthopsis macdonnellensis*. In the former, two specimens measured showed the length of the tooth-lows to be 18 mm. The posterior premolar is in an advanced stage of reduction, so that the species presents a dental length characteristic of Group II. and the premolar characters of Group III. A similar condition is found in the latter species<sup>\*</sup>, where, in animals of general proportions like the larger members of Group II., the posterior premolar is greatly reduced.

With regard to the premolar transformations in the later carnivorous stages, it has already been mentioned that while during the reduction of the posterior premolar there is a compensatory enlargement of the median tooth, there is subsequently a slight reduction both of the latter tooth and of the anterior premolar. Neither of these teeth

<sup>\*</sup> Only spirit-specimens of this species and of *Chaetocercus* and *Dasyuroides* were available, so that the tooth-rows could not be exactly measured.

is as functional in the carnivorous forms as in the insectivorous prototypes. The explanation of this apparently anomalous condition is doubtless to be sought in the progressive increase in the functional value of the canines. In the insectivorous forms the latter teeth are at most only moderately developed, so that the premolars possess their full functional value as grasping and piercing organs. In the carnivorous forms these functions become largely usurped by the enlarging canines, and the incisors and premolars become reduced. In *Sarcophilus* and *Dasyurus* the premolars present an appearance as if the material formerly used for their development had been utilized in the development of the canines.

## MYRMECOBIINÆ.

The dentition of the single representative of this subfamily is of great interest on account of its marked departure from the usual conditions in the recent Mammalia, in respect to the peculiar characters and extraordinary number of the molar teeth, and the alliance thereby suggested between *Myrmecobius* and the Mesozoic Mammalia.

It is a noteworthy coincidence that the original description of Myrmecobius by Waterhouse (1836) was published only shortly before a vigorous discussion, marked by the opinions of such eminent zoologists as de Blainville, Owen, and Agassiz, took place as to the nature of the first of the famous jaws from the Stonesfield Slate. The discovery of Myrmecobius, with its peculiar dentition, furnished Owen (1836) with a strong argument in favour of the view that their affinities were not only mammalian, but also marsupial. Owen repeated his opinion in his subsequent publications (1846, 1871), and even went so far in his estimation of the primitiveness of Myrmecobius as to suggest a community of dental characters between it and the theriodont reptile Galesaurus (1887). Following Owen, Thomas (1888, p. 312) has characterized Myrmecobius as an "unmodified survivor from Mesozoic times," and its possible affinities have been commented upon by other writers in almost every case in which the Mesozoic mammals have been described.

New interest has lately been added to the question through the discovery by Poulton of the true teeth of *Ornithorhynchus*, the patterns of which were compared by that writer (1888, p. 20) with those of *Myrmecobius*, and by Cope (1888, p. 259) with those of the Multituberculata. Following Poulton's comparison, Leche (1891, p. 152) suggested a possible community of type between the molars of the Multituberculata and those of the Dasyuridæ, through *Myrmecobius*, although he subsequently (1893, p. 114, footnote) withdrew his opinion as to the resemblances between *Ornithorhynchus* and *Myrmecobius* on the publication of Stewart's description (1891) of a specimen of the former animal in the collection of the Royal College of Surgeons with more complicated teeth than those in the specimens previously described by Poulton (op. cit.) and Thomas (1889).

Winge (1882, 1893) has expressed the opinion that the relations of *Myrmecobius* are with the Dasyuridæ, the extraordinary number of the molariform teeth being in his estimation the result of a retention of the normally deciduous premolars. Leche (1891), however,

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dissents from this proposition, and believes the increased molar formula to represent a primitive character inherited from Mesozoic forms \*.

In a former paper (1901 a) the writer expressed the opinion that the dental characters of *Myrmecobius* have been derived by retrogression from those of the normal Dasyuridæ, and this position has been amply confirmed by the examination of the extensive series of specimens in the British Museum collection. Many of the characters of the incisors, canines, and premolars, which appear at first sight to be primitive, are repeated in the Peramelidæ, where they are undoubtedly the result of retrogression. The patterns of the lower molars are directly derivable from those of the smaller Dasyurinæ. In fact, the only real difficulty in the derivation of the dentition relates to the patterns of the upper molars, these being so extremely variable that the cusp-homologies are difficult of determination. Nevertheless, even in them it is possible to recognize a ground-type running through the variations, and this ground-type represents approximately the pattern characteristic of the normal Dasyurinæ.

With reference to the origin of the excessive molar formula in *Myrmecobius*, it will be seen that there are three possible explanations :—(a) That it is due to the retention of the normally deciduous teeth (Winge); (b) that it represents a primitive condition carried over from the Mesozoic Mammalia (Owen, Leche, and others); (c) that it is due to a simple reduplication of teeth from the posterior portion of the dental lamina, or to a reappearance of formerly vestigial teeth in the same region.

As to the possibility of a retention of the deciduous teeth, a description will be found, on pp. 106–107, of a young specimen in the collection in which the posterior premolars have not yet begun to develop; and of three molariform teeth already formed, the first are comparatively minute, while the second are approximately equal in size to the unworn first molars of the adolescent animal. This appears to indicate that the minute first molariform teeth represent deciduous premolars, which are afterwards replaced. It may be observed that, even assuming a retention of the deciduous teeth, we would still have to account for the occasional presence of an additional lower molar.

With reference to Leche's suggestion that the increased formula is a primitive character, the writer believes it to be counterindicated by the following facts :—(a) The extreme variability of the dentition and the abundant evidence of retrogression from a normal Dasyurine condition, added to the fact that there is an intimate correspondence between Myrmecobius and the Dasyuridæ in other respects, and more especially in the reduced incisor formula of  $\frac{4}{3}$ , indicate that the relations of the animal are in every way with the latter family. That this relation is, however, not an ancestral one, as the increased molar formula would seem to indicate, is apparent from the fact that the ancestral modifications of the Dasyuridæ are to be found in Didelphyidæ, which forms present a more primitive condition of the incisor formula than is found in Myrmecobius. (b) The data collected by Bateson (1894) show that reduplication of teeth may occur

<sup>\* &</sup>quot;Es scheint mir somit festzustehen dass das *Myrmecobius*-Gebiss, was die Form der Backen-Zähne betrifft, theilweise reducirt ist, und demselben Typus wie dasjenige der Dasyuridæ und *Ornithorhynchus* angehört, dass aber die grössere Anzahl etwas Primitives, von Mesozoischen Säugethieren Ererbtes ist."

without reference to homology, while the observations of Thomas (1888) and Allen (1901) show, further, that an excessive number of molars may be found as a variation in normal Marsupials (*Bettongia* and *Didelphys*). (c) The minute size of the molars in *Myrmecobius* and the elongation of the palate and lower jaw offer just those conditions favourable for the intercalation of new teeth, or, as indicated above, their origin by reduplication from the posterior part of the dental lamina.

Unlike Leche, the writer sees nothing incompatible in the recognition of a retrogressive development of the already existing teeth and the synchronous addition of new ones. The reduction of the function of an organ is not immediately followed to its obliteration, the latter only taking place after a longer or shorter period of attempted development. While, therefore, the molar teeth of Myrmecobius may be found in a semi-reduced condition, the mere fact of their presence is sufficient evidence of their tendency to develop in a normal way. It is accordingly reasonable to suppose that under the favourable conditions of increased space in the molar region, the same tendency as is seen under less favourable conditions in Bettongia and Didelphys to produce new teeth should not only be present, but also be more strongly marked. In fact, the existence of such a tendency is in evidence in the case of the antemolar teeth, although the latter are admittedly less reduced than the others. Two of the British Museum specimens already mentioned by Thomas (1888) show four instead of three lower incisors, and Leche (1891) has described a specimen in which there is an additional premolar in the left ramus of the lower jaw behind the posterior premolar. In the Peramelidæ we find several instances in which reduction of the canines is accompanied by the appearance of new basal cusps, and an analogous case is seen in the Didelphyidæ, where in Caluromys a retrogressive development of the external styles of the upper molars (cf. Pl. 5. fig. 27) is proclaimed by a reduction of the larger elements normally present, and the development of a large number of smaller ones.

No surprise need be expressed that such new teeth should resemble in their characters the already existing ones. The results of Bateson (1894) show that in the intercalation of new teeth without definite homologies the same principle determines their patterns as those of the normal teeth of the region in which they occur.

With reference to the comparisons which have been made between the molars of *Myrmecobius* and those of *Ornithorhynchus* and certain of the Multituberculata, there is no doubt that certain resemblances exist, but they are of much too general a kind to be interpreted as indicating affinities. A careful study of the patterns presented by *Plagiaulax, Microlestes, Ornithorhynchus*, and *Myrmecobius* fails to reveal any evidence of homologous cusps. The fact, already referred to above, that the relations of *Myrmecobius* are in most respects with the Dasyuridæ, whose prototypal characters are those of the Didelphyidæ, strengthens the view that such resemblances as do exist are merely the result of convergent development. The molars of *Myrmecobius* differ from those of the normal Dasyuridæ chiefly in lacking the angularity both of the general contour and the constituent cusps, which, in the latter, is due to the mechanical precision with which the teeth are fitted together. It is exactly in these obviously secondary

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features that *Myrmecobius* resembles the plagiaulacid Multituberculata. As to what kind of adaptations the teeth of the latter animals represent is wholly obscure. In the writer's opinion the tabulate teeth of *Ornithorhynchus* are highly specialized, and represent an adaptation for crushing the shells of small molluses. They are comparable, in a general way, with those of the Trichechidæ, or, better, the Sea-Otters. The excessive crenulation of the molar margins in the specimen described by Stewart (1891, pl. 8), which enhances their multituberculate character, is undoubtedly secondary, and represents a development of much the same order as that seen in the teeth of the Suidæ and Ursidæ. Without expressing an opinion as to the Multituberculata, the writer considers the superficial resemblances existing between *Myrmecobius* and *Ornithorhynchus* to be referable to different adaptations, and therefore not only secondary, but also much less worthy of being designated as convergent developments than, for example, those seen in the molars of the Phalangeridæ and Primates, where similar quadrituberculate teeth have been evolved independently for similar purposes.

Before considering the dental characters of *Myrmecobius* in detail, it may be observed that the whole dentition is extremely variable, and that no adequate conclusions can be formed from a study of single specimens. The variability is much more pronounced in the upper molars than in any of the remaining teeth, there being in them not only no correspondence between the homologous teeth of different individuals, but also none between those of opposite sides of the jaw in the same animal. The cause of the variability is partly to be sought in the uneven mechanical wearing to which the teeth are subjected, through the presence of particles of earth in the food. This is especially noticeable in the case of the molars, where, as Leche (1891, p. 151) has shown, the outer parts of the lower teeth and the inner parts of the upper ones tend to be obliterated with age, while the remaining parts are, in each case, only slightly affected. Beyond this, however, there is a variability of an inherent kind which is not the result of wear, but of the retrogression which is taking place throughout the dentition. It is interesting to note that a similar tendency towards variability is seen under similar conditions in the Peramelidæ.

Molar Patterns.—The lower molars are much more constant in their characters than the upper, and also depart to a less extent from the normal dasyurine type, so that they may be more conveniently described first.

As already mentioned, apart from their minute size, the molars of *Myrmecobius* differ from those of the Dasyurinæ chiefly in lacking the angularity both of the general contour and of the constituent cusps. The lower teeth (Pl. 6. fig. 9) are roughly oval in section, and their cusps are either conical or slightly curved. The crown of an unworn posterior tooth shows exactly the same number and arrangement of the cusps as is seen in the teeth of normal dasyurine forms (*cf.* fig. 3), there being in all six cusps, of which the three anterior together represent a trigonid, while the remaining three represent a talonid. These two portions of the tooth are not differentiated as in normal forms, the reason being partly that the crown-surface of the talonid is placed almost at the level of that of the trigonid, and partly that the cusps of both portions have much the same characters. In fig. 9b is represented a tooth which had not yet appeared above the bone, and in this the trigonid will be seen to show indications of the angularity characteristic of normal forms. This specimen is of great interest, not only as indicating the former presence of this condition in the lower molars, but also as implying a similar condition in the more highly modified upper teeth. In some cases it is possible to recognize in the lower molars an anterior tubercle representing the anteroexternal shelf characteristic of normal forms.

The most peculiar feature of the lower teeth is, however, the marked differentiation between the outer and inner cusps, the protoconid and hypoconid being reduced, while the paraconid, metaconid, entoconid, and sometimes the hypoconulid are large and elongated. These relations are exactly the reverse of those in the Dasyurine. As Leeche has pointed out, the condition is partly attributable to mechanical wear. In the anterior molars, which, being older, have been in use for a longer time, the protoconid and hypoconid are found in a much more advanced stage of reduction than in the newer posterior teeth. In extreme cases, where the outer cusps have been worn down to their bases, the teeth present a curious appearance; when viewed internally in profile they appear triconodont, or, in cases where the hypoconulid is well developed, quadriconodont, the cusps being arranged in a linear series from before backwards. The basal ledge, which formerly supported the two outer cusps, presents the appearance of a wide external cingulum. The reduced condition of the protoconid and hypoconid is not, however, wholly attributable to mechanical wear, since the same tendency is seen in the unworn teeth, although naturally in a lesser degree. It appears as if the repeated obliteration of the outer cusps by wear had produced a development in that direction.

The first lower molar, believed by Winge to represent a formerly deciduous tooth, is usually found in a much more reduced condition than the remaining teeth. Leche regards this also as the result of use. In all of the older specimens which I have examined, and also in the young specimen represented in Pl. 6. fig. 9 c, the tooth shows three or four cusps arranged in a linear series. These apparently represent the inner cusps of the posterior teeth, although apart from this their homologies are usually obscure. In the young specimen represented in text-figure 3 (p. 106) of the second pair of molariform teeth, that of the left side shows one outer and two inner cusps of doubtful homologies, while that of the right side shows all of the cusps characteristic of the posterior teeth. It is probable that the same remark made for the posterior teeth is true to a greater extent of the first, namely, that the reduction is partly a natural one and partly the result of mechanical wear.

Examples of the patterns of the upper molars are given in Pl. 5. fig. 5. The cusp designations, and also the descriptions here given, are based on a study of seven specimens. As already intimated, these teeth present an infinite variety of minor characters, but it is possible to recognize a ground-type apparently representing a modification of the condition in normal forms.

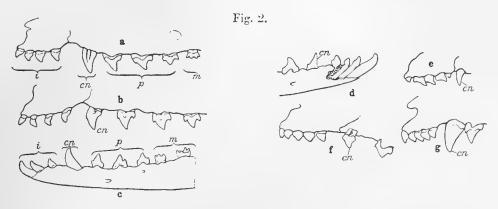
Taking the intermediate members of the molar series as more typical than the extreme

anterior and posterior ones, we first notice the fact that as regards contour a roughly triangular shape predominates, and that, further, the apex of the triangle is internal and is formed of a large cusp (pr.), identifiable with the protocone in normal forms. In some cases the protocone-like cusp is well developed, but the triangular shape is obliterated by the great development of the more posteriorly placed cusps. In one case the protocone was found to be considerably elongated and its edge crenulated. The anterior portion of the tooth is usually occupied by one internal (pa.) and two external (ab and c) cusps. The anterior position of these elements is partially disturbed by the occasionally anterior position of the protocone. The internal cusp, from its small size and position, probably represents a paracone, while of the two external cusps the anterior one, which stands in close relation with the paracone, is probably equivalent to style ab of the Dasyurinæ, and the more posterior one, judging from its large size and position, is probably equivalent to style c. The paracone is often worn down and sometimes wholly absent. The posterior part of the tooth is usually occupied by two cusps, one of which (me.), situate internally, is usually conspicuous for its large size. These cusps probably represent together the metacone of normal forms. The reasons for this view are: first, that their posterior position indicates a connection with the metacone; secondly, that they are sometimes connected by a trenchant edge (cf. fig. 5a); and, thirdly, that all of the well-developed cusps of the molars of *Myrmecobius* are elongated, and that an elongation of such a cusp as the metacone of normal forms would very likely result in the formation of an extra cusp from the distal extremity of its spur. It must be admitted, however, that it is sometimes difficult to explain the relations of these elements on this supposition, on account of a reversal of their relative sizes, although it is probable that the latter condition is due in some cases to the wearing to which the internal cusps are subjected.

As in the case of the lower teeth, the first molars are much simpler than the others. The best-developed specimen examined showed four cusps arranged in a linear series, the two intermediate members being much larger than the others ; and, in addition, two minute cusps placed between the larger median elements, the one internally, the other externally. The greatest departure from the condition in this specimen was found in another case, in which the tooth formed a flat plate, with no indication of cusps beyond that arising from a slight concavity of the edge. The homologies of the cusps, even in the better-developed teeth, are extremely doubtful, except that they show a general resemblance, when seen in profile, to the external styles in normal forms. The general conclusion with regard to the derivation of the upper molars is that they

The general conclusion with regard to the derivation of the upper molars is that they represent modifications of a trituberculate type. The examination of a larger series of specimens is, in the writer's opinion, necessary before this proposition can be accepted as certain.

Incisors.—All of the incisor characters of Myrmecobius are directly derivable from those of the Dasyurinæ or Didelphyidæ. The median upper teeth (text-fig. 2, a, b) are more rounded in section than the lateral ones, and are also slightly procumbent, so that, while they are not differentiated to the same extent as in normal insectivorous forms, they show signs of having been so at an earlier stage. It is interesting to note that a similar lack of differentiation characterizes the homologous teeth in the Peramelidæ (fig. 2, e). The lateral incisors present a curious appearance, due to a subcaniniform modification of their tips. This condition is only an extreme development of that seen in the Dasyurinæ and Didelphyidæ (fig. 2, g), where the tips of the lateral teeth are already acute and directed slightly backwards. A very similar appearance to that seen in Myrmecobius has been figured by Flower and Lydekker (1891, p. 539) in the degenerate



The antemolar teeth of Myrmecobius fasciatus compared with those of other Marsupials.

a-c. Myrmecobius, upper and lower dentition of normal specimens; d. Lower dentition of abnormal specimen with four lower incisors; e. Perameles obesula, upper incisors; f. Charopus castanotis, upper incisors and canine;
g. Metachirus opossum, upper incisors and canine. Abbreviations: i., incisors; cn., canine; p., premolars; m., molars.

carnivore *Eupleres*, and a similar tendency towards a posterior extension of the tips of the lateral teeth is found as a secondary character in certain of the Peramelidae (fig. 2, e). All of the lower incisors tend to be caniniform. Their contour is much less angular than in the upper teeth, and a similar difference is observable in normal forms. The median lower incisors are slightly enlarged, as in *Phascogale penicillata*<sup>\*</sup>.

Canines.—These teeth show a distinct departure from the usual type found in the Dasyuridæ, this being particularly the case with the upper ones. The latter (fig. 2, b) tend to be laterally compressed, and in some cases present accessory anterior and posterior cusps. In addition, they sometimes show a grooving of the root. These characters give them an almost premolariform appearance, and this is further enhanced by the fact that there is a gradual reduction in size of the cheek-teeth proceeding from the canine to the posterior premolar.

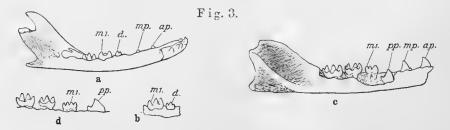
The fact that morphologically the canines are modified premolars might at first sight

\* The incisors of *Myrmecobius*, like all of the remaining teeth, tend to be separated by diastemata, and thus present an appearance not unlike that seen in certain of the Mesozoic Mammalia. The condition is, however, a purely secondary one, and is due to the elongation of the muzzle common to this and other ant-eating mammals. It is interesting to note that even the comparatively advanced young show no indications of the elongated muzzle characteristic of the adult, the facial region presenting a curious abbreviated appearance, which Leche has aptly referred to as "cine wirkliche Mopsform."

lead one to regard the condition in *Myrmecobius* as primitive. That it is not so, however, may be seen from a comparison of the Peramelidæ, certain species of which present canine modifications of the same kind and even of a more extreme degree. An example is given in text-fig. 2 of the teeth of *Chæropus castanotis*. In all cases among the Peramelidæ the modification is not only secondary but also purely local.

*Premolars.*—Apart from a marked tendency to develop accessory cusps, which is doubtless due to their separation by diastemata, these teeth present the same characters as those of the Dasyurinæ. As already mentioned above, they decrease in size from before backwards. The exact explanation of this condition is doubtful; the small size of the posterior tooth may be due simply to the circumstance that it forms an intermediate member between the larger anterior teeth and the greatly reduced molars, or that it has been formerly reduced as in the normal Dasyurinæ. As regards the presence of accessory cusps, it may be observed that exactly the same tendency is found in the Peramelidæ under similar conditions of increased space in the premolar region.

Milk premolars.—In describing the dentition of the Dasyurinæ no reference has been made to the modifications of the deciduous teeth for the reason that their characters do not pertain to the category of secondary adaptations here considered, but to the primary differentiation of the Marsupials as a group. Some reference to them is, however, necessary in the case of *Myrmecobius*, on account of their possible connection with the origin of the increased molar formula.



Doubtful case of dental replacement in Myrmecobius fasciatus.

a. Internal view entire left ramus of jaw of young specimen (nat. length of jaw=23 mm.); b. External view of part of right ramus of same specimen; c. Right ramus of older specimen; d. External view of right posterior premolar and anterior molars of adult animal. Abbreviations: ap., mp., pp., anterior, median, and posterior premolars; d., doubtfully deciduous premolar; m. 1, first true molar. All figures drawn to same amplification.

The milk-premolars have been recognized by Woodward (1896) in the young, but their subsequent fate has not been elucidated. According to the view of Thomas (1887) and Leche (1891) they are replaced by the posterior premolars in the ordinary way, while in Winge's (1882) opinion they remain in place, the posterior premolars being unable to dislodge them on account of the elongation of the jaw.

The accompanying text-fig. 3 represents the anterior molariform teeth of the lower jaw in three specimens, all of which have been drawn to the same amplification. Of these a and b represent the teeth of a young specimen, in which the posterior premolars are not yet formed. In a the first member of the molariform series is comparatively

### OF THE AUSTRALIAN MARSUPIALIA.

minute, and in **b** the corresponding tooth of the opposite jaw is only slightly larger. In **d**, which is the specimen described and figured by Thomas (*op. cit.*, pl. 27. fig. 5), the posterior premolar is almost fully formed, but is still beneath the bone. The first members of the molariform series are considerably larger than in the younger specimen, approximating more nearly in size to the second members of the latter. A somewhat similar size relation is seen in c, in which the posterior premolars are fully in place. The minute size of the first molariform teeth in specimen a appears to point out these teeth as milk-premolars, which are afterwards replaced as in normal forms. The dental variability is, however, so great in *Myrmecobius* that the evidence of a single specimen must be regarded as suggestive rather than conclusive.

#### THYLACININÆ.

In a former paper (1901 a) the molar patterns of the Tasmanian Wolf (*Thylacinus cynocephalus*) were described as representing the final stage in the carnivorous evolution of the Dasyuridæ. To this conclusion, which turns out to be erroneous, the writer was led partly by a comparison of the molars of the animal with those of *Dasyurus*, the only other member of the family at that time available, and partly by the view expressed by Thomas (1888), that the relations of *Sarcophilus* are with *Thylacinus* rather than with *Dasyurus*. In the present paper *Thylacinus* is assigned to a separate division, and even suggested as a foreign or unrelated element in the Australian family.

Reference has already been made to the fact that the various genera of the Dasyurinæ present successive phases of an extremely homogeneous dental evolution, the chief features of the transformation being: (a) reduction of the protocone in the upper molars and of the talonid in the lower; (b) approximation of the external styles of the upper molars to their respective cusps; and (c) reduction with final obliteration of the posterior premolars and of the paraconid in the first lower molars. In all of these characters *Thylacinus* stands apart from the typical Dasyuridæ, so that while it presents a degree of carnivorous dental specialization only slightly inferior to that presented by *Sarcophilus*, its evolution must have proceeded independently of that of the Dasyurinæ, at any rate in so far as the carnivorous stages of the latter are concerned.

The resemblances between *Thylacinus* and the Sparassodonta of the South-American Miocene have been noted by different writers and regarded as indicating affinity between the latter group and the Dasyuridæ. Lydekker (1899) has suggested the Sparassodonta as the ancestral forms of the Australian family. The characters in which *Thylacinus* resembles the Sparassodonta, however, prove to be exactly those in which it differs from the advanced Dasyurinæ, whose evolution can be directly traced to minute insectivorous forms such as *Sminthopsis* and *Phascogale*. If the resemblances between *Thylacinus* and the Sparassodonta represent affinity rather than parallel development we can assume no closer relation between both of them and the Dasyuridæ than is implied by a possibly common origin of the South-American and Australian faunas.

It must not be supposed that *Thylacinus* presents any dental characters which would prevent it from being theoretically derived from one of the smaller dasyurine forms. SECOND SERIES.—ZOOLOGY, VOL. IX. 16

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It is only the fact that all of the remaining members of the Dasyuridæ as at present defined, with the exception of *Myrmecobius*, present a uniform dental evolution which is thus the predominant and characteristic one for the Australian radiation, which accentuates the resemblances of such an isolated form as *Thylacinus* to the Sparassodonta, whose type of evolution is just as characteristically South American, and lends probability to the view that its origin is to be sought in the latter group.

Length of Tooth-rows.—On comparing the tooth-rows of Thylacinus with those of Sarcophilus or the more advanced species of Dasyurus, we notice a conspicuous difference in their relative lengths. In the latter, notwithstanding the lateral compression of the molars, there has been a shortening of the whole dental series, while in the former an elongated condition has been retained and possibly increased. It is interesting to note that similar differences characterize the dental evolution of the placental Creodonta and Carnivora, although in the latter Orders they are closely associated with the elaboration of posterior or more anterior cheek-teeth as sectorials. The elongated condition in Thylacinus is repeated in the South-American group.

Molar Patterns.-The characters of the upper molars are represented in Pl. 5. figs. 6 & 7, of Thylacinus cynocephalus (m. 3) and T. spelæus (m. 2). The protocone is well developed, and is supported on a separate root. In this character *Thylacinus* differs from the carnivorous members of the Dasyurinæ, and points back to the insectivorous forms. The crown-surface of the protocone in the adult presents a curious spur-like appearance. Its posterior border tends to be slightly trenchant. The metacone is much enlarged and trenchant. As in Sarcophilus, its tip is lanceolate from a filling out of the concavity originally present on its outer side. The metacone-spur is well developed and trenchant, but its distal extremity has not been rotated inwards to the same extent as in Sarcophilus. The paracone is small and comparatively undifferentiated. Unlike those of the Dasyurinæ, the external styles are vestigial or wholly absent. Style ? ab is apparently always present in the first, second, and fourth molars. Style c is not represented, but a small element probably equivalent to style  $c_2$  (cf. Pl. 5. fig. 1 b, Peratherium) is apparently always present in the first molar, variable in the second, and scarcely distinguishable in the third. The vestigial nature of the external styles gives the teeth a very different appearance from that seen in Sarcophilus, where their great development and approximation to their respective cusps result in the production of a double cutting-edge. The fourth molar is small, and of much the same character as that of the Dasyurinæ. The cusps represented are the protocone, paracone, and style ab, the metacone being barely indicated by a small posterior protuberance.

The patterns of the lower molars are represented in Pl. 6. figs. 10 & 11, of the third and first teeth of T. cynocephalus. As in Sarcophilus, the paraconid and protoconid are modified to form trenchant blades. The metaconid is wholly absent, as in Prothylacinus and Amphiproviverra. The anterior portion of the base of the trigonid in the first and second molars bears a small protuberance representing an antero-external shelf. Except in the fourth tooth the talonid is well developed, and its crown-surface is flat and shelflike. In this character *Thylacinus* differs markedly from the Dasyurinæ, more especially the carnivorous forms, but resembles *Prothylacinus* and *Amphiproviverra*. The talonid shows indications of the three original cusps. Of the latter the hypoconid is best developed and tends to be slightly trenchant. In the fourth molar the talonid is reduced to a small spur, as in *Amphiproviverra*. An interesting character is seen in the first molar, where the paraconid is comparatively well developed, as again in the lastnamed form. As already pointed out, this structure is absent in the carnivorous Dasyurinæ.

Antemolar Teeth.—The incisors are very similar to those of Sarcophilus. The median upper teeth show signs of having been formerly procumbent, as in the insectivorous Dasyurinæ, in being more rounded in section, or, in other words, less completely spatulate than the lateral teeth, and also in being separated at their bases and approximated at their tips. The incisor-rows, unlike the premolar- and molar-rows, show the same shortening exhibited by Sarcophilus. In this case the lower canines are almost apical in position.

The canines show no essential difference from those of *Sarcophilus*, except that they are rather more slender and more evenly curved.

The chief feature of the premolars is that they increase in size from before backwards, the posterior tooth, as in the Prothylacinidæ, showing no indications of the reduction which is so marked a feature of the Dasyurinæ.

# PERAMELIDÆ.

Reference has already been made to the fact that the dental characters found in the smaller insectivorous members of the Dasyuridæ are prototypal not only to those of the larger carnivorous forms of that family but also to a considerable extent to those of the omnivorous Peramelidæ and Phalangeridæ. The close sequence of modifications which is observable in the dental evolution of the Dasyurinæ, and which is of so perfect a kind that it is impossible to distinguish where the insectivorous evolution ceases and the carnivorous evolution begins, shows at once that one is a direct natural continuation of the other. Nevertheless, on the omnivorous side we find, in certain of the Peramelidæ and Phalangeridæ, modifications which are almost as inseparable from those of the insectivorous Dasyuridæ as are those of their carnivorous relatives, but which at the same time usher in advanced medifications of a widely divergent kind. While, therefore, it may be shown that the differentiation of the Phalangeridæ in some respects represents an insectivorous specialization, there is abundant evidence that as regards dentition the primary division of the Australian radiation has been the differentiation of a carnivorous and an omnivorous line from insectivorous prototypes.

It is interesting to note that the Peramelidæ, or including with them the Phalangeridæ, occupy much the same position as intermediate omnivorous types with reference to the Dasyuridæ on the one hand, and the members of the herbivorous section on the other. that, among the Placentals, the Condylarthra do with reference to the Creodonta and the Ungulata respectively. It is also an interesting fact that among the existing Insectivora, a group showing a fairly wide range of dental differentiation, we find in the Soricidæ molar patterns of an incipient omnivorous type which parallel almost exactly those of the Peramelidæ, just as in the Talpidæ and Chrysochloridæ we find insectivorous modifications paralleling those of the Dasyuridæ and Notoryctidæ respectively.

Unlike that of the Dasyurinæ, the dental evolution of the present family does not represent a uniform progression in one direction. In the members of the dominating genus Perameles the molars will be seen to present a progressive omnivorous development, associated with an increasing hypsodontism, which is quite as gradual as the carnivorous development of the Dasyurinæ; while the antemolar teeth, on the other hand, will be seen to present a varied assortment of local and more or less retrogressive characters. The cause of this condition may be found in the peculiar manner in which the family has been derived. The ancestors of the Peramelidæ were arboreal animals, and were probably either purely insectivorous or at most only slightly omnivorous. On becoming terrestrial they have gradually become more completely omnivorous, as shown by the successive modifications of the molars. But they have also become fossorial to a varying extent, and this development appears to represent the prime cause of the antemolar variation. The hypsodontism of the molar crowns represents a compensatory development, the object of which is to counteract the effects of the mechanical wearing down of the teeth caused by the presence of particles of earth in the food. It owes its uniformity to its association with the omnivorous development of the molars. The local and retrogressive characters of the antemolar teeth may be due to a slight extent to the reduction of their function in the omnivorous evolution, but are more closely connected with the displacement of these teeth from their original relations by a varying elongation of the muzzle. The latter is here, as in many other cases, the result of fossorial or semifossorial habit.

The family may be divided on a basis of molar characters as follows :---

Α.	Upper molars normal; triangular, becoming quadrate by the development of a	
	hypocone. External styles not conspicuously enlarged	Peramelinæ.
	Genera: Perameles, Chæropus.	
В.	Upper molars aberrant; quadrate through displacement inwards of the meta-	
	cone; external styles greatly enlarged and forming with the protocone and	
	metacone the main cusps of the crown	Thylacomyinæ.
	Genus: Thylacomys.	

Some doubt may be expressed as to the advisability of making a major division in the Peramelidæ on account of the fact that the family is a small one and the three genera closely related. The type of molar modification found in *Thylacomys* is, however, unique in the Marsupials, and rare in the Mammals generally, so that this form seems fairly entitled to distinction.

#### PERAMELINÆ.

Of sixteen species composing the whole family of the Peramelidæ twelve belong to the genus *Perameles* of the present division. The latter, therefore, presents nearly all of the dental modifications of evolutionary interest found in the family. It also represents the parent form from which the less inclusive genera *Chæropus* and *Thylacomys* have been derived.

Although the modifications of the molars are comparatively uniform in this series, the specific variability of the antemolar teeth is so great that a general synopsis of the dental sequence is scarcely permissible.

Sequence of Molar Patterns.—The order of specialization is as follows:—Perameles Doreyana and P. Raffrayana, P. Bougainvillei, P. nasuta and P. Gunni, P. Cockerelli, P. moresbyensis, P. macrura and P. obesula. Chæropus castanotis is in some respects as specialized as the extreme form P. obesula, but appears to be a derivative of P. Bougainvillei or a closely allied form.

As indicated in the above plan, the most primitive modifications relate to P. Doregana and P. Raffrayana. This remark, however, applies only to the species studied. The collection contains no examples of the presumably primitive forms P. Broadbenti and P. longicaudata (cf. Thomas, 1888, pp. 240-242).

The following description of P. Doreyana will apply almost equally well to P. Raffrayana. The third upper molar of P. Doreyana (Pl. 5, fig. 8) is of an insectivorous type approximating closely to that found in the Dasyurinæ (cf. fig. 2, Sminthopsis leucopus). The only important points of departure are seen in the arrangement of the external styles, and in the addition of a new cusp, the hypocone (hy.). As regards the arrangement of the external styles, the Dasyurinæ have already been described as presenting a specialized condition, style c being greatly developed, while two anterior styles have been fused together to form a single element ab. In P. Doreyana, as, in fact, in all of the Peramelinæ, style c is only moderately developed \*, while the anterior styles a and b are much more completely separate. In both of these characters the Peramelinæ approximate much more closely to the Didelphyidæ (cf. Pl. 5, figs. 1 & 26, Peratherium, Metachirus opossum) than do the Dasyurinæ.

The appearance of the new cusp, the hypocone, is of great significance, since it marks the first stage in the transformation of a piercing, cutting, and crushing tooth into a grinding one, or, in other words, the passage from an insectivorous to an omnivorous condition.

The remaining upper molars of P. Doreyana differ from the third in exactly the same way as in the Dasyurinæ. The first and second are more laterally compressed, and the fourth is reduced through the loss of the metacone.

The lower molars of P. Doreyana (Pl. 6. fig. 12) also approximate closely to those of

\* In the Peramelinæ, and also in the Didelphyidæ, as in the Dasyurinæ, style c is better developed in the first and second molars than in the third. Allowance should be made for this fact when comparing the figure here given of the third molar of *P. Doregana* with those of the second molars of other forms. the Dasyurinæ (cf. figs. 2 & 3, Sminthopsis leucopus, Dasyurus viverrinus). Three points of departure are, however, indicated. There is, first, a slight reduction of the paraconid; secondly, a partial elevation of the crown-surface of the talonid; and, lastly, a slight reduction of the hypoconulid. These remarks apply to all three anterior molars, but not wholly to the fourth, the latter having the talonid reduced, as in the Dasyurinæ (cf. fig. 16, P. Bougainvillei).

Proceeding from *P. Doreyana* and *P. Raffrayana* we find the following changes in the molar patterns. In the upper teeth (Pl. 5. figs. 9 & 10, *P. Bougainvillei*, *P. obesula*) the general shape from being triangular becomes quadrate, the spaces originally existing between the internal apices of the teeth being gradually filled partly by the growth of the hypocone and partly by a very slight rotation of the body of the metacone. The metacone-spur becomes partially reduced, and the former disproportion in size between the paracone and metacone becomes less obvious. In the lower teeth (Pl. 6. fig. 13, *P. obesula*) there is a further reduction of a practically quadritubercular pattern. It is interesting to compare the tooth of *P. obesula* here figured with that of *Thylacomys leucura* (fig. 14), which shows a more advanced stage of the same evolution. In this form the paraconid has completely disappeared, and the remaining cusps of the trigonid have now the same characters as those of the talonid.

Viewing the molar changes from an adaptive standpoint it is seen that the teeth of *P. Doreyana* and *P. Raffrayana* perform the same piercing, crushing, and cutting functions as those of the smaller Dasyurinæ. In the insectivorous stage the general movement of the teeth is vertical. In the omnivorous stage the teeth assume a transverse grinding action, and the cusps become arranged in such a way as to present a uniform crown-surface, and at the same time to obliterate all of the interspaces. The crown-surface of the talonid, originally low, is raised to the level of that of the trigonid. The protocone and hypocone are similarly raised. The change in the latter cusps is, however, not so essential as that in the talonid, since the movement of the teeth is necessarily vertical and internal as well as transverse, and is accordingly slower. It is, in fact, only completed in the more advanced Phalangeridæ (*cf.* Pl. 5. figs. 13 & 16, *Distæchurus pennatus, Trichosurus vulpecula*). The triangular spaces between the internal apices of the upper molars become obliterated by the growth of the hypocone, and the somewhat similar spaces between the external apices of the trigonids and talonids in adjacent lower teeth become obliterated by the reduction of the paraconid and hypoconulid.

Hypsodontism of the Molar Crowns.—The molars of the various members of the Perameline furnish an interesting example of the perfect correlation of two adaptive changes, which are due to different causes, in the association of a gradually increasing hypsodontism of the molar crowns with the omnivorous elaboration of the patterns. The hypsodont development is scarcely perceptible in the teeth of the primitive forms P. Doreyana and P. Raffrayana, but becomes more and more obvious as we pass to the final forms P. obesula and P. macrura. Unlike the hypsodontism which is found in the Macropodidæ, that of the Peramelidæ affects the bodies of the teeth rather than the cusps. The appearance presented in an extreme stage is well represented in Pl. 6. fig. 15 of the lower molar of *Chæropus castanotis*. The same modification of otherwise comparatively simple teeth is found in the Notoryctidæ (Pl. 6. fig. 17 b) and in many of the placental Insectivora.

Incisors.—The most important feature of these teeth is the retention in all forms, except *P. Doreyana* and *P. Cockerelli*, of a fifth upper pair. In this feature, which is also presented by *Thylacomys*, the members of the family are more primitive than any of the remaining Marsupials of Australia, but exactly resemble the Didelphyidæ.

With the partial exception of the fifth upper pair, the incisors present a very characteristic appearance on account of the great broadening of their tips. The median upper teeth are not differentiated from the lateral ones as they are in the Dasyurinæ, the Didelphyidæ, and the primitive Phalangeridæ. This condition is apparently secondary, as in *Myrmecobius* and *Notoryctes*. The anterior four pairs of upper incisors are usually seen to have their cutting-edges squarely truncated, but this condition is probably the result of wear. In young specimens of *Chæropus castanotis* and *Perameles nasuta* the upper incisors show the same curious triangular shape as found in the Didelphyidæ and Dasyuridæ (*cf.* text-fig. 2, f & g, p. 105). As already noted above, the unworn teeth of *P. obesula* show a backward prolongation of the tips somewhat like that found in *Myrmecobius*. The fifth upper incisors tend to be more or less caniniform, like all of the upper lateral teeth of the latter form.

The lower incisors are fairly constant in their characters. Their cutting-edges are rounded and point to the type found in the Dasyuridæ and Didelphyidæ. The third tooth shows a prominent posterior accessory cusp. This element probably represents a secondary development. It is not present in the Didelphyidæ, which have four lower incisors, but is frequently present in the Dasyuridæ, where, as in the Peramelidæ, the incisors have been reduced to three.

The relative positions of the fifth upper incisors and their occasional absence furnish the first instance of the variability of the antemolar teeth already referred to. In the otherwise primitive form P. Raffrayana the muzzle is moderately elongated and the fifth incisors are separated from the fourth by short diastemata; in the intermediate forms P. nasuta and P. Gunni the muzzle is excessively elongated and the diastemata are correspondingly increased; while in the final forms P. obesula and P. macrura, as also in Charopus castanotis, the muzzle is again shorter and the diastemata are scarcely in evidence. Again, of the two primitive forms P. Doreyana and P. Raffrayana, the fifth upper incisors are present in one and absent in the other, while they are present in all of the specialized forms with the exception of P. Cockerelli. These characters may be taken, in connection with certain others of the canines and premolars, as showing that the sequence indicated by the modifications of the molars cannot be relied upon as indicating the true relationships of the various species.

Canines.—These teeth are even more variable in their characters than are the fifth upper incisors in their position. In *P. Raffrayana* the upper tooth is short, moderately stout, and curved. The lower tooth is so short as to be scarcely caniniform, and bears a small posterior accessory cusp. In P. Doreyana we find both upper and lower teeth greatly reduced, the former showing usually small anterior and posterior cusps like those of the premolars, and also a slight grooving of the root. The lower tooth shows indications of a posterior cusp, and its root is also slightly grooved. A somewhat similar condition is seen in Chæropus castanotis, except that in this form there is an anterior cusp on the lower tooth. Perameles Bougainvillei also shows a similar condition, except that the upper tooth is not grooved. In P. nasuta both upper and lower teeth are of a normal caniniform type; they are, in fact, better developed in this form than in other members of the family, excepting the species of Thylacomys. In P. obesula, P. macrura, P. moresbyensis, and P. Gunni the upper canines are short and curved, as in P. Raffrayana. The lower teeth of P. moresbyensis and P. macrura are not so caniniform as those of P. obesula. They show a posterior cusp as in P. Raffrayana, but in addition an anterior one. Apart from their stouter build, they thus resemble those of P. Doreyana, P. Bougainvillei, and Chæropus. In P. obesula and P. Gunni the lower teeth are rather short, but are otherwise normal.

Apart from special phylogenetic considerations, the characters of the canines in this series are of interest as illustrating the effects of retrogressive development. The reduction in length, the addition of anterior and posterior basal cusps, and the grooving of the root mark the return of a caniniform tooth to a premolariform one, from which it originally evolved. The retrogressive characters of the Peramelidæ find a direct parallel in *Myrmecobius*. It is interesting to note that retrogressive characters of a somewhat similar kind are seen in *Cænolestes (cf.* Pl. 5. fig. 38) and in the Phalangeridæ, and further that in certain members (*Dactylopsila, Phalanger*) of the latter family the opposite development is illustrated, namely the conversion of an anterior premolar into a caniniform tooth.

**Premolars.**—Except for a slight tendency towards the reduction of the posterior teeth in *Chæropus castanolis*, the premolars are well developed throughout the series. They resemble in their general characters those of the Dasyurinæ and Didelphyidæ. Except in *Chæropus* they increase in size backwards, and this character places the Peramelidæ in a more primitive condition than the Dasyurinæ or even the existing Didelphyidæ. In their relative positions the premolars show considerable variation. In cases where the diastemata separating the teeth are of moderate length, the latter show a pronounced tendency towards the enlargement of the basal cusps. The separation of the teeth being due to the elongation of the muzzle, the characters show much the same relations in the different species as those of the fifth upper incisors.

From their association with the molars, the posterior premolars show indications of a progressive evolution. In *P. Doreyana* and *P. Raffrayana* they are laterally compressed and of the usual primitive trenchant type common to the Dasyuridæ and Didelphyidæ; in the more specialized forms they become more massive and rounded in section, as in the more advanced Phalangeridæ.

#### THYLACOMY1N.E.

The antemolar teeth of *Thylacomys* call for no description, since they resemble in their characters those of the Peramelinæ and throw no further light on the evolution of the family.

The most important features relate to the characters of the upper molar patterns. As will be seen from a comparison of Pl. 5. fig. 11 with figs. 8, 9, 10, the upper molars show a quadrate contour very like that seen in the more advanced forms of the Peramelinæ, but that while in the latter the quadrate shape is due to the development of a hypocone, in Thylacomys it is due to the displacement inwards of the metacone, or, what amounts to the same thing, a shortening of the protocone. The paracone retains its original characters and position. Of the external styles, only b and c are represented. They are greatly enlarged and form with the protocone and metacone the main cusps of a functionally quadrituberculate crown. The second tooth here figured will be seen to show a small hypocone wedged in between the protocone and the metacone. This element is absent in all of the other teeth of this specimen, including the corresponding one of the opposite side. As to the extent of its occurrence in Thylacomys, no further data have been available, except that it has not been figured or described by Spencer (1896) in the new species T. minor. The specimen of T. leucura here described is unfortunately the only example of this genus in the collection which shows the unworn molar patterns.

The first molar of T. *leucura* resembles the second and third here figured. The fourth is not visible in this specimen, but in adults of T. *lagotis* it appears to be of the same reduced type as in the Peramelinæ and Dasyuridæ.

The upper molar patterns of *Thylacomys* have apparently been derived from such a primitive type as is presented by P. *Doreyana* or P. *Bougainvillei*, the rudimentary hypocone having been in all probability obliterated by encroachment of the metacone.

The lower molars of T. leucura (Pl. 6, fig. 14) are not modified away from the perameline type, but present a much more advanced stage of development than is found in any of the Peramelinæ. The anterior lobe of each tooth no longer bears any resemblance to a trigonid, the paraconid having completely disappeared. The broad ledge occupying the anterior border of the tooth represents the antero-external shelf, a structure which is better developed in all of the Peramelidæ than in the Dasyurinæ. In the talonid the hypoconulid is quite vestigial, while the entoconid and hypoconid are greatly enlarged and raised to the level of the anterior cusps.

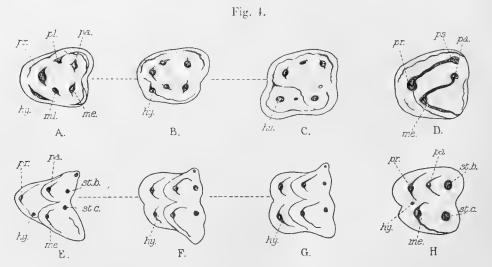
The lower molars of T. lagotis resemble those of T. leucura so far as can be judged from worn specimens. In both species the hypsodont development is present to a marked degree.

# The Cusp-homologies of Quadrate and Quadrituberculate Molars.

The occurrence of two distinct lines of molar development in the Peramelidæ raises an interesting question as to the homologies of the cusps in more specialized forms. SECOND SERIES.—ZOOLOGY, VOL. IX. 17 1

It will be seen that both in *Perameles obesula* and in *Thylacomys leucura* the upper molars are functionally quadrituberculate, the main cusps being in the former the protocone, hypocone, paracone, and metacone, but in the latter the protocone, metacone, and styles b and c. The upper molars of the Phalangeridæ present in most cases an actually quadrituberculate pattern, which is ancestral to the advanced patterns of the Macropodidæ, Phascolomyidæ, and Diprotodontidæ. The question therefore arises as to whether the four cusps of the Phalangeridæ are homologous with those of *Perameles* or those of *Thylacomys*.

In the more primitive forms of the Phalangeridæ (cf. Pl. 5. figs. 14 & 15, Dromicia concinna, Petaurus sciureus) the upper molars show a vestigial external cingulum, which appears to be equivalent to that bearing the external styles in polyprotodont forms, and in one section of the family (Phascolarctinæ) vestigial styles are actually present. This indicates that, although resembling them in many respects, the two outermost of the main cusps in the Phalangeridæ are not equivalent to the modified external styles in



Normal and aberrant production of quadrate upper molars in Marsupials and Placentals.

Flacentals :- A. Protogonodon; B. Euprotogonia; C. Phenacodus (Condylarthra); D. Coryphodon (Amblypoda).
 Marsupials :- E. Perameles Doreyana; F. P. Bougainvillei; G. P. obesula; H. Thylacomys. Abbreviations:
 pr., protocone; pa., paracone; me., metacone; hy., hypocone; ps., parastyle; st.b., style b; st.c., style c.

Thylacomys. Furthermore, in the primitive Phalangeridæ (cf. Pl. 5. fig. 13, Distæchurus pennatus) the postero-internal cusp is relatively small, but increases in importance in the more advanced stages (fig. 16, Trichosurus vulpecula) in precisely the same way that the hypocone does in the Peramelinæ, and is therefore more probably homologous with that cusp than with the displaced metacone of Thylacomys. Finally, in the Placentalia the formation of a quadrituberculate tooth by the addition of a hypocone to an originally triangular crown is the normal procedure, since it is indicated in various members of the Condylarthra, Primates, Insectivora (Soricidæ, Macroscelidæ, Erinaceidæ). The formation of a quadrate tooth by displacement of the metacone is rare, being only found, so far as the writer is aware, in the Amblypoda. The significance of this will be more apparent from the accompanying diagrams (text-fig. 4), in which the typical method of the formation of a quadrate tooth is illustrated by the teeth of the Condylarthra and Peramelinæ, on the one hand, and the atypical method by those of the Amblypoda and *Thylacomys*. All of these facts indicate that the main cusps represented in the typically quadrituberculate Phalangeridæ and their herbivorous derivatives are directly homologous with those of the Peramelinæ.

The lower teeth of the advanced quadrituberculate forms call for no consideration, since in the Thylacomyínæ, as also in the Amblypoda, they show no departure from the condition in other forms.

#### NOTORYCTIDÆ.

During the twelve years which have elapsed since the original description of *Notoryctes* by Stirling (1891), the dental characters of the animal have been commented upon by several writers, including Ogilby (1891), Cope (1892), Gadow (1892), Winge (1895), Forsyth Major (1897), Spencer (1896), and Tomes (1899). The following remarks are therefore largely directed towards an arrangement and discussion of opinions already expressed.

It may be observed at the outset that no adequate conclusions concerning the affinities of Notoryctes can be formed from a study of the dentition alone. While the median lower incisors present an undifferentiated condition, which shows the animal to be related to the members of the polyprotodont section, namely the Dasyuridæ and Peramelidæ, the dentition is otherwise so completely modified away from the usual polyprotodont type that it does not present any of those special characters which distinguish the latter families from one another. As will be pointed out in detail in a subsequent section, in the absence of definite characters of dental affinity in Notoryctes the primary characters which separate the Dasyuridæ from the Peramelidæ do not relate to dentition, and in addition do not represent merely a family distinction, but, on the other hand, serve to separate the Dasyuridæ from all of the remaining Australian forms. These characters may be mentioned as relating to the non-syndactylous and syndactylous modifications of the second and third digits of the pes, respectively characteristic of the two series. Notoryctes, in its foot-structure, shows affinities with the syndactylous section, indicating that of the two polyprotodont families its relations are rather with the Peramelidæ than with the Dasyuridæ. These relations should be borne in mind in attempting to derive the characters of its dentition.

**Dental Formula.**—A conspicuous feature of the dentition of Notorycles, and one which is in all probability responsible for most of the remaining characters presented, relates to the foreshortened condition of the tooth-rows. One of the effects of this development is seen in the variability of the dental formula, implying a reduction, which is still in progress, of certain of the less functional teeth. The formula has been variously determined by Stirling, Ogilby, Gadow, and Spencer, the most trustworthy figures being those given by the last-named writer. Spencer states that the full formula, "as far as at present known," is:  $i.\frac{4}{3}$ ,  $c.\frac{1}{1}$ ,  $p.\frac{2}{3}$ ,  $m.\frac{4}{4}$ . Concerning this he remarks as follows (p. 47):— "It was only after examining twenty-nine specimens that one was found in which the full number of incisors was present in the upper jaw, whilst in only a comparatively few specimens an additional premolar was present in the lower jaw, always small and pushed out to the side of the jaw in front of the first molar." The formula given by Spencer differs only from that determined by Gadow from Stirling's specimens in the addition of one upper incisor and one lower premolar.

Gadow has expressed the opinion that the affinities of *Notoryctes* are with the Dasyuridæ, and the subsequent discovery of a fuller incisor formula of  $\frac{4}{3}$  appears at first sight to support this view. It must be borne in mind, however, that the upper incisor formula of 4 only represents one limit, so far as known at present, of the variability which is normal for this genus; it cannot be regarded as indicating the presumably stable formula of the ancestral form from which *Notoryctes* has been derived. Furthermore, no greater importance can be attached to the occurrence of a fourth upper incisor in one of twenty-nine specimens than, for example, to the occasional presence of a fourth lower incisor in *Myrmecobius* or a fifth in *Didelphys*, even though the latter be regarded as reversional, a proposition which, as Bateson (1894) has shown, is rather doubtful.

With reference to the premolar formula, Gadow considered the number  $\frac{2}{2}$  determined by him to represent the anterior and median premolars of other Marsupials, the posterior teeth having disappeared as in the Dasyuridæ. This, again, cannot be regarded as indicating a special affinity with the latter family, since the same process of reduction of the posterior premolars is found in other families. In the Phalangeridæ the genus *Acrobates* shows a reduced condition of the posterior premolars, and in *Distæchurus* (cf. Pl. 5. fig. 39) the upper teeth are much reduced and the lower are absent, as in the more advanced members of the Dasyuridæ. The same tendency towards reduction is seen in the Didelphyidæ, and in two species, *Thylacomys lagotis* and *Chæropus castanotis*, of the Peramelidæ.

The dental reduction of *Notoryctes* appears to be confined to the antemolar teeth, the molars always presenting the formula  $\frac{4}{4}$  characteristic of all of the remaining Marsupials with the exception of *Myrmecobius*, *Acrobates*, *Distæchurus*, and two species of *Dromicia*. The cause of the stability of the molar formula is to be sought in the greater functional importance of these teeth. Like the antemolar teeth they have been affected by the shortening of the jaws, but only to the extent of an antero-posterior compression.

Derivation of the Molar Patterns.—The characters of the upper teeth are represented in Pl. 5. fig. 12, and those of the lower in Pl. 6. fig. 17.

The appearance of the molar crowns has been figured by Stirling (1891) in connection with his original description. Tomes, however, remarks that, "in Dr. Stirling's figures of the grinding-surfaces of the molar teeth, it is shown that the middles are worn into concavities, and that the retention of the cuspidate form is not due to the retention of sharp enamelled cusps, but that it is due to the upstanding of the edges." While this is probably true of the lower molars figured by Stirling, the prominences shown in his illustrations of both upper and lower teeth will be found to correspond with those here given, which have been taken from a specimen in which no signs of wearing are apparent.

Both the upper and lower molars are extremely simple in structure. Each of the upper teeth is composed of a high triangular pillar, to which is attached two small external cusps and a large internal one. The apex of the triangular pillar forms a large cusp, which in the pointed character and the triangular section of its tip resembles the paracone or metacone of a normal insectivorous tooth. Of the external cusps, one is attached anteriorly to the tip of the triangular pillar, while the other occupies a similar position posteriorly. The former shows indications of a composite structure. The large internal cusp is crescentic in shape when viewed from the crown, and its tip is placed at a much lower level than that of the median pillar. Each of the lower teeth shows a triangular pillar similar to that of the upper teeth, but with the section-apex reversed. The crown-surface bears three cusps, showing the same arrangement and proportions as those of the trigonid in the Dasyuridæ and primitive Peramelidæ. The talonid, which in the latter forms is well developed, is, however, only represented by a minute tubercle attached to the postero-internal angle of the trigonid in the first and second molars.

It will be observed that the molars of *Notoryctes* present a less complicated condition than is found in any of the other polyprotodont families; and this raises the interesting question, involving the origin not only of *Notoryctes* but that of all recent Marsupials, as to whether the modification represents a more primitive phase or is the result of special development proceeding from the type represented by the teeth of the Dasyuridæ and Peramelidæ.

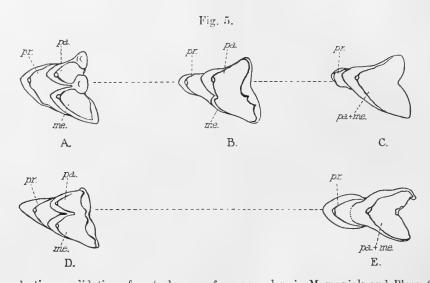
Cope has called attention to the fact that there is an intimate resemblance between the molars of *Notoryctes* and those of *Chrysochloris*, and has further stated that "the tritubercular molars .... show *Notoryctes* to be a primitive type"; while Winge, on the other hand, has expressed the opinion that the teeth of *Notoryctes* have lost some of their cusps, and has further compared them with those of the Centetidæ. A similar comparison with the Centetidæ has been made by Forsyth Major.

Whether the teeth of *Notoryctes* are primitive or specialized, one thing is apparent, namely that there are no intermediate stages connecting them with those of any other marsupial forms. Their relations can therefore only be surmised from the parallel case of the Centetidæ. The evolution of the teeth in the latter family has been carefully studied by Forsyth Major (1897), and the following statement of the case is based to a considerable extent upon this writer's views:—In certain of the Insectivora (Talpidæ) (cf. text-fig. 5, p. 120) the upper molars show an arrangement of the cusps which is very similar to that seen in the Didelphyidæ, there being in each case a triangle of three main cusps and an outer row of styles. In the Potamogalidæ the two outer cusps of the triangle, the paracone and metacone, are partially fused together, while the protocone and the external styles tend to retain their original characters. In all of the Centetidæ, and also in the Chrysochloridæ and Solenodontidæ, the paracone and metacone are completely fused together to form a median pillar, in which it is not

possible to recognize the constituent elements. The protocone is either reduced (*Oryzoryctes*) or in the final stages (*Ericulus, Echinops, Centetes*) wholly vestigial or absent.

Referring to the consolidation of the paracone and metacone in the upper molars, Forsyth Major adds:—" It is only in *Notoryctes*, which in other respects also is highly specialized and forms a parallel to the Centetidæ and still more to the Chrysochloridæ, that this fusion likewise occurs in all molars; the protocone in *Notoryctes* is still developed to a considerably greater extent than in the Centetidæ."

With reference to the lower molars of the Centetidæ, this writer points out that the chief feature is the reduced condition of the talonid, a character which he believes to be secondary, from the fact that this structure is well developed both in the lowest Tertiary and Cretaceous Mammalia.



Homoplastic consolidation of central cusps of upper molars in Marsupials and Placentals. A. Talpa; B. Potamogale; C. Oryzoryctes; D. Peramys; E. Notoryctes. (Abbreviations as in text-fig. 4, p. 116.)

According to this view, the molars of *Notoryctes* bear the same relation to those of the Dasyuridæ, primitive Peramelidæ, and Didelphyidæ as those of the Centetidæ and especially *Oryzoryctes* bear to those of the Talpidæ. The triangular pillar of the upper molars represents the conjoined paracone and metacone, the large internal cusp a protocone. The external styles, which are virtually three in number, the anterior one being composite, represent a, b, and c of the normal polyprotodonts. The triangular pillar of the lower teeth represents an elongated trigonid, the talonid being vestigial.

It is apparent that Cope's designation of the molars of *Notoryctes* as trituberculate, although quite applicable to the lower teeth, is misleading as applied to the upper, if by the term "trituberculate" we mean to designate such teeth as those of the Didelphyidæ, Talpidæ, and primitive Creodonta, which present a triangle of three main cusps with or without intermediate conules or external styles. It is further apparent that his view that the minute proportions of the talonid in the lower molars of *Notoryctes*, *Chrysochloris*, and the Centetidæ represent a primitive condition, which is prophetic of one in which this structure is well developed, is also erroneous. While the fact pointed out

by Forsyth Major that in the early Tertiary and the Cretaceous Mammalia the talonid is found in a well-developed condition, does not in itself invalidate the view that the reduced condition of this structure in the Centetidæ represents a primitive character, the reverse is indicated by the fact that the modifications of the talonid in the lower molars of the Insectivora follow those of the paracone and metacone and also the protocone in the upper. In the Talpidæ, where the protocone is well developed, and the paracone and metacone entirely separate from one another, the talonid is found in a well-differentiated condition. In the Potamogalidæ, where the paracone and metacone are partially fused and the protocone slightly reduced, the talonid is also reduced; while, finally, in the Centetidæ, where the fusion of the paracone and metacone is complete and the protocone vestigial, the talonid is also vestigial. Such an assumption, therefore, as that the changes of the lower molars in the above-mentioned Insectivora represent successive stages in the development rather than the reduction of the talonid, implies the further assumption of a similar sequence in the upper molars, namely the gradual development of a protocone and the formation of a paracone and metacone by the splitting apart of an originally single cusp, a proposition which could not be seriously This conclusion, however, in nowise affects the general thesis that the entertained. tuberculo-sectorial type of lower molar, as exemplified by the Didelphyidae, Dasyuridae, Talpidæ, and the Creodonta, has arisen by the addition of a talonid to a previous existing trigonid, nor that the trituberculate condition of the upper molars of the same forms represents a primitive type from which many other modifications have proceeded. The conditions in Notoryctes, the Chrysochloridæ, Centetidæ, and Potamogalidæ simply represent another line, similar to those leading to the carnivorous Dasyuridæ and the placental Carnivora, or to the diprotodont Marsupials, the Primates and Ungulata, along which the transformation of trituberculate, tuberculo-sectorial teeth may proceed.

The dominating principle in the molar evolution of *Notoryctes* appears to be the economy of space in the molar region, involving an antero-posterior compression of the teeth, but the development has probably been assisted by the hypsodont modifications of the molar crowns. In the upper molars of the Dasyuridæ and Didelphyidæ, the paracone and metacone are not placed on exactly the same level as the protocone, but arise together from a short median platform, to the base of which the latter cusp is attached. The hypsodont development of such a crown would tend to produce just such a condition as is seen in *Notoryctes*, providing it were accompanied by antero-posterior compression. In the Peramelidæ, where there is a tendency towards an elongation rather than compression of the paracone and metacone, although even in these forms the latter cusps, instead of being individually elongated, are borne on an elongated median pillar very similar to that seen in *Notoryctes*. The reduction of the longitudinal diameter of the lower molars by obliteration of the talonid calls for no explanation.

As already pointed out, the dentition of *Notoryctes* gives no indications of special affinity either with that of the Dasyuridæ or that of the Peramelidæ. The only molar characters on which reliance may be placed in the distinction of the latter families from one another relate to the presence of a hypocone in the Peramelidæ and its absence in

the Dasyuridæ. The hypocone, however, represents at most an outgrowth from the protocone, the crown-surfaces of the two cusps being practically continuous. Even supposing the upper molars of *Notoryctes* to have originally possessed a hypocone, we could scarcely expect to find this element differentiated in teeth which have undergone a consolidation of two cusps, namely the paracone and metacone, which are originally much more distinct from one another than are the protocone and hypocone in the Peramelidæ.

As shown in Pl. 6. fig. 16, there is considerable resemblance between the fourth lower molar of *Perameles Bougainvillei* and the normal molars of *Notoryctes*. This resemblance is largely due to the hypsodont condition of both, and since the original condition in the Peramelidæ is a brachyodont one, it cannot be strictly regarded as indicative of affinity. A certain resemblance also exists between the fourth upper molars of the Peramelidæ with the normal molars of *Notoryctes*, but this resemblance also extends to the Dasyuridæ and Didelphyidæ.

Antemolar Teeth.—Apart from their variability in numbers, the chief feature of these teeth is their lack of differentiation, the incisors, canines, and posterior premolars being all of the same short peg-like character. The median upper incisors are separated at their bases and approximated at their tips, but, like those of the Peramelidæ, show otherwise no indications of having been formerly differentiated as in the Dasyuridæ, Didelphyidæ, and primitive Phalangeridæ. The last (morphologically median) premolar is better developed than any of the remaining antemolar teeth, probably on account of its association with the better developed molars.

### PHALANGERIDÆ.

The present family has already been referred to as forming with the Peramelidæ an intermediate group, with dental characters connecting those of the insectivorous Dasyurinæ with those of the herbivorous section. The association of the two families will be seen to depend fundamentally on the recognition of the Peramelidæ as Omnivora rather than as Polyprotodontia. The polyprotodont characters may now be considered together with certain progressive omnivorous ones of a lower rank than those seen in the Phalangeridæ, as defining the position of the latter family with reference to the Peramelidæ as in many respects a derived one. These characters are as follows :----(a) Retention in the Peramelidæ of an undifferentiated condition of the median lower incisors, which is replaced in the Phalangeridæ by a differentiated condition involving extensive reductions of the antemolar teeth. (b) Retention in the Peramelidæ of the piercing character and pyramidal shape of the molar cusps; replaced in the Phalangeridæ by a bunoid or selenoid modification of these structures. (c) Retention of a full complement of external styles; in the Phalangeridæ these elements are either wholly vestigial (Phascolarctinæ) or absent (Phalangerinæ). (d) Retention of the constructive stages in the formation of either functionally or actually quadrituberculate molars from others of insectivorous type, only indicated in the Phalangeridæ, and to a very limited extent, in the development of the hypocone in the upper molars.

Considered alone, the above characters might be regarded as indicating that the dental evolution of the Phalangeridæ represents a continuation of that of the Peramelidæ. That this is not the case, however, will be seen from the following additional characters :--(a) The primitive members of the Phalangeridæ retain a differentiated (insectivorous) condition of the median upper incisors. This is not indicated in any of the Peramelidæ, although present in all other primitive polyprotodonts (Dasyuridæ, Didelphyidæ). (b) The same forms show signs of dasyurid affinity in the retention of normal insectivorous characters in the upper canines and premolars, in which respect they are quite as primitive, and, in view of their smaller size and the tendency towards retrogression of these teeth, especially the canines, in the Peramelidæ, even more so than the latter family. (c) The primitive members of both families present an incomplete condition of the hypocone in the upper molars, while the advanced members in each case show this element in a perfect condition. (d) Finally, the Phalangeridæ show none of those hypsodont developments of the molars which characterize the other family.

The explanation of these two series of characters becomes more apparent on comparison of the foot-structure in the two families. The present facts may be taken as indicating that the common ancestors of the Peramelidæ and Phalangeridæ were in all probability animals combining the incipient omnivorous molar characters of the primitive members of the former family, and also their incisor formula, with the normal antemolar characters of the smaller Dasyurinæ, and it may be mentioned in anticipation that the two families have undergone a divergent evolution in the foot-structure—the Peramelidæ having become terrestrial, while the Phalangeridæ have remained arboreal, so that their omnivorous dental evolution must have proceeded independently as far as the later stages are concerned.

# The Origin of the Diprotodont Modification.

Closely connected with the question of the dental relations of the Phalangeridæ and Peramelidæ is that of the origin of the diprotodont modification, which appears for the first time in the former family, although characteristic to a marked degree of the whole herbivorous section.

It is a familiar fact that of the recent Marsupials the Didelphyidæ, Dasyuridæ, and Peramelidæ on the one hand, and the Phalangeridæ, Macropodidæ, Phaseelomyidæ, and Diprotodontidæ on the other, form two broad divisions, differing markedly in the characters of the antemolar teeth, which distinction led Owen to propose a primary division of the whole group into Polyprotodontia and Diprotodontia. The: relative merits of this division will be discussed in a subsequent section, the object of the following remarks being to show that the diprotodont modification, although characteristic of the herbivorous section of the Marsupials, is the result of an insectivorous adaptation which must have been developed in the minute ancestors of the Phalangeridæ during the incipient stages of the omnivorous evolution, but after the separation of the peramelid stem.

The fundamental characters of the diprotodonts may be enumerated as follows:— (a) Reduction of the upper incisor formula to 3 or even 1. (b) Reduction of the lower SECOND SERIES.—ZOOLOGY, VOL. IX. 18

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functional inciser formula to 1, the median teeth becoming greatly enlarged, while the lateral ones, together with the canines and anteriorly placed premolars, become reduced or disappear.

The fact has already been noticed that the insectivorous members of the Dasyurinæ, like the Didelphyidæ and many of the placental Insectivora, show a procumbent development of the median upper incisors, which adds considerably to their functional value as grasping and piercing organs in the capture of insect prey, but that, with the partial exception of certain forms such as *Phascogale penicillata* and its prototype *P. calura*, they show no corresponding differentiation of the median lower incisors; further that in the placental Soricidæ the latter teeth are enlarged and elongated in such a way as to act in concert with the median upper ones after the manner of the tips of a pair of forceps. The primitive members of the Phalangeridæ (*Acrobates, Distæ-churus, Dromicia*) show exactly the same differentiation of the median lower ones as is found in the Soricidæ. This circumstance furnishes a complete clue to the origin of the diprotodont modification, since it can be shown that all of the changes which take place in its formation are directly dependent on the differentiation of the median lower incisors as grasping and piercing organs.

It may be observed that none of the actually constructive stages in the development of the diprotodont modification are illustrated in the existing Phalangeridæ, the most primitive condition found in that family being of the kind represented in Pl. 5. fig. 39, of the dentition of *Distachurus pennatus*. Outside of the Australian group, however, we find in the Epanorthidæ and their allies much more primitive relations, and a comparison and figure of the dentition of *Cænolestes obscurus*, the existing representative of that family, has accordingly been introduced.

If we suppose such a polyprotodont animal as Phascogale penicillata to undergo a further enlargement of the median lower incisors, the result would be twofold. In the first place, the elongation of these teeth would be accommodated by a shortening of the anterior portion of the lower jaw, and this would disturb the relations of all of the more anteriorly placed lower teeth with the corresponding upper teeth. On comparison of the figure of Canolestes (Pl. 5. fig. 38) \*, it will be seen that, while the lower molars, as well as the median and posterior premolars, occupy their normal positions with reference to the corresponding upper teeth, all of the remaining lower teeth situate behind the enlarged median incisors have been displaced backwards, and are now in a vestigial A continuation of the same development will be seen in Distachurus condition. (fig. 39), where, with a further shortening, at least two teeth, probably representing the canine and anterior premolar, have wholly disappeared. In the second place, there would be a reduction of the posterior upper incisors, since only those teeth with which the tips of the median lower incisors come into contact could persist. Thus in

<sup>\*</sup> This specimen of *Canolestes*, kindly lent to me by Mr. Thomas, differs from the type specimen described by him (1895 b) in possessing an additional "intermediate" tooth on each side of the lower jaw. The full antemolar formula, which is thus 8 in this specimen, is greater than in any of the existing Marsupials excepting the Didelphyidæ.

*Cœnolestes* the fourth upper incisor shows a tendency towards reduction, while in *Distæchurus*, as, in fact, in all of the Phalangeridæ, the number of upper incisors is already reduced to three, the lateral two together serving as a stop for the enlarged lower teeth.

The presence of the diprotodont modification in herbivorous Marsupials is accordingly not to be explained on the supposition that it represents an advantageous condition, but rather that these animals are the descendants of minute forms, which, like *Acrobates*, *Distachurus*, and *Dromicia*, had undergone a special insectivorous development of the median lower incisors, and that their ancestors were able to remodel the original insectivorous condition to suit the necessities of an herbivorous evolution. In the Macropodidæ both the upper and lower incisors present trenchant modifications adapting them more or less perfectly for a grazing habit; while in the Phascolomyidæ and Diprotodontidæ (Pl. 5. figs. 40, 41) the median upper and lower teeth present an open-rooted condition, and a formation of anterior enamel bands fitting them for a rodent habit.

Apart from its bearing on the evolution of the Phalangeridæ, the origin of the diprotodont modification as an insectivorous modification, primarily concerning the median upper and lower incisors, and its conversion into a rodent modification in the Phascolomyidæ, is of interest as furnishing a possible clue to the origin of the placental Rodentia.

With regard to the special dental evolution of the Phalangeridæ, we may distinguish three lines of development, characterized by the modifications of the molar patterns as follows :—

A. Molars quadrituberculate, with selenoid cusps. Upper teeth with reduced external styles; with or without intermediate conules	Phascolarctinæ.
B. Molars quadrituberculate, with bunoid cusps. Upper teeth without external styles or intermediate conules	Phalangerinæ.
Petaurus, Dactylopsila, Phalanger, Trichosurus. C. Dentition degenerate; cheek-teeth haplodont, wholly vestigial Genus: Tarsipes.	Tarsipedinæ.

## PHALANGERINÆ.

As compared with the Phascolarctinæ and Tarsipedinæ the present group will be seen to represent the dominating division of the family, the bundont modifications of the molars by which it is distinguished being found in eight of a total number of twelve genera. It also represents the ancestral group from which the herbivorous families have been derived.

The various genera of the Phalangerina form a progressive series of much the same order as that seen in the case of the Dasyurina, the dominating principle appearing to be, as before, the increase in size of the body. The more primitive forms, such as *Acrobates, Distachurus*, and *Dromicia*, in their comparatively minute proportions and,

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apart from the diprotodont modification, in their dental characters, make an interesting approximation to the insectivorous Dasyurinæ, while the most specialized forms, such as *Phalanger* and *Trichosurus*, in their large size and incipient herbivorous modifications, present an opposite extreme, bordering on the conditions in the smaller of the Macropodidæ.

It may be observed, however, that the sequence of dental modifications in the present division does not indicate an evolution as completely homogeneous as that of the Dasyurinæ. Each genus will be seen to present one or more specialized modifications which, while not disturbing the general sequence, prevent it from being wholly prototypal to a succeeding one. The cause of this condition will be better discussed after a review of the dentition of the group, but it may be mentioned at this point that the omnivorous-herbivorous evolution, preceded as it is by the diprotodont modification, appears to represent a critical stage in the general dental progression. There appears to have been a double conflict between the continuation of the reduction of the posterior premolars and their elaboration as sectorials, and between the use of the incisors as piercing and cutting organs and the transference of their functions to the posterior premolars. The molars will be seen to show an evolution as gradual as that of the Dasyurinæ and Peramelinæ, the only important exception being that in *Acrobates, Distæchurus*, and two species of *Dromicia* there is a reduction of the formula by one tooth above and below.

Sequence of Molar Patterns.—Apart from certain characters of specialization, to which reference will be made below, the molars of *Distachurus pennatus*, the form selected for illustration, may be taken as representing the starting-point for the evolution of the bundont section, as far as the stages of this are indicated in recent forms.

The upper molars of *Distachurus* decrease in size from before backwards, the first tooth being more than three times as large as the third. This character and also that represented by the reduced condition of the molar formula are secondary and not prototypal. Each of the upper teeth (Pl. 5. fig. 13) is roughly triangular in shape, and shows only four cusps, representing the protocone, paracone, metacone, and hypocone (cf. p. 89, text-fig. 1). The protocone and hypocone are placed below the level of the remaining cusps, as in the Peramelinæ and, in the case of the protocone, the Dasyurinæ and Didelphyidæ. Together they appear to form an internal ledge attached to the bases of the outer cusps. The hypocone is not fully developed, and this accounts for the somewhat triangular contour of the crown. Both the paracone and metacone are well developed, and present a very different appearance from that seen in the Dasyurinæ and Peramelidæ, there being no disproportion in their relative sizes, and no tendency towards any excavation of their external faces, so that, apart from a fine trenchant line extending over their tips, they are wholly bunoid. External styles are entirely unrepresented. There are also no traces of a metacone-spur.

The lower molars of *Distæchurus* do not show the disproportion in size characteristic of the upper teeth. The first is only slightly, if at all, larger than the second, and the latter is slightly larger than the third. The second (Pl. 6. fig. 18) and third are oblong

in shape and quadrituberculate, only the protoconid, metaconid, hypoconid, and entoconid being present, as in *Thylacomys*. The protoconid and hypoconid are not yet completely bunoid, but tend to retain the triangular section characteristic of more primitive forms. As in the latter also the two cusps are separated externally by an angular notch. At the anterior and posterior margins of each tooth a minute ledge is seen to be connected with a fine ridge running over the tips of the outer cusps. This structure is not very pronounced in the present form, but becomes very conspicuous in the more advanced species.

The first lower molar of Distechurus (Pl. 6. fig. 20) shows an insectivorous specialization, the protoconid being elongated and curved after the manner of a canine, while the metaconid is reduced so as to form a small tubercle attached to the inner side. This curious development also appears in a reduced state in more advanced forms.

The molars of *Acrobates* are very like those of *Distachurus*. The upper teeth are, however, more definitely quadrate, in which character they are more specialized, but they also decrease only moderately in size backwards, in which respect they are more primitive. In the first lower tooth the protoconid has not been elevated to the same extent, so that the disproportion in size between it and the metaconid is not so marked.

The anterior upper molars of *Dromicia* resemble those of *Acrobates* in their proportions and the completeness of the hypocone, but this is more nearly true of *D. lepida* and *D. nana* than of *D. concinna*, which tends to resemble *Distachurus*. In the third upper molar the hypocone is absent, so that the tooth is triangular and trituberculate. In the first lower molar the anterior cusp is elongated only in *D. concinna*. The metaconid is fairly separate in *D. lepida*, as in *Acrobates*, but is absent in *D. concinna* and *D. nana*.

Passing from Acrobates, Distachurus, and Dromicia, it is probable that the next higher member of the series is Gymnobelideus. This genus is, however, not represented in the collection. Its volant form, Petaurus, which is said by Thomas to be identical with it in dentition, presents the following features. The molar formula is unreduced, and the teeth decrease gradually in size from before backwards. The upper molar patterns almost repeat those of the preceding species, this being especially true of P. breviceps and P. sciurcus. It is interesting to note in this connection that P. breviceps makes the closest approach in size to Dromicia, P. sciurcus being intermediate in size between P. breviceps and P. australis. The upper molars of the lastnamed species begin to show advanced characters. In those of P. sciureus (Pl. 5. fig. 15) a thin ridge is seen to pass over the protocone and hypocone, and to terminate anteriorly and posteriorly in narrow ledges. This structure is very faintly indicated in P. breviceps as in Distachurus, but is more definite in P. australis. The internal sides of the paracone and metacone show slight indications of transverse ridging. The lower teeth differ from those of Distachurus in having the protoconid and hypoconid more completely bunoid, and in having the external band slightly more pronounced. The anterior lobe of the first molar shows the same modification as in Distachurus, except that the protoconid is not so conspicuously clongated, and the metaconid is absent. It now becomes apparent that this tooth has been formerly modified as a piercing-organ and is undergoing reduction.

Dactylopsila represents the next higher member of the series both in size and dental characters. It differs from *Petaurus* in having the protocone and hypocone fully differentiated in the upper molars and placed on a level with the outer cusps, except in the case of the first tooth, where these elements are low as in the smaller species. The external cusps do not, however, show quite so marked a tendency towards transverse ridging as those of *Petaurus*. *Dactylopsila* appears to be very slightly aberrant in this character and in its insectivorous habit as compared with its size, judging from the conditions presented by *Petaurus* and more advanced forms. In the first molar the protoconid is low, as in *Petaurus*. The remaining teeth have their cusps completely bunoid.

With *Petaurus* and *Dactylopsila* the omnivorous development of the molars may be regarded as complete. In the next member of the series, *Phalanger*, and also in the final form, *Trichosurus*, herbivorous modifications begin to be apparent. The upper teeth of the latter genus (Pl. 5. fig. 16) are oblong in shape; the hypocone is fully developed, and the cusps are all of the same height. The internal band described for *Petaurus* is now extremely conspicuous and involves completely the inner cusps. The internal sides of the outer cusps are sharply ridged, each of the ridges extending from the tip of an outer cusp towards the base of an inner one. In *Phalanger* this ridging is slightly less prominent than in *Trichosurus*.

In the lower molars of *Trichosurus* (Pl. 6. fig. 19) the same lophodont developments are again in evidence, the opposite (internal) cusps being affected. The external band, like the corresponding internal band of the upper teeth, is very pronounced and involves completely the outer cusps. The first molar, both in *Trichosurus* and *Phalanger* (Pl. 6. fig. 21), shows the protoconid enlarged but low, as in *Petaurus* and *Dactylopsila*; the metaconid is practically absent.

The development of transverse crests in the final members of the Phalangerinæ represents the beginning of the herbivorous evolution. As will be seen from a consideration of the Macropodidæ and Diprotodontidæ, it is on these structures that the herbivorous evolution of the molars is mainly developed. It is interesting to observe the transverse ridges already appearing so far back in the evolution as *Petaurus*.

Origin of Bunodont Molars.—On following the modifications of the molar patterns in the Phalangerinæ, it will be seen that the conditions obtaining in the final members *Phalanger* and *Trichosurus* represent a considerable advance on those of the initial forms *Acrobates*, *Distæchurus*, and *Dromicia*. Nevertheless, the molar patterns even of the latter animals do not represent an actually incipient, but a fairly advanced phase of the bunodont evolution, the first constructive stages having already been obliterated.

The available evidence goes to show that the upper molar patterns of the Phalangerinæ have been derived from a trituberculate type like that seen in the Dasyurinæ, the main facts being as follows :—In the first place, we find the earlier stage represented in the group characterized by an imperfectly developed condition of the hypocone. This appears to indicate that the hypocone is now in process of development as a supplement to an originally trituberculate crown. The same differences in the degree of development

of the hypocone are seen in the Peramelidæ, whose molars are undoubtedly of trituberculate origin (cf. Pl. 5. figs. 8, 9, & 10). Secondly, while in the majority of the existing Didelphyidæ we meet with molar patterns of the same insectivorous type as those seen in the Dasyurinæ, in one form, Caluromys, we find indications of a bunodont omnivorous development, which is now in its very incipient stages, but which if continued would probably give rise to exactly the same conditions as are seen in Distachurus and its allies. Comparing the upper molars of Caluromys (Pl. 5. fig. 27) with those of a normal didelphyid form (fig. 26), we notice the following modifications :- The cusps are lower and their triangular section not so sharply indicated. The protocone is conspicuously broadened. The disproportion in size between the paracone and metacone is not so obvious, the metacone-spur being reduced. The external styles are reduced, and the ridge bearing them is thin and usually crenulated. In all of these characters the pattern of Caluromys is prophetic of that of Distachurus (Pl. 5. fig. 13), and if the protocone were still further broadened to a stage of differentiation of a hypocone, and the triangular section of the outer cusps slightly more reduced, the result would be much as in the latter genus.

Confirmatory evidence may be obtained from a consideration of *Cænolestes*. In this form (*cf.* Thomas, 1895 b, pl. 1. fig. 6) the first and second upper molars show a bunodont quadrituberculate condition, which is very similar to that seen in *Petaurus*, while the third shows a trituberculate condition, which is intermediate between that in *Caluromys* and that in *Distæchurus*, the outer cusps being bunoid and the external styles absent, as in the latter. A somewhat similar relation may, in fact, be seen between the second and third molars of the three-molared Phalangerinæ themselves.

The derivation of the lower molars of the Phalangerinæ presents no great difficulties. The quadrituberculate pattern is the same as that seen in *Thylacomys*, the latter being shown by analogy with the Peramelinæ to be of tuberculo-sectorial origin. A prototypal condition is again seen in *Caluromys*, where there is a tendency towards the reduction of the paraconid and hypoconulid, and a rounding off of the remaining cusps. As already mentioned, the molars of *Distæchurus* show a tendency to retain the original angular character of the protoconid and hypoconid.

Incisors.—The general characters of these teeth have already been referred to in connection with the origin of the diprotodont modification, so that only the sequence of their special modifications calls for consideration.

As in the case of the molars, the most primitive conditions are to be found in the three genera *Acrobates*, *Distachurus*, and *Dromicia*. In all of these the median incisors are of much the same procumbent piercing type as those of the Dasyurinæ, the only noteworthy difference being seen in a slight tendency towards the lateral compression of the tips. The upper lateral teeth (*cf.* Pl. 5. fig. 39) are relatively small, this being especially true of the anterior one (i. 2). In the unworn condition they are spatulate, as in the Dasyurinæ, but their edges are now slightly turned inwards so that they stop the tips of the lower teeth instead of letting them pass inside. The latter are recurved and sharply pointed.

The larger forms *Petaurus* and *Dactylopsila* show a more advanced stage of the same modification. In the former the median upper incisors are decidedly procumbent. They tend to be triangular in section from a thickening of their antero-internal edges. In *Dactylopsila* they are still more completely triangular in section, and the procumbent character is very conspicuous (cf. Thomas, 1888, p. 127, profile figure). The upper lateral teeth of *Petaurus* are like those of the smaller forms, and the same is true of *Dactylopsila*, except that here the edge of the posterior tooth (i. 3) is much broader, and its anterior portion slightly more inwardly rotated than in *Petaurus*. In both genera the lower teeth are elongated and recurved, as in the smaller species, and this character is again more pronounced in *Dactylopsila* than in *Petaurus*.

Phalanger and Trichosurus show a more specialized modification of the incisors, but it is of a different type from that seen in the preceding forms. The procumbent development of the median upper teeth, which is so pronounced in the next lower member of the series, Dactylopsila, is here scarcely in evidence. In Phalanger these teeth are more rounded in section, and their length is reduced, so that their tips project only slightly beyond those of the lateral teeth. In Trichosurus the length is still further reduced, and, except for their greater curvature, they begin to show the characters of the lateral teeth. In Phalanger ursinus and P. melanotis the upper lateral teeth are much like those of Petaurus and Dactylopsila, the second serving chiefly as a stop for the lower ones, while the third, which are again spatulate at their tips, have their anterior portions rotated inwards. The remaining species of Phalanger show a specialized condition, the third upper teeth being reduced through the encroachment of In Trichosurus the upper lateral teeth are like those of P. ursinus the canines. and P. melanotis. In both genera the lower teeth are flattened, lanceolate, and only slightly curved. In neither case do they show any tendency to continue the progressive elongation and piercing developments characteristic of the lower members, especially Dactylopsila.

The incisor modifications just described furnish the first instance of the conflict of developments above referred to as characterizing the omnivorous evolution of the Phalangerinæ. In the minute forms Acrobates, Distachurus, and Dromicia the insectivorous purpose of the diprotodont modification is fully realized, the procumbent character of the median upper teeth, and the elongated, recurved, and sharply-pointed character of the lower ones, combining to make these structures of obvious value in the prehension of food. Proceeding from these more or less initial forms we meet with a series of genera showing a gradual increase in the size of the body, which we might reasonably suppose, both on general principles and from the analogous case of the Dasyurinæ, to demand the abandonment of insectivorous habit and a gradual reduction of insectivorous characters. What we do find in the present case, however, is a tendency to continue the insectivorous developments. This is not surprising in the case of Petaurus, especially the smaller species P. breviceps and P. sciureus, but it certainly is so in the case of Dactylopsila, both on account of its larger size and its actually insectivorous habits. Passing to the still larger forms Phalanger and Trichosurus we find the conditions abruptly changed, the insectivorous characters being replaced by

others which can be easily shown from their constant occurrence in the Macropodidæ to be of a herbivorous type. As will be seen from a further consideration of the antemolar teeth of this series, the changes noticeable in the incisors of the latter genera are closely associated with others in the premolars which are almost as abrupt in their appearance and are also characteristic of the Macropodidæ.

Functional Canines.-These teeth show a fairly homogeneous evolution. As before, the most primitive conditions are found in the three genera Acrobates, Distechurus, and Dromicia. In the two former the teeth are long, curved, and sharply pointed, and are apparently quite as functional as in the Dasyurinæ. As will be seen from the figure of Distachurus (Pl. 5. fig. 39) they work over the sides of the lower incisors. In both forms they have undergone an anterior progression, so that the space originally occupied by the notch for the reception of the lower canines, and presumably also by additional posterior incisors, has been obliterated, the third incisors being in close contact with the canines. In Dromicia the canines are not so well developed, being shorter, less curved, and slightly compressed; they are also separated from the third incisors by short diastemata. Their shortened condition in this genus represents the beginning of a process of reduction which characterizes the canine evolution in the present series. In Petaurus the canines are so short as to project only slightly beyond the third incisors; their tips are rounded and laterally compressed. In some cases the compression is accompanied by a grooving of the root as in P. Doreyana, Chæropus, and Myrmecobius. In Dactylopsila the canines are reduced as in Petaurus, and are also slightly compressed. In Phalanger we find two different conditions. In P. ursinus and P. melanotis the canines are short and rounded as in Dactylopsila, and they project to about the same extent as the third incisors, while in the remaining species they are enlarged, in all probability secondarily, and present the characters of normal canines. Trichosurus shows much the same condition as P. ursinus and P. melanotis, the only noteworthy difference being a slightly greater reduction. In this form the third incisors frequently project beyond the canines.

Functional Premolars.—The most primitive conditions are found in Acrobates. In this form the upper premolars are of a piercing insectivorous type, exactly as in the Dasyurinæ. The resemblance to the latter is increased by the fact that the posterior teeth are slightly reduced as compared with the median, while the latter are slightly larger than the anterior teeth. The lower functional premolars are the median and posterior teeth. They also resemble those of the Dasyurinæ in being of a primitive piercing type; the posterior teeth are again slightly reduced. Distæchurus (Pl. 5. fig. 39) shows a slightly more advanced stage of the same modification. The upper anterior and median premolars are simply enlarged, while the posterior teeth are still further reduced. In the lower jaw the posterior teeth have entirely disappeared, recalling the condition in advanced forms of the Dasyurinæ. The median lower teeth show an elongated and subcaniniform condition.

The three species of *Dromicia* present considerable differences in their premolar second series.—ZOOLOGY, VOL. IX. 19

characters. Those of *D. lepida* are of interest as being prototypal to those of *Petaurus*. In this species the upper anterior and median teeth are small as compared with the posterior ones, the latter, unlike those of Acrobates and Distachurus, being enlarged instead of reduced. They present a rather different appearance from those of Acrobates, being relatively short and provided with accessory cusps. The tips of the upper posterior premolars are slightly flattened and bifid. Of the lower premolars the only functional members are the posterior teeth, which are comparatively well developed and also bifid. In D. concinna the disproportion in size between the upper anterior and median and the posterior premolars is almost more marked than in D. lepida, not, however, on account of the enlargement of the latter, these being in reality less enlarged, but because of the styliform and wholly vestigial character of the former. In the lower jaw of this species none of the premolars are functional. In D. nana, a larger and more specialized form than the others, the anterior and median upper premolars are vestigial, as in D. concinna, while the posterior teeth are greatly enlarged, and much more completely bifid than those of D. lepida. As in the latter, only the posterior premolars are functional in the lower jaw; they are enlarged but not bifid.

As already mentioned, *Petaurus* approximates to *D. lepida*. This is especially true of *P. breviceps*, the smallest of the three species. The upper anterior and median premolars are low, with prominent accessory cusps. The median teeth, which in *D. lepida* are reduced as compared with those of *Acrobates* and *Distæchurus*, are here further reduced. The upper posterior premolars are moderately developed; they are not bifid at the tips, although they show a tendency towards such a development in a grooving of their outer sides in the region of the edge. The lower posterior premolars are reduced; they show a faint tendency towards a grooving of the edge. It appears probable that both upper and lower teeth have been formerly modified as in *D. lepida*.

Dactylopsila shows an advance on Petaurus, except as regards the upper anterior premolars. The latter are seen to be undergoing a new development, becoming less compressed, single-rooted, and subcaniniform. Apart from its striking character, this development is of great interest as being carried over from the present form to the succeeding genus *Phalanger*. The median premolars are still more reduced than in *Petaurus*, being wholly vestigial or even absent. The posterior teeth are moderately developed, and their edges are slightly compressed in an oblique direction, the anterior portion of the edges being placed internally. This is the reverse of the condition in *Phalanger*, where the cdges are compressed in such a way that the anterior portions are external. None of the lower premolars are functional in *Dactylopsila*; the posterior teeth are still more reduced than in *Petaurus*.

In the succeeding genus *Phalanger* the anterior and median upper premolars show the same trend of evolution as those of *Dactylopsila*, while the posterior teeth above and below show a pronounced departure. Of the former teeth the anterior elements are single-rooted and subcaniniform, except in *Phalanger ursinus*, while the median ones are vestigial or wholly absent. The posterior premolars are enlarged as sectorials, as in *Dromicia nana*. The various steps in the elaboration of the sectorials are illustrated to a certain extent in the different species. In the upper teeth of *P. celebensis*, *P. breviceps*, *P. melanolis*, *P. orientalis*, and *P. maculatus* we find that the original tip (protocone) is anterior and more or less external in position, and that the posterior slope is compressed and slightly trenchant. The cutting-blade thus formed bears one or two short superficial grooves ending in notches at the edge. In *P. melanotis*, where only one groove is present, the teeth resemble those of *Dromicia nana* and *D. lepida*. In all cases the posterior portion of the trenchant edge tends to be elevated, but this tendency is much more apparent in certain forms (*P. orientalis*) than in others (*P. breviceps*, *P. celebensis*). In *P. lullulæ*, *P. leucippus*, and *P. Rothschildi* the trenchant character of the edge is much more pronounced, the posterior portion of the edge being still more elevated and bearing three grooves.

An interesting feature of the development of the trenchant edge is its axial rotation. In *P. melanotis*, *P. ursinus*, and *P. maculatus* we find a practically unrotated condition, so that a line drawn through the cutting-edge, if it passes through the middle line of the skull at all, will pass posteriorly in the region of the condyles. In the case of *P. orientalis*, *P. lullulæ*, and *P. leucippus* it will pass through the middle line forwards in the region of the palatal vacuities. Increase in relative size seems also to be a part of the sectorial elaboration. In *P. celebensis* and *P. breviceps* the teeth are small, while in such extreme forms as *P. leucippus* and *P. Rothschildi* they are considerably enlarged, now exceeding the first molars.

It is interesting to note at this point that in the Macropodidæ the sectorial evolution has proceeded along two lines, one of which, represented by *Hypsiprymnodon* and *Bettongia*, appears to present in an extreme degree the grooved and rotated condition found in *Phalanger*, while the other seems to represent a modification of the simpler, practically ungrooved and unrotated type found in *Dromicia* and *Petaurus*.

In Trichosurus the upper anterior premolars are single-rooted, as in the two preceding genera, Phalanger and Dactylopsila; they are on the whole, however, more reduced. The median teeth have now disappeared. The posterior premolars above and below show much the same conditions of sectorial elaboration as are seen in the more specialized forms of Phalanger. Their trenchant edges are elevated, as in P. leucippus, and are rotated to about the same extent as in the latter form or P. orientalis. They show indications of three notches. A significant feature is that the sectorial teeth show, as a rule, more decided indications of wear in Trichosurus than in Phalanger, this character supplementing the evidence of the molars, canines, and incisors as to the greater herbivority and more advanced position of the former genus.

Apart from special phylogenetic considerations, the modifications of the premolars in *Phalanger* and *Trichosurus* possess a general significance. While these genera may be shown by their lack of development of the median premolars to be not very nearly related to the ancestors of the Macropodidæ, they show the incipient phases of a sectorial development of the premolars, which is continued and perfected in the latter family. The fact that the formation of sectorials may have taken place not only within the limits of the family but within the limits of two genera, indicates the futility of such general comparisons as have been made in suggesting affinities between the specialized sectorials of the Macropodidæ and those of certain of the South-American Miocene forms, or of the Plagiaulacidæ.

The modifications of the posterior premolars in the Phalangerinæ will be seen to furnish a further example of the conflict of developments already described for the incisors. In *Acrobates* and *Distæchurus* these teeth present two stages of a reduction similar to that which is so characteristic of the Dasyurinæ. Within the limits of the three species of *Dromicia*, we find the same tendency towards reduction indicated in *D. concinna*, but an opposite tendency towards enlargement as sectorials in *D. lepida*, and still more in *D. nana*. In *Petaurus* and *Dactylopsila* the posterior premolars are comparatively poorly developed, this being especially the case with the lower teeth, while in the succeeding forms *Phalanger* and *Trichosurus* they are greatly developed as sectorials. The marked difference in this respect between *Phalanger* and *Dactylopsila* is doubtless due in part to the retention in the latter of insectivorous modifications of the incisors, the latter teeth being thus the more functional elements; but, in general, the modifications of the whole series represent a conflict between a reduction of the posterior teeth, as in the Dasyurinæ, and their elaboration as sectorials, as in the Macropodidæ.

Lower intermediate Teeth.—The functional or vestigial character of the various teeth situate between the median lower lower incisors and the first molars in this series probably depends on several circumstances, the elongation of the median incisors being, however, the most important factor in the reduction of the elements of this region. In all forms, except *Trichosurus* and *Phalanger*, there are normally two vestigial teeth situate immediately behind the median functional ones. They are sometimes separated from the median premolars by diastemata which, in all probability, were formerly occupied by the canines and anterior premolars. The vestigial nature of these teeth can only be ascribed to the enlargement of the median incisors. The latter would doubtless have brought about the reduction of the median and posterior premolars in all forms, as in *Petaurus* and *Dactylopsila*, were it not for the fact that it has been prevented from so doing by other developments. Thus, in *Acrobates* and *Distæchurus* the median premolars have been prevented from becoming vestigial by being developed as sectorials.

The only feature of phylogenetic interest presented by the intermediate teeth concerns their relations in *Phalanger* and *Trichosurus*. In the former three vestigial teeth are usually, although by no means always, present\*, while in *Trichosurus* only one is as a rule indicated, although two may occur as a variation. This fact supports the evidence already given as to the more advanced position of the latter genus.

#### TARSIPEDINÆ.

The single representative of this division, *Tursipes rostratus*, owes its distinction from the remaining members of the family to the wholly degenerate character of its dentition, the only teeth represented being the upper incisors, the median lower incisors, the upper

<sup>\*</sup> Bateson (1894, p. 253) has given a detailed account of the variability of these disappearing elements in *Phalanger* and other members of the present family.

canines, and a varying number of undifferentiated cheek-teeth, all of which are vestigial \*. The upper incisors are usually two in number, judging from four specimens in the collection, and are always extremely minute and styliform. Apart from their minute size, the upper canines bear a certain resemblance to those of *Dromicia* in being only slightly curved and rounded at the tips. The median lower incisors are almost straight and extremely slender, but are otherwise of the usual diprotodont type. The cheek-teeth (Pl. 6. fig. 24), like the upper incisors, are minute and either simply styliform or slightly curved. Their number appears to be usually three, and their homologies are indeterminable.

The exact dental relations of *Tarsipes* with the remaining Phalangeridæ are doubtful, and its mode of origin can only be conjectured from the association of its reduced dentition with its mellivoroūs habit. It is extremely probable that the omnivorous evolution of the Phalangeridæ began with diminutive animals which, like *Acrobates*, *Distæchurus*, and *Dromicia*, were able to live among the smaller branches of trees, and to supplement their insectivorous fare with blossoms and honey. Certain of these must have continued the omnivorous evolution in a normal way, giving rise to the Phalangerinæ and Phascolarctinæ, while others resorted largely to a mellivorous habit, giving rise to *Tarsipes*<sup>‡</sup>. The reduction of the dentition is due to the same cause as in ant-eating forms, the food requiring no mastication, and its collection being perfectly provided for by the prehensile development of the tongue.

# PHASCOLARCTINÆ.

The three genera forming the present division are of general interest as presenting a fresh instance of the remarkable parallelisms between marsupial and placental types. In the Macropodidæ, and in their prototypes the Phalangerinæ, we have two groups, roughly distinguishable by the hypsilophodont and brachybunodont modifications of the molars. In respect to these modifications the two groups parallel the perissodactyl Ungulata, especially the tapiroid representatives of the latter, and the Condylarthra. The Phascolarctinæ now present selenodont modifications similar to those of the artiodactyl Ungulata, especially the more primitive forms which retain the brachyodont condition.

In the case of the Marsupials the evolution of the selenodont section is of very limited extent, the reason being that, unlike the case of the bundont Phalangerina, none of the members of the original arboreal stock have given rise to terrestrial successors. The evolution of the bundont section would be searcely less limited were it not for the existence of the terrestrial Macropodidæ, Phascolomyidæ, and Diprotodontidæ.

With regard to their special relationships, the dental characters indicate that the genus *Pseudochirus* represents the ancestral type from which the remaining genera *Petauroides* and *Phascolarctus* have been derived. Like *Phalanger*, *Pseudochirus* is

<sup>\*</sup> Cf. Waterhouse (1846).

<sup>&</sup>lt;sup>†</sup> The interesting observation of Gould (1863) with reference to the fly-catching propensities of a captive *Taesipes* may be noted in this connection.

conspicuous for its wealth of species, a condition which is doubtless due in a large measure, as in the former genus, to the advent of a new and successful adaptation—in the present case the formation of quadrate sclenodont molars, in *Phalanger* of sectorials. *Petauroides*, as pointed out by Thomas (1888) is indistinguishable in dentition from *Pseudochirus*, and otherwise represents simply a volant form of the latter. *Phascolarctus*, although seemingly isolated by its great specialization, shows in all of its dental characters a direct advance on *Pseudochirus*.

Sequence of Molar Patterns .- Notwithstanding their wealth of numbers, the species of Pseudochirus are remarkably constant in their molar characters, and the following description of P. peregrinus will apply almost equally to all. In P. peregrinus (Pl. 5. fig. 17) first, second, and third upper teeth are fully quadrate in shape, like those of the advanced Phalangerinæ and Peramelinæ, so that they are not separated internally by angular spaces. The functional cusps are arranged in three longitudinal rows, a condition which at first sight suggests that seen in the Peramelinæ. On closer examination, however, the teeth are seen to possess a fourth (external) row of vestigial cusps representing the external styles of the third row in the Peramelinæ and the polyprotodont families in general. The predominant cusps of the crown are those of the first and third rows, these representing, as in the Phalangerinæ, the protocone, paracone, hypocone, and metacone. The protocone is slightly predominant. The hypocone is complete. There is no disproportion in size between the paracone and metacone, and no trace of a metacone-spur. The main cusps are comparatively low and are crescentic in section, each being concave in its outer face. The protocone and metacone are placed slightly below the level of the outer cusps. The cusps of the second row are comparatively small, but are of the same crescentic character as the larger ones. They are usually smaller than in the specimen here figured. They represent the subsidiary protoand metaconules, which are fairly common in the Placentals, but rare in Marsupials. The vestigial external styles are two in number; they appear to represent b (or ab) and c of polyprotodont forms. Their presence in the Phascolarctinæ is of considerable interest, since in all the remaining members of the diprotodont section they have completely disappeared. Style c shows a slight tendency to be bifid, a condition which is partly natural and partly the result of wear. In mastication the crowns of the lower teeth sweep transversely across those of the upper in such a way that the triangular tips of the hypoconid and entoconid pass through the triangular spaces separating the paracone and metacone. Style c is placed directly in the line of passage, so that its tip becomes notched by those of the hypoconid and entoconid. In unworn teeth of P. peregrinus and P. Cooki there is seen a slight indication of a cleavage of this element, showing that the mechanical notching of its tip has produced a natural development in that direction. In other species of *Pseudochirus* there is a slight variation in the external styles: they are obsolete in *P. Dahli*, and almost so in *P. Forbesi* and in *Petauroides volans*.

Like those of the Phalangerinæ, the upper molars decrease in size backwards. The fourth tooth is reduced, although not to the same extent as in polyprotodont forms. This element is in fact now undergoing a progressive evolution. In P. peregrinus it is

triangular in shape as in the Phalangerinæ, and it shows three cusps, probably representing the protocone, paracone, and metacone. In some species the metacone-like element shows a tendency towards division, and this condition appears to be prophetic of that in Phascolarctus, where the posterior lobe of the fourth molar bears two distinct cusps. The same process of development, resulting in the formation of new cusps, with apparent, but without actual, homologies, is also observable in the same teeth of the Macropodidæ, and also in the first lower molars of that family. Apart from its special significance, this condition throws an interesting light on the general problem of the fate of vestigial members. In the most primitive of the polyprotodont forms we find the fourth upper molars in an advanced condition of reduction, while passing through a series of intermediate forms in the Phalangeridæ and lower Macropodidæ we find these teeth becoming finally the largest and most perfect elements of the upper molar series. Both in the Macropodidæ and the Phascolarctinæ the cause of this peculiar development is to be sought in the greater possibilities of service involved in the substitution of a transverse grinding action of the teeth for a vertical cutting and piercing one. In primitive polyprotodonts, as already indicated, the action of the metacone of the anterior upper molars is directed backwards against the trigonid of the succeeding lower teeth. In the fourth upper molar the metacone is reduced, the reason being that there is no trigonid working behind it, that of the lower tooth being in relation with the third upper one. In the Phascolarctinæ, as in the Macropodidæ, on the other hand, the action of the metacone is directed forwards against the hypoconid and entoconid. The fourth tooth may therefore become capable of service by the development of its vestigial metacone into a functional cusp, and may increase its utility by the addition of a new cusp simulating the hypocone in normal teeth.

The lower molars of P. peregrinus (Pl. 6. fig. 22) are brachyodont, and, like those of *Thylacomys* and the Phalangerinæ, completely quadrituberculate. The selenoid modifications are confined for the most part to the outer cusps, the inner cusps being rather blade-like than crescentic. It will be seen that the concavities of the outer cusps occupy their internal faces, this condition being the reverse of that in the upper molars. In the first lower molar the protoconid is greatly reduced and flattened against the side of the metaconid. In P. Albertisi, however, it tends to be set apart, a condition which is found to recur in *Phascolarctus*. From the presence of two distinct cusps in the latter form, however, it is possible that the element here designated as a metaconid may be in reality a protoconid, the former having disappeared as a result of an insectivorous specialization, as it undoubtedly has in the case of the Phalangerinæ. According to this view, the outer element represents a new accessory cusp. Such a development of a new protoconid-like element can be directly traced in the Macropodidæ.

Passing from *Pseudochirus* to *Phascolarctus* we find a more specialized stage of the same modification found in the former genus. In the upper teeth (Pl. 5. fig. 18) only the main cusps are well developed, the intermediate conules being very minute. All of the main cusps are more completely selenoid than in *Pseudochirus*. The protocone is

usually more prominent than the hypocone from an inward extension of its base. This condition appears to be a remnant of that seen in more primitive trituberculate forms. The spaces between the cusps present a curious appearance, the surface being thrown into small ridges. The posterior shearing edge of the paracone is frequently supplemented by a larger ridge passing down its postero-internal side. The external styles are almost as conspicuous as in *Pseudochirus*, not, however, on account of their better development, but from the greater concavity of the outer cusps; they are in reality more vestigial than in the latter genus. Style b does not project beyond the level of the paracone ridge which joins it; style c is very minute and bifid.

In the fourth upper molar the posterior lobe bears two perfectly developed selenoid cusps, so that the tooth is almost completely quadrate like the others. As already mentioned above, this represents the final stage of a process of cleavage of an originally single cusp.

The lower molars of *Phascolarctus* (Pl. 6. fig. 23) resemble those of *Pseudochirus* even more closely than do the upper. The selenoid character is more pronounced in the outer than in the inner cusps. The latter are, however, more selenoid than in *Pseudochirus*, a slight concavity having now appeared on their inner faces. These teeth show a tendency towards the addition of an external cingular ridge, obliterating the notch originally present between the protoconid and hypoconid.

Origin of Selenodont Molars.—Like those of the Phalangerinæ, the molars of the present division are comparatively well specialized. Apart from the more or less completely selenoid modifications of the cusps, the hypocone will be seen to be well developed in the upper teeth, while the paraconid and hypoconulid are wholly absent in the lower. They are thus considerably removed from the second type characteristic of the polyprotodont section. The question here arises as to the intermediate stages which have been passed in the development of the selenodont molars up to the *Pseudochirus* stage.

It may be admitted at the outset that the evidence on this subject is of a rather fragmentary kind. There is, in the first place, no marsupial group outside of the Phascolarctinæ which shows incipient stages of the same evolution, as *Caluromys* does with reference to the Phalangerinæ, and, in the second place, the evidence as to the origin of the selenodont molars in the parallel case of the artiodactyl Ungulata is not wholly satisfactory \*.

Winge has expressed the opinion that the molar patterns of *Phascolarctus* are ancestral to those of the Phalangerinæ, intermediate conditions being found in *Pseudochirus*. The main reason advanced for this view is that *Phascolarctus* shows the same angular character of the molar cusps as is found in the polyprotodont forms, and further that it possesses vestigial external styles, which have disappeared in the Phalangerinæ.

Three propositions may be considered, namely: (a) that the molar patterns of the Phascolarctinæ are ancestral to those of the bundont Phalangerinæ; (b) that the reverse

\* The available evidence favours bunodont origin of selenodont (artiodactyl) types.

is the case; (c) that the molar patterns of each group have been independently derived from a second type, like that seen in *Perameles Doreyana*.

On comparing the melars of *Phascolarctus* with those of the polyprotodonts, it will be seen that there is ample evidence in favour of Winge's view that certain characters of the former are directly derivable from those of the latter. For example, the selenoid modifications of the protocone, paracone, metacone, hypoconid, and protoconid are already present in the polyprotodont forms, and are only more fully elaborated in the Phascolarctinæ. The hypocone is crescentic in the Peramelidæ. It may also be shown that the selenodont molars could not have originated from a bunodont type: in the first place, on account of the fact that the external styles are absent in the latter; in the second place, that the outer and inner cusps in the lower molars of the Phascolarctina present a differentiated condition which would in all probability not be indicated if all of the cusps had been derived from a common bunoid type. In the polyprotodonts the outer cusps are quite selenoid, with their concavities external as in the Phascolarctinae. The inner cusps, and especially the metaconid, also tend to be selenoid, but their concavities are on their external sides, or, in other words, on the wrong side, with reference to the Phascolarctinæ. The blade-like character of the inner cusps in the latter seem therefore to indicate an intermediate stage in the conversion of semiselenoid cusps with external concavities into selenoid cusps with internal concavities. The condition found in Pseudochirus is just on the line between the two phases, and that of Phascolarctus just beyond.

There are, however, no reasons for concluding from this that the selenodont molars of the Phascolarctinæ are ancestral to the bunodont patterns of the Phalangerinæ, while to regard the dental characters of Phascolarctus as ancestral to those of Pseudochirus is simply to reverse the order of evolution. As already mentioned above, the various members of the Phalangerinæ show a close general sequence of dental modifications, the most primitive conditions being found in Acrobates, Dromicia, and Distachurus. The ancestors of the Phalangerinæ were minute insectivorous forms, which, apart from the diprotodont modification of the antemolar teeth, possessed a full antemolar formula. Their secodont molars began to be modified in the same way as those of Caluromys are being changed at the present time. They could not have possessed any of the special characters which now distinguish the Phascolarctine, with the exception of the crescentic character of certain of the cusps and the possession of external styles. The Phascolarctinæ are comparatively large specialized forms, which are well advanced in an herbivorous evolution, the latter being here, as in the Macropodidæ, Phascolomyidæ, Diprotodontidæ, and specialized Phalangerinæ, secondary, and succeeding, not preceding, the insectivorous evolution as exemplified by the primitive Phalangerinae. The fact that the Phascolarctine show resemblance to the polyprotodonts in the character of certain cusps means nothing more than that in the formation of selenodont molars from others of secodont type these cusps have been able to undergo a complete change of function with little alteration of their original character. The molars of the Phascolarctine and Phalangerinæ have been derived by a divergent evolution from a common insectivorous second type. It is possible that, as in the primitive Perameline, this

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type involved an incipient hypocone and slightly reduced paraconid and hypoconulid. The omnivorous stage in the evolution of the Phascolarctinæ must have been of extremely short duration.

*Incisors.*—Within the limits of the genus *Pseudochirus* we find several variations in the characters of the incisors, especially those of the upper jaw. There is, however, cvidence of a ground type corresponding in a general way to that represented by the smaller Phalangerinæ.

In *P. Forbesi*, a small form showing, for the most part, primitive conditions, the median upper incisors are of an almost insectivorous type. Their tips are rounded in section and pointed, and they project a considerable distance beyond those of the lateral teeth. They are directed towards one another in the middle line. The second and third upper teeth are subequal in size, the second shows a very slight thickening of the tips. The enlarged lower teeth are lanceolate and only slightly curved; their tips, which are rounded, work against the posterior sides of the median upper teeth, while their sides cut against the lateral ones, especially the second.

In *P. Albertisi* the median upper incisors are much as in *P. Forbesi*, but are stouter. The second upper teeth have bulb-like tips. The third upper teeth are relatively small and unmodified. The lower teeth are flattened like those of *P. Forbesi*, but, unlike the latter, their external cutting-edge is concave, so as to fit the convexity of the upper lateral teeth. Somewhat similar conditions are found in *P. Corinnæ*, *P. cupreus*, and *P. Dahli*. In *P. Corinnæ*, however, the median upper incisors are very much elongated, projecting downwards, but only slightly forwards, and are also separated from one another in the middle line, this development producing an appearance similar to that seen in certain of the Insectivora and Hyracoidea. Much the same modification is found in *P. Dahli*, although the teeth are not elongated to the same extent as in *P. Corinnæ*. With reference to the second upper teeth, it is difficult to decide whether or not their tips are bulbous in *P. Dahli* the external cutting-edges of the lower incisors are not concave as in the remaining species except *P. Forbesi*.

In *P. peregrinus*, *P. occidentalis*, *P. Cooki*, and in *Petauroides volans* we find modifications of a slightly different kind. The median upper incisors are reduced, so that they project only slightly beyond the lateral teeth. They present a compressed appearance which is due to the excavation of their postero-internal surfaces where they come in contact with the lower teeth. They are separated at their bases and approximated at their tips. Apart from their more reduced characters, they resemble somewhat those of *Petaurus*. The second and third teeth are much as in *P. Forbesi*, being subequal, slender, and on the whole unmodified. The lower teeth are only slightly curved and are fully lanceolate. The internal edges are not concave.

The above facts, although not exhaustive, are sufficient to indicate that the main feature on which the variations develop in this genus is one in which the median upper incisors are pointed, elongated, and procumbent, the lateral incisors subequal and inturned to act as stops for the lower teeth. The lower incisors appear to be already modified throughout as cutting rather than simply piercing organs.

The incisor modifications of *Phascolarctus* indicate a much more specialized condition than those of *Pseudochirus*. The chief difference relates to the tendency towards the development of rodent characters. The lower teeth meet the upper at a wide angle (about 90°), so that instead of cutting by their edges against the tips of the upper lateral teeth they cut entirely by their tips against those of the median upper ones. The upper lateral teeth therefore act as stops. The median upper teeth are rounded in section and flattened from before backwards at the tips. The lateral teeth are slender, and at most only slightly thickened distally as in most species of *Pseudochirus*. The lower teeth are lanceolate when unworn, and scalpriform when worn. In the peculiar manner in which the median upper and lower teeth are fitted together, as also in the slenderness of the lateral teeth, *Phascolarctus* shows an interesting approximation to *Diprotodon*, although there is no tendency in the former towards the differentiation of enamel bands.

As in the case of the molars, there is nothing primitive in the characters presented by *Phascolarctus* as compared with those of the *Pseudochirus* type. The unworn lower teeth of *Phascolarctus*, on the other hand, furnish direct evidence that a cutting modification like that of the latter type is the original condition from which the scalpriform one has been derived.

Upper Canines.—These teeth show few points of phylogenetic interest. In all members of the series they are reduced and apparently functionless, this condition being a specialized one, as in the advanced Phalangerinæ, and contrasting with the primitive one in the smaller members of the latter group. They are short, often laterally compressed, and in general bear little resemblance to normal canines.

Functional Premolars.—Pseudochirus and Petauroides are primitive in respect to the possession of a full upper premolar formula. The anterior teeth are reduced, the median moderately developed, and the posterior slightly enlarged, the condition being also fairly primitive. The median teeth show slight indications of compression of the edges, and this character is still more pronounced in the posterior teeth. The latter, unlike the compressed teeth of the advanced Phalangerinæ, have their original tips in the centre instead of at the anterior end. These teeth show signs of the formation of an internal ledge and of a postero-internal cusp. In the lower jaw the conditions are. more advanced, the only functional teeth being the posterior. Like the upper teeth their edges are compressed, and they also show indications of an anterior accessory cusp.

The condition in *Phascolarctus* appears to be a direct advance on this type. The anterior and median upper premolars have disappeared, while the posterior have become enlarged. The latter are of much the same character as in *Pseudochirus*, but the edge is more uniformly trenchant and the internal ledge better developed. The lower

teeth show much the same relations. The cutting-edge tends to be duplicated behind, and a trace of this formation is also observable in *Pseudochirus*.

Lower intermediate Teeth.—The only interesting feature of these teeth is the fact that they are usually indicated in *Pseudochirus* and *Petauroides*, but are absent in *Phascolarctus*, thus supporting the evidence of incisors, canines, and molars as to the more advanced position of the latter genus. Even in *Pseudochirus* there is considerable variation in the extent of development of these vestigial members as in the Phalangerinæ, the number varying from none to four.

# MACROPODIDÆ.

From what has been said with reference to the preceding families, it will be apparent that on passing successively through insectivorous and omnivorous modifications in the Dasyuridæ, Peramelidæ, and the primitive Phalangeridæ, we finally meet with incipient herbivorous characters in the advanced members of the latter family. As will be pointed out in greater detail in a subsequent section, if we follow the modifications of the footstructure in the same forms we find that these successive phases of dental evolution are closely associated with successive phases of arboreal adaptation. The development of each new phase of dental evolution in arboreal animals appears to have opened a field for the continuation of that evolution in terrestrial ones. At any rate, we find that at the insectivorous stage the arboreal Dasyuridæ have given rise to a number of terrestrial forms which now form a prominent section of the family, while at the omnivorous stage another series of arboreal forms, now without typical representatives, have given rise to the terrestrial Peramelidæ. In the same manner the appearance of incipient herbivorous characters in the Phalangeridæ appears to have been marked by the origin of a series of terrestrial herbivores differentiating into the Macropodidæ, Phascolomyidæ, and Diprotodontidæ.

All of the last-named families are of bundont origin—that is, if we may judge the derivation of the lophodont molars of the Diprotodontidæ by analogy with those of the Macropodidæ. Of the two principal divisions of the Phalangeridæ their relations are accordingly with the Phalangerinæ.

On comparing the dental characters of the herbivorous families it becomes apparent that the phalangerine dentition is capable of giving rise to more than one line of herbivorous evolution. Thus the Phascolomyidæ present rodent modifications throughout the dentition, while the Diprotodontidæ present rodent modifications of the incisors combined with lophodont characters of the molars. The Macropodidæ alone show a uniform continuation of that type of herbivorous evolution which is found in its incipient stages in the advanced members *Phalanger* and *Trichosurus* of the Phalangerinæ, although it may be shown from the retention of the median premolars that they are the descendants of forms slightly more primitive than the latter genera. Generally speaking, the dental evolution of the Macropodidæ has been connected with the perfection of the dentition for a grazing habit, and this, in turn, appears to have been closely associated with increasing capabilities of the animals for terrestrial progression. Judging from the sequence now presented, the ancestors of the family possessed a type of dentition fully as primitive as that of *Petaurus*, and their sphere of action must have been greatly limited by their small size and the shortness of their limbs. Taking these phalangerine characters into consideration, it is probable that the original forms lived among the low scrub, subsisting on leaves and shoots, and possibly supplementing this fare with roots and grasses. The most specialized members of the family, namely, the Kangaroos, judging from the present characters and habits of the smaller forms, are the descendants of such phalangerine forms, which, on becoming larger and longer limbed, and from browsing on the herbage of the scrub, have taken to grazing in its open spaces, then to the open forest-glades, and finally to the open plains.

In ascribing to the Macropodidæ the perfection of grazing adaptations as the chief feature of their dental evolution, a few reservations must be made. The most primitive members of the existing family (Bettongiinæ, Potoroinæ) are forms which have not taken part in the grazing evolution, the direction of their special evolution being, with one exception, away from rather than towards the typical forms. Furthermore, it seems probable that certain of the extinct forms, such as *Procoptodon*, judging from the characters of the incisors, possessed feeding-habits of a different kind from those of their grazing contemporaries. Finally, certain of the more advanced existing members of the family, embracing the Tree- and Dorca-Kangaroos, from being terrestrial, have become temporarily or permanently arboreal, and while retaining many primitive characters have undergone a divergent evolution of sectorial premolars as a result of shoot-eating habits.

The various existing genera of the family may be arranged, on a basis of their premolar and molar characters, as follows:—

A. Molars lophodont, their anterior and posterior pairs of cusps completely connected

(a) Molars brachyodont: sectorial premolars excessively developed.

Genera: Dendrolagus, Dorcopsis, Setonyx.

(b) Molars hypsodont; sectorial premolars moderately developed.

Genera: Lagorchestes, Lagostrophus, Onychogale, Petrogale, Macropus.

B. Molars quadrituberculate, their cusps only incipiently lophoid.

- (a) Sectorial premolars with from two to four short superficial grooves . . . Potoroinæ. Genera: Potorous, Caloprymnus.
- (b) Sectorial premolars with six or more long, narrow, and prominent grooves . Bettongiinæ. Genera: Hypsiprymnodon, Bettongia, Epyprymnus.

## BETTONGIINÆ.

The three genera *Hypsiprymnodon*, *Bettongia*, and *Epyprymnus*, which are included in this division, owe their distinction to the possession of well-differentiated sectorial premolars associated with primitive characters in the remaining teeth. They present a line of dental evolution entirely distinct from that beginning in the Potoroinæ and continuing in the Macropodinæ, and have in all probability originated independently from phalangerine forms possessing the same peculiarities. The extinct form *Burramys*, described by Broom (1896), is a member of the same general series, although, as mentioned by that writer, its position cannot be exactly determined at present beyond that it presents phalangerine as well as macropodine resemblances, and that it is not directly ancestral to *Hypsiprymnodon*.

The special evolution of the group is chiefly marked by the progressive modifications of the molars and sectorial premolars, the canines and incisors retaining for the most part primitive relations throughout. The various forms, with the exception of *Bettongia* cuniculus, appear to be related in the following order:—*Hypsiprymnodon moschatus*, *Bettongia penicillata*, *B. Gaimardi*, *B. Lesueuri*, and *Epyprymnus rufescens*. *B. cuniculus* appears to represent a side development of *B. penicillata*, or possibly *B. Gaimardi*.

Sequence of Molar Patterns.—The progressive characters noticeable in the molars are as follows:—(a) tendency towards reversal of the relative proportions of the three anterior teeth above and below; (b) rotation inwards of the posterior ends of the toothrows; (c) slight hypsodontism of the crowns.

In the most primitive form, *Hypsiprymnodon moschatus*, the first and second upper and lower teeth are approximately equal in size, while the third are slightly smaller than the second and the fourth smaller than the third. The tooth-rows are straight, as in some of the Phalangerinæ. The teeth are quadrituberculate and brachybunodont, as in the latter group. In the upper teeth the protocone and hypocone are placed on a level with the outer cusps, and the internal sides of the latter elements tend to form low transverse ridges, both as in the Phalangerinæ. There are no traces of external styles. The last upper molar is triangular, as in the Phalangerinæ, but its posterior lobe shows indications of division into two cusps. In the lower molars the inner cusps, like the outer cusps of the upper teeth, show indications of the development of low ridges. As in the advanced Phalangerinæ, the first lower molar has but one cusp on its anterior lobe.

Passing through the remaining members of the series we find these characters changing as follows:—The second teeth from being equal in size to the first in Hypsiprymnodon and in some specimens of *Bettongia penicillata* become slightly larger than the latter in other specimens of *B. penicillata*, in *B. Gaimardi*, and in *B. Lesueuri*, and considerably larger in  $\pounds pyprymnus$ . The third teeth from being smaller than the second in Hypsiprymnodon and *Bettongia* become larger in  $\pounds pyprymnus$ . The changes in size of the fourth molars are not serial: in *B. penicillata* and *B. Lesueuri* they are of about the same size as in Hypsiprymnodon, and as the former are much larger animals they appear out of proportion to the remaining teeth. In *B. Gaimardi* and in  $\pounds pyprymnus$  they are of about the same relative size as in Hypsiprymnodon.

The changes just described, namely, the reversal of the relative proportions of the molars, are of considerable significance, in that they represent a necessary feature of the herbivorous evolution, since they are indicated not only in the present group but also

## OF THE AUSTRALIAN MARSUPIALIA.

in the Potoroinæ and Macropodinæ. As will be more apparent from a consideration of the last-named division, the advent of herbivorous habits involves extensive wearing of the molar crowns, which in the course of evolution is counteracted in part by a hypsodont development and in part by a functional replacement of the teeth from behind forwards. The anterior molars, since they come into service before the posterior ones, are naturally worn down in the young animal, and if the teeth decreased in size backwards, as in the Phalangerinæ, the adult would be provided with a molar dentition totally inadequate for its needs. Instead of this, the posterior molars increase at a greater rate than the anterior ones, and also replace the latter when worn down, so that the animals are provided with an efficient dentition up to an advanced age. In the Phalangerinæ and in those forms of the Macropodidæ which have not yet advanced to a definite herbivorous phase, the anterior molars imay conveniently be larger than the others, because they come into service at an earlier period and are functional throughout life.

In Hypsiprymnodon the molars are wholly brachyodont, as in the Phalangerinæ, in Bettongia their crowns are slightly elongated, and in  $\pounds pyprymnus$  considerably so. The molar patterns of Bettongia present the same characters as those of Hypsiprymnodon. In  $\pounds pyprymnus$  the increasing hypsodontism of the crowns causes the transverse ridges to be more prominent than in the remaining forms. The posterior lobe in the fourth upper molars shows indications of two cusps in all of the forms. The anterior lobe of the first lower molars, both in Bettongia and  $\pounds pyprymnus$ , bears an accessory cusp on its outer slope. The new cusp takes up the position of a protoconid, but is obviously not homologous with that element, the true protoconid being the inner cusp, the true metaconid having been lost in the phalangerine stage.

Incisors.—Throughout the series the median upper incisors are enlarged and elongated. They are scarcely procumbent, and in this respect resemble those of the Potoroinæ and some species of *Pseudochirus*. The tips of the upper lateral teeth are spatulate when unworn, and turned inwards so as to stop the passage of the lower teeth. The latter are lanceolate. The general condition is little removed from that of the advanced Phalangerinæ. The special developments are few. *Bettongia penicillata* practically repeats the characters of *Hypsiprymnodon*. *B. Lesueuri* shows a slight curving of the median upper teeth with antero-posterior compression of their tips, and also a turning inwards of the anterior parts of the tips of the third teeth. All of these characters are indicated in *Epyprymnus*, and in a more marked degree.

Canines.—These elements are fairly constant throughout, being greatly reduced but not wholly vestigial. The canines are the last of the reduced elements to disappear in the antemolar region. Their reduction is not, as in the case of the lower intermediate teeth, attributable to the presence of the diprotodont modification, since they are seen to persist long after its introduction, but, as in ungulate Placentals, to the effects of herbivorous evolution.

Median and posterior Premolars .- The modifications of these teeth are of interest as showing much more clearly than those of the remaining teeth the sequence of species in the present series and their general relations with the Potoroinæ. It appears to be on the present series and their general relations with the recording. It appears to be on them that the dental change in this series has been mainly developed. The evolution is marked by the following characters:—(a) increase in size and functional importance, with increase in the number of the grooves; (b) gradual rotation of the cutting axis inwards anteriorly. In Hypsiprymnodon (Pl. 5. figs. 31, 34) the posterior upper premolars are comparatively short and their cutting-edges rounded. They are marked by six prominent curved grooves ending in notches. In *Bettongia penicillata* (Pl. 5. fig. 32 b) these teeth are more elongated, and the number of grooves is increased to seven. The most interesting feature, however, is that their anterior portion has the same characters as the whole tooth in *Hypsiprymnodon*, showing approximately the same number of grooves and the same rounding of the edge. They have apparently been derived from such a type as is seen in Hypsiprymnodon, simply by the lengthening of the posterior portion. In *B. Gaimardi*, *B. Lesueuri*, and Epyprymnus the anterior portion of the cutting-edge is successively levelled, so that all parts of it come to project to about the same extent. In *B. Gaimardi* the number of grooves is increased to eight, in B. Lesueuri to ten, and in  $\pounds pyprymnus$  to eight. Correlated with these modifications is a rotation of the cutting-edge, by which the latter from being directed outwards anteriorly comes to be directed inwards. The main features of this peculiar change are represented in Pl. 5. figs. 34, 35, 36, where the upper teeth of the left side in Hypsiprymnodon, B. penicillata, and B. Gaimardi have been drawn so that their cutting axes form the same angle with reference to the border of the Plate that they do with reference to the middle line of the palate. In Hypsiprymnodon the tooth is rotated outwards anteriorly, so that the edge forms a considerable angle with reference to the middle line. In B. penicillata what has been referred to as the original or anterior portion of the tooth is rotated outwards, as in *Hypsiprymnodon*, while the newer posterior portion is approximately parallel to the middle line. In *B. Gaimardi* the whole tooth is straight, while in *B. Lesueuri* it is slightly rotated inwards, and in *Epyprymnus* considerably so.

It appears at first sightly lotated inwards, and in  $\Sigma pyprymnas$  considerably so. It appears at first sight extraordinary that such a change as that just described, involving a torsion of a sectorial tooth through an angle of nearly 90°, should represent a natural progression. The explanation becomes apparent, however, on comparing the modifications of the muzzle in the different species. In *Hypsiprymnodon* the latter is relatively long, but in the succeeding members it becomes gradually shorter and broader. At the same time the sectorial premolars become elongated antero-posteriorly. If under both of these changes the premolars should retain their original outwardly rotated condition, either their anterior and presumably most essential portion would have to be supported on a weak projecting pillar or their inner portion would have to encroach on the palate. As it is, the rotation of the teeth in the opposite direction enables them to be constantly supported directly in the line of the outer border of the jaw.

The above descriptions of the upper posterior premolars apply almost equally to the lower teeth. The median premolars, which perform the same functions in the young as the posterior teeth, replacing them in the adult, also show a progressive development of much the same kind. It is an interesting and suggestive fact, however, that the modifications of the median premolars always represent a more primitive stage of the same modifications seen in the posterior premolars of the same forms. Thus the median upper premolar of *B. penicillata* (Pl. 5. fig. 32 *a*) is much simpler than the posterior tooth, being shorter and bearing a smaller number of grooves. It will be apparent that if the present series is a natural one then the posterior premolars of the more primitive forms should resemble the median premolars of more advanced forms. The species of *Bettongia* and *Epyprymnus* are scarcely removed to a sufficient extent from one another to present such relations; but between *B. penicillata* and *Hypsiprymnodon*, two forms which, except for the dental resemblances already described, we would scarcely suspect to be related as successor and ancestor, from a comparison of other characters, the correspondence is exact and unmistakable, the median premolar of the former (fig. 32 *a*) almost repeating the characters of the posterior premolar of the latter (fig. 31).

A further application of this principle to the median premolars of *Hypsiprymnodon*, the existence of which is, however, only presumed at present, might throw some light on the characters of the posterior teeth in its phalangerine ancestors, and also facilitate the comparison of the animal with the peculiar form *Burramys* (Broom, 1895), in which the posterior premolars are modified, as in the present series, while the median teeth, although placed far back in the jaw, are not modified and not replaced in the tooth change.

## POTOROINÆ.

The chief interest of the two genera *Potorous* and *Caloprymnus*, composing the present division, lies in their general prototypal relations with the Macropodinæ. It will be seen on comparison of the present series with the Bettongiinæ that while both groups present primitive phalangerine characters in the general dentition, the Potoroinæ alone present premolar characters which correspond to those found in the more primitive forms of the Macropodinæ; none of the members of the two latter groups show the finely grooved and rotated condition of the sectorials found in the Bettongiinæ.

The species of *Potorous* form a natural series, of which the incipient or most primitive member is *P. platyops*, a form which shows an interesting approximation in many of its dental and also of its cranial characters to *Petaurus*, suggesting an affinity with *Gyanobelideus*, the non-volant form of the latter. The remaining members of the series are, in order, *P. Gilberti* and *P. tridactylus*, the typical Tasmanian form of the latter (*P. apicalis*) being more advanced than the New South Wales form. It is interesting to notice that the evolution of this series is associated with an elongation of the muzzle, a modification which is exactly the reverse of that characterizing the Bettongiinæ. *Caloprymnus* does not continue the evolution of *Potorous*, but probably represents a side development from a primitive species of the latter. It combines nearly all of the ancestral phalangerine characters seen in *Potorous*, it shows no tendency towards an elongation of the muzzle.

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## DR. B. A. BENSLEY ON THE EVOLUTION

The evolution of *Potorous* presents a further instance of the principle of increase in size of the body already noticed in the case of the Dasyuridæ and Phalangeridæ. An interesting exception is, however, found in the final forms, where of the two Tasmanian derivatives of the New South Wales species, *P. tridactylus*, one is a more progressive and larger form, while the other (*P. rufus*) is a dwarf (*cf.* Thomas, 1888, p. 120).

Sequence of Molar Patterns .- In Potorous platyops the molars are comparatively small and lightly built, as in Petaurus. The tooth-rows are very slightly bent inwards posteriorly. In the upper jaw the first molars are equal in size to the second, from which point they decrease gently in size backwards. The same conditions obtain in the lower jaw, except that the first teeth are slightly smaller than the second. It will be observed that we have here the same primitive size-relations common to the incipient members of the Bettongiinæ and to the Phalangerinæ. Both upper and lower teeth are of the usual quadrituberculate bundont type. The protocone and hypocone in the upper molars are placed on a level with the outer cusps, and the latter, as well as the inner cusps of the lower teeth, show a tendency towards the formation of transverse The fourth upper teeth are almost quadrate; they have evidently been ridges. triangular at an earlier stage, but now show a division of the posterior lobe into two cusps. The patterns of the first lower molars are doubtful, these teeth being much worn in the specimens examined. All of the molars are longer in the crown than those of *Petaurus*, but would nevertheless be described as brachyodont.

Passing through the remaining species of *Potorous* we find the molars showing but little modification. They become slightly more robust and more hypsodont. Their proportions change, so that the three anterior teeth above and below become equal in size. In *P. Gilberti* and *P. apicalis* the anterior lobe of the first lower molar bears an accessory outer cusp. As in the Bettongiinæ, this tooth is probably changing from the insectivorous modification characteristic of the Phalangerinæ to the quadrituberculate one scen in normal molars.

In Caloprymnus the general characters of the molars are as in Potorous. The upper teeth decrease gently in size backwards, while the lower increase in size to the third. The tendency towards hypsodontism is almost more pronounced than in the final form P. tridactylus (apicalis) of Potorous. The patterns of the molars are as in Potorous, except that the ridging of the cusps is, if anything, more pronounced. On the whole, this form points towards the Macropodinæ.

The molar patterns of *Caloprymnus* are represented in Pl. 5. fig. 19, and Pl. 6. fig. 25, for comparison with those of the phalangerine genus *Trichosurus* (Pl. 5. fig. 16, Pl. 6. fig. 19), on the one hand, and with those of the Macropodinæ (Pl. 5. figs. 20–23, Pl. 6. figs. 26–29), of which they may be taken as representing the ancestral type. The chief progressive changes relate to the development of the transverse ridges. As already described, in the case of the Phalangerinæ, Bettongiinæ, and Potoroinæ, with the exception of *Caloprymnus*, to a certain extent also of *Æpyprymnus*, what little ridging is indicated is confined to the outer cusps of the upper molars and the inner cusps of the lower ones. In *Caloprymnus* the ridges in both upper and lower teeth will be seen

to show a tendency towards extension to the remaining cusps. This development is continued in the Macropodinæ with the rapid obliteration of the originally cuspidate character. It is associated with a vertical lengthening of the newly formed crests, and the partial conversion, in most cases, of the internal longitudinal bands of the upper teeth, and the corresponding external bands of the lower teeth, into longitudinal crests.

Incisors.—In Potorous platyops these teeth are much as in Petaurus. The median upper incisors are prolonged beyond the others, and are also stout, gently curved, and slightly flattened. The second upper teeth are small, and act as a stop for the lower teeth, while the third are flattened and have their cutting-edges elongated. The lower incisors are not greatly elongated as in *Petaurus*, but have their tips gently curved upwards as in that form.

Passing through the remaining species of *Potorous*, we find much the same conditions as in *P. platyops*, except that the median upper incisors become slightly straighter, stronger, and more angular, the second teeth larger, and the lower teeth straighter and more elongated, so as to project forwards but only slightly upwards.

The incisors of *Caloprymnus* resemble those of *P. platyops*, but show some characters pointing towards the Macropodinæ. These relate chiefly to the tendency of the median upper teeth to become flattened so that their edges shear against the tips of the lower teeth instead of simply piercing against them. Both the second and third upper teeth serve as a stop for the lower ones, but show a slight tendency to shear against their sides. The latter show much the same proportions as those of *P. platyops*.

Canines.—These teeth are reduced, but not wholly vestigial, in all of the species of *Potorous*, as in the Bettongiinæ. In *Caloprymnus* they are quite vestigial, more so, in fact, than in many of the Macropodinæ.

Median and posterior Premolars.—As in the case of the Bettongiinæ, these teeth furnish the most valuable indications as to the direction of the dental evolution. Unlike those of the latter division, their axes are never rotated, but are always placed in a line with the molars, as in Macropodinæ. In Potorous platyops the posterior premolars are extremely simple. The upper teeth are small; their edges are emarginate and bear two short superficial grooves. In P. Gilberti these teeth are more elongated, and the number of grooves is increased to three. In P. tridactylus (N.S.W.) the teeth bear three grooves and indications of a fourth, while in the Tasmanian form, P. apicalis, there are four fully developed grooves. In both of the latter species the teeth are still more elongated. In the lower teeth a similar sequence is observable. In P. platyops and P. Gilberti there are two grooves, in P. tridactylus and P. apicalis there are three with indications of a fourth. The dwarfed Tasmanian form (P. rufus) shows three grooves in both upper and lower teeth.

In Caloprymnus (Pl. 5. figs. 33, 37) the posterior upper premolars are slightly elongated, and the edge bears two superficial grooves, with indications of a third.

These grooves are, however, so poorly marked that they do not produce the conspicuous notching of the edge seen in *Potorous*. A noteworthy feature is the presence of a postero-internal cusp. While indicated in *Hypsiprymnodon* and *Bettongia*, this element is highly characteristic of the Macropodinæ. The lower teeth are similar to the upper, but the accessory cusp is external.

As in the Bettongiinæ, the modifications of the median premolars follow those of the posterior teeth, but represent a backward stage of development. These teeth are unfortunately not indicated in any of the specimens of P. platyops and P. tridactylus. In P. Gilberti they are decidedly more primitive than the posterior teeth, the upper ones being comparatively small and broad, and bearing two notches like the posterior teeth of P. platyops, while the lower ones show only one. In both of the Tasmanian species the upper teeth show two notches, while the lower show two. In Caloprymnus they show indications of two notches, above and below.

A comparison of the most primitive member Potorous platyops of the present series with the most primitive form of the Bettongiinæ, Hypsiprymnodon moschatus, in respect to the characters of the posterior premolars, will show sufficiently the necessity of regarding the existing Macropodidæ as of diphyletic origin. In the Bettongiinæ the premolars are well developed, conspicuously grooved, and their axes rotated outwards in the most primitive of the known forms, and the occurrence of similar modifications in the allied form Burramys, which shows indications of phalangerine affinity in its median premolar, as in its mandibular characters, furnishes some evidence of the former existence of the same peculiarity in a section of the Phalangerinæ now without representatives. The posterior premolars of Hypsiprymnodon resemble in a very general way those of the more specialized forms of Phalanger. In the Potoroinæ the posterior premolars, in the most primitive condition known, are small and scarcely grooved, and their axes are in the same line with the remaining teeth. We can only assume, therefore, that their characters have developed from somewhat similar ones in phalangerine ancestors. The single-notched lower premolar of P. platyops is not far removed from the type found in the upper teeth of D. lepida or the upper and lower in D. nana, in both of which the tips are bifid. During the development of the Phalangeridæ there has been a development of sectorial premolars along at least four different lines, one of these being indicated in the two genera Phalanger and Trichosurus, a second in the Phascolarctinæ, a third in the ancestors of the Bettongiinæ, and a fourth in Dromicia and the ancestors of the Macropodinæ and Potoroinæ. It is interesting to note that if one may judge from the somewhat similar bifid condition in the less specialized forms of Phalanger and in Dromicia, on the one hand, and the somewhat similar rotated and grooved condition in the more specialized forms of Phalanger and in Hypsiprymnodon, the first, third, and fourth lines are more closely related to one another than any one of them is to the second.

# MACROPODINÆ.

In the case of the Potoroinæ and Bettongiinæ the dental evolution is of an extremely limited range, and for the most part of an indecisive kind. In the present series, on the other hand, it is much more comprehensive, the herbivorous adaptations being taken up at a stage not far in advance of that represented by *Caloprymnus*, and rapidly brought to a high state of perfection.

The extent of modification may be briefly summarized as follows: -(a) In the molars, complete conversion of the anterior and posterior pairs of cusps into transverse crests, the latter becoming successively elongated; development of longitudinal crests from already existing longitudinal bands, or as new structures; reversal of the relative proportions of the teeth, by which they come to increase in size backwards; retardation of the posterior teeth, with functional replacement from behind forwards. (b) In the upper incisors, reduction of the length of the median upper teeth, by which they cease to project beyond the lateral ones; compression of their edges; elongation of the cutting-edges of the lateral teeth, frequently accompanied by reduplication. (c) In the lower incisors, perfection of the spatulate development, by which they come to cut against all of the upper incisors, and in some cases against one another. (d) In the canines, rapid obliteration proceeding from an already reduced condition. (e) In the median and posterior premolars, successive elaboration of the teeth as sectorials.

As mentioned above, the dental evolution of the existing Macropodinæ appears to have proceeded along two different lines. One of them is represented as a series of typical forms, whose evolution has been a terrestrial one throughout and has culminated in the true Kangaroos; while the other is represented by an aberrant series, whose evolution, at least in the case of two genera, has been effected by a return to arboreal life. In the following descriptions these groups are respectively referred to as the hypsodont and brachyodont series.

# The Brachyodont Series. (Dendrolagus, Dorcopsis, Setonyx.)

The derivation of *Dendrolagus* and *Dorcopsis* is an interesting question, on account of the fact that while both forms are more primitive in their general dental characters and more specialized in their premolar characters than the true Kangaroos, *Dorcopsis* appears, and has been commonly supposed from its terrestrial habit and its limb proportions, to represent a connecting-link between the latter and the tree-living *Dendrolagus*. On tracing the dental sequence, it is found that neither one of the two genera is nearly related to the true Kangaroos, the resemblances shown by *Dorcopsis* to the latter being the result of convergent development. The evolution appears to represent a Papuan migration, the sequence of species being as follows:—*Dendrolagus Lumholtzi* and *D. Bennettianus* (Queensland forms); *D. inustus*, *D. Dorianus* (both Papuan forms); *Dorcopsis Macleayi*, *D. luctuosa*, *D. Muelleri* (all Papuan forms). The species of *Dorcopsis* are derivatives of *Dendrolagus Dorianus*, or a closely allied form, which have become terrestrial and have begun to assume characters similar to those of the true Kangaroos.

The relations of Setonyx (= Macropus brachyurus, Quoy & Gaim.) are rather obscure. It resembles *Dorcopsis* and *Dendrolagus* in the characters of its incisors and molars, and also in the general characters of its sectorial premolars. In the relative size of its premolars it is, however, more primitive than *Dendrolagus Lumholtzi*, while in the extent of reduction of its canines it is more advanced than the final members of *Dorcopsis*. There is no evidence that the dental characters of this form are the result of arboreal habit. Thomas (1888) estimates its systematic position to be with the members of the small Wallaby section of the genus *Macropus*, and it probably represents an aberrant form of this group which has assumed feeding-habits similar to those of the arboreal forms.

Molars.—The characters of these teeth are almost constant throughout the series. In all forms the tooth-rows are either straight or but slightly bowed outwards in the middle. The upper teeth increase gently in size from before backwards from the first to the third, the fourth being slightly smaller on account of the meagre development of their posterior lobes. The lower teeth increase in size from the first to the fourth. These proportions are more primitive than those seen in the true Kangaroos, but represent an advance on those of the Potoroinæ and Bettongiinæ. All the teeth are functional at the same time, the first teeth being only partially worn when the fourth are fully in place. Their tips accordingly project to the same extent, and thus present a very different appearance from that seen in the Wallabies and Kangaroos, where the functional rotation of the teeth produces an arcuate arrangement of the tips. Both in the upper and lower teeth (cf. Pl. 5. fig. 20; Pl. 6. fig. 26) the originally anterior and posterior pairs of cusps are completely connected by transverse crests. In this character and in the relative shortness of the crests they represent a transitional stage between the cuspidate condition of the Potoroinæ and Bettongiinæ and the hypsilophodont condition of the Wallabies and Kangaroos. Longitudinal crests formed by the modification of the original longitudinal bands are indicated, and only to a moderate extent, in the median valleys of the upper molars.

Incisors.—Although essentially macropodine rather than phalangerine in their general characters, these teeth are noticeable for their comparative primitiveness. The median upper incisors are rounded in section, but slightly flattened at their tips. They tend to project slightly beyond the lateral teeth. The latter are comparatively small, and appear to serve as much for grasping as for cutting organs. Their crown-surfaces are basin-like, the rims of the basins being, however, incomplete externally. This modification recalls that seen in the incisors of the Equidæ, the pseudo-invagination having, however, taken place internally in the latter. The lower incisors are distinctly lanceolate and sharp-edged, as in the members of the hypsodont series. In *Setonyx* the incisors are more as in the hypsodont series, both median and lateral upper teeth being distinctly flattened, the lower lanceolate.

Canines.—These teeth are present in a reduced condition in all the species of *Dendrolagus* and *Dorcopsis*. They are in general more primitive as regards the extent of reduction than in the hypsodont series; in the latter they are, as a rule, either wholly vestigial or absent. In *Setonyx*, notwithstanding its small size and general primitiveness, the canines have wholly disappeared.

Posterior Premolars.-As in the Bettongiinæ and Potoroinæ, these teeth furnish the most decisive evidence concerning the sequence of the different species. Leaving out of consideration for the present the genus Setonyx, the most primitive conditions are found in the two species Dendrolagus Lumholtzi and D. Bennettianus. In both forms the upper teeth are scarcely as long as the first and second molars. Their length is about equal to that of the upper incisor rows. They are comparatively broad, but the cutting-edge is thin and emarginate. The edge ends anteriorly in a pyramidal column, probably representing the protocone. There is a prominent internal ledge, ending posteriorly in a welldeveloped cusp like that seen in Caloprymnus. There is also a postero-external cusp. In the Papuan species, D. Dorianus, we find a more advanced stage of sectorial evolution. The teeth are of about the same size as in the preceding forms, and show the same anterior pyramidal cusp, internal ledge, and postero-internal cusp. The postero-external cusp is, however, absent; and the internal ledge is present in the form of two rounded protuberances. The emarginate portion of the edge is furthermore thickened, and now bears two distinct vertical ridges with corresponding grooves. In the remaining Papuan form of Dendrolagus, D. inustus, we find a transitional stage between D. Dorianus and D. Lumholtzi, the cutting-edge of the premolars being thin, the internal ledge not in the form of protuberances, the ridges scarcely distinguishable, and the postero-external cusp absent.

Passing to Dorcopsis, we find a more advanced stage of the same evolution. In D. Macleayi the teeth are slightly longer than the first and second molars, and decidedly longer than the upper incisor rows. The edge is uniformly thickened and not emarginate, so that the differentiation of the anterior pyramidal cusp is not so marked. The sides of the teeth are marked by four prominent ridges, with indications of a fifth, the most anterior ridge corresponding to that formed by the anterior pyramidal cusp in Dendrolagus. As before, there is a postero-internal cusp, but no postero-external one. There is probably an internal ledge: this part of the teeth was found to be worn in the single specimen examined. In D. luctuosa the teeth have the same characters as in the preceding species, except that they are still more elongated, being now equal in length to the first and second molars together with the tip of the anterior crest of the third. There are again four ridges, with indications of a fifth. The internal ledge is prominent and tuberculate, as in D. Dorianus. In D. Muelleri we find the last stage of the evolution. The teeth are exactly similar to those of D. luctuosa, except that they are again more elongated, their length being now equal to that of the first and second molars together with the whole anterior lobe of the third. The character of the internal ledge is doubtful.

In Setonyx the outer premolars show the same stout proportions as those of Dendrolagus. Their length is about equal to that of the first and second molars combined. In this character they approximate to Dendrolagus Lumholtzi and D. Bennettianus. There are no traces of a postero-external cusp found in the latter forms. The cutting-edge is not emarginate; it bears three stout ridges, with indications of a fourth. There is a well-developed postero-internal cusp and an internal ledge which does not appear to be tuberculate.

# The Hypsodont Series. (Lagorchestes, Lagostrophus, Onychogale, Petrogale, Macropus.)

The present group scarcely calls for generic consideration, since the characters by which the genera are distinguished are for the most part others than those of the dentition. Generic differentiation appears in this case to have resulted from the assumption by the animals concerned of different kinds of environment while still pursuing a grazing habit.

The main stages of progressive dental evolution concern the species of the predominant genus *Macropus*. As recently pointed out by de Vis (1895), the three sections into which the latter have been classified by Thomas (1888)—namely, the Small Wallabies, Large Wallabies, and Kangaroos—represent successive phases of herbivorous evolution. It is interesting to notice that, as in the Dasyuridæ, Phalangeridæ, and Potoroinæ already referred to, the successive phases indicate increase in size of the animals as well as dental specialization.

Progressive Characters of Molars.—Reference has already been made to the fact that the assumption of an herbivorous habit involves an extensive wearing-down of the molar crowns, rendering necessary a change from such a condition as is seen in the Phalangerinæ, where the teeth are short-crowned, and being functional throughout life tend to decrease in size backwards, because those first formed, namely the anterior ones, are longest in use and may advantageously be largest. This change is now seen to include in its entirety ( $\alpha$ ) reversal of the relative proportions of the teeth, by which they come to increase in size backwards; (b) hypsodont development of the crowns; (c) functional replacement of the teeth from behind forwards, the anterior teeth being worn off and shed while the posterior are coming into service.

As already pointed out, the tendency to reverse the proportions of the molars is indicated, although to a very limited extent, in the Bettongiinæ and Potoroinæ. In the brachyodont division of the Macropodinæ, where we meet with dental modifications intermediate in extent of specialization between those of the foregoing smaller divisions and the present hypsodont series, the upper teeth are seen to increase gently in size from the first to the third, the fourth being smaller on account of the imperfect development of its posterior lobe, while the lower teeth increase in size backwards throughout. In the present series we find both the upper and lower teeth increasing markedly in size from the first to the fourth. In respect of this character there is little progressive variation, the modification being only carried to such a stage as to provide the adults with a dentition as functional as that of the young. The forms which are highest in other respects, namely those of the Kangaroo section of *Macropus*, are at most only slightly more advanced in this character than the smaller more primitive forms of the same genus.

With regard to the functional replacement of the molars, it is seen that in the brachyodont series this principle is scarcely indicated, the first molars being only slightly worn and still very obviously functional when the fourth molars are fully in place; so

that, as in more primitive forms, all of the teeth are functional at the same time. In the present series the first molars may be worn to the bases of their transverse ridges before the fourth teeth come into place. This functional rotation is much more conspicuous in the Kangaroos than in other forms, and has there been aptly compared by Thomas (1888) to that found in the Proboscidea and some Sirenia. Correlated with the functional rotation is a throwing-off of the worn-out anterior teeth. On examining a series of individuals of different ages, it is seen that the worn median premolars and milk-premolars are first thrown off by the eruption of the posterior premolars, and that afterwards the latter, and finally the first molars, are thrown off; so that, of seven cheek-teeth, only the last three to appear remain. In the Kangaroos that portion of the margin of the jaw which bears the cheek-teeth is raised above the anterior edentulous portion; and De Vis, in his interesting paper on the fossil Kangaroos, has pointed out that the anterior teeth are in a way pushed over the edge of this platform, the posterior premolars not being large enough in these forms to retain their own position and that of the succeeding first molars. However this may be, the condition in the Kangaroos represents a distinct adaptive advance on that in the Wallabies, where even in small premolared forms the anterior teeth are retained.

Hypsodontism of the molar crowns is more pronounced in the Kangaroos (Pl. 5. fig. 23 & Pl. 6. fig. 29, *Macropus rufus*) than in the smaller forms (Pl. 5. fig. 21 & Pl. 6. fig. 27, *Lagorchestes*), and is better indicated in all of the group than in *Dendrolagus* or *Dorcopsis*. *M. Eugenii* furnishes a partial exception, the length of the molar crests in this form being scarcely greater than in the last-named genera.

In respect to the molar patterns, the present group shows an advance on the brachyodont series in the formation of longitudinal crests supplementing the transverse ones. Mention has already been made of the presence in the Phalangerinæ, the Bettongiinæ, and Potoroinæ of longitudinal bands connecting the protocone and hypocone in the upper molars and the protoconid and hypoconid in the lower, and ending anteriorly and posteriorly in both cases in thin ledges. In the brachyodont series these elements are scarcely indicated; but in the present group they appear as longitudinal crests. One of these crests connects the anterior and posterior transverse crests. It is placed on the internal side in the upper melars and on the external side in the lower. The upper longitudinal element opposes the posterior transverse crest of a lower tooth, while the lower longitudinal crest opposes the anterior transverse crest of an upper tooth. In the lower teeth the longitudinal band is represented in front by a ridge extending from the tip of the protoconid to the anterior ledge. Passing from such a type as Caloprymnus (Pl. 6. fig. 25) to the Kangaroos (Pl. 6. fig. 28), we find this ridge assuming a more internal position, its outer wall becoming pouched in such a way that a structure resembling the antero-external shelf of polyprotodonts is formed. In the upper molars the anterior ledge has lost its connection with the protocone, but tends to be connected externally with the paracone. This connection is obvious in all of the forms, with the exception of the Large Wallabies and Kangaroos : in the former it is barely indicated, while in the latter the anterior ledge is practically free externally. In the Kangaroos an apparently new ridge is developed internally. It is well developed in all forms SECOND SERIES .- ZOOLOGY, VOL. IX. 22

excepting *M. rufus* and *M. magnus*, in the latter of which the anterior ledge has been reduced. In certain fossil Kangaroos, as shown by the descriptions of Owen (1877) and De Vis (1895), a greater degree of molar complication is found than is indicated in existing forms. In *Procoptodon* accessory ridges are very numerous and conspicuous.

Incisors.-In the two lower subfamilies of the Macropodidæ the median upper incisors tend to retain the original predominating size-relations and the grasping character found in the smaller Phalangerinæ, Caloprymnus alone (like the higher Phalangerinæ, Phalanger and Trichosurus) showing the opposite tendency to reduce the vertical length of these teeth while flattening their tips in order to adapt them for a cutting function. The members of the brachyodont series also tend to preserve the original relations, although in a lesser degree. In the present group the modifications begun in Caloprymnus are followed throughout, these teeth being always of a distinctly cutting nature. The median lower teeth present the lanceolate cutting modification throughout. The upper lateral teeth show successive stages of sectorial elaboration; but there is not a perfect progression in this respect from the smaller towards the larger forms. Primitive conditions are found in Lagorchestes, Lagostrophus, Petrogale, Onychogale, certain of the Small Wallabies (M. Eugenii), and also in certain of the Large Wallabies (M. irma and M. Greyi) which appear to be derivatives of M. Eugenii. In these forms, especially Onychogale, the cutting-edges of the upper lateral teeth are comparatively narrow. In the Small Wallabies, with the above exception, the edges of the third upper teeth tend to be elongated. A more primitive condition is found in M. Coxeni and M. Billardieri than in M. Thetidis, M. Wilcoxi, and M. stigmaticus. The same expansion is noticeable in the Large Wallabies, except in the species referred to, and also in the Kangaroos. Even the latter present differences of a somewhat similar kind to those in the lower forms-M. robustus and M. giganteus, for example, showing a condition of greater expansion than is found in M. rufus and M. magnus. It is an interesting fact that in this elaboration of cutting-edges, which is so important a feature of the grazing evolution, the second upper incisors play a much less important rôle than the third, their edges being at most only slightly expanded. The explanation is probably to be found in the greater freedom of the third teeth, there being no teeth situate behind them to oppose their posterior elongation.

Reduplication of the edges of the upper lateral teeth, already referred to in the case of the brachyodont group, is also indicated in the present series, although the tendency is here in the direction of reduction. In such forms as *Dendrolagus* and *Dorcopsis*, where no expansion of the edges is indicated, the tips of the teeth are basin-shaped; while in more specialized forms, such as those of the present series, where the upper internal teeth cease to act as stops for the lower and become definite cutting-organs, reduplication is less apparent on account of the transverse compression. It is still indicated, however, by a notching of the posterior or lateral sides of the teeth. In the Kangaroos the notching is absent in the second incisors and barely indicated in the third, while scarcely more primitive conditions are found in the Large Wallabies. It is apparent that in the development of these forms there has been an increase of muscular perfection admitting of a finer adjustment of the incisor teeth.

Sectorial Premolars.-The posterior upper teeth may be taken as typical of these elements, which include the upper and lower median and lower posterior teeth. Their modifications are of interest as throwing a side-light on the evolution of the series, since they are not connected with the development of the grazing habit, but with the passage of the shoot- or twig-eating habit. In their general character they preserve the orthal position in the jaw, as in the Potoroinæ. They are never so well developed as in the typical shoot-eating forms of the brachyodont series. In Onychogale the teeth are extremely small as compared with the first molars. They are pear-shaped in section, the larger end being posterior. There are three cusps-two outer, and one inner and posterior: the former appear to represent the fore and aft portions of the cutting-edge of Caloprymnus, and the latter the postero-internal cusp. In Lagostrophus, Lagorchestes, and Petrogale the posterior premolars are fairly well developed. In the first-named genus and in Lagorchestes hirsutus the teeth are equal in length to the first molars, and their cutting-edges bear three well-developed grooves; in Lagorchestes conspicillatus, L. leporoides, and Petrogale they are slightly longer than the first molars and bear four grooves on their cutting-edges. Among the Small Wallabies, M. Wilcoxi, M. Thetidis, M. sligmaticus, and M. Billardieri have the posterior premolars equalling in length the first molars, with the tip of the anterior crest of the second, with two grooves on the cutting-edges. In M. Eugenii and M. Bedfordi the length of the posterior premolars is almost equal to that of the first molars; the postero-external cusp tends to be grooved. The whole condition is not far removed from that seen in Onychogale. Among the Large Wallabies we find M. ruficollis, M. Parryi, and M. Greyi showing a similar approximation to Onychogale; the posterior premolars are here shorter than the first molar. In M. agilis, on the other hand, the teeth are well developed, their length being equal to that of the first molars and the anterior crests of the second. In the Kangaroos the posterior premolars are shorter than the first molars, and resemble those of the small premolared lower forms. The explanation of these facts seems to be that in the lower genera, including the Small Wallabies, there has been local elaboration of sectorials in connection with a shoot-eating habit, grazing adaptations being incomplete at that stage. Small-premolared and large-premolared Small Wallabies have apparently given rise to similarly conditioned Large Wallabies. The relatively small size of the posterior premolars in the Kangaroos appears at first sight to indicate that elaborated sectorials have formerly been present in some of the lower forms and have been subsequently reduced; but the more probable explanation is that these animals are the descendants of successively small-premolared Small and Large Wallabies, which have become more and more dependent on grazing habit and the development of grazing adaptations.

Canines.—With the partial exception of Lagorchestes conspicillatus, none of the members of this group show such well-developed canines as those of the brachyodont series (excepting Setonyx), the Potoroinæ and Bettongiinæ, although even in the latter they are greatly reduced. These teeth are present in a vestigial condition in Lagorchestes hirsutus and L. leporoides, vestigial or absent in Onychogale, and typically absent in the remaining forms (except L. conspicillatus).

## PHASCOLOMYIDÆ.

The dental characters of *Phascolomys*, the single living representative of the family, are of interest as indicating another line along which the herbivorous evolution begun in the Phalangeridæ has proceeded, and also as furnishing still another example of convergent developments between Marsupials and Placentals, the general condition being here very similar to that in the Rodentia.

The exact relations of *Phascolomys* with the phalangerid genera are not wholly demonstrable as regards the dentition. The main evidence is (a) that the unworn molar patterns present resemblance to those of the advanced bunodont Phalangerinæ; (b) the incisor modifications represent a more advanced stage than is found in any of the latter forms or in the Diprotodontidæ; (c) the moderately elaborated posterior premolars bear a general resemblance to those of *Dromicia* on the one hand and, at least in the case of the lower, to those of *Nototherium* and *Diprotodon*. The animal appears to represent a specialized offshoot of the same line leading from the more primitive Phalangerinæ to the Diprotodontidæ.

Molars.—In the upper molars of the adult Phascolomys the sectional area is seen to decrease in proceeding from before backwards, while in the lower it is more uniform. As in the more specialized members of the Rodentia, the teeth are elongated and openrooted. Their bodies are curved, outwards in the case of the upper teeth and inwards in that of the lower; so that the grinding-stress does not fall on the unsupported bases, but on the side of an arch. Each tooth shows two triangular pillars; the sectional apices are directed outwards in the lower teeth and inwards in the upper. In the adult animal, the crown-surfaces being entirely worn down, the tips present the appearance of two triangles joined together by their contiguous basal angles. In all of the above characters, with the exception of the first, *Phascolomys* is not only highly specialized, but also unique among existing Marsupials.

The only safe evidence concerning the molar derivation is afforded by the unworn patterns. The latter are represented in Pl. 5. fig. 24 & Pl. 6. fig. 30. Both the figures and accompanying descriptions are based on a young specimen in which only three molars above and below are formed, the first and second having barely pierced the gum, while the third is still concealed in the alveolus. The upper molars bear a close resemblance to those of *Trichosurus* (Pl. 5. fig. 16). The two triangular pillars represent the anterior and posterior lobes of the phalangerine tooth. Each of the pillars bears two large cusps; those of the anterior one correspond almost exactly in their characters and position to the protocone and paracone of *Trichosurus*, while those of the posterior pillar similarly correspond to the hypocone and metacone of that genus. As in *Trichosurus*, the cusps are wholly bunoid, and the protocone and hypocone take part in the formation of a conspicuous internal band enclosing the internal anterior and posterior portions of the tooth. The paracone and metacone are massive, and their internal sides show indications of the development of transverse ridges. A peculiar feature is the presence of a large number of small nodules arising from the sides of the main cusps. Apart from the obvious quadrituberculate ground-pattern, the presence of these structures gives the teeth an almost multituberculate appearance. This development appears to be unique among the Marsupials.

The lower teeth also present a quadrituberculate pattern similar to that in *Trichosurus* (Pl. 6. fig. 19). As in the latter, the protoconid and hypoconid take part in the formation of an external band enclosing the external anterior and posterior portions of the teeth. The entoconid and metaconid are massive. The development of accessory nodules is again in evidence. The appearance of these elements is well illustrated in the internal profile view of the second lower molar given in Pl. 6. fig. 30 b.

A conspicuous feature of the unworn molars is the small sectional area of the crowns. The crown-surface of the second upper molar of an adult *Phascolomys* may be twice as long as in the young and more than twice as broad; and similar proportions are observable in the remaining molars. In the young the upper teeth decrease in size backwards from the second; the lower teeth increase in size from the first to the third.

Incisors.—As in the Rodentia, with the exception of the Duplicidentata, the incisors are limited to one on either side of the jaw above and below. They are greatly enlarged, arched, and open-rooted. In the unworn condition (Pl. 5. fig. 41) they are pointed at the tips, and thus resemble those of the Phalangerinæ; while in the worn condition they are scalpriform, as in the larger Rodentia. The scalpriform modification is, however, incomplete, the reason being that the teeth meet at such a narrow angle ( $40^{\circ}$ ) that the wear falls obliquely on their tips rather than on their posterior sides. The degree of differentiation of the enamel bands appears to vary in different individuals; while always thicker on the anterior sides of the teeth than anywhere else, the enamel sometimes extends to their sides or even all the way round to their posterior surfaces.

**Posterior Premolars.**—With the exception of the incisors, these are the only members of the antemolar series present in the genus. Like the molars they are elongated, curved, and open-rooted, but unlike them are not definitely bilobed. In the unworn lower teeth there are indications of three cusps, including a somewhat larger anterior element and two smaller posterior ones; the latter are connected by a small transverse ridge. The lower teeth bear a certain resemblance to those of *Nototherium* and *Diprotodon*. The upper teeth are bifid at the tip, and resemble somewhat those of *Dromicia*.

# DIPROTODONTIDÆ.

The available evidence concerning the dental derivation of this family points to a connection with the Phalangerinæ, in part through the Phaseolomyidæ. Nototherium appears to represent one of the ancestral types leading towards Diprotodon.

Molars.—Apart from their comparatively huge size, the molars of Diprotodon resemble closely those of the Macropodine in having the opposite cusps completely connected by

transverse crests (cf. Pl. 5. fig. 25 & Pl. 6. fig. 31). If one may judge by analogy with the latter family, these teeth are of quadrituberculate bundont origin, as are also those of the Phascolomyidæ. In both upper and lower teeth the transverse crests are greatly elongated vertically, as in the Macropodinæ, but unlike the latter they are also curved. The longitudinal crests characteristic of most of the Macropodinæ are not represented. The upper molars show the anterior basal cingular ridge which is commonly developed in the latter group. The lower molars show a posterior cingular ridge which is not represented in the Macropodinæ.

The molar characters of the smaller form, *Nototherium*, are much as in *Diprotodon*. There is a trace of a longitudinal band in the median valley. In this character *Nototherium* is slightly more primitive, because, while longitudinal bands are highly characteristic of the more specialized of the Macropodidæ, their actual presence is a primitive phalangerine character, and their absence is secondary.

Incisors.—The incisors of *Diprotodon* are in general intermediate in character between those of the Phalangeridæ and those of the Phascolomyidæ. The median upper teeth are open-rooted, arched, and scalpriform, as in the latter family. They are even more specialized as regards the differentiation of the enamel bands. The second and third are retained, and serve as stops for the lower teeth, as in the Phalangeridæ; but, unlike the latter, they are also open-rooted.

Nototherium approaches Diprotodon in that the second and third upper teeth are present and those of opposite sides are in contact in the middle line. The median upper and lower teeth are of a more primitive type, neither being scalpriform. The lower especially are rounded in section and definitely pointed. It is interesting to note that among the fossil forms referred to the Macropodidæ we find two types of lower incisors, the latter being usually of a spatulate cutting type, as in the existing forms of grazing Macropodinæ, but sometimes (*Procoptodon*) of a pointed piercing type, as in Nototherium. Considered alone, the lower incisors of *Procoptodon* would be readily taken as belonging to a lower and smaller member of the Nototherium-Diprotodon line.

Premolars.—As in the Phascolomyidæ, only the posterior teeth are represented. The following comparisons include only the lower ones. In Nototherium these teeth are very much as in Phascolomys, except that they are not open-rooted. They are comparatively poorly developed; they show a main anterior cusp, and a posterior crest formed by the connection of two cusps. In Diprotodon, also, these teeth are poorly developed. When slightly worn they present anterior and posterior crests, the former appearing imperfect. The posterior crest obviously corresponds to that in Nototherium, although better developed than in that form. The anterior crest cannot be regarded as having arisen from the connection of two opposite cusps, as in the molars, because no case occurs in the herbivorous Marsupials where these are found in posterior premolars, the only conclusion being, therefore, that it is the result of compression of the anterior cusp found in the smaller forms, Nototherium and Phascolomys.

It will be seen that, although the dental characters of both families are highly modified

away from what would be considered a primitive type in comparison with the Phalangeridæ, and also from one another, the Phascolomyidæ and Diprotodontidæ appear to be allied in several features, namely : (a) the (presumably) quadrituberculate bundont origin of their molars; (b) the rodent modifications of the incisors; (c) the similarity in size and arrangement of the cusps of the lower posterior premolars; (d) the obliteration of the anterior and median premolars. To these may be added: (e) reduction of the deciduous premolars.

of the alterior and median premolars. To these may be added: (e) reduction of the deciduous premolars. It is a question not wholly answerable, however, whether or not some of these characters may be the result of convergent development. *Phascolarctus* presents points of general resemblance with *Phascolomys*, and as regards its dentition shows three of the characters above referred to, namely, b, d, and e. There is good reason for believing all of the latter to be the result of convergent development. *Phascolarctus* is isolated by its advanced selenoid molar patterns; and while there is overwhelming evidence, both in Marsupials and Placentals, of the conversion of the bundont type of molar into a lophodont one, no case is known of the conversion of the selenodont type into a similar lophodont one. As already pointed out, although the molars of *Phascolarctus* and the other Phascolarctine have retained, with but little modifications, certain of the cusp-characters of the polyprotodont forms, which are alike ancestral to them and to the Phalangerine, they are much too advanced in a special selenodont direction to have given rise to those of the Phalangerine, such as *Acrobates*, are far more primitive in their general dental characters than the Phascolarctine. We have, however, no such proofs of convergence between the Diprotodontidæ and Phascolary b and d. Finally, the smaller members of the Phalangerine, such as *Acrobates*, are far more primitive in their general dental characters than the Phascolarctine. We have, however, no such proofs of convergence between the Diprotodontidæ and Phascolomyidæ as we have between both families and *Phascolarctus*; so that if it is permissible to generalize on the evidence available, we may assume that their common features are characters of affinity—on the whole, that they have diverged from common ancestors possessing a reduced premolar formula, a reduced tooth-change, bunodont quadrituberculate molar patterns, and incipiently rodent incisors. As mentioned be

#### THYLACOLEONTIDÆ.

The recent discussion by Broom (1898) of the controversial question of the habits of the extinct form *Thylacoleo* appears to allow of no further doubt as to its predaceous carnivorous character. The question now arises as to how the relationships of the animal with the Phalangeridæ are to be explained. Throughout the present paper the effort has been made to show that the Australian radiation began with insectivorous prototypes and proceeded along two primary lines, one of them carnivorous, the other omnivorous and finally herbivorous. In the second line all the advanced forms are diprotodont, and all the typical terminal forms are highly specialized herbivora. *Thylacoleo* is clearly a member of the second line, which, in all probability after the connivorous stage, has become carnivorous instead of herbivorous. In view of the general sequence in the Australian group, this development is to be looked upon as an aberrant one. Analogous cases of perverted habit and dental adaptation are to be found in the Placentalia, a conspicuous case being afforded by the fish-eating rodent *Ichthyomys* (Thomas, 1893) of South America, in which the herbivorous principle of the Rodentia has not been adhered to.

The presence of enlarged posterior premolars in *Thylacoleo* points to a former condition of at least incipient herbivority. The excessive enlargement and ungrooved character of the teeth represent more special carnivorous adaptations, repeated in the placental Carnivora, but without parallel in marsupial carnivores.

The reduced character of the upper canines possesses a similar significance. In the smaller members of the Dasyuridæ the canines are moderately developed, and following the carnivorous evolution they show a successive increase in functional importance. In the Phalangeridæ we find the smaller members presenting well-developed upper canines, but following the omnivorous-herbivorous evolution there is a successive decrease in functional importance, and in derived families total obliteration. *Thylacoleo* is quite as advanced in the reduction of the canines as *Phalanger* or *Trichosurus*.

In *Thylacoleo* the piercing elements of the dentition are the median upper and lower incisors. It is interesting to note that in the Dasyuridæ a piercing modification of the upper incisors appears as a prototypal insectivorous character, and that in the carnivorous evolution the piercing function is taken over by the canines. In the more primitive Phalangeridæ we find both upper and lower median incisors modified as piercing-organs; while in more advanced forms the lower teeth assume a cutting character, and the upper become slightly reduced. It is difficult to say whether the incisors of *Thylacoleo* were formerly modified as cutting elements; but it is apparent that the animal must have developed along normal phalangerine lines to such an extent that only the median incisors were left as possible piercing-organs.

The reduction of the molars, although repeated in the most specialized of the placental Carnivora, contrasts strongly with the sectorial elaboration met with in the typically carnivorous Dasyuridæ, and has probably resulted from the presence in the ancestral form of inadaptive quadrituberculate bunodont patterns as much as from the sectorial elaboration of the posterior premolars.

# THE ADAPTIVE MODIFICATIONS OF THE FOOT-STRUCTURE IN THE AUSTRALIAN MARSUPIALS.

On comparing the general types of foot-structure in the Placentalia it is seen that certain forms, more especially some of the Creodonta, present an extremely close approximation to the ideal pentadactyl type, which we assume to represent the startingpoint for the foot-evolution of the Mammalia generally, and, further, that the great majority of the remaining forms present advanced modifications of this type bearing a decidedly terrestrial stamp. The predominance of terrestrial modifications and the presence of prototypal conditions in such a central group as the Creodonta indicate that the evolution of the Placentalia is typically a terrestrial one.

In the Marsupials the reverse appears to be the case. As already pointed out by Huxley in 1880, none of the members of this group present an ideal pentadactyl pes, the hallux, whenever present, showing more or less extensive indications of opposability. And, as recently further shown by Dollo (1899), all of the primary modifications of the pes found in the group are in the direction of prehensilism, while all other modifications, whether indicative of terrestrial or aquatic (*Chironectes*) adaptation, are derivatives of arboreal phases. Unlike that of the Placentals, therefore, the evolution of the Marsupials is primarily arboreal, and secondarily terrestrial.

The following summary, representing to a considerable extent an adaptation of Dollo's views to the present case, is designed to show the general sequence of arboreal and terrestrial phases in the various marsupial families :---

(Unidentified Marsupio-Placental stock.)	Pes adapted for slow terrestrial progression: plantigrade, pentadactyl, with short meta- podials and more or less radiating digits.			
b. Primary arboreal phases.				
b <sup>1</sup> . First arboreal phase	Pes prehensile for arboreal progression. Hallux opposable.			
$b^2$ . Second arboreal phase	Characters of $b^1$ . 4th digit elongated; 2nd and			
(Some Didelphyidæ, Phalangeridæ except	3rd digits reduced and syndactylous.			
Tarsipes.)				
$\dot{\boldsymbol{\delta}}^{\mathfrak{d}}$ . Third arboreal phase	Characters of $b^2$ . Claws of 4th and 5th digits con-			
(Tarsipedinæ.)	verted into nails.			
c. Secondary terrestrial phases.				
c <sup>1</sup> . First terrestrial phase	Derivative of b <sup>1</sup> . Pes elongated; hallux reduced			
(Dasyuridæ in part.)	or absent. Plantigrade or subdigitigrade.			
c <sup>2</sup> . Second terrestrial phase	Derivative of $b^2$ . Pes variable. Plantigrade or			
(Notoryctidæ, Phascolomyidæ, Diprotodon-	digitigrade ; pentadactyl, tetradactyl, or func-			
tidæ, Peramelidæ, Macropodidæ.)	tionally monodactyl.			

# DASYURIDÆ.

On comparing the distribution of arboreal and terrestrial phases in the Australian Marsupials, we find that they are, as a rule, so completely differentiated as to be distinctive of family divisions. The Dasyuridæ, however, present a notable exception, there being evidence of a main line of arboreal or semi-arboreal evolution, with several subsidiary lines of terrestrial adaptation. The general principle of the whole radiation is here illustrated in a single family.

The main line is represented by the numerous species of *Phascogale*, together with the two species *D. hallucatus* and *D. maculatus* of *Dasyurus*. Its identification does not depend on the presence of progressive changes, but on the retention of primitive characters in successively larger animals. The subsidiary lines are constituted as

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follows:—The first by the species of Sminthopsis and by Antechinomys laniger; a second by Chætocercus cristicauda and Dasyuroides Byrnei; a third by Dasyurus Geoffroyi and D. viverrinus; and a fourth by Sarcophilus ursinus. The species described by Spencer (1896) as Phascogale macdonnellensis may represent another terrestrial line, but the animal is doubtfully separable from Sminthopsis. The genera Myrmecobius and Thylacinus represent two more terrestrial lines whose exact connections are doubtful.

The above reference to the main line of the evolution as arboreal or semi-arboreal calls for some explanation. It will be seen from a general survey of the family that even in the most primitive species the hallux, although of an opposable type, is much smaller than in typical arboreal forms, such as those of the Phalangeridæ and Didelphyidæ, and the digits present a parallel rather than a primitive radiate arrangement. Thomas (1888) remarks that the species of *Phascogale* are strictly arboreal, while Winge (1893) states that the foot of *Phascogale* is more modified for terrestrial service than in the Didelphyidæ.

The fact that the forms here referred to as constituting successive lines of terrestrial evolution present definite terrestrial characters, shows that modifications presented by *Phascogale* must be explained on some other assumption than that they represent terrestrial adaptations.

It is a well-known fact that the Didelphyidæ, which approximate very closely to the present family, present typical prehensile developments both in the pes and in the tail. In the Dasyuridæ these prehensile developments are absent, if we except the presence in some of striated plantar pads and the opposability of the reduced hallux. The conditions in the Dasyuridæ thus appear at first sight to indicate that the family has been derived originally from forms which had already embarked on a terrestrial evolution. This proposition may, however, be dismissed with the simple statement, since in another section of the Australian fauna, namely the Phalangeridæ, we meet with hallucal characters of the same primitive arboreal stamp as those of the Didelphyidæ. The alternative explanation is that the Dasyuridæ have abandoned modifications of prehensilism for others better suited for either arboreal or terrestrial progression in connection with their insectivorous habits. Comparison with the Placentals shows that arboreal habit does not necessarily demand the adoption of prehensilism, although it is indicated to a marked degree in some forms (Primates), as it is in the Marsupials. The modifications of the pes in the primitive Dasyuridæ indicate a cursorial development involving elongation of the pes and parallel arrangement of the digits as well as recession of the hallux. The ancestral forms of the family appear to have abandoned their prehensile modifications for semi-cursorial ones of undoubted advantage in insectivorous life, the pes having thus been made serviceable for rapid progression either in the trees or on the ground. At the same time they have lost nothing in the abandonment of modifications of prehensilism, these being unnecessary in animals which are capable of balancing their bodies in arboreal progression by means of rapid locomotion. Those of their successors which have become definitely terrestrial are not necessarily more completely cursorial, although their special characters are largely the result of

For descriptive purposes the foot of Phascogale flavipes may be taken as representing the type from which the modifications of the remaining forms have been derived. In this animal the foot is relatively short and broad. In the specimen here figured (Pl. 7. fig. 2) the ratio of the breadth, measured directly behind the hallux, to the length, measured from the tip of the hallux to that of the third digit, excluding the claw, was found to be in the proportion of 1:3.5. The hallux is greatly reduced as compared with that of the Didelphyidæ and Phalangeridæ. As in the latter, however, it is set at a considerable angle to the remaining digits, and is, further, clawless and provided with a slightly swollen terminal pad. The remaining digits are approximately equal in size and provided with strong curved claws. Their most conspicuous feature is their parallel arrangement and consequent restriction of lateral motion. The plantar surface is naked and granulated, and bears five prominent pads, all of which are elongated and transversely striated. One of these is placed at the base of the hallux, and extends from the notch separating that digit from the second backwards towards the heel; its posterior two-thirds is separated from its anterior third by a sharp constriction. Three other pads are situated at the bases of the outer digits; they are completely separated from one another, and the middle one is placed somewhat in advance of the others. A fifth pad is placed on the outer margin of the sole opposite the middle of the hallucal pad. It is probable that even in arboreal progression these structures are not so functional as in those arboreal forms in which the hallux is well developed and the outer digits are radially arranged. The original function of the hallucal pad is to oppose the outer digital pads anteriorly and the marginal pad posteriorly, just as the hallux opposes the outer digits.

In the remaining species of *Phascogale* and in *Dasyurus hallucatus* we find much the same condition as in *P. flavipes*, such differences as do exist, apart from the progressive increase in size, being of a minor character. In *P. Sucainsoni* and its Tasmanian representative *P. minima* the pads are shorter and more oval than in *P. flavipes*. The proportion of breadth to length in *P. minima* is approximately 1:3. In *P. dorsalis* these characters are repeated, except that the constriction seen in the hallucal pad is here replaced by a distinct gap. The proportion of breadth to length is  $1:3\cdot8$ , and in *P. Thorbeckiana* 1:4. In the latter the hallucal pad is undivided. *P. apicalis*, which was seen to be aberrant in its premolar relations as compared with its size, is also aberrant in its foot-structure, the heel being elongated, so that the ratio of breadth to length becomes  $1:4\cdot2$ . The hallucal pad is undivided, and the marginal pad is very thin posteriorly. In *P. calura* and its larger representative *P. penicillata* the pads are elongated as in *P. flavipes*; the proportions are respectively 1:5 and  $1:3\cdot75$ .

The form described by Spencer as *Phascogale macdonnellensis* shows a partial departure in foot-structure from the normal members of that genus. The foot is relatively short, the proportion of breadth to length being 1: 3.26. It presents a peculiar swollen appearance. The hallux is reduced to scarcely more than a tubercle. All of the pads are comparatively well developed, and their surfaces are transversely striated as in *Phascogale*. The hallucal pad is here subdivided. According to Spencer's account, the

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habits of the animal are terrestrial. Its foot-characters appear to represent an intermediate stage between the condition in *Phascogale* and that in the most primitive form (*S. leucopus*) of *Sminthopsis*, with, however, a substitution of a plantigrade for the saltatorial modification which distinguishes the latter genus.

Passing from *Phascogale* to *Sminthopsis* and *Antechinomys*, we meet with a comparatively well-graded series of minute forms which show a terrestrial and saltatorial evolution. The most primitive condition is found in *Sminthopsis leucopus* (Pl. 7. fig. 3), the foot-structure of which approximates very closely to the type presented by *Phascogale flavipes*. The foot is relatively longer than in *P. flavipes*, the proportion being 1:5.5. The hallux is slightly more reduced and its terminal pad scarcely swollen. The plantar surface is not wholly naked as before, the marginal hairs of both sides of the foot showing a tendency to encroach on its posterior portion. The heel is almost completely hairy. The hallucal pad is scarcely distinguishable from the surrounding granular surface; its striated area is minute and oval. The digital pads are as well marked as in *P. flavipes*, but are much more rounded and less distinctly separated. The striated surface does not extend over the whole pad, but is confined to a small area at the apex, the granulated surface having encroached on the base. The marginal pad is practically absent, its position being only indicated by certain larger granules.

Sminthopsis larapinta while agreeing with S. leucopus in the proportions of the foot  $(1:5\cdot1)$  presents a more advanced stage in respect to the characters of the pads. The hallucal pad is practically absent, being only represented by a row of three large smooth granules. The digital pads are closely set together and their bases are fused. The basal granules of each have now encroached to such an extent that the formerly well-developed and striated surfaces have become much reduced. The marginal pad is absent; its former presence is indicated by one or two larger granules.

Sminthopsis murina shows a variation or side development of the condition seen in S. leucopus. The proportion of breadth to length is 1:5. There is a small elevation at the base of the hallux, with a larger granule anteriorly. The digital pads are well developed and separate, except at their bases; but their surfaces are completely granular. There is in each case a larger granule representing a formerly striated area. The marginal pad is absent.

In Sminthopsis crassicaudata (Pl. 7. fig. 4) we find a more advanced stage than that in S. leucopus and S. larapinta. The ratio of breadth to length is 1:7.5. Except for a slightly enlarged granule at the base of the hallux, the hallucal pad is unrepresented. The digital pads are still more completely fused together basally. Their surfaces are entirely granular, but the apex of each is occupied by a large differentiated granule, which obviously represents the remains of a formerly striated surface, as in S. murina. The marginal pad is wholly absent. In Sminthopsis hirtipes (Pl. 7. fig. 5) we find what is apparently another modification of the condition in S. larapinta. The proportion of breadth to length is 1:6:3, the foot being relatively shorter than in the preceding species. The hallux is more reduced than in S. larapinta. The hallucal pad is represented by a small protuberance. The digital pads are more specialized than those of the preceding species, being so completely fused together that their former distinctness might be questioned were it not for the fact that the compound structure shows a trilobate contour.

In Antechinomys laniger (Pl. 7. fig. 6), which is the final member of the series, we find a further advance on S. crassicaudata. The proportion of breadth to length is 1:10. The hallux is absent, as are also the hallucal and marginal pads. At the bases of the outer digits there is a single large pad representing the now completely fused pads of the more primitive forms. The whole surface is covered with granules, which increase in size towards the apex. The posterior portion of the sole is completely hairy as far forwards as the base of the digital pad.

A second line of terrestrial evolution, with relations with the larger instead of the smaller species of *Phascogale*, is represented by *Chætocercus cristicauda* and *Dasyuroides Byrnei*. These forms repeat, on a larger scale, the special modifications found in *Sminthopsis*. In *Chætocercus* (Pl. 7. fig. 8) the proportion of breadth to length is 1:4.53, much the same as in *Phascogale*. The hallux is more minute than in the latter genus. The hallucal pad is represented only by a small protuberance, bearing granules which are slightly larger than those of the surrounding surface. The digital pads are well developed, but are laterally compressed and fused at their bases: their surfaces are entirely granular; but, as in *S. crassicaudata*, there is an enlarged apical granule representing a formerly striated area. The middle line of the plantar surface is hairy for about 10 mm. posteriorly.

Dasyuroides Byrnei (Pl. 7. fig. 9) shows an advance on the preceding species. The proportion is 1:7.5. The hallux is absent, as are also the marginal and hallucal pads. The digital pads are well developed and fused basally. As in *Chaetocercus*, their surfaces are granular, and a larger apical granule is present; the latter shows signs of transverse striation. The sole is hairy for 10 mm. posteriorly, as in the latter species, and the marginal hairs of both sides of the foot, as far forwards as the pads, tend to encroach on its granular surface.

Within the genus *Dasyurus* we find both arboreal and terrestrial phases. In *Dasyurus hallucatus* (Pl. 7. fig. 10), the smallest and most primitive of four species \*, we find an arboreal foot type which is scarcely distinguishable from that of *Phascogale*. The proportion of breadth to length is 1:3.7. All of the pads are well developed and

\* The collection contains no examples of the Papuan form, D. albopunctatus.

transversely striated. The sole is completely naked. The hallucal pad is subdivided and its posterior portion moderately elongated.

Dasyurus maculatus is represented in the collection only by dried skins. So far as can be judged from these, the pes practically repeats the arboreal type of D. hallucatus. The plantar pads are well developed and transversely striated. The proportion of breadth to length is 1:4. The hallux appears to be relatively more reduced than in D. hallucatus.

The terrestrial forms *Dasyurus Geoffroyi* and *viverrinus*, on the other hand, show resemblances to *Chatocercus* and *Dasyuroides*. In the former the proportion of breadth to length is 1:4.7. The hallux is relatively smaller than in *D. hallucatus*. The digital pads are partially fused together, and their surfaces are completely granular. The hallucal and marginal pads are entirely absent. The posterior portion of the sole is hairy, as in *Chatocercus*. In *Dasyurus viverrinus* (Pl. 7. fig. 11) we find a direct advance on the terrestrial type of *D. Geoffroyi*. The pes is more elongated, the proportion being 1:6. The marginal fur of the foct tends to encroach to a greater extent on the sole. The digital pads are still more definitely fused, and the hallux has disappeared.

In all of the terrestrial forms above described, with the exception of *Phascogale* macdonnellensis, the tendency is towards digitigrade modifications. In Sarcophilus (Pl. 7. fig. 12) plantigrade conditions have been retained, the foot being relatively short, as in *Phascogale*, the proportion of breadth to length being in the neighbourhood of 1:3.5. The hallux is absent, as in other advanced terrestrial forms. There are no plantar pads, the sole being uniformly covered with a papillated skin. The whole condition is unique in the family, but is derivable from an arboreal *Dasyurus* type.

In three of the four terrestrial lines here recognized we have animals of respectively small, medium, and large size showing the same type of foot-modification. This appears, at first sight, to indicate genetic sequence, but such a view is rendered improbable by the fact that the evolution of the family is primarily an arboreal one, and that in the arboreal series we have animals of successively larger size. The terrestrial lines have arisen in succession with the development of larger and larger species in the arboreal series. It, furthermore, seems impossible to regard the generic characters of *Dasyurus* as the result of convergent development in two sets of species, one of arboreal, the other of terrestrial derivation, as we should be obliged to assume in adopting the former view.

The foot-structure of the terrestrial form Myrmecobius is, in many respects, unique, and there is little in the way of direct evidence concerning its relations with the *Phascogale* type. The proportion of length to breadth is 1:5.5, the foot being thus slightly elongated. The sole is naked anteriorly and provided with a smooth tough skin; its posterior portion is hairy for about 12 mm. forwards. There is no external hallux. An oval elevation in the region of the tip of the reduced hallucal metatarsal bone appears to represent the hallucal pad of *Phascogale*. Digital pads are present as in the latter genus; they are well developed and separate. Each pad has a punctate area at its tip, probably representing a formerly striated surface. The first digital pad tends to be approximated to the second, as in some syndactylous forms.

The derivation of the type met with in *Thylacinus* is quite as obscure. The modification is a digitigrade one, as in the smaller terrestrial forms. The foot is not greatly elongated, the proportion being in the neighbourhood of 1:4. The hallux is absent, as in other advanced terrestrial forms. A single large pad, placed at the bases of the digits, shows signs of trilobate structure, and may have originated from the fusion of three separate pads, as in smaller forms. It is difficult either to demonstrate a connection of this type with those represented by other members of the family, or even to prove that it is of arboreal derivation.

# PHALANGERIDÆ.

In this family the same general principle is exemplified as in the arboreal line of the Dasyuridæ. We have a series of animals showing increase in size of body and progressive characters in other respects, but with foot-patterns of much the same type throughout. The modification is an arboreal one, and in some respects more primitive, in others more specialized than in the primitive Dasyuridæ. Just as in the case of the dentition, the exact prototypal characters are not found associated in any single form, but are distributed over two families—in this case, the present one and the Dasyuridæ.

The pes of *Dromicia* (Pl. 7. fig. 13, *D. nana*) may be taken as representing the prototypal condition not only for the Phalangeridæ, but for all of the Australian families with the exception of the Dasyuridæ. The general characters are those of the second arboreal phase (*cf.* p. 163). The primitive characters, as compared with the Dasyuridæ, are: (a) the short broad proportions of the foot and the radiating character of the digits; (b) the unreduced character and wide opposability of the hallux; (c) the more typical development of the five striated plantar pads and of the terminal pads of the digits. The more advanced characters are: (a) the great development of the fourth toe \*; (b) the reduction and syndactylism of the second and third toes.

In the remaining members of the family, excepting *Tarsipes*, the modifications of this type are few and insignificant. *Acrobates pygmæus* presents the same conditions as *Dromicia nana*, except that there is an accessory pad on the postero-external side of the hallucal pad and another smaller one on the outer side of the third digital pad. *Tarsiper*,

• With reference to the recognition of the enlarged nature of the fourth toe as an arboreal adaptation (Winge, Dollo), it is interesting to note that a different explanation was given by Owen (1879). While acknowledging the fact that there has been a successive enlargement of this member in the Macropodidæ, Owen considered its original predominance to be a reptilian character. A somewhat similar opinion has been expressed by Leche (1891). This writer remarks as follows :—" Bis auf Weiteres neige ich zu der Ansicht hin, dass die Prevalenz der 4. Zehe bei Marsupialia ebenso wie diejenige der 3. bei Ungulata unabhangig von der besondern Function durch Vererbung erworben ist."

as pointed out by Dollo (1899), presents a more extreme type (third arboreal phase, p. 163), the second and third digits being greatly reduced, and almost completly enclosed in a common integument; while the fourth digit is greatly enlarged, and like the fifth is provided with a nail instead of a claw, as in the placental Primates. In addition to these obviously progressive characters, *Tarsipes* presents certain other peculiarities. The terminal pad of the hallux is not swollen to the same extent as is usual in arboreal forms. The hallucal plantar pad is very short. The second digital plantar pad is subdivided and its outer portion has migrated on to the base of the fourth digit.

The larger forms *Petaurus* (*breviceps*) and *Dactylopsila* almost repeat the characters of *Dromicia*. In the former there is an accessory hallucal pad as in *Acrohates*. *Dactylopsila* differs only in that the claws are very powerful and the digits appear to be permanently bent at the joints of the first and second phalanges.

Among the species of *Phalanger* we find in *P. orientalis* and *P. lullulæ* a slight deviation from the general type. Except for a small area on the inner side of the foot between the hallucal and the first digital pad, and another between the marginal and the outer digital pad, the whole plantar surface is occupied by striations. This condition is obviously the result of a fusion of the originally separate pads. The hallucal pad is very broad, and its striations, which run in an oblique direction, join posteriorly with those of the marginal pad. The striations of the digital pads cross from one to the other, and, in the case of the second and third, they also extend backwards on the sole to meet those of the hallucal and marginal pads. The hallux is set rather further back than in *Dromicia*, so that its opposability is more perfect.

In *Trichosurus* the extension of the plantar striations is not indicated. The hallucal pad is well developed, but is not sharply differentiated from the sole on the outer side. Its striations are very short. The digital pads are oval and well separated from one another. The marginal pad shows much the same characters as the hallucal one. At first sight the non-extension of the plantar pads appears to represent a distinction between this form and *Phalanger*; but in *P. celebensis* we find much the same condition as in *Trichosurus*, showing that the condition in the above-described species of *Phalanger* is a special one.

In the structure of the pes there is no such difference between the phascolarctine and phalangerine groups as is observable in dentition. The foot of *Pseudochirus (Forbesi)* conforms to the type in *Dromicia*. The first and second digital pads are closely set together and have their striations concentrically arranged. The conditions in *Phascolarctus* give no indication of special relationship with *Pseudochirus*. The general conformation of the digits is the same, but the plantar pads have all been reduced, the sole being uniformly covered with a soft granulated skin somewhat as in *Sarcophilus* and *Phascolomys*. The hallux is, however, set back to a much greater extent than in *Pseudochirus*, so that it is more perfectly opposable. With only a slightly greater displacement, its axis would be in the same line as that of the fourth digit which it opposes.

#### NOTORYCTIDÆ.

Apart from the original description by Stirling (1891), the chief observations on the foot-structure of Notoryctes are those of Gadow (1892), Winge (1893), and Dollo (1899). Of the last-named writers, Gadow and Dollo have made comparisons with other Marsupials with conflicting results, the former finding resemblances to the Didelphyidæ and Dasyuridæ, the latter to members of the syndactylous series, more especially the Peramelidæ. The following remarks are designed to show that the balance of evidence is in favour of the latter view.

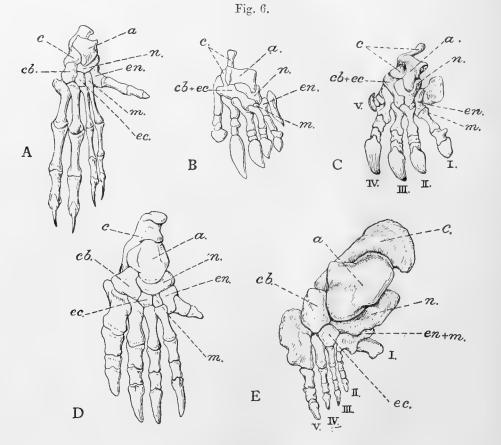
It may be observed at the outset that the pes of Notoryctes is so highly specialized that the exact manner of derivation cannot be affirmed with certainty.

The plantar surface shows no indications of arboreal pads, being covered by a leathery wrinkled skin. The hallux is well developed and possesses the full number of phalanges as in the Phalangeridæ and Didelphyidæ. Its terminal phalanx is provided with a flattened claw. In this respect Notoryctes is unique among the Marsupialia. Winge, who follows Gadow's view as to the dasyurid affinity of the animal, suggests the possibility that the hallucal claw is of secondary origin; and this explanation is in all probability the correct one-Notoryctes being highly specialized in other respects. The entocuneiform bone is comparatively long. As pointed out by Owen, and by Dollo for the present form, this character represents an arboreal adaptation. Gadow mentions the presence of a prehallucal element attached to the entocuneiform as indicative of affinity with Didelphys, in which it is also present. An examination of other genera of Didelphyidæ shows that the element is of fairly general occurrence in this family. It is absent in the adults of all the Australian forms, but Emery has described it in embryos of certain species.

The hallucal articular facet of the entocuneiform is figured by Stirling as terminal (cf. text-fig. 6, B, p. 172). In an exhibition skeleton in the B.M. Collection (text-fig. 6, C) the terminal portion of the entocuneiform is wedge-shaped, the one side of the wedge being applied to the proximal portion of the second metatarsal, while the other bears the articular facet. The hallux thus occupies a position of partial opposability. This condition is more apparent in one foot than in the other. A somewhat similar tendency towards variation is found under the same conditions in Phascolomys. In Notoryctes a formerly opposable hallux is apparently returning to an orthal position while remaining functional, while in *Phascolomys* a formerly opposable hallux retains a more or less opposable position, but is becoming vestigial.

Gadow regards the second and third digits of Notoryctes as free as in "Didelphyidæ, Dasyurus, Thylacinus, Phascogale, Myrmecobius, Phascolomys. . . . There is at the utmost a very slight indication of syndactylism of the second and third toes, far less obvious than it is even in *Phascolomys.*" Dollo, on the other hand, recognizes a slight reduction and syndactylism of these digits, as in the arboreal Phalangeridae. A spirit-specimen (cf. Pl. 7. fig. 19) examined by the writer shows very definite indications of syndactylism. It is true that the condition is not so marked as in normal forms, because SECOND SERIES .- ZOOLOGY, VOL. IX. 24

in Notoryctes all the digits are much less distinctly separated from one another. The same condition is observable in *Phascolomys*, also a terrestrial plantigrade type. As shown below, there is not the slightest doubt as to the derivation of the latter from a normal syndactylous type such as is represented by the arboreal Phalangeridæ. As regards the size of the second and third digits in the skeleton of *Notoryctes*, they are not distinctly more slender than the others, especially the fourth, as in phalangerine forms. The same condition is again observable in some specimens of *Phascolomys*, although in others they are of the slender phalangerine type. Notwithstanding their uniformity in size, however, the relations between second and third digits in *Notoryctes* are plainly with one another rather than with those on either side of them. They show a very



Dorsal views of phalangerine pes and terrestrial plantigrade modifications.

A. Trichosurus (after Flower); B. Notoryctes (after Stirling); C. Notoryctes (B.M. specimen); D. Phascolomys (after Owen); E. Diprotodon (from Dollo, after Stirling and Zietz). Abbreviations: a., astragalus; c., calcaneum; n., navicular; en., entocuneiform; m., mesocuneiform; ec., ectocuneiform; cb., cuboid.

close correspondence in the general size and length of the metatarsals and phalanges, which is strongly suggestive of former syndactylism.

Dollo points out a predominance of the fourth digit as a further indication of affinity with the syndactylous series. In Stirling's figure (text-fig. 6, B), here reproduced, the fourth digit is seen to project a considerable distance beyond the third. In the spiritspecimen above referred to (Pl. 7. fig. 19) the fourth digit does project, in a sense, but the projection is due entirely to the elongation of the claw. In the skeleton examined (text-fig. 6, C) the fourth digit projects to about the same extent as the third. It is nevertheless to be regarded as predominant. The metatarsal of the fourth digit is displaced backwards, so that the head of that of the third articulates with it as much as with the conjoined trapezoid and cuboid. Its head is prolonged backwards beyond this articulation, so that its tip extends to the margin of the foot, overlapping that of the enlarged fifth metatarsal. The fourth digit is thus still predominant, but has simply been displaced backwards for better support. It appears to be one of the most functional digits of the pes, and the fact that the sole is turned outwards and the hallux downwards in action, the longest digit thus becoming subjected to great lateral stress, shows sufficiently the reason of this adaptation.

The available evidence is decidedly in favour of the derivation of the *Notoryctes* type of pes from one of ordinary phalangerine type. The resemblance pointed out by Gadow between *Notoryctes* and *Didelphys* is probably indicative of affinity, since, considering the polyprotodont character of its dentition, *Notoryctes* must have been one of the first derivatives of the arboreal syndactylous line. The latter is directly traceable to the Didelphyidæ.

## PHASCOLOMYIDÆ.

The pes of *Phascolomys* (Pl. 7. fig. 20) represents a derivative of the second arboreal phase. The original plantigrade condition has been retained, as in *Notoryctes* and *Diprotodon*. The hallux is reduced to a tubercle externally. In the skeleton (*cf.* text-fig. 6, D) it occupies a position of opposability. The entocuneiform to which it is attached is elongated, and its articular facet is external, so that the axis of the hallux is placed at right angles to that of the second digit. The terminal phalanx of the hallux has disappeared, and the proximal phalanx may also be absent. Externally there is little indication of syndactylism of the second and third digits, the reason being that all of the digits are more or less connected by integument. The condition is more apparent in the immature specimen here illustrated than usually in the adult. In the skeleton there is some variation in these digits. In some specimens they are very distinctly slenderer than the fourth and fifth, while in others this disproportion is not indicated. The fourth digit is always well developed, as in the Phalangeridæ, the whole of it being occupied by a tuberculate skin, as in *Phascolarctus* and *Sarcophilus*.

# DIPROTODONTID.E.

In their original description of the foot-structure of *Diprotodon*, Stirling and Zietz (1899) show that it presents resemblances with the Phalangeridæ and the Phaseolomyidæ. Dollo (1899) has pointed out that the pes is of arboreal derivation, as shown by the opposability of the hallux, the reduction of the second and third digits and predominance of the fourth. The following summary, which is based partly on the original description of Stirling and Zietz and partly on the plaster-casts recently acquired by the British Museum, is designed to show that, as in the case of the

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dentition, there are general characters of resemblance and special characters of divergence between the pes of *Diprotodon* and that of *Phascolomys*, pointing to a common origin of the two genera or the families they represent.

Both in Diprotodon (cf. text-fig. 6, E) and Phascolomys the plantigrade condition is retained. The hallux is reduced; in the former only the metatarsal element is retained, and its distal portion is swollen to form a knob-like structure. Although reduced in respect to the loss of phalanges, this digit was apparently functional in Diprotodon, serving as an antero-internal support, the remaining antero-internal elements, especially the second and third digits, being poorly developed. In both forms the entocuneiform is elongated and its articular facet (as opposed to terminal) is external, as in the Phalangeridæ; so that the hallux is set away from the remaining digits. The two forms differ in the relations of the mesocuneiform element. This is free in Phascolomys and joined to the entocuneiform in Diprotodon. In both forms the second and third digits are disproportionately smaller than the fourth. Dollo has correctly pointed out that the larger size of the fourth digit in Diprotodon is partly inherited and partly adaptive. In Phaseolomys the second and third digits have regained their functional importance, while in Diprotodon they have not. In the former the walking-stress is uniformly distributed to all of the digits; in *Diprotodon* it must have fallen on the outer side of the foot, only the hallucal metatarsal, beyond the more posterior navicular and calcaneal protuberances, serving for support internally. This is apparent not only in the general disproportion between the fourth and fifth digits on the one hand, and the second and third on the other, but also in the massiveness of the astragalus, with its internally directed facet, calcaneum, cuboideum, and fifth metatarsal. The shifting outwards of the walking-axis is attributable in the first place to the reduction of the opposable hallux common to all terrestrial forms, and in the second to the reduction of the second and third digits as a phalangerine arboreal adaptation, the three internal digits being thus largely thrown out of service. The divergent characters presented by *Phascolomys* and *Diprotodon* are explainable on the assumption that in the former the second and third digits have regained their functional importance, and that in the latter the hallux has remained functional to a slight extent by being modified as a prop or internal balancer. There is little doubt that the two forms are divergent members of a single terrestrial plantigrade line leading from the Phalangeridæ.

### PERAMELIDÆ.

The general type of pes in the Peramelidæ agrees with that of the three preceding families in that it represents a derivative of the second arboreal phase. It differs, however, in the substitution of digitigrade developments for plantigrade ones, with a tendency towards functional monodactylism.

The Peramelidæ are without existing arboreal representatives. The only way in which it is possible to arrange their foot-patterns in proper sequence is, therefore, according to the extent to which they depart from the arboreal type as presented by the Phalangeridæ. In such an arrangement the most primitive conditions are seen to be presented by the two forms *Perameles Raffrayana* and *P. Cockerelli*. It is an interesting fact that *P. Cockerelli* is very closely related to *P. Doreyana*, and that the latter, together with *P. Raffrayana*, are the most primitive forms in dentition; also that all three are Papuan in their distribution. The foot-patterns of the Australian or mainland forms are traceable to that of *P. Raffrayana*. These species present a division into short- and long-footed series: the former including *P. macrura*, *P. obesula*, and *P. barrowensis*; the latter *P. Bougainvillei*, *P. nasuta*, *P. Gunni*, *Thylacomys*, and *Chæropus*. In the longfooted series development has probably proceeded along three subsidiary lines.

In P. Cockerelli (Pl. 7. fig. 14) we find a very close approximation to the typical condition in the Phalangeridæ. The foot is comparatively short; the proportion of breadth measured immediately behind the hallux to the length measured from the heel to the tip of the fourth digit, excluding the claw, is approximately 1:4.3. It is not possible to make a similar measurement of a phalangerine foot, but it may be observed that if the foot of P. Cockerelli were provided with a well-developed instead of a reduced opposable hallux, its proportions would be almost exactly as in the Phalangeridæ. In other words, the plantigrade and non-elongated condition has been perfectly retained. P. Cockerelli is specialized after the manner of all other secondarily terrestrial forms in the reduction of the opposable hallux. It is primitive, as compared with other Peramelidæ, in the more radiate arrangement and greater freedom of the outer digits, this being a phalangerine character which is lost in the more advanced forms. Another primitive character is observable in the position of the notch separating the conjoined second and third digits from the fourth on a level with that separating the latter digit from the fifth. Of the plantar pads characteristic of the prioreal type of pes, only the digital elements are represented; they are well separated, but have no striated areas, their surface being granular like the rest of the sole. The claws of the fourth and fifth digits are slightly curved: this is also a primitive character-in the more specialized subdigitigrade forms the claws are stouter and also straighter.

The above description of *P. Cockerelli* applies almost equally to *P. Doreyana*. In *P. Raffrayana* (Pl. 7. fig. 15) the pes is more specialized in its proportions, the ratio of breadth to length in a specimen measured being 1:6:3. The hallux, however, is almost better developed, its proximal phalanx and metatarsal being quite large. The plantar pads are also more primitive. At the base of the hallux there is a small elevation representing a hallucal pad, the apex of which bears a smooth area, probably representing a formerly striated surface. The digital pads are well developed and show the same characters as the hallucal one.

In *P. moresbyensis* we find much the same characters as in *P. Raffrayana*. The proportion of breadth to length in a specimen measured was found to be  $1:6\cdot1$ . The hallux is more reduced. There are no signs of a hallucal pad and the first digital pad is obsolete. The second and third digital pads are well developed, but their apical smooth areas are not so well marked. Practically the same characters are found in *P. obesula*. The proportion of breadth to length in a specimen measured was found to be  $1:6\cdot3$ . A dried preparation of *P. macrura* showed a proportion of  $1:7\cdot5$ , but this measurement cannot well be compared with those of spirit-specimens.

The species just referred to are essentially short-footed forms. In the remaining ones, with the partial exception of the annectant form P. nasuta, the pes shows definite signs

of elongation and digitigrade development. In P. Bougainvillei (Pl. 7. fig. 16) the proportion in a specimen measured was found to be  $1:11\cdot3$ . The hallux is now reduced almost to a tubercle. The second and third digits are more completely bound together and also more reduced; they are set backwards in such a way that the notch separating them from the fourth digit is placed considerably behind that separating the fourth digit from the fifth. There is no hallucal or first digital pad. The second and third digitals are well developed and show faint signs of striation. The sole is hairy as far forwards as the base of the hallux.

In *P. nasuta* and *P. Gunni* the conditions are more primitive, although the animals are larger and approximate more closely to those of the short-footed series. A dried specimen of *P. nasuta* showed a proportion of 1:6.5. A spirit-specimen of *P. Gunni* showed a proportion of 1:8. In the latter species the hallux is not so reduced as in *P. Bougainvillei*, and the second and third digits are not displaced backwards. The characters are otherwise much as in that species.

Thylacomys leucura (Pl. 7. fig. 17) presents an advance on P. Bougainvillei. The proportion of breadth to length is about 1:15. The two digital pads (morphologically second and third) are fused together basally, but the compound structure thus formed shows two small, smooth, apical areas representing the formerly striated surfaces. The sole is completely hairy. Judging from a dried specimen, the pes of T. lagotis corresponds closely with that of T. leucura just described.

Charopus (Pl. 7. fig. 18) presents a more advanced stage of the digitigrade development than Thylacomys. In a dried specimen the proportion was found to be 1:21:4. The sole is extremely narrow and completely hairy. The hallux is absent and the second and third digits wholly vestigial. There is a large digital pad which is probably the result of fusion of the second and third pads, as in *P. Bougainvillei*. It is an interesting fact that while in *P. Bougainvillei* the second and third digits are placed behind the fifth, in *Charopus* they are placed in front. Thus, in the reduction of the second, third, and fifth digits, in connection with the monodactylous elaboration of the fourth, the recession, as shown by *P. Bougainvillei*, first influences the second and third, but ultimately, as shown by *Charopus*, these elements are passed by the fifth\*.

\* It is interesting to notice, in connection with this form, the peculiar conditions which must have attended the origin of its foot-modifications. In both the front and hind feet *Chaeropus* presents digitigrade cursorial developments analogous to those of the placental Ungulata. The hind feet have become functionally monodactyl like those of the Equidæ in the perissodactyl series; but whereas in the latter the third digit is the predominant member, in *Charopus* it is the fourth. Dollo has already shown that the reason of this is that while in the Equidæ the monodactyl condition has proceeded from a normal pentadactyl one, in *Charopus* it has proceeded from a specialized arboreal type like that seen in the Phalangeridæ, in which the third digit was already reduced and the fourth digit predominant. The front feet present an analogous case. They are functionally didactyl, as in the artiodactyl Ungulata; but whereas in the latter division the predominant digits are the third and fourth, in *Charopus* they are the second and third. The reason is that before becoming cursorial the foot of *Charopus* was already specialized in a fossorial direction. In the species of *Perameles* the first and fifth digits, and to a lesser extent the fourth, are reduced, and the second and third enlarged for digging purposes. It is interesting to note that in *Charopus* the two functional toes are not exactly of the same size, the second being slightly but perceptibly smaller.

In developing into a cursorial animal, Charopus has been, in a sense, hampered by the possession of arborcal characters in its hind feet and of fossorial characters in its front ones.

#### MACROPODIDÆ.

The general type of pes in the Macropodidæ represents a terrestrial derivative of the second arboreal phase. The tendency is towards digitigrade modification and functional monodactylism. There is an almost perfect parallelism between this family and the Peramelidæ \*, although the two are easily proved to be of totally independent derivation.

The pes of Hypsiprymodon (Pl. 7. fig. 21) is familiar as presenting an intermediate condition between the general type represented by the arboreal Phalangeridæ and that characteristic of the Macropodidæ. The whole foot is comparatively short. The hallux is fairly well developed and possesses the full number of phalanges. It is opposable, although not to the same extent as in the Phalangeridæ. This condition contrasts strongly with that in the remaining Macropodidæ, where the hallux is invariably absent. The plantar surface presents the full number of transversely striated pads. The first and second digital ones tend to fuse together in connection with the incipient narrowing of the foot.

Contrary to what might be expected from their dental relations, Hypsiprymnodon shows no points of special affinity in its foot-structure with *Rettongia* and *Epyprymnus*. In both of the latter the pes is already well specialized; it is very narrow and greatly elongated, much more so, in fact, than in many otherwise more specialized forms. There are no indications of plantar pads, with the exception of a large elevation at the base of the functional digits. The various species show comparatively little variation.

In Potorous (Pl. 7. fig. 23) we find a fairly close approximation to Hypsiprymnodon. The pes is much shorter than in the preceding genera, and the digits show the lesser degree of elaboration and also the freedom of lateral movement characteristic of Hypsiprymnodon and the Phalangeridæ. The full number of plantar pads has been retained, but their transverse striations are broken by irregular longitudinal markings. The hallucal and marginal pads are in process of reduction, as in the Peramelidæ. The first and second digital pads are partially joined together, as in Hypsiprymnodon. So far as can be judged from dried specimens, there is little variation in the different species. Caloprymnus shows a much closer approximation in its foot-structure to Bettongia and *Epyprymnus* than to *Potorous*, as seen in the greater elongation, the greater elaboration of the fourth digit, and the absence of plantar pads, with the exception of the large basal structure described for the former genera. The length of the pes as compared with the breadth is greater in Caloprymnus than in Bettongia, with the exception of B. Gaimardi, and almost twice as great as in Potorous. These relations appear at first sight to oppose the serial arrangement arrived at from a study of the dentition; but there is no doubt that the dental relations are of a more fundamental character. The fact that the foot-structure of the Phalangerinæ is practically homogeneous throughout shows that the greater resemblance of Hypsiprymnodon to Potorous means only

\* The arrangement of the tarsals and metatarsals furnishes a point of distinction. In the Peramelidæ the enlarged fourth metatarsal is supported in part by the ectocuneiform and in part by the cuboid, while in the Macropodidæ it is practically supported by the cuboid alone.

derivation from the same type. *Potorous* has retained primitive characters by assuming a more or less fossorial habit, while the remaining genera *Bettongia*, *Æpyprymnus*, and *Caloprymnus*, of both subfamilies, have, like the Macropodinæ, assumed a freer ground-living habit, with the development of a more elongated saltatorial modification in the pes.

Passing to the Macropodinæ, we find two chief types, respectively characteristic of the arboreal forms (species of *Dendrolagus*) and the terrestrial ones. The pes of *Dendro*lagus (Pl. 7. fig. 22) is comparatively short. The proportion of breadth to length in a spirit-specimen of D. ursinus and also in a skeleton of D. inustus was found to be approximately 1:3. This appears to indicate a more primitive condition than even in Hypsiprymnodon, where, disregarding the hallux, the proportion is about 1:6; but it is very probable that the shortened condition of the pes has been reacquired. The plantar surface shows no indications of pads. These, like the hallux, have been lost during the antecedent terrestrial phase. The second, third, fourth, and fifth digits resemble more closely those of the Phalangeridæ than those of the terrestrial Macropodinæ, and similar conditions characterize the metapodials and phalanges in the skeleton. In the fourth and fifth digits the claws are definitely curved. It is difficult to state exactly how far these characters have been secondarily developed or have been carried over from the phalangerine ancestors through a primitive terrestrial form. As to whether there is a special resemblance between Dorcopsis and Dendrolagus in foot-structure as there is in dentition has been difficult to ascertain from a comparison of the available specimens, all of those representing the former genus being dried preparations. The general conformation of the pes in *Dorcopsis* is as in other terrestrial macropodine forms. The ratio of breadth to length is approximately 1:7-9, the foot being relatively short as in *Potorous*. It is an interesting fact that the pes of D. luctuosa presents a distinctly swollen condition as compared with that of D. Muelleri or D. Macleayi, and the heel, and in fact the whole pes, is less elongated than in the latter species. These characters point to those of Dendrolagus, and afford some evidence for the conclusion arrived at from a study of the dentition, namely, that Dorcopsis is a secondary terrestrial derivative of the secondarily arboreal Dendrolagus.

The members of the macropodine series, *Petrogale*, *Onychogale*, *Lagorchestes*, *Lagostrophus*, and *Macropus*, show very great uniformity in the general pattern of the pes, and the specimen of *Macropus dorsalis* here figured (Pl. 7. fig. 34) may be taken as representative of the group. The ratio of breadth to length in this specimen is 1:13.5. The fifth and the intimately joined second and third digits are now more closely associated with the fourth, and thus show a great reduction of the free movement characteristic of more primitive plantigrade forms. The fourth digit is perfectly axial in position, and corresponds very closely in stoutness with the middle portion of the foot. The plantar surface is covered with a tuberculated skin, and of the plantar pads the marginal as well as the hallucal one has completely vanished; while the three digital pads are completely fused together, forming a prominent protuberance which shows not the slightest traces of the striated areas formerly present.

Comparison of the proportions of the feet in the various genera reveals a slight

variation, inasmuch as those of Lagorchestes, Lagostrophus, and Onychogale are relatively more elongated than those of the remaining species with which they are most closely associated in size. The following data will suffice to illustrate this difference, although the figures given must be taken as roughly approximate, being based on dried preparations:—Three specimens representing the three species of Onychogale, O. frenata, O. lunata, and O. unguifera, show a ratio respectively of 1:14.5-14.6-17.1; a specimen of Lagostrophus fasciatus, 1:15.1; three specimens representing the species of Lagorchestes, L. leporoides, L. hirsutus, and L. conspicillatus, respectively 1:15-15.7-18. On the other hand, specimens representing the species of Petrogale, P. penicillata, P. brachyotis, P. concinna, and P. inornata, show a ratio respectively of 1:10.7-10.9-11.8-14; while the Small Wallabies of the genus Macropus show a range from 1:7(M. Coxeni) to 1:13.5 (M. Eŭgenii). In Lagorchestes and Lagostrophus, moreover, the sole of the foot tends to become hairy.

As regards the three sections of the genus *Macropus*, namely the Small Wallabies, Large Wallabies, and Kangaroos, there is a marked increase in the actual size of the foot as in the size of the body proceeding from one group to the next, and this difference has been made use of by Thomas (1888) in defining the three sections. There appears, however, to be no broad differences in the proportions of the feet separating these sections, although it is possible to demonstrate by measurement that the members of the Small Wallaby group show a greater tendency towards the retention of the original shortened form than do those of the other two. This is indeed what we should expect, because while the initiation of a saltatory method of progression demands the development of an elongated pes, yet its perfection is more a matter of the actual size of the animals and the proportion of the hind limb as a whole.

The species referred to as *Setonyx brachyurus* corresponds in the proportion of the foot with with the Small Wallabies, the ratio in a specimen measured being 1:7.9.

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THE IDENTIFICATION OF THE STEM-FORM OF THE AUSTRALIAN MARSUPIALS.

So far as deducible from the modifications of dentition and foot-structure, the data already given in the two preceding sections are sufficient for the construction of a phylogenetic or morphogenetic plan, except in one important particular, namely, that they fail to express the relationships of the primary families Dasyuridæ, Peramelidæ, and Phalangeridæ. None of the latter present the characters of a prototype, such characters being distributed over all three. Thus the Dasyuridæ in dentition occupy a prototypal position, except in respect to the upper incisor formula and the characters of the upper molar styles, in which they give place to the Peramelidæ; while the Phalangeridæ occupy a prototypal position in foot-structure, except in the syndactylous condition of the second and third digits, in which they give place to the Dasyuridæ. The Australian fauna considered by itself represents a radiation without a recognizable source, and in order to complete it it is necessary to add a hypothetical form combining the prototypal characters of the three primary families.

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Such a generalized type while not represented in the Australian group is, except for a more primitive condition of the lower incisor formula, exactly represented by the American Didelphyidæ, and the present section is devoted to a consideration of the various members of this family both in their relations to the Australian fauna and to one another.

Reviewing the opinions already expressed with respect to the relationships of the Australian fauna, we find them to be of the most diverse kind. Writing in 1871 Owen remarked :—"Among these initial forms of Marsupialia [referring to the Mesozoic Mammalia] we may see in *Amphitherium* the prototype of *Myrmecobius*; *Peralestes* has culminated in *Sarcophilus*; *Triconodon* in *Thylacinus*; *Plagiaulax* is to *Thylacoleo* what the Weasel is to the Lion. But derivative change has not advanced to the long-limbed saltatory type of Marsupial; nor has any evidence yet been had of a Mesozoic predecessor of the climbing Koala, the volant Petaurist, or the burrowing Wombat.

"The Marsupial type . . . has in America progressed to and been succeeded by the more specialized form of *Didelphys*.

"If Australia possessed Marsupials as far back in time as did America and Europe, analogy would lead us to suppose that the primitive diminutive multimolar insectivorous type prevailed. It has not there yet become extinct; but it seems to have been reduced to the solitary exceptional form of *Myrmecobius*."

Wallace, in his 'Geographical Distribution of Animals' (1876, v. p. 2), has expressed a similar view of a connection of the Australian fauna with northern Mesozoic forms:—"As, however, no other form but that of the Didelphyidæ occurs there [in Europe] during the Tertiary period, we must suppose that it was at a far more remote epoch that the ancestral forms of all the other marsupials entered Australia; and the curious little mammals of the Oolite and Trias offer valuable indications as to the time when this really took place. . . . It was probably far back in the Secondary period that some portion of the Australian region was in actual connection with the northern continent, and became stocked with the ancestral forms of marsupials."

To the same order belong the views of Falconer and others who have sought to establish a relationship between the Australian diprotodont forms and the Plagiaulacidæ, and that of Cope (1882, 1884), who actually referred the form *Thylacoleo* to the family Plagiaulacidæ, at the same time connecting the family with the Macropodidæ through a hypothetical ancestor *Tritomodon*.

The 'Systematische Phylogenie' of Haeckel (1895) contains much more definite views of a connection of the Mesozoic Mammalia with existing Marsupials. This writer recognizes a Jurassic group of Prodidelphia giving rise to the Marsupials along polyprotodont and diprotodont lines.

Apparently the only writers who have anticipated what is probably the true relationship of the Australian fauna are Winge (1893) and Lydekker (1896), both of whom favour a more direct connection with the existing American Didelphyidæ than with Mesozoic forms. In a general scheme of the marsupial families Winge indicates three lines of development—one of them represented by a group composed of *Diprotodon*, *Thylacoleo*, Phascolomys, and Phascolarctus, a second by the Peramelidæ, and a third by the Dasyuridæ, from didelphyid prototypes. Lydekker, in his 'Geographical History of Mammals,' remarks as follows :—" Recent researches have tended to show that the alliance between the Dasyuridæ and the Didelphyidæ is much more intimate than was formerly supposed to be the case. This being so, it is a fairly safe assumption that both families are descended from a single common ancestral stock. . . . Not improbably polyprotodont Marsupials survived in south-eastern Asia till the early portion of the Eocene division of the Tertiary epoch, and in this region both Dasyuridæ and Didephyidæ were differentiated. Representatives of the former family soon afterwards found their way into Australia, while the Opossums would appear to have dispersed in one direction into Europe, and in the other into North America."

Certain opinions have, however, been expressed in favour of a South-American origin of the Australian fauna. Ameghino (1891) regards the forms described by him as Microbiotheriidæ as ancestral to both polyprotodont and diprotodont Marsupials, as well as to the Insectivora and Chiroptera. Spencer (1896) has pointed out the possibility that the Australian Marsupials and the Didelphyidæ may have originated at some time during the Cretaceous period from South-American ancestors. In a recent paper Lydekker (1899) has suggested the origin of the Dasyuridæ from South-American Prothylacinidæ (Sparassodonta), this view being based for the most part on the resemblances of *Thylacinus* to that family.

The main evidence as to the general relationships of the different groups of Marsupials may be summarized as follows:—During the Oligocene period the Didelphyidæ, represented by *Peratherium*, were widely distributed in the northern hemisphere, and if, as seems very probable, the Microbiotheriidæ of Ameghino, or at least some of them, are in reality members of this family, they were present at a slightly later period in South America as well. Of fossil forms at present known, the Oligocene Didelphyidæ are the earliest which may definitely be referred to the Marsupialia. The idea that the more ancient fossil Mammals must be Marsupials is untenable, and the only evidence on which the identification of the Jurassic forms as Marsupials now depends is the presumed existence of a single tooth-change in *Triconodon*, concerning which, as Lydekker (1899) has pointed out, there is room for doubt.

But whether the Oligocene Didelphyidæ were the first true Marsupials to be differentiated, or whether they were the descendants of earlier Marsupials as yet unrecognized, they are the ancestors of all of the later-appearing forms. In the development of the latter there is evidence of at least three different radiations. The first and most extensive one is that represented by the Australian fauna. A second is, in all probability, represented by the Miocene fauna of South America. The existing Didelphyidæ of South America, which might at first sight be regarded as surviving remnants of the original didelphyid radiation, may be shown to represent a third radiation which is at the present time in its very incipient stages. Of these three radiations the Australian and the existing South-American ones are directly traceable to minute primitive didelphyid forms like the existing genera Marmosa and Peramys, or the extinct Peratherium. Winge (1893), who has made a careful study of the existing Didelphyidæ, divides the family as follows \*:---

I. Hindmost of the three outer cusps of the upper molars well developed.

- A. p. 1 and m. 3 comparatively well developed. Molar teeth with high sharp cusps. Body of the lower jaw shallow. Proc. angularis sharply inflected. Ribs narrow. No marsupium. Grymæomys [=Marmosa].
- B. p. 1 and m. 3 reduced. Molar teeth with low rounded cusps. Body of the lower jaw deep. Proc. angularis only slightly inflected. Ribs broad. Marsupium in the form of folds. Philander [=Caluromys].

II. Hindmost of the three outer cusps of the upper molars reduced.

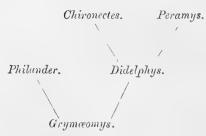
A. Tail long. Terminal phalanx of hallux broad.

- (a) No swimming-membrane between the toes. Skin of palms and soles normal. Didelphys [= Didelphys and Metachirus].
- (b) Swimming-membrane between toes. Skin of palms and soles provided with peculiar papillæ.

Chironectes.

B. Tail short. Terminal phalanx of hallux compressed. Hemiurus [=Peramys].

He considers the relationships of the above genera to be as follows :---



The genus *Peramys* is regarded by Winge as derivative of *Didelphys*, but in many respects it is prototypal not only to that genus but also to *Marmosa*. It will be observed that Winge's main division associating *Didelphys* and *Peramys* is based on the characters of those elements of the upper molars here referred to as external styles. These structures are regarded by him as typically three in number and as the original cusps of the crown (triconodont type). Winge remarks with reference to *Phascogale*, *Dasyurus*, and their allies in the Dasyuridæ that they present a more primitive condition of the upper molars than is found in any other of the existing Mammalia, the three outer cusps being persistent, and the median one of them, like the median one of the three internal cusps of the lower molars, being larger than the others. He also states that in *Grymæomys* (*Marmosa*) the three outer cusps are present, but the median one has lost its predominance, while again in *Hemiurus* (*Peramys*) and in *Didelphys* the hindmost cusp has become reduced. He illustrates these cases by the teeth of *Phascogale penicillata*, *Marmosa cinerea*, and *Peramys domestica*, designating the three cusps numerically in the order of their occurrence from before backwards.

<sup>\*</sup> On account of these results being written in the Danish language the writer has taken the liberty to substitute a translation for the original text.

That the Dasyuridæ should present more primitive characters than the Didelphyidæ, a family which is otherwise so completely prototypal, appears at the outset improbable. In addition it may be shown that the three cusps figured by Winge in *Marmosa cinerea* and *Phascogale* are not homologous, the third cusp of the latter animal not being present in *Marmosa*, whose third cusp is equivalent to the second of *Phascogale*, and whose second cusp represents a new development.

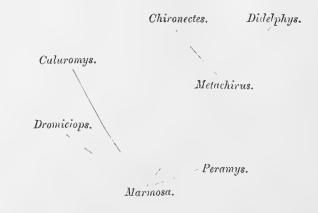
In Pl. 5. fig. 1 b will be found a carefully drawn external profile view of the inner molar of *Peratherium*, in which the outer cingular ridge will be seen to bear in all six elevations. The latter may be designated in the order of their occurrence from before backwards as a, b,  $b_1$ ,  $c_1$ , c,  $c_2$ \*, the letters indicating those elements which are well developed and have, for the most part, definite homologues in other polyprotodont forms, while the letters to which numerals are appended indicate smaller and more subsidiary elements. The cusps b (or ab)—see account of Dasyuridæ, -c, and  $c_2$  represent the three outer cusps figured by Winge in Phascogale penicillata. On examining the arrangement of these structures in the various species of Marmosa and Peramys, with reference to the type presented by Peratherium, there is found to be not a single character of them which will serve to separate one genus from the other. The stylar formula varies to a certain extent in different individuals of a species, and even in different teeth of the same animals, the range being from a formula of a, b, c to one of a, b,  $b_1$ ,  $c_1$ , c,  $c_2$ . In *Peramys* the more subsidiary cusps are on the whole poorly represented;  $c_2$ (Winge's 3) may be present or absent. In Marmosa  $c_1$  is nearly always present and comparatively well developed, the only notable exception being in M. elegans, in which only two of some twelve or fourteen specimens presented signs of intermediate cusps. In Marmosa murina, M. cinerea, and M. rapposa,  $c_1$  is better developed, as compared with the other cusps, than in the remaining species of the genus, and a similar condition is found in some cases in Caluromys. This cusp is that designated as 2 in Winge's figure of Marmosa cinerea. Its developmental stages, as here interpreted, are represented in Pl. 5. figs. 1, 28, 29, 30 of Peratherium, Peramys Iheringi, Peramys americana, and Marmosa cinerea.

The question here arises—How can it be shown that the cusp  $c_2$  is a subsidiary element which is becoming enlarged in such forms as M. cinerea rather than an original cusp which is becoming reduced? According to Winge's view, the molars of M. murina are more primitive than those of the smaller forms M. microtarsus and M. pusilla, because in the former the median outer cusp is better developed and the teeth are less compressed in an antero-posterior direction. But in reality they are much more specialized, because not only M. cinerea but also M. murina and M. rapposa are closely allied to Caluromys, of which they represent an ancestral type. Their teeth are transitional in pattern between those of Caluromys and those of the smaller forms, and this is true in respect to the peculiarly elongated canines and the reduced anterior premolars as to the molars. The molars of Caluromys are noticeable for their lateral compression and the obsolete character of the external cingulum (cf. Pl. 5. fig. 27). The apparently well-

\* Cf. text-fig. 1, p. 89.

developed condition of style  $c_2$  in Marmosa murina, M. cinerea, M. rapposa, and in some specimens of Caluromys in reality represents a general levelling down of the whole stylar series prior to its obliteration. In some specimens of Caluromys, as in that here figured, the cingular ridge is seen to be extremely small and thin, and to bear, instead of definite styles, a number of minute crenulations. All of the molar characters of this genus are indicative of an incipient omnivorous development, pointing towards that seen among the Australian Marsupials in the Phalangerinæ, where, even in the most primitive forms (cf. Pl. 5. fig. 13, Distæchurus), the external styles have already disappeared.

In the writer's opinion the relationships of the Didelphyidæ are as indicated in the following modified plan :---



This represents an incipient radiation, since the diverging lines are directly traceable to Marmosa. It is an interesting fact that the representatives of these lines are still scarcely separable systematically from that genus. As in the Australian families, increase in size of the body appears to have been an essential feature of the evolution. With the exception of Dromiciops, the two genera Marmosa and Peramys include the smallest and most primitive forms of the family. Peramys bears much the same relation to Marmosa as Sminthopsis does to Phascogale, being in general more primitive in dentition, but specialized in a terrestrial direction in foot-structure. The most important dental character demonstrating the prototypal position of Peramys relates to the posterior premolars, which are, as a rule, larger than the median teeth. In Peratherium they are apparently always larger, but in Marmosa, as well as in the more specialized forms, they show definite signs of reduction. The foot-characters in which Peramys is specialized relate to the reduction of the terminal phalanx of the hallux, reduction of the striated plantar pads, and shortening of the fifth digit, all of which modifications are connected with a secondarily terrestrial habit. Peramys is also more specialized than Marmosa in the shortened, hairy, and, apparently, non-prehensile character of the tail. It is interesting to note that in the Didelphyidæ the tail ranks with the teeth and feet as an As indicated in Winge's plan, Marmosa represents the organ of adaptive change. The existing species have, however, parent form of all the remaining genera. undergone a specialization of the posterior premolars, a reduction similar to that found on a larger scale in Phascogale. Some of the species have further undergone a special development of the molars, canines, and anterior premolars pointing towards the genus Caluromys. Marmosa is completely prototypal in foot-structure, apart from a slight tendency in some species towards syndactylism of the second and third digits, the pes being of a primitive arboreal type, with widely opposable hallux and well-developed, striated, plantar pads. The tail is long and prehensile. The minute form *M. velutissima* forms a connecting-link between *Marmosa* and *Peramys*.

Caluromys is an advanced form of one of the larger species of Marmosa, such as *M. rapposa*, *M. murina*, or *M. cinerea*. In its foot-structure, as also in the character of its tail, it continues the arboreal developments of Marmosa. In dentition the main progressive character is the omnivorous type of molar pattern in an early stage of differentiation. The anterior premolars are reduced and the canines are elongate and compressed. This character, at first sight appearing to indicate carnivorous habit, is in all probability of secondary sexual significance.

The peculiar form *Dromiciops* (Thomas, 1894) is a derivative of *Marmosa*, approximating to *Caluromys* in the characters of its molar teeth, and to *Peramys* in the shortened and hairy condition of the tail.

The two genera *Metachirus* and *Didelphys* are so closely allied that it is not possible to separate them on the characters of the dentition or foot-structure. Their dentition repeats on a larger scale the characters of *Marmosa*. In the upper molars style  $c_2$  is usually indicated on account of the greater space available on the metacone-spur. Intermediate styles are poorly represented. Both genera show a slight tendency towards terrestrial specialization in foot-structure. In other respects *Metachirus* is more primitive than *Didelphys*, approaching *Marmosa* in its smaller size and the incomplete development of the marsupium and its uniform coloration, the homogeneous character of the fur, and the conformation of the ears. It is possibly related to *Marmosa* through *M. elegans*.

Chironectes has been pointed out by Thomas (1888) as very closely allied to Metachirus, and in its cranial characters indistinguishable from that genus. Apart from its obvious metachirine derivation, the special features of Chironectes are remarkable and unique among Marsupials, as indicating an aquatic adaptation, the tail being flattened and the feet, which have a modified opposable hallux, being provided with swimmingmembranes connecting the digits.

In identifying the characters in which the Didelphyidæ occupy a prototypal position to the Australian Marsupials, it is not possible to rely entirely on fossil forms, the information available concerning them not being sufficiently full. In utilizing the characters of the existing Didelphyidæ to supplement the evidence of *Peratherium*, the facts pointed out above must be borne in mind, namely, that they represent a contemporaneous, although less extensive, radiation. Three different classes of characters may thus be expected, namely: (a) those which indicate a more primitive condition than is found in any of the Australian forms, as, for example, the increased lower incisor formula or the arboreal type of pes with opposable hallux and non-syndactylous second and third digits; (b) those representing conditions exactly equivalent to those already mentioned as prototypal for the Australian series, as, for example, the tritubercular type of upper molar; (c) those which indicate a similar potential of evolution, such as the reduction of the posterior premolars and the development of syndactylous modifications in the pes. It will be observed that all the characters of the dentition and foot-structure described as prototypal, and distributed over three families in the Australian series, may occur together in the Didelphyidæ in a single species.

# Deutition.

Molar Patterns.—The upper molars of the smaller Dasyurinæ have already been mentioned as completely prototypal, except in the arrangement of the external styles. We may now notice the fact that their patterns are practically identical with those of *Peratherium* and the existing Didelphyidæ (cf. Pl. 5. figs. 1 a-b, 2 a-b, 26, of *Peratherium*, *Sminthopsis leucopus*, and *Metachirus opossum*). The only important exceptions to this general statement are as follows:—In the first place, the molars of the more advanced Didelphyidæ (fig. 26), while differing from those of the Australian forms (advanced Dasyurinæ and Peramelidæ) in tending to retain the original insectivorous character, show less antero-posterior compression than those of the smaller forms, and also *Peratherium* and the smaller Dasyurinæ. Secondly, one member of the family, *Caluromys*, shows indications of an omnivorous development, which, if continued further, would parallel that of the Phalangerinæ. Thirdly, there are minor variations in the arrangement of the external styles; all of them, however, both in the Didelphyidæ and the Australian forms, are easily traceable to the *Peratherium*-type.

Comparing the second molar of Sminthopsis leucopus here figured with that of Peratherium, it is seen that in the former styles a and b are fused together. Intermediate styles are not represented. Style c is greatly enlarged. In other members of the Dasyurinæ style  $c_1$  is occasionally developed. In the British Museum Collection it is present in m. 2 of eight specimens of Phascogale flavines, in m. 1 and m. 2 of one specimen of P. Swainsoni, in m. 1 of three (of five) specimens of P. penicillata, and in m. 2 and m. 3 of two. One specimen of P. minutissima shows both style  $c_1$  and  $b_2$  in m.1. Style  $c_2$  is generally absent in the smaller forms. Even in *Peratherium* it is so small as to be scarcely recognizable. It is altogether absent in all of the British Museum specimens of Sminthopsis. It is present in m. 2 in one specimen P. Swainsoni; it is absent in all of eleven specimens of P. flavipes. In Phascogale penicillata, the type figured by Winge in connection with this element, it is present in m. 1 and m. 2 in three of five specimens. It is absent in m.3 of three specimens, and in each of the two others it is represented by two minute tubercles. It is present as a trace in m.1 and m.2 of one specimen of *P. dorsalis* and one of *P. Thorbeckiana*, and is barely indicated in most specimens of *Dasyurus* (cf. Pl. 5. fig. 3).

The arrangement of the external styles in the existing Didelphyidæ has already been referred to. It needs only to be added that not only are the variations traceable to a *Peratherium*-type, but also that there is less departure from that type than is seen in the Dasyurinæ. The same tendency towards the fusion of styles a and b is noticeable (cf. Pl. 5. figs. 28, 29), but is not so apparent as in the Dasyurinæ. The condition is

nearer that shown by the Peramelidæ (Pl. 5. fig. 8). Style c does not become greatly enlarged as in the Dasyurinæ, but retains more the proportions seen in *Peratherium* and the Peramelidæ. Finally, there is a greater tendency towards the retention of the intermediate styles  $b_1$  and  $c_1$ .

The following additional characters of resemblance between the Didelphyidæ, including *Peratherium*, and the Dasyurinæ and Peramelidæ may be noticed. The first molar is always more laterally compressed than the second, while the reverse is true of the third. In the latter also the external styles are poorly developed. The fourth molar is in every case reduced.

Passing to the lower molar patterns, we note the fact that the smaller Dasyurinæ present prototypal relations which are exactly duplicated in the Didelphyidæ. The pattern figured for *Sminthopsis leucopus* (Pl. 6. fig. 2) will be seen to be practically identical with that of *Peratherium* (fig. 1) and *Metachirus* (fig. 32). An exception will be noticed in the absence of the entoconid in *Sminthopsis*, but, as already mentioned in connection with the Dasyurinæ, the condition in this form and other species of *Sminthopsis* is not typical of the subfamily. It is interesting to note that, notwithstanding the increase in size of the body in the advanced members of the Didelphyidæ, the primitive molar type is for the most part retained, while in the similarly advanced members of the Dasyurinæ carnivorous modifications begin to appear.

As noticed above, the first lower molar in the Dasyurinæ shows a series of reductions of the paraconid and metaconid, beginning with a type like that figured for *Sminthopsis crassicaudata* (Pl. 6. fig. 6), in which these cusps are fairly well developed. In the primitive Peramelidæ, in *Peratherium*, and all of the existing Didelphyidæ (*cf.* Pl. 6. fig. 33) we find prototypal relations, these elements being well developed throughout.

In the fourth lower molar of the Dasyurinæ there is a marked tendency towards the reduction of the talonid. The same tendency is seen in a somewhat lesser degree in the existing Didelphyidæ. Five specimens of *Peratherium* in the British Museum Collection show the characters of these teeth, and in three of them the talonid is fairly developed, and all of the three cusps are recognizable, while in two others the talonid is reduced \*.

Incisors.—On account of the lack of information concerning the incisors of *Pera*therium the following comparisons include only the existing Didelphyidæ. In the Australian series, and apart from the incisor formula, the smaller Dasyurinæ are the only forms showing prototypal characters. In these we find no less than five points of resemblance with the Didelphyidæ. The median upper teeth are procumbent and subcaniniform. The upper lateral teeth, when unworn, have triangular tips. The median lower incisors are unmodified. Like the lower lateral teeth their tips are rounded. The insertion of the three anterior lower teeth is arranged so that the root of the second

<sup>\*</sup> These specimens are *P. arvernensis* (Puy-de-Dôme, M. 27700), an undetermined species from Auvergne (M. 27811), an undetermined species from Hordwell, Hants (M. 30350), *P. Lamandini* (Caylux, M. 2388 d), and *P. affinis* (Tarn-et-Garonne, M. 2388 a). *Cf.* Lydekker (1887).

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is placed behind that of the first, while that of the third is placed externally to that of the second.

In the incisor formula the Peramelidæ are the most primitive of all the Australian forms, the number being  $\frac{5-4}{3}$ . The Dasyuridæ come next with the uniform formula of  $\frac{4}{3}$ . The Didelphyidæ present the prototypal condition of  $\frac{5}{4}$ . The mutual homologies of the teeth in the three families are not at all clear. Thomas (1888), Winge (1895), and Dependorf (1898) have estimated the original marsupial formula as  $\frac{5}{5}$ , but there is no agreement as to how reduction from this type has been effected in the different families. The various views may be tabulated as follows :—

	Thomas (1888).	Winge (1895).	Woodward (1895).	Wilson and Hill (1897).	Dependorf (1898).
Didelphyidæ	$ \frac{12345}{12340} $	$\begin{array}{r}1&2&3&4&5\\\hline0&2&3&4&5\end{array}$			
Peramelidæ	$\cdots  \frac{1\ 2\ 3\ 4\ 5}{1\ 2\ 3\ 0\ 0}$	$\frac{1\ 2\ 3\ 4\ 5}{0\ 2\ 3\ 4\ 0}$	*****	$\frac{12345}{0234?}$ *	$\frac{1\ 2\ 3\ 4\ 5}{1\ 0\ 3\ 4\ 0}$
Dasyuridæ	$\cdots  \frac{1\ 2\ 3\ 4\ 0}{1\ 2\ 3\ 0\ 0}$	$\frac{1}{0} \frac{2}{2} \frac{3}{3} \frac{4}{4} \frac{0}{0}$	$\frac{1\ 2\ 0\ 4\ 5}{0\ 2\ 0\ 4\ 5}$		$\frac{1}{0}\frac{2}{2}\frac{3}{3}\frac{4}{4}\frac{0}{0}$

The evidence on this point is admittedly unsatisfactory, but it is probable that the plan of reduction suggested by Winge is the correct one. In the first place, there is evidence to show that the anterior lower incisor has disappeared throughout. Winge has pointed out that the median lower incisors are in relation with the second upper teeth, with which they are accordingly homologous. There are no lower teeth corresponding to the median upper ones, and it may thus be supposed that the development of a procumbent caniniform condition in them may have disturbed the relations of their original homologues in the lower jaw, leading to their reduction. Furthermore, both Woodward and Dependorf have described vestigial germs situate in front of what are later on the first functional lower teeth in embryos of *Dasyurus*. Wilson and Hill mention a possibly equivalent germ in *Perameles*, although this is not mentioned by Dependorf for that genus.

In the second place, there are reasons for believing the three lower incisors of the Dasyuridæ and Peramelidæ to be homologous with one another and with the first three lower incisors of the Didelphyidæ. Wilson and Hill have called attention to the fact that in embryos of *Perameles* the germs of the lower functional teeth occupy a peculiar relation to one another, the second being situate in a line posterior to the first, while the third, in consequence of a sharp bending outwards of the dental lamina, is situate externally to the second, so as to appear in the same transverse sections. Röse (1898) has figured the same condition in a model of the tooth-germs of *Didelphys aureus*, although he has mistaken the homologies in designating the external germ as second instead of the third, and *vice versá*. Exactly the same conditions are seen in the adults of all three families, Dasyuridæ, Didelphyidæ, and Peramelidæ, where the second tooth is inserted behind the first and the third tooth externally to the second, the tips at the same time forming a uniform row. According to Dependorf's idea, the lower teeth of

\* As determined from their description of the tooth-development of Perameles (1897).

Perameles and Dasyurus are not homologous throughout, since in the former he recognizes a vestigial germ of a morphological second incisor (di. 2). This element, however, is probably not a member of the same series as the functional teeth, but is more likely equivalent to the calcified germ described as di. 2 by Wilson and Hill, or, in other words, the predecessor of the functional second (morphological third incisor), and also homologous with the germ described as di. 3 in the upper jaw, which, according to Wilson and Hill, is large, but degenerates early in Perameles, and is present and calcified in Dasyurus.

Finally, there is evidence of the presence of vestigial germs in the posterior incisor region in the Dasyuridæ and Peramelidæ. Dependorf describes, in his fourth and fifth stages in *Perameles*, a vestigial germ (di.5), presumably corresponding to the fourth lower functional tooth of the Didelphyidæ. This element is not mentioned by Wilson and Hill for *Perameles*, but is described by Woodward for *Thylacomys (Peragale)*, and by both the latter writer and by Dependorf for *Dasyurus*. A fifth upper vestigial germ is also mentioned by Dependorf for *Dasyurus*, although it is not mentioned by Woodward, this writer having apparently concluded that the reduction took place in the middle of the series. Dependorf states his inability to recognize either the upper or lower intermediate teeth described by Woodward for *Dasyurus*. Further study of the whole question from the standpoint of comparative embryology is greatly to be desired.

Canines.—These teeth call for little consideration. They present exactly the same insectivorous characters in the smaller Dasyurinæ, and, in the case of the upper, in the more primitive of the Phalangerinæ (Acrobates and Distachurus), as in the Didelphyidar, with the partial exception of Caluromys.

**Premolars.**—In the general characters of the premolars the smaller Dasyurinæ and the Didelphyidæ are inseparable. The chief special features relate to the proportions of the posterior teeth. As already mentioned above, the Dasyurinæ present successive stages of reduction of the posterior premolars, beginning with a condition in which they are slightly or disproportionately larger than the median teeth, and ending in their total obliteration. This reduction has also been mentioned for certain of the Phalangerinæ (Acrobates and Distæchurus), and for two members, Thylacomys lagotis and Chæropus castanotis, of the Peramelidæ. Peratherium presents a prototypal condition, the posterior premolars being apparently always larger than the median teeth \*. In the existing Didelphyidæ we find indications of the same process of reduction scen in the Dasyurinæ, with the difference that it does not proceed to the obliteration of the teeth or even to the loss of their functional value. Of all the existing Didelphyidæ Peramys makes the closest approach to Peratherium, the upper posterior premolar being always larger, and the lower posterior tooth slightly larger than, or equal to, the median.

<sup>\*</sup> This statement is based on five specimens in the British Museum collection, including *P. Aymardi* (2388), *P. arvernensis* (27700 and 27810), an undetermined species (27811), and *P. exilis* (27806, type), and also on the description given by Gervais (1859), by whom two of the specimens have been figured. *Cf.* Lydekker (1887).

Deciduous Premolars.—Except in the case of Myrmecobius, these teeth have not been considered in dealing with the dentition of the Australian forms, the reason being that their characters do not relate to the secondary evolution of the group \*, but with the primary differentiation of the Marsupials as a whole. They furnish such conspicuous proof of the prototypal position of the Didelphyidæ, however, that their characters may well be used to supplement the evidence already given.

It is a well-known fact that in the differentiation of the Marsupials one of the dentitions has been obliterated, although as to which dentition is indicated is still a matter of controversy. Wilson and Hill (1897), in expressing the opinion that it is the milk-dentition which has been reduced, have pointed out the fact that in the Didelphyidæ the deciduous premolars are well developed, while in the Dasyuridæ and Peramelidæ they are reduced to vestiges. This they regard as indicating a final stage in the obliteration of the milk-dentition, the posterior deciduous premolar being at the present time in process of reduction. The following remarks, although specially designed to show the prototypal position of the Didelphyidæ, may be taken as con-firmatory of that view.

The deciduous premolars are well represented in the British Museum specimens of the Didelphyidæ, partly on account of the completeness of the collection, and partly from the fact that the teeth are not replaced until well on in life, and thus appear in all of the younger specimens. They show very little variation throughout the family. The lower teeth resemble almost exactly the true molars, and the same remark applies to the upper teeth, except that here there is a fusion of the paracone with style b. The most important feature of the teeth is, however, their large size and obvious functional condition. They are at most only slightly smaller than the first true molars.

The deciduous premolars are to be seen in only a few of the British Museum specimens of Dasyuride, as Sminthopsis murina, Phascogale flavipes, P. minima, P. penicillata, and Thylacinus cynocephalus. In all of these the deciduous teeth are found in an advanced state of reduction. They are, in fact, quite vestigial. In all except Thylacinus they tend to retain a molariform shape. There is an internal cusp, a large central cusp, a metacone, and a third anterior smaller cusp, respectively representing protocone, metacone, and paracone. The teeth are relatively more reduced in P. penicillata than in the smaller forms. In Thylacinus we find an extreme stage of reduction, the teeth being represented by minute triangular plates which are displaced before birth (cf. Flower, 1869). In Dasyurus, where the posterior premolars are absent, the deciduous premolars only occur as calcified vestiges in the embryo (Woodward, 1895; Dependorf, 1898).

Thomas (1887) has expressed the opinion that the reduction of the deciduous premolars in the Dasyuridæ is associated with the reduction of their successors, the posterior premolars. While this is in a certain sense true, it must be remembered that the association is only incidental. In *Thylacinus*, where the deciduous teeth are greatly reduced, the permanent teeth are well developed and predominant. The same condition is seen in the Peramelidæ and in *Phascolarctus*.

\* A partial exception is afforded by the Macropodidæ and advanced Phalangerinæ (vide infrå).

Of the Peramelidæ the deciduous premolars are represented in specimens of three species of *Perameles* (*P. obesula*, *P. nasuta*, and *P. Cockerelli*), as well as in *Charopus* and *Thylacomys*. In all of these, as in the Dasyuridæ, they are greatly reduced as compared with those of the Didelphyidæ. The specimen of *P. nasuta* presents the same appearance as one figured by Wilson and Hill (1897, pl. 32. fig. 78), the minute deciduous tooth being supported on the posterior slope of its enlarged successor. A reduced condition of the deciduous teeth has been figured by Flower (1869) for *P. Bougainvillei* and by Röse (1892) for *P. Doreyana*.

None of the specimens representing the smaller species of the Phalangeridæ show the deciduous premolars. In Phaseolarctus, as pointed out by Thomas (1887 b) and Dependorf (1898), they are wholly vestigial. In the final members of the Phalangerinæ, Phalanger and Trichosurus, as well as in the Macropodidae, we find a modification of quite the reverse kind, the deciduous teeth being well developed and functional until well on in life. In the phalangerine forms they perform the same sectorial functions for the young as the posterior premolars do for the adult, while in the Macropodidæ, where the median premolars are retained as sectorials in the young, the deciduous teeth take on, or perhaps retain, a molariform shape. In the Phascolomyidæ the deciduous teeth have apparently been reduced in the ordinary way. In view of the concise evidence in the Dasyuridæ and Peramelidæ of retrogression from a didelphyid type, it is surprising to find the deciduous teeth so well developed in the most advanced forms of Marsupials, such as the advanced Phalangerinæ and Macropodidæ, where one might expect to find them wholly absent. Whatever may have been the original cause of the reduction of one dentition-Leche has ascribed it to the peculiar suckling conditions attendant on premature birth-it appears probable that in these forms the reduction of the last element, namely, the deciduous premolar, has been checked by its becoming scrviceable in the secondary herbivorous evolution.

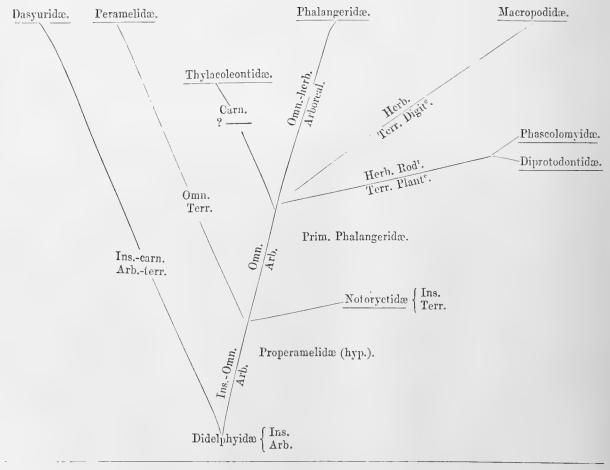
Foot-structure.-With regard to the foot-structure of the Australian forms it will be seen that the prototypal characters are distributed over two families. The Dasyuridae are primitive in the non-syndactylous and unreduced condition of the second and third digits. The Phalangeridæ are primitive in the possession of a full complement of welldeveloped and transversely striated plantar pads, and of a fully developed and completely opposable hallux associated with a non-clongated condition of the whole pes. It is apparent that the two types respectively characteristic of these two families are derivatives of a common form combining the prototypal characters of both. This common form is exactly represented by Marmosa (Pl. 7. fig. 7) among the Didelphyidae, with the partial exception that there is here, in some species, an indication of the syndactylous condition of the Phalangeridæ. Marmosa is completely arboreal, just as the ancestor of the Australian forms must have been. The conditions in this genus are repeated in Peramys, the genus which is most primitive in dentition, is slightly Caluromys. specialized in a terrestrial direction in foot-structure (Pl. 7. fig. 1), but, except for the partial reduction of the plantar pads and a tendency to shorten the fifth digit, retains the character of a prototypal form. It is an interesting fact that we have here in

Marmosa and Peramys a beginning of separation of persistent arboreal from terrestrial or semiterrestrial types, just as must have taken place in the original separation of the Dasyuridæ from the common ancestors of the Phalangeridæ, Peramelidæ, and Notoryctidæ. It is also an interesting fact that the larger members of the Didelphyidæ are conservative in foot-structure exactly as they are in dentition. Both Metachirus and Didelphys, the larger terminal forms of this incipient radiation, like Peramys, tend to depart from arboreal conditions, but in doing so do not become modified to an appreciably greater extent from the original arboreal type.

# THE PHYLOGENETIC ARRANGEMENT OF THE AUSTRALIAN MARSUPIALS.

In the three preceding sections the attempt has been made to bring together and classify the data at present available as to the origin and sequence of forms in the Australian radiation, by reference to the characters of the dentition and foot-structure, the latter being considered for the most part separately. In the present section a general statement is given of the phylogenetic \* conclusions which may be drawn from their combination.

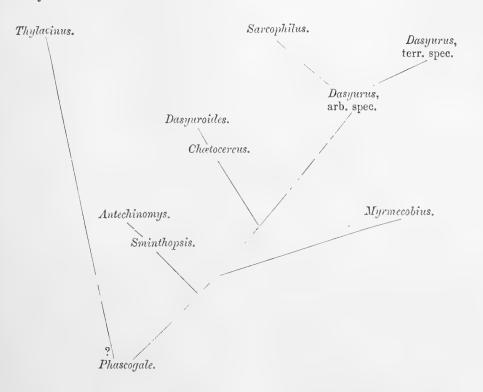
The accompanying plan, showing the main lines of the radiation, may be consulted as preliminary to the more detailed statement of generic and specific relationships given below.



\* Cf. closing paragraph of introductory section.

## DASYURIDÆ.

Beginning with the hypothetical stem-form, to which we assign the characters of the Didelphyidæ, we first note the fact that the radiation has proceeded along two primary lines. One of these, distinguished by its insectivorous-carnivorous dental evolution, and by its arboreal-terrestrial foot-evolution, in which the primitive eleutherodactylous condition of the digits has been retained throughout, leads to and culminates in the present family.



As shown by the dentition, the stem-form for the Dasyuridæ must have been a small species of *Phascogale*. Considering size, dentition, and foot-structure together it is probable that *P. flavipes* makes the closest approach to this prototypal form. The dental evolution of the predominant section of the family, or Dasyuriæ, has been referred to as homogeneous and progressive throughout, but the general sequence is disturbed by the occurrence of successive lines of terrestrial modification in foot-structure. We are thus obliged to recognize a main insectivorous-carnivorous arboreal line extending through the species of *Phascogale* and ending in *Dasyurus*. *Sminthopsis*, which has been referred to as, on the whole, more primitive than *Phascogale* in dentition, this remark referring chiefly to the less reduced or wholly unreduced character of the posterior premolars, in reality represents a terrestrial derivative of that genus, the various species, beginning with *S. leucopus*, showing successive stages in the development of a digitigrade type of pes. The small size of the species of *Sminthopsis* and their primitive dental characters, together with the transitional type of pes presented by *S. leucopus*, distinguish them from the larger terrestrial forms, and establish the fact of

their origin from a diminutive form of Phascogale. Antechinomys is a derivative of Sminthopsis, since it shows the same dental characters as the latter genus, and a more advanced stage of the same digitigrade modification of the pes characterizing that genus. Chatocercus cristicauda represents a terrestrial modification of Phascogale, which parallels Sminthopsis, but is distinguished by its dental characters and size as a derivative of a larger species. Dasyuroides represents a more advanced member of the same terrestrial line leading to Chatocercus. Within the genus Dasyurus we find D. hallucatus directly continuing the evolution of Phascogale in size, dental characters, and foot-structure. The advanced carnivorous form D. maculatus represents a further continuation of the same line and also its culminating point as far as the arboreal evolution is concerned. D. viverrinus and D. Geoffroyi, which are intermediate between the two last-named species in dentition, represent terrestrial derivatives in respect to foot-structure. Of the two species D. viverrinus is the more advanced, the hallux having Sarcophilus, which, in dentition, represents the culminating entirely disappeared. stage of the carnivorous evolution of the Dasyurinæ, is a terrestrial plantigrade derivative of Dasyurus. It has no relation with the remaining specialized carnivorous form Thylacinus.

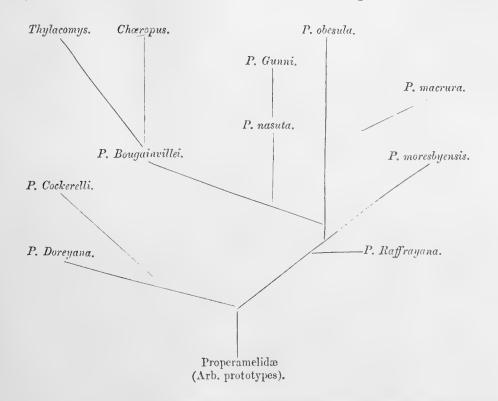
The foot-structure of *Myrmecobius* cannot be relied on for evidence of the special affinity of the animal. A close study of the dentition shows a balance of evidence in favour of derivation by retrogression from *Phascogale* rather than any direct relation with the Mesozoic Mammalia.

Thylacinus, so far as one may judge from the dentition and foot-structure, may be a derivative of *Phascogale*; if this is the case, it must be derived from a very primitive form of the latter genus, since it retains the original proportions of the posterior premolars. The evidence of the dentition, however, favours a relation with the Sparasso-donta of the South-American Miocene, the most important considerations being, first, that the dentition is well advanced in the carnivorous evolution, but its characters are in many respects different from those gradually developed in the Dasyurinæ and perfected in *Sarcophilus*, so that *Thylacinus* comes to occupy an isolated position in the Australian family, and, secondly, that the dentition resembles that of the carnivorous Sparassodonta in exactly those characters in which it differs from that of *Sarcophilus*. This may not be regarded as indicating that the Dasyuridæ are the descendants of Sparassodonta through forms like *Thylacinus*, but that *Thylacinus* is a foreign element in the Australian series.

# PERAMELIDÆ.

The line of evolution leading to the Dasyuridæ has already been referred to as one of two primary lines along which the Australian radiation has proceeded. The fundamental characters of the second line include an insectivorous-omnivorous progression in dentition, coupled with a continuation of the arboreal evolution of the stem-form in footstructure, up to what has been designated as the second arboreal phase or that in which syndactylism appears. The arboreal evolution of the pes culminates in the Phalangeridæ, but the dental evolution changes from omnivorous to herbivorous, and only culminates in terrestrial derivatives of that family. The latter include the Macropodidæ, Diprotodontidæ, and Phascolomyidæ. The present family and the Notoryctidæ are early terrestrial derivatives of the same general line, in which the dental evolution has been arrested at the omnivorous or insectivorous stage, thence proceeding in special directions.

The relations of the Peramelidæ are shown by the following characters :—(a) the retention of the polyprotodont modification of the antemolar teeth; (b) the development of omnivorous modifications of the molars; (c) the development of terrestrial, and more or less digitigrade, modifications of the pes, the latter being otherwise of an arboreal



phalangerine type. The first two characters indicate a general ancestral relation of the Peramelidæ to the remaining members of the main line, with the partial exception of the Notoryctidæ, while the third is a primary character of divergence. The presumed common ancestors of the Peramelidæ and Phalangeridæ are designated in the general plan (p. 192) as Properamelidæ (hyp.).

The present family is notable for the paucity of characters of generic rank. Its special evolution largely concerns the distribution of the species of *Perameles*. The two forms *Thylacomys* and *Chæropus* are independent derivatives of a form not far removed from *Perameles Bougainvillei*.

No member of the family combines the characters of a stem-form. *P. Doreyana* and *P. Raffrayana* are prototypal in their molar patterns, which are only slightly specialized in an omnivorous direction from the insectivorous type presented by the Didelphyidae and smaller Dasyurine. *P. Cockerelli* and *P. Doreyana* are prototypal in the proportion

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of the pes, which shows on the whole little departure from the phalangerine type. Both species are specialized in the reduction of the upper incisor formula and in the reduction of the plantar pads. *P. Cockerelli* is more specialized than *P. Doreyana* in its molar patterns. *P. Raffrayana* is not far removed from the stem-form of all the Australian mainland species, as shown by its retention of a full upper incisor formula, in common with all of the latter, retention of prototypal characters in the molars, retention of more primitive proportions of the pes and of plantar pads.

The evidence of the dentition and foot-structure will be seen to favour the view of a Papuan origin of the family, the three forms *P. Doreyana*, *P. Raffrayana*, and *P. Cockerelli*, possessing the most primitive characters, being confined to New Guinea, while all the advanced forms are Australian.

Thomas (1888) has remarked that the Australian species fall into two series typified by P. obesula and P. Gunni respectively. These divisions indicate two lines of development, giving rise respectively to short- and long-footed types. The former includes P. obesula, with its dwarfed relative P. barrowensis, and P. macrura, the latter the remaining species of Perameles, together with Thylacomys and Chæropus. The short-footed forms are, speaking generally, also distinguished by the retention of the original shortened condition of the muzzle, in which character they are even more primitive than P. Raffrayana, and by the possession of highly specialized molar patterns, the latter being of the most advanced type found in the family.

Assuming a Papuan origin of the family, the question arises as to whether the Australian mainland species are derivatives of a single stem-form or are diphyletic. This question is not easy to decide because of the lack of adherence to type which is so conspicuous a feature of the whole family. The Papuan species P. moresbyensis is, as pointed out by Thomas (1888), closely allied to the North-Australian P. macrura. It represents a very slight advance on P. Raffrayana in foot-structure, and a very decided advance in its molar patterns, the latter being almost as specialized as those of P. obesula. P. macrura is not, as might be expected, prototypal to the southern and Tasmanian P. obesula, but is more specialized both in dentition and foot-structure. The long-footed series must be traced to a form combining the dental characters of P. Bougainvillei with the pedal characters of P. nasuta. The presence in New Guinea of P. moresbyensis with affinities with P. macrura and P. obesula appears at first sight to indicate that there has been a differentiation in New Guinea of two stem-forms, one combining a primitive type of dentition with a slightly elongated type of pes, the other combining a specialized type of dentition with retention of the original shortened type of pes. It is much more probable, however, that P. moresbyensis has arisen independently of the Australian forms P. macrura and P. obesula, and has become specialized in dentition. If this is the case, it bears the same relation to P. Raffrayana as P. Cockerelli does to P. Doreyana. P. Cockerelli, it will be observed, is also independently specialized in its molar patterns. There is a remote possibility that the presence of P. moresbyensis in New Guinea is secondary.

Of the mainland species P. macrura may be safely regarded as a more specialized offshoot of the same form which gave rise to P. obesula. The distribution of the two

series does not indicate that P. obesula is an original or ancestral form. P. nasuta, although recognized as a member of the long-footed series, is not far removed in the proportions of the pes from P. obesula. It is more primitive in foot-structure than its ally P. Gunni, with which it agrees in dentition. Both forms are more primitive than P. Bougainvillei in foot-structure, but more specialized in dentition. P. Gunni is undoubtedly a derivative of P. nasuta, and in this relation it is interesting to note the typically Tasmanian distribution of the latter and the South-east Australian distribution of the former.

*P. Bougainvillei* is probably the ancestral form of both *Thylacomys* and *Charopus*. The chief derivative features of *Thylacomys* are the further digitigrade development of the pes and the peculiar elaboration of the molars, in which an incipient hypocone, like that of *P. Bougainvillei*, has-been obliterated by displacement inwards of the metacone. It is interesting to compare the distribution of the two forms: *P. Bougainvillei* is West, South, and South-east Australian, and *Thylacomys* West, South, and Central Australian.

Charopus is the most specialized member of the family in foot-structure, and presents a great advance in this respect on *Thylacomys*, which comes second. *Charopus* is, however, to be regarded as an independent derivative of *P. Bougainvillei*, since it does not show the peculiar type of molar found in *Thylacomys*. It is interesting to note again the distribution, which includes, in this case, West and South Australia, with Western New South Wales and Victoria.

## NOTORYCTIDÆ.

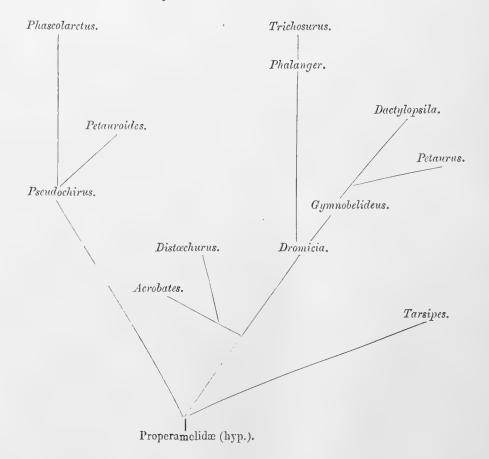
The different opinions as to the affinities of *Notoryetes* have already been mentioned. The available evidence is decidedly in favour of Dollo's \* suggestion of a relationship with the syndactylous Peramelidæ. In the general plan (p. 192) *Notoryetes* is placed as a terrestrial derivative of the Properamelidæ (hyp.), the presumed arboreal ancestors of the Peramelidæ and Phalaugeridæ. The main facts determining this position are as follows:—(a) Excluding *Notoryetes*, the primary lines of the Australian radiation may be defined as insectivorous-carnivorous and insectivorous-omnivorous in their composition, and may be distinguished by the respective absence and presence of a hypocone in the upper molars. *Notoryetes* is too far advanced in a special insectivorous reduction of the molars to show definite resemblances with either series. (b) The two main lines may also be distinguished by the fact that they are made up respectively of eleutherodactylous and syndactylous types, *Notoryetes* showing definite affinities with the latter. (c) Unlike all the remaining members of the syndactylous line, with the exception of the Paramelidæ, *Notoryetes* has retained the polyprotodont modification of the antemolar teeth, indicating

<sup>\* &</sup>quot;Caractères communes aux Peramelidæ et aux Notoryctidæ, polyprotodontie, prédominance du quatrième orteil, réduction du deuxième et du troisième, syndactylie de ceux-ci, entocunéiforme allongé, caisse tympanique volumineuse, rotule osseuse, poche s'ouvrant en arrière. Ces deux familles proviendraient-elles d'un ancêtro commun?" (Dollo, 1899.)

that its divergence as a terrestrial type must have taken place, as in the case of the latter family, at a comparatively early stage. (d) Its Central-Australian range and the probability of a Papuan origin of the Peramelidæ do not favour the view of a very intimate relationship with the latter family.

## PHALANGERIDÆ.

The phylogenetic position of this family may be estimated as follows:--(a) By the retention in foot-structure of the second arboreal stage through which all the remaining members of the second or syndactylous line have passed; (b) by the appearance of the diprotodont modification of the antemolar teeth; (c) by the loss of the insectivorous characters of the molar cusps; (d) by the retention of a number of dental characters ancestral to those of the Macropodidæ, Diprotodontidæ, and Phascolomyidæ. In respect to character a the family is prototypal. In characters b and c it is more advanced than the Peramelidæ and Notoryctidæ.



The Phalangeridæ are the derivatives of minute insectivorous or incipient omnivorous prototypes combining the dental characters of the more primitive of the Peramelidæ with the type of pes at present characteristic of the group. The diprotodont modification was developed in these forms as an insectivorous adaptation primarily affecting the median lower incisors.

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The foot-structure is so homogeneous throughout the family that it may practically be neglected in making a phylogenetic arrangement of the genera. Evolution has proceeded along two main lines leading respectively to the Phalangerinæ and Phascolarctinæ, the chief distinctive features of these being the development of selenodont and bunodont modifications of the molars. A third subsidiary line, represented by *Tarsipes*, is characterized by dental retrogression and the development of a more advanced stage of arboreal elaboration in the pes than is found in the remaining members of the family.

The facts of the dentition show that the phascolarctine line cannot be derived from the phalangerine one, or *vice versá*. In the former the most primitive form is *Pseudochirus*. *Petauroides*, which agrees with *Pseudochirus* in dentition, must be placed as a derivative of that genus on account of its volant character. *Phascolarctus*, the terminal form, represents, in all its dental characters, a direct advance on *Pseudochirus*\*.

In the Phalangerinæ the most primitive members are Acrobates, Distæchurus, and Dromicia, these forms showing in some respects an interesting approximation to an insectivorous prototype. Acrobates and Distachurus are more closely related to one another than either of them is to Dromicia. They are derivatives of a common stemform, from which they have become specialized by the reduction of the posterior premolars; they have diverged through the development of Acrobates into volant animals. In the extent of reduction of the posterior premolars, and in the development of special insectivorous characters in the lower median premolars and first lower molars, Distachurus represents a more advanced form. Dromicia shows a more marked tendency towards the omnivorous modifications characteristic of the larger specialized genera. The volant form *Petaurus* occupies a derived position with reference to *Dromicia*, so that its non-volant relative Gymnobelideus, which is said by Thomas to be identical with it in dentition, is probably a derivative of that genus. Dactylopsila represents a direct advance in dentition on Petaurus, and is to be regarded as another derivative of Gymnobelideus. The derivation of the genus Phalanger is a somewhat difficult matter. As noted above, it represents a direct advance on *Dactylopsila* in the reduction of the vestigial teeth, especially the median upper premolars, and also in the development of incipient herbivorous characters in the molars. On the other hand, it departs from both Dactylopsila and Petaurus in the abrupt substitution of herbivorous for insectivorous characters in the incisors, and of well-developed sectorial premolars, somewhat like those of Dromicia nana, for vestigial ones. Trichosurus is plainly a slightly more specialized form of *Phalanger*. The fossil form *Burramys* (Broom, 1896) should probably be included in the Phalangerine, on account of the lack of development of the median premolars, which removes it from the Bettongiinæ. The characters of the sectorial premolars

\* In connection with the present interpretation of the affinities of *Phascolarctus* it is interesting to note that in the structure of the manus the animal agrees with *Pseudochirus*, and differs from all the remaining members of the family, the first and second digits being arranged so as to oppose the third, fourth, and fifth. The peculiar straightening out of the normally inflected angle of the jaw, which is so noteworthy a feature of *Phascolarctus*, is also indicated in *Pseudochirus Cooki*, and to a certain extent in some other species. Other species of *Pseudochirus*, such as *P. Albertisi* and *P. Corinnæ*, have the angle fully inflected as in normal phalangerine forms.

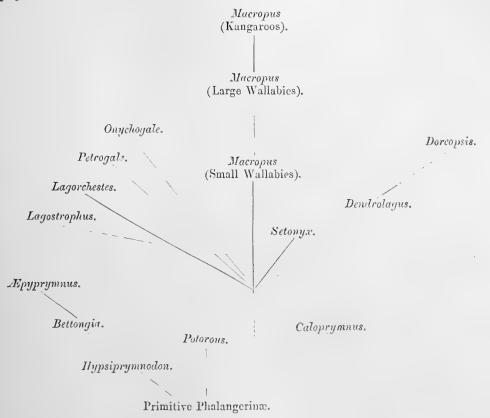
offer a slight suggestion of special relationship between *Burramys*, the Bettongiinæ, and *Phalanger*.

Spencer has recently described under the designation Wyniardia bassiana a fossil Marsupial from the Table Cape Beds of Tasmania, in which he identifies characters of resemblance to both polyprotodont and diprotodont sections, and which he states "may be regarded as intermediate between the former and the latter, and as indicative of a stage in the development of the Australian Marsupials when the ancestors of the recent Diprotodontia were beginning to diverge from the original polyprotodont stock, from which they have been developed within the limits of the Australian region." This view is based on a detailed study of the parts preserved, which unfortunately include neither the dentition nor the front or hind feet. While it would be difficult to add to the excellent comparisons presented by Spencer, it is probable that the reference to the animal as an intermediate form must be excluded, if for no other reason, on account of its large size. Throughout the present paper the effort has been made to show that the actual prototypal or central forms must have been comparatively minute insectivorous animals. In the Didelphyidæ, which occupy an ancestral position to all of the Australian Marsupials, we find that the most primitive forms are the minute animals belonging to the genera Marmosa and Peramys. The species of the Oligocene Peratherium, which is closely related to the preceding genera, and probably the actual ancestor of the Australian series, were animals of small size. The most primitive members of the Dasyuridæ, and even of the Phalangeridæ, are of like proportions. Thus all the forms which approach the hypothetical intermediate type are of small size. Not only this, but the diprotodont modification itself may, as already explained, be shown to represent an insectivorous adaptation which could only have taken place in comparatively small animals. The relations of Wyniardia are more probably with one of the advanced genera, such as Pseudochirus, Phascolarctus, or Phalanger.

# MACROPODIDÆ.

With regard to the relationships of the Potoroinæ and Bettongiinæ it has been mentioned above that the modifications of the pes appear to contradict the general subfamily division and generic sequence as determined by reference to the dentition, *Hypsiprymnodon* showing a closer approach to *Potorous* than to *Bettongia*, while *Caloprymnus* shows a closer approach to *Bettongia* than to *Potorous*. There is no doubt, however, that the correct plan of division is according to dentition, because the divergent characters of the sectorial premolars, on which the dental division mostly depends, are of a very fundamental kind. It is impossible to derive the straight and comparatively unelaborated sectorials of the Potoroinæ and Macropodinæ from the multigrooved rotated sectorials of *Hypsiprymnodon*. On the other hand, while *Bettongia* is widely separated from *Hypsiprymnodon* in foot-structure, it must have passed through a *Hypsiprymnodon*-stage in arriving at its present condition. The Potoroinæ have also passed through a *Hypsiprymnodon*-stage in foot-structure, but this does not prove affinity with that genus, because there was probably, in the phalangerine ancestors of both forms, as in the existing Phalangeridæ, several types of dentition, but only one general type of pes. *Potorous* has retained a fairly primitive type of pes on account of its more fossorial and less saltatorial habit.

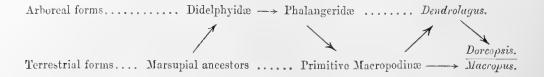
The connections of the Bettongiinæ with the Phalangeridæ are doubtful, but the characters of the sectorials afford a slight suggestion of a common origin of three lines ending in the present division, in *Burramys*, and in *Phalanger*. *Hypsiprymnodon* is closely allied to, if not itself the actual ancestor of *Bettongia*. The annectant species is *B. penicillata*. *Bettongia* is further the prototype both in dentition and foot-structure of  $\mathcal{E}pyprymnus$ .



In the Potoroinæ, a common stem-form, not far removed from *Petaurus* or, better, *Gymnobelideus*, has given rise to *Potorous platyops* as a short-limbed fossorial form and to *Caloprymnus* as a free plains living cursorial form. The former appears to have spread from West Australia castward to Tasmania, giving rise to the remaining species. *Caloprymnus* shows the closest approach of all the Potoroinæ and Bettongiinæ to the Macropodinæ.

In the brachyodont section of the Macropodinæ we have first the genus *Dendrolagus*, representing an arboreal derivative of some primitive form rather than a specialized one such as *Macropus*. *Dorcopsis* represents a secondarily terrestrial derivative of *Dendrolagus*, which begins to parallel *Macropus*. The sequence of modifications of the sectorial premolars and the retention of certain primitive characters in the general dentition preclude the possibility of a derivation of *Dendrolagus* from *Macropus* through *Dorcopsis.* The evolution of the series indicates a migration from Australia to New Guinea.

The derivation of *Dorcopsis* is interesting from a general biological standpoint, inasmuch as there is direct evidence that in the whole course of its evolution it has been three times terrestrial and twice arboreal. The alternation of arboreal and terrestria phases may be expressed as follows :---



Setonyx does not appear to be nearly related to *Dendrolagus* and *Dorcopsis*, although it agrees with those forms in the peculiar characters of the sectorials and the small degree of hypsodontism of the molar crown. It is removed partly by its small size and complete canine reduction, and partly by the purely terrestrial character of the pes; all the secondarily terrestrial species of the brachyodont line, namely those of *Dorcopsis*, are Papuan, while *Setonyx* is Australian. It is probable that *Setonyx* is a member of the Small Wallaby section of the genus *Macropus* which has assumed feeding-habits somewhat similar to those of the tree-living *Dendrolagus*. The fact that *Dorcopsis*, although terrestrial, continues the sectorial evolution begun in *Dendrolagus*, shows that such developments do not necessarily begin and end with arboreal life.

The members of the hypsodont series are best arranged as representing a minor radiation, the divergent characters of the various genera being, for the most part, associated with differences of environment, and not affecting to any appreciable extent the dentition or foot-structure. Onychogale, however, appears to be more nearly related to Macropus than to the remaining genera, and Lagorchestes, of which Lagostrophus is a modified form, appears to be similarly related to Petrogale. The typical and predominant forms of this radiation are the species of Macropus. It is an interesting fact that this genus, in which the most important stages of the grazing evolution are to be found in point of numbers of species, stands out as the successful type of the family, just as the genus Phalanger does in the Phalangerinæ, and Pseudochirus in the Phascolarctinæ. Within the genus the Small Wallaby, Large Wallaby, and Kangaroo sections represent successive stages of the same graminivorous and saltatorial evolution. The predecessors of the Small Wallabies appear to have undergone a distributional differentiation with the production of the various species comprising the section. The latter appear to have given rise locally to Large Wallabies, and these in turn to Kangaroos. This sequence is indicated, first, by the obvious affinities and wide distribution of the Small Wallabies; secondly, by the fact that it is possible to differentiate between small and large premolared species, especially in the two lower sections; and, thirdly, that there are indications of relationships between certain members of the Small and Large Wallaby sections having similar geographical ranges. Thus the West-Australian Small Wallaby (Macropus Eugenii) is prototypal to the Large Wallaby (M. irma) of the same region, and also to

the more southern M. Greyi, and a similar relation is observable between M. Bedfordi and M. dorsalis. The existing Kangaroos are apparently the descendants of successively small-premolared forms.

### THYLACOLEONTIDÆ.

The evidence available concerning the phylogenetic position of Thylacoleo is very incomplete, partly on account of the absence of annectant types, and partly because of the lack of information as to the foot-structure. The dentition furnishes indications of two lines of development-one of normal phalangerid type, represented by the diprotodont modification, involving enlargement of the median incisors and reduction of the posterior antemolar teeth, and by the enlargement of the posterior premolars as sectorials; the other of a special carnivorous type, represented by the piercing development of the median incisors, the reduction of the molars, and the excessive enlargement and smoothing of the cutting-edges of the sectorials. This evidence does not warrant a closer estimation of the relations of the animal than that it is a derivative of the Phalangeridæ, which, unlike all the remaining derivatives of that family, has, after the passage of the omnivorous stage, or even during the herbivorous stage, become carnivorous instead of continuing the herbivorous evolution in the normal way.

# PHASCOLOMYIDÆ AND DIPROTODONTIDÆ.

The vailable evidence concerning the phylogenetic position of these families may be briefly mmed up as follows :-- It is possible to recognize, both in the dentition and foot-strikure, three kinds of characters-primary ones of phalangerine affinity, secondary ones of a vity with one another, and characters of divergence. The first refer to the diprotodon haracter of the dentition and the bunodont origin of the molars, and, in the foot-struture, the reduction of the second and third digits, enlargement of the fourth, and opsability of the hallux. The second refer to the rodent modifications of the incisors, the eduction of the premolars to the posterior pair, which present somewhat similar patterns, d the terrestrial plantigrade modification of the pes. The divergent characters refer the retention in the Diprotodontidæ of the upper lateral incisors, the presence of lophod rooted molars, and the shifting of the walking axis to the outer side of the pes, with largement of the astragalus, calcancum, and cuboid, fusion of the mesocuneiform with entocuneiform, and functional retention of the hallux as an internal balancer. In Phascolomyidæ the upper lateral incisors have been obliterated, and the molars have one rootless and rodent in their character while remaining bunodont. There has be re-development of the second and third digits by which the shifting of the walking ax f the pes has been avoided. The latter is thus of a more normal or less differentiate. The antermolform has been avoided. in the same way as in other the not been modified as a balancer, but has been reduced second series.—ZOOLOGY,

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These relations point to the origin of the Phascolomyidæ and Diprotodontidæ from a common stem-form, which is in turn traceable to the Phalangerinæ. The absence of annectant types makes it impossible to fix the affinities of the two families with any existing phalangerine genera.

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The Question of the Time and Mode of Origin of the Australian Radiation.

Partial reference has already been made to the views of different writers as to the time and conditions under which the Australian fauna originated in dealing with the identification of the stem-form.

With regard to the direction from which the ancestral forms entered Australia there appear to be only two possibilities—that they came either from the North, as supposed by Wallace (1875) and Lydekker (1896), or from South America, as thought by Ameghino (1891) and Spencer (1896).

According to Lydekker's view the Dasyuridæ and Didelphyidæ may have originated from common ancestors inhabiting South-eastern Asia, from which region the former family migrated into Australia, while the latter one dispersed in two directions into Europe and North America. In advocating a South-American origin of the family Spencer takes exception to this view on the general grounds of the paucity of polprotodont types in New Guinea, through which the ancestral forms would have pass the difficulty of explaining the absence of Didelphyidæ in Australia, and the la

lestion With reference to the first of these objections, it may be pointed out that the Guinea does not concern so much the relative numbers of polyprotodont forms in Ner. and Australia, since, in view of the greater area and greater possibilities of dis differentiation of the latter region, we may expect to find, as we actually question is differentiation of the latter region, we may expect to find, as we actually question is contains a greatly predominating portion of the polyprotodont fauna. T'ay be fairly rather whether or not New Guinea contains prototypal forms. This in addition to answered in the affirmative. On referring to the Dasyuridæ we find than Thorbeckiana, the specialized forms Phascogale Doriæ, P. dorsalis, P. Wallacei, and s occurs there as which are confined to the Papuan region, the prototypal form P. flavie Peramelidæ all well as in the eastern and south-eastern parts of Australia. Of three genera of the the species presenting prototypal characters are Papuan. Of thapuan representative Phalangerinæ which present primitive characters, Dromicia has on confined to that region. (D. caudata), Acrobates one (A. pulchellus), while Distachurus is New Guinea, and this It is true that migrations may have taken place from Australiques there is evidence of factor should be kept in mind as bearing on the question, be to a certain extent of the such migration in the distribution of Phalanger, Dorcopsis, and Small Wallabies.

Small Wallabies. Spencer's further objection as to the lack of evidence couly the indications of faunal of Marsupials in Asia is, of course, unanswerable. We have community between Asia and North America, poir tog now Behring Straits, and the occurrence of fossil opossums in the Oligocene rocks of Europe and North America.

The difficulty as to the absence of Didelphyidæ in Australia presents itself whether we assume a northern or a South-American origin. Spencer explains the condition by assuming that the land-connection between South America and Australia was broken at a time soon after the ancestral forms of the Australian Marsupials had passed across, and while the Didelphyidæ were being developed in the more northerly portion of South America. If this explanation be the correct one, we may ask why the form *Thylacinus*, whose affinities are decidedly with the South-American Sparassodonta, gained access to the Australian region, while the Microbiotheriidæ, some of which at least present the characters of the Didelphyidæ and are found fossil in the same formations, were excluded. The same question might be asked of the Edentate fauna of those formations. There is also the difficulty of recognizing a definite period of rupture of the antarctic connection and that of accounting for the origin of the Didelphyidæ of the northern hemisphere.

In a former paper the writer referred to the difficulty presented by the absence of the Didelphyidæ in Australia as an apparent one, due to the recognition of the family as a modern derived group. We are accustomed to look upon the Didelphyidæ not only as contemporaries of the Australian Marsupials, but also as forms possessing fixed family characters. When we consider, first, that the modern family represents an exceedingly plastic group, the members of which are at the present time undergoing an incipient radiation; secondly, that the structural differences separating the family from the Dasyuridæ and the presumed common ancestors of the Peramelidæ and Phalangeridæ are extremely slight; and, thirdly, that the ancestors of the Australian fauna on entering that region must have found themselves under conditions most favourable for differential development in a place offering diverse and unoccupied sources of food-supply-it is not difficult to conceive that the Didelphyidæ in establishing the foundation of an extensive radiation may have thrown aside their original didelphyid characters. It seems preferable to believe that the Didelphyidæ were formerly present in Australia, as well as Europe and North and South America.

The evidence in favour of a South-American origin of the Australian fauna is based partly on the general faunal evidence of an antarctic land-connection, concerning which there seems to be little doubt, and partly on the presumed special resemblances between the Australian fauna and that of the Patagonian Miocene. Fuller reference to these resemblances will be made in the next section, but it may be mentioned at this point that those occurring between the diprotodont forms of both series are of too general a kind to be interpreted as indicating more than a parallel development from common ancestral types, and that those between *Thylacinus* and the Sparassodonta do not indicate a South-American origin of the Australian fauna, since there are no definite reasons for believing *Thylacinus* to have a special affinity with the Dasyuridæ, and it has not the slightest resemblance to a prototypal form. The evidence of a connection of the Patagonian with the Australian forms at present limits itself to the possibility that *Thylacinus* may have migrated from South America, and a further possibility of a former distribution of

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Didelphyidæ across the Antarctic continent with centres of radiation in Australia and South America.

It may be mentioned in passing that if an antarctic connection existed there is evidence from the Marsupials that it did not include Tasmania, because the fauna of that region is made up for the most part of specialized forms having identical or prototypal representatives on the mainland. In the Dasyuridæ we have *Phascogale minima*, a typically Tasmanian form, and in *P. Swainsoni* a closely related form inhabiting Tasmania and the adjacent portion of the mainland. While both of these forms are fairly primitive, they are specialized as compared with the Papuan and Australian form *P. flavipes*. Of the species of *Dasyurus*, two are common to East Australia and Tasmania. One of them, *D. maculatus*, is the most specialized member of the Dasyuridæ, with the exception of *Sarcophilus* and *Thylacinus*. The remaining form, *P. viverrinus*, is only slightly less specialized. The actually primitive species, *D. hallucatus* and *D. albopunctatus*, are North Australian and Papuan respectively. Nothing can be inferred from the present Tasmanian distribution of *Sarcophilus* and *Thylacinus*, since both are found fossil on the mainland.

Passing to the Peramelidæ we find two Tasmanian forms, P. Gunni and P. obesula. The former species is easily shown to be a specialized derivative of the East-Australian P. nasuta, while the latter, itself one of the most specialized members of the family, enjoys a wide distribution on the mainland.

In the Phalangeridæ only one of the three primitive genera, namely *Dromicia*, possesses Tasmanian representatives. These are *D. lepida*, a fairly primitive type, possibly ancestral, in some respects at least, to *Gymnobelideus*, and *D. nana*, which is not only highly specialized but is also not typically Tasmanian, since remains of it have been found in cave-deposits of New South Wales.

Passing to the Potoroine division of the Macropodidæ, we find in the distribution of the species of *Potorous* a clear case of migration from Australia to Tasmania. Proceeding from the West-Australian P. *platyops* we find a progressive specialization passing through the South-Australian P. *Gilberti*, the New South Wales form P. tridactylus, to the Tasmanian P. "apicalis."

These facts are suggestive of a comparatively recent derivation of the Tasmanian fauna from forms inhabiting the adjacent portions of the mainland.

As to the time at which the ancestral forms of Marsupials gained access to Australia, the most diverse opinions have been expressed. Owen supposed the group to have been present there in Mesozoic times, while Wallace estimated the time of entry as Jurassic. According to Spencer's view it was Cretaceous, while in Lydekker's opinion it was early Eocene. While it is interesting to notice in these opinions an increasing appreciation of the newness of the Australian fauna, it is probable that even the lowest estimate of the duration of their evolution is still much too large. In the first place, on comparing the Australian radiation with the general radiation of Placentals, we note the fact that the former is in a backward stage of development. For example, the differentiation has not proceeded beyond the production of families, although, as recognized by several writers, these families have the potential value of placental orders. In the existing didelphyid

radiation, which is of still more recent origin, differentiation has not proceeded beyond the production of genera. Furthermore, in some cases, even the family differentiation has proceeded to such a meagre extent that family divisions are based on comparatively trivial characters. In fact, the Marsupials present much the same composition as must have existed at a very early stage of the placental radiation. The Australian radiation, confined as it has been, has not proceeded to the stage of very great specialization or to over-population, with the obliteration of less specialized intermediate types. We have such cases as that of Myrmecobius, in which, while dental reduction has taken place as a result of ant-eating habits, it has not proceeded to the stage of total obliteration of the teeth, as in placental ant-eating forms. All these facts indicate that the Australian radiation is of comparatively recent origin, and if, as appears probable from the central position of the Creodonta, the placental radiation began in the early Eocene or late Cretaceous, it seems unlikely that the marsupial radiation could have begun until well on into the middle of the Tertiary period. To this structural evidence we may add the final fact that the Didelphyidæ are the ancestral forms of the Australian radiation, and that they are typically Oligocene forms.

# THE MAJOR CLASSIFICATION OF THE MARSUPIALS IN GENERAL.

The recognition of the Dasyuridæ as a primary division in the Australian radiation raises a doubt as to the applicability of Owen's classification of the Marsupials into Polyprotodontia and Diprotodontia. The difficulty presented by the Peramelidæ, which while essentially polyprotodont possess a syndactylous type of pes otherwise characteristic of the diprotodont series, has already been commented upon by Flower, but the relations of this family have been explained by Thomas on the assumption that their syndactylism has been independently acquired.

The diprotodont modification has obviously been derived from a polyprotodont one; it is traceable to an insectivorous specialization of the median lower incisors. The members of the diprotodont section may be shown to have passed through an omnivorous stage, and to have possessed omnivorous molar characters similar to those of the primitive Peramelidæ. The primitive Phalangeridæ are to be connected with the Peramelidæ not only as syndactylous, but also as omnivorous forms, rather than separated as Diprotodontia, while the Dasyuridæ are to be separated as eleutherodactylous and progressively carnivorous forms.

In selecting a differential character on which a classification may be based we are obliged to turn to other structures than the dentition. The absence of a definite hypocone in the upper molars of the Dasyuridæ would furnish exactly the kind of character required, since the addition of this element is highly characteristic of the omnivorous evolution, were it not for the aberrant developments presented by *Notoryctes* and *Thylacomys*. Turning to the foot-structure, we find in the respectively eleutherodactylous and syndactylous condition of the pes a differential character of sufficient importance and applicability. If by a major classification we intend to designate primary lines of descent, the division should not be into Diprotodontia and Polyprotodontia, but rather into Syndactyla and Diadactyla.

Owen's divisions of the Polyprotodontia naturally included the Didelphyidæ as well as the Australian Dasyuridæ and Peramelidæ. Such a group as the Didelphyidæ could have no place in the above classification on account of the fact that its component genera present both syndactylous and eleutherodactylous types of foot-structure. The Epanorthidæ present similar difficulties both with reference to this and to Owen's classification. In commenting on the systematic position of *Cænolestes*, the living representative of the Epanorthidæ, Thomas remarks: "As to the general classification of the Marsupials, a subject already difficult in view of the puzzling possession by the Peramelidæ of polyprotodonty combined with syndactyly, *Cænolestes* apparently only adds to the difficulty, being non-syndactylous like most polyprotodonts, while it has by dentition nothing whatever to do with them. If anything, however, this fact tends to confirm the tentative opinion expressed in the 'Catalogue of Marsupials,' that the primary division of the order should be by dentition and that syndactyly is a secondary character. Were syndactyly the primary character, the Epanorthidæ would be thrown with the Didelphyidæ with which they have clearly nothing to do, and separated from what appear to be their nearest allies, the Phalangeridæ."

Difficulties such as these are only apparent, arising from the attempt to apply the same principles of classification to isolated and independently evolved groups. In the first place, how have the various marsupial faunas arisen? As to the origin of the Didelphyidæ, the evidence is wholly unsatisfactory. They may have come from a spur of an earlier Jurassic radiation, or they may have been themselves the original stock of the marsupial division. As to the subsequent history of the family, the evidence is more complete. They enjoyed a wide distribution in the northern hemisphere during the Oligocene period, and were probably present in South America as well. The Australian fauna shows indications of didelphyid origin. The existing Didelphyidæ of South America represent a minor radiation, proceeding from forms approximating closely, so far as may be judged from the dentition, to Peratherium. It is extremely probable that at least some of the Miocene Microbiotheriidæ of South America were in reality Didelphyidæ, and were the ancestors of the Epanorthidæ and their allies and of the Sparassodonta. In other words, the derivation of the different marsupial faunas is the history of successive radiations of Didelphyidæ. Now it will be apparent that it is impossible to apply the same principles of classification to two geographically isolated faunas unless their resemblances are of such a nature as to lead us to suppose that two or more differentiated portions of one of them represent migrated portions of the other. In the case of the marsupial faunas we have to ask whether the resemblances between them can be traced to such migration or whether they are the result of convergent development.

There appears to be no possibility of a connection of the existing didelphyid radiation with the Australian one, the former being much too modern. We may take advantage of this to point out certain resemblances as due to convergent development. We notice especially that the Didelphyidæ parallel the Dasyuridæ in the tendency towards reduction of the posterior premolars. Certain of them parallel the Phalangeridæ in the development of syndactylous modifications of the pes, and *Caluromys* shows signs of the parallel development of omnivorous characters in the molars as in the latter family. These resemblances are not indicative of affinity except in the broader sense that they possibly imply a similar potential of evolution carried over from common ancestors.

The case of the South-American Miocene and Australian groups is admittedly difficult of discussion on account of the lack of definite information as to the primary differential characters of the former. The dental resemblances of *Thylacinus* to the Sparassodonta are sufficiently close to warrant a belief in their common origin. Even so, however, there is no evidence that the evolution of *Thylacinus* has been connected in any way with that of the Dasyuridæ, the reverse being indicated by the fact that the various forms of the Dasyuridæ present successive stages of a dental evolution, which, while carnivorous in its character as in *Thylacinus*, is otherwise of a totally different facies.

The fact that the diprotodont modification of the dentition occurs in the South-American as well as in the Australian forms has been regarded as a mark of affinity. As indicated above, even the most primitive forms of the existing Phalangeridæ are well removed as regards dentition from the condition which must have obtained at the time of introduction of the diprotodont modification. Furthermore, the origin of the peculiarly grooved sectorials of the Bettongiinæ is not illustrated in the Australian series. In view of the presence of such gaps in the series, we could not wish to deny the possibility that the prototypes of these forms may yet be found in the South-American group. The mere fact of the presence of diprotodont modifications in each series, however, means nothing. The development of a diprotodont modification has taken place in the Soricidæ, in the Rodentia, and in the Multituberculata. The bunodont molars of the Epanorthidæ resemble those of the Phalangeridæ, but such teeth have been developed in the Condylarthra and the Primates. If convergent development may occur between groups which have little in common beyond their mammalian character, how much greater is the chance of convergent development in smaller groups of common parentage? If resemblances between the Australian and the South-American groups are to be recognized as indicative of affinity they must not be of a broad general kind such as those already pointed out between the Epanorthidæ and their allies and the Australian diprotodonts, but must be of much more special application. The forms presenting them should not differ in a greater degree from one another than do the successively specialized genera of the Australian families. For all we are able to say at present, the South-American radiation may have proceeded on general lines of polyprotodonty and diprotodonty or on some other unrelated character.

If the above interpretations are correct, how are the Marsupials to be classified? The farther the identification of intermediate types proceeds, the more difficult becomes the systematic classification to which we are accustomed. We are now placed in the somewhat paradoxical position of attempting to recognize and characterize concrete groups which our knowledge of evolutionary sequence tells us could have had no separate existence. If natural classification recognizes lines of descent, major classification must recognize radiations, and distinctions of time and geographical distribution are as valuable as those of anatomical structure. From this point of view the Marsupials may be arranged as follows :---

- 1. Primary marsupial radiation.—Arboreal derivatives of Metatheria. Jurassic —? Arctogæic. Jurassic Mammalia in part. (The identification of this group is wholly problematical.)
- 2. Arctogaic and Neogaic didelphyid radiation.—Derivative of ?1. Oligocene—Lower Miocene. Didelphyidæ, Microbiotheriidæ ? in part.
- 3. Notogeic radiation. Derivative of 2. ? Mid-Tertiary recent. Dasyuridæ, Peramelidæ, Phalangeridæ, &c.
- 1. First Neogeic radiation.—Derivative of 2. Lower Miocene—recent (Cænolestes). Prothylacinidæ (Sparassodonta), Epanorthidæ, Decastidæ, Abderitidæ, &c.
- 5. Second Neogaic radiation .- Derivative of 2. ? Pliocene-recent. Existing Didelphyidae.

THE SYSTEMATIC ARRANGEMENT OF THE AUSTRALIAN FAMILIES.

In the case of the Australian radiation the systematic arrangement which most nearly expresses the lines of family derivation is as follows :---

- A. Diadactyla (second and third digits of the pes separate). Incisor formula  $\frac{4}{3}$ ; upper molars with no postero-internal cusp (hypocone). B. Syndactyla (second and third digits of the pes conjoined). a. Dentition polyprotodont. Incisor formula  $\frac{5-4}{3}$ ; posterior premolars well developed. Upper molars with paracone and metacone separate, with hypocone (except Thylacomys). Lower molars with well-developed talonid. Pes terrestrial, subdigitigrade ; Incisor formula  $\frac{4-3}{3-2}$ ; posterior premolars absent. Upper molars with conjoined paracone and metacone; no hypocone. Lower vestigial talonid. Pes terrestrial, plantigrade; hallux well developed, not opposable, with . . . . . . . . . . . . Notoryctid.e. secondary claw . . . . . . . . b. Dentition diprotodont. les arboreal; hallux well developed, fully opposable. Antemolar dentition primitive. Anterior upper premolars always, and vestigial intermediate teeth usually present. Functional incisor formula  $\frac{3}{1}$ . Median lower incisors piercing or trenchant. Molars rooted, brachyodont, quadrituberculate (except in Pes terrestrial; hallux not definitely opposable, reduced or absent. Antemolar dentition specialized. Anterior upper premolars and vestigial intermediate teeth absent. Pes plantigrade. Incisors scalpriform. Median premolars absent.
  - Upper lateral incisors present. Molars hypsilophodont, rooted. Pes with walking-axis external; axial elements of tarsus enlarged. Hallux retained as an internal balancer. Mesocuneiform fused with entocuneiform . . . . . . . . . . . . . . . . DIFROTODONTID.E.

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<ul> <li>Upper lateral incisors absent. Molars quadrituberculate, bunodont, hypsodont, rootless. Pes of normal proportions. Mesocuneiform free; hallux vestigial.</li> <li>Pes digitigrade; incisors trenchant. Median premolars developed as sectorials in young.</li> </ul>	Phascolomyid.e.
Incisor formula $\frac{3}{1}$ . Molars rooted, bunodont, brachybunodont and quadrituberculate, or lophodont. Sectorial premolars grooved . Incertæ sedis. Pes? Functional incisor formula $\frac{1}{1}$ . Incisors piercing.	Macropodid.E.
Sectorial premolars excessively enlarged and smooth-edged. Molars vestigial or absent	THYLACOLEONTIDÆ.

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#### EXPLANATION OF THE PLATES.

# PLATE 5.

# Illustrating the patterns of the upper teeth.

Nore.—In the preparation of Plates 5 and 6 the figures have been arranged, wherever convenient, in lines, indicative of adaptive sequence, and numbered accordingly. No attempt has been made to represent the relative sizes of the teeth, those of the smaller forms having been enlarged to a much greater extent than those of the larger ones for the purpose of illustrating, to the best advantage, the peculiarities of their patterns. In all of the crown-views the uppermost margin of a figure represents the anterior side, and the left-hand margin the internal side. In the profile views the left-hand margin represents the anterior side. The external profile is represented throughout in the upper molars and premolars, and the internal profile in the lower molars (except Pl. 6, figs. 14 & 15).

The numbers given in brackets are those by which the figured specimens are designated in the registers of the British Museum.

- Fig. 1. Peratherium sp. Right m. 2 reversed. a, crown; b, profile. (Lower Miocene, Antoign: No. 27807.)
  - 2. Sminthopsis leucopus, Gr. Left m. 2. a, crown; b, profile. (No. 52. 1. 13. 3.)
  - 3. Dasyurus maculatus, Kerr. Left m. 2 and m. 3. (No. 983 b.)
  - 4. Sarcophilus ursinus, Harr. Left m. 2 and m. 3. (No. 42 b.)
  - Myrmecobius fasciatus, Waterh. Left m. 2 and m. 3. a, crown; b, m. 3, profile (No. 76. 11. 27. 3);
     c, left m. 2, crown (No. 44. 1. 22. 21).
  - 6. Thylacinus cynocephalus, Harr. Left m. 3. (No. 65. 10. 9. 17.)
  - 7. Thylacinus spelæus, Owen. Left m. 2. (No. 43887.)

- Fig. 8. Perameles Doreyana, Quoy & Gaim. Left m. 3. a, crown; b, profile. (No. 95. 5. 8. 13.)
  - 9. Perameles Bougainvillei, Quoy & Gaim. Left m. 2. (No. 41. 1178.)
  - 10. Perameles obesula, Shaw. Left m. 2. (No. 87. 5. 18. 8.)
  - 11. Thylacomys leucura, Thomas. Right m. 2 and m. 3 reversed. (No. 83. 10. 19. 17.)
  - 12. Notoryctes typhlops, Stirl. Left m. 2. (No. 97. 11. 3. 13.)
  - 13. Distachurus pennatus, Pet. Left m. 1. (No. 94. 2. 14. 1.)
  - 14. Dromicia concinna, Gould. Left m. 1. (No. 60. 1, 5. 27.)
  - 15. Petaurus sciureus, Shaw. Left m. 1. a, crown; b, profile. (No. 245 d.)
  - 16. Trichosurus vulpecula, Kerr. Left m. 1. (No. 43. 8. 12. 40.)
  - 17. Pseudochirus peregrinus, Bodd. Left m. 2. a, crown; b, profile. (No. 55. 12. 24. 69.)
  - 18. Phascolarctus cinereus, Goldf. Left m. 2. (No. 253 c.)
  - 19. Caloprymnus campestris, Gould. Left m. 2. (No. 46. 4. 4. 45.)
  - 20. Dorcopsis luctuosa, D'Alb. Left m. 2. (No. 76. 10. 28. 3.)
  - 21. Lagorchestes hirsutus, Gould. Left m. 2. (No. 289 e.)
  - 22. Macropus giganteus, Zimm. Left m. 3. (No. 40. 2. 28. 1.)
  - 23. Macropus rufus, Desm. Left m. 3 (worn pattern). (No. 56. 4. 7. 2.)
  - 24. Phascolomys Mitchelli, Owen. Left m. 2 and m. 3. (No. 87. 3. 1. 3.)
  - 25. Diprotodon australis, Owen. Right m. 3 reversed. (No. 38609.)
  - 26. Metachirus opossum, Linn. Left m. 3. (No. 98. 9. 5. 9.)
  - 27. Caluromys philander, Linn. Left m. 2. (No. 51. 8. 30. 5.)
  - 28. Peramys Iheringi, Thomas. Left m. 2. (No. 61. 12. 2. 9.)
  - 29. Peramys americana, Müll. Left m. 2. (No. 55. 12. 24. 74.)
  - 30. Marmosa cinerea, Temm. Left m. 1. (No. 99. 4. 3. 23.)
  - 31. Hypsiprymnodon moschatus, Rams. Posterior upper premolar. (No. 1691 a.)
  - 32. Bettongia penicillata, Gray. a, median; b, posterior upper premolar. (Nos. 42. 6. 29. 16 and 46. 4. 4. 41.)
  - 33. Caloprymnus campestris, Gould. Posterior upper premolar. (Nos. 46. 4. 4. 44 and 46. 4. 4. 45.)
  - 34. Hypsiprymnodon moschatus, Rams. Crown view of fig. 31.
  - 35. Bettongia penicillata, Gray. Crown view of 32 b.
  - 36. Bettongia Gaimardi, Desm. Posterior upper left premolar. (No. 55. 12. 29. 199.)
  - 37. Caloprymnus campestris, Gould. Crown view of fig. 33.
  - 38. Canolestes obscurus, Thomas. Profile view of dental series.
  - 39. Distachurus pennatus, Pet. Profile view of dental series. (No. 94. 2. 14. 1.)
  - Diprotodon australis, Owen. Profile view of incisors, greatly reduced. After Owen (1877, vol. ii. pl. xix. fig. 1).
  - 41. Phascolomys Mitchelli, Owen. a, profile view of incisors in young animal, enlarged; b, ventral view of lower incisors. (No. 87. 3. 1. 3.)

(For cusp-abbreviations vide text-fig. 1, p. 89.)

# PLATE 6.

#### Illustrating the patterns of the lower molar teeth.

- Fig. 1. Peratherium Aymardi, Filh. Right m. 3. a, crown; b, profile. (No. M. 2388; Upper Eocene, Caylux, Tarn-et-Garonne.)
  - 2. Sminthopsis leucopus, Gray. Right m. 3. a, crown; b, profile. (No. 52. 1. 13. 3.)
  - 3. Dasyurus viverrinus, Shaw. Right m. 3. a, crown; b, profile. (No. 44. 2. 29. 1.)
  - 4. Dasyurus maculatus, Kerr. Right m. 3. a, crown; b, profile. (No. 31a.)

- Fig. 5. Sarcophilus ursinus, Harr. Right m. 3. a, crown; b, profile. (No. 42 b.)
  - 6. Sminthopsis crassicaudata, Gould. Right m. 1. (No. 46. 8. 3. 37.)
  - 7. Dasyurus Geoffroyi, Gould. Right m. 1. (No. 86. 1. 26. 10.)
  - 8. Sarcophilus ursinus, Harr. Right m. 1. (No. 42 b.)
  - Myrmecobius fasciatus, Waterh. a, crown views of right m. 2, m. 3, m. 4; b, internal profile of m. 2, m. 3; c, external profile view of median and posterior premolars and first three molars. (No. 44, 1, 22, 21.)
  - 10. Thylacinus cynocephalus, Harr. Right m. 3. a, crown; b, profile. (No. 93. 4. 13. 1.)
  - 11. Thylacinus cynocephalus, Harr. Right m. 1. (Drawn from No. 77. 2. 6. 12 and a foetal specimen in the Index Collection.)
  - 12. Perameles Doreyana, Quoy & Gaim. Right m. 3. a, crown; b, profile. (No. 95. 5. 8. 13.)
  - 13. Perameles obesula, Shaw. Right in. 2. a, crown; b, profile. (No. 87. 5. 18. 8.)
  - Thylacomys leucura, Thomas. a, right m. 2, crown; b, left m. 2, external profile. (No. 83. 10. 19. 17.)
  - 15. Chæropus castanotis, Gray. Left m. 3, external profile. (No. 48. 1. 27. 41.)
  - Perameles Bougainvillei, Quoy & Gaim. Right m. 4 (for comparison with 17 b). (No. 41. 1178.)
  - 17. Notoryctes typhlops, Stirl. Right m. 2. a, crown; b, profile. (No. 97. 11. 3. 13.)
  - 18. Distachurus pennatus, Pet. m. 2. (No. 94. 2. 14. 1.)
  - 19. Trichosurus vulpecula, Kerr. Right m. 2. (No. 43. 8, 12. 40.)
  - 20. Distachurus pennatus, Pet. Right m. 1. (No. 94. 2. 14. 1.)
  - 21. Phalanger orientalis, Pall. Right m. 1. (No. 67. 4. 12. 90.)
  - 22. Pseudochirus peregrinus, Bodd. Right m. 2. a, crown; b, profile. (No. 55. 12. 24. 69.)
  - 23. Phascolarctus cinercus, Goldf. Right m. 2. (No. 253 c.)
  - 24. Tarsipes rostratus, Gerv. & Verr. Three of the vestigial cheek-teeth. (No. 1381 b.)
  - 25. Caloprymnus campestris, Gould. Right m. 2. (No. 46. 4. 4. 45.)
  - 26. Dorcopsis luctuosa, D'Alb. Right m. 2. (No. 76. 10. 28. 3.)
  - 27. Lagorchestes leporoides, Gould. Right m. 2. (No. 41. 1127.)
  - 28. Macropus giganteus, Zimm. Right m. 3. a, crown; b, profile. (No. 40. 2. 28. 1.)
  - 29. Macropus rufus, Desm. Right m. 3. (No. 56. 4. 7. 2.)
  - 30. Phascolomys Mitchelli, Owen. Right m. 2 and m. 3. a, crown; b, profile (m. 3). (No. 87. 3. 1. 3.)
  - 31. Diprotodon australis, Owen. Left m. 3 reversed. (No. M. 474.)
  - 32. Metachirus opossum, Linu. Right m. 3. a, crown; b, profile. (No. 98. 9. 5. 9.)
  - 33. Caluromys sp. Right m. 1. (No. 95. 8. 17. 19.)

[Note.—In figs. 6, 7, 8, 11, pa. should read pa<sup>d</sup>.; figs. 2 a, 9 a, 10 a, 13 a, he<sup>d</sup>. should read hl<sup>d</sup>.; fig. 9 c, pm. 3 and pm. 2 should read pp. and mp.]

#### PLATE 7.

Illustrating the modifications of the pes in the Australian Marsupialia.

NOTE.—All the figures on this Plate, with the exception of fig. 19, refer to the plantar surface of the right foot. All, with the exception of figs. 11 and 18, are drawn from spirit-specimens.

Fig. 1. Peramys brevicaudata, Erxl. (No. 89. 10. 26. 14.)

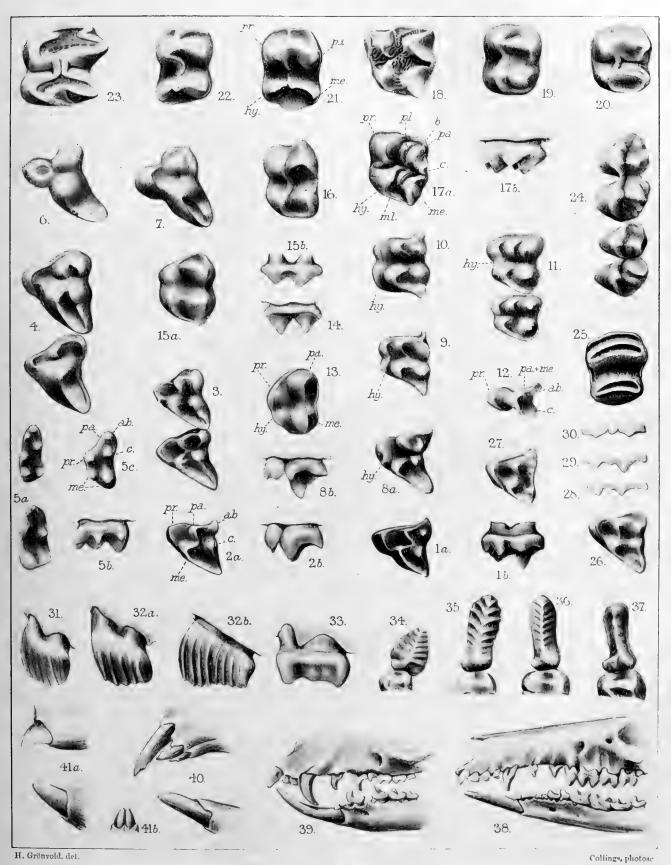
- 2. Phascogale flavipes, Waterh. (No. 86. 5. 15. 8.)
- 3. Sminthopsis leucopus, Gray. (No. 86. 5. 15. 9.)

- Fig. 4. Sminthopsis crassicaudata, Gould. (No. 97. 11. 3. 9.)
  - 5. Sminthopsis hirtipes, Thos. (No. 97, 12, 17, 1.)
  - 6. Antechinomys laniger, Gould. (No. 97. 11. 3. 12.)
  - 7. Marmosa pusilla, Desm. (No. 82. 9. 30. 42.)
  - 8. Chætocercus cristicauda, Krefft. (No. 97. 11. 3. 2.)
  - 9. Dasyuroides Byrnei, Stirl. (No. 97. 11. 3. 7.)
  - 10. Dasyurus hallucatus, Gould. (No. 84. 9. 11. 3.) (Immature.)
  - 11. Dasyurus viverrinus, Shaw.
  - 12. Sarcophilus ursinus, Harr. (No. 52, 1, 15, 2.) (Immature.)
  - 13. Dromicia nana, Desm. (No. 60. 11. 29. 34.)
  - 14. Perameles Cockerelli, Rams. (No. 82. 10. 27. 10.)
  - 15. Perameles Raffrayana, M.-Edw. (No. 83. 3. 29. 2.)
  - 16. Perameles Bougainvillei, Quoy & Gaim. (No. 70. 8. 30. 1.)
  - 17. Thylacomys leucura, Thos. (No. 83. 10. 19. 17.)
  - 18. Chæropus castanotis, Gray. (No. 44. 7. 9. 22.)
  - 19. Notoryctes typhlops, Stirl. Dorsal view of left foot.
  - 20. Phascolomys Mitchelli, Owen. (No. 87. 3. 1. 3.)
  - 21. Hypsiprymnodon moschatus, Rams.
  - 22. Dendrolagus ursinus, Schl. & Müll. (No. 84. 4. 22. 7.)
  - 23. Potorous tridactylus, Kerr. (No. 90. 5. 19. 1.)
  - 24. Macropus dorsalis, Gray. (No. 85. 1. 30. 1.)



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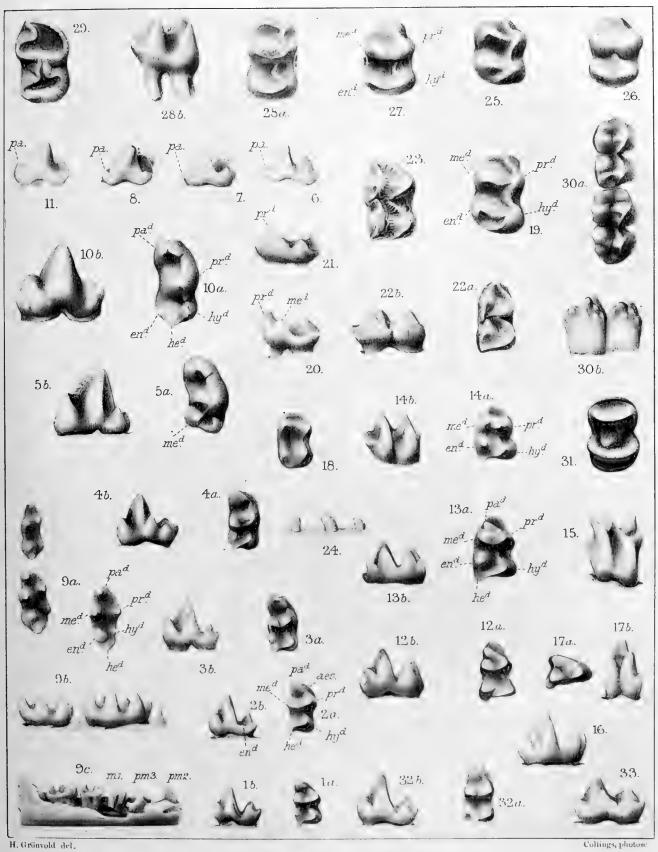


TEETH OF MARSUPIALS.



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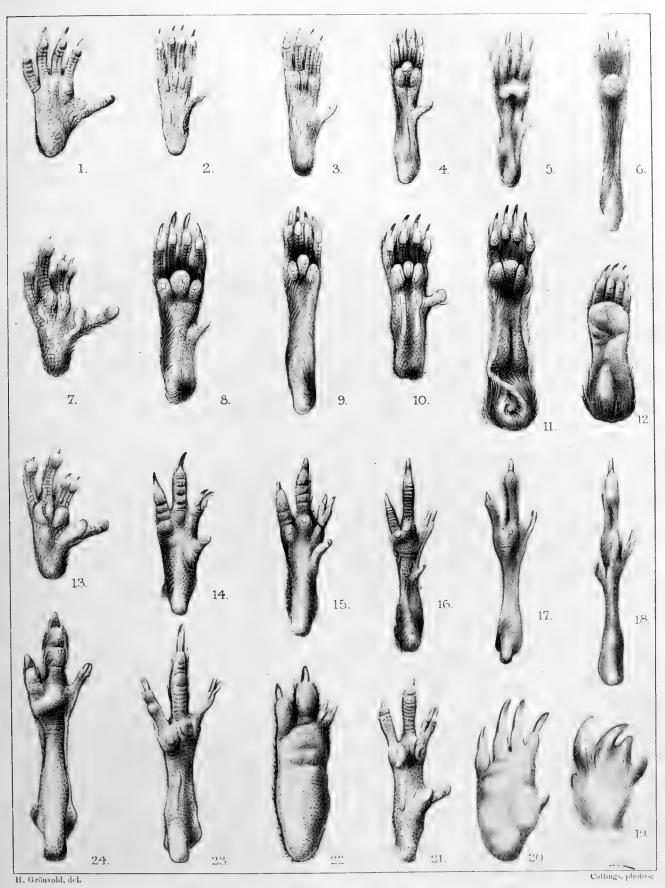
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TEETH OF MARSUPIALS.







FEET OF MARSUPIALS.



# IV. The Labial and Maxillary Palpi in Diptera. By WALTER WESCHE, F.R.M.S. (Communicated by G. MASSEE, F.L.S.)

### (Plates 8-10.)

Read 16th April, 1903.

HITHERTO only one pair of palpi have been known in Diptera, and these have generally been regarded as homologous throughout the order. They are described as maxillary by Savigny, and this nomenclature has been accepted and adopted by the large majority of morphologists.

The mouth-parts in the various families differ much in shape and armature: the Estridæ have only a few tubercles, while the Tabanidæ have a nearly complete organ. The trophi of the Muscidæ are considered typical of the order, and Calliphora, on account of its large size and great abundance, has usually been selected for study; consequently, the rudiments of palpi, absent in *Calliphora*, but present in a very minute form in Musca domestica and many species related to it, have escaped notice. The second pair of palpi have been searched for, as Kirby and Spence \* mention that Savigny thought he had seen the rudiments of the labial palpi in Tabanus †. Westwood gives as a character of the order, "always destitute of labial palpi" ‡. Later writers who have studied the proboscis in the Muscidæ hold similar views.

Dr. Benjamin T. Lowne worked at Calliphora erythrocephala in the larval, nymph, and imago stages. The subject has been most exhaustively treated, sections of the various parts having been largely used in his studies. He says § that the disc on the end of the proboscis (presumably the labella) is derived from the first pair of maxillae, and the palpi present are, "without the slightest doubt, maxillary palpi."

Kraepelin ||, Chatin ¶, and Macloskie \*\* are of opinion that the extremity of the proboscis is derived from a fusion of the labial palpi in the median line. Macloskie thus translates Kraepelin :--- "The labella which Burmeister and Erichson have shown to be

\* ' Introduction to Entomology,' Letter xxxv.

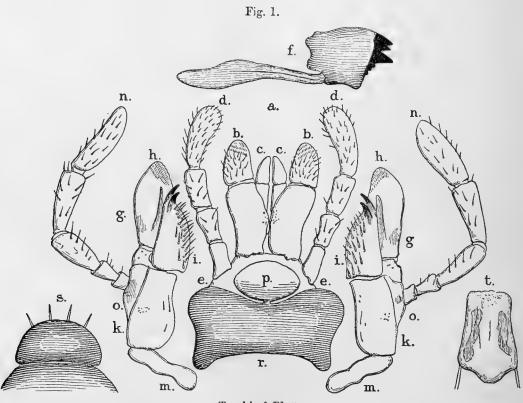
+ Savigny, in the first part of his 'Mémoires sur les Animaux sans Vertèbres,' entitled "Théorie de la bouche," gives a figure of the labium of Tabanus italicus (plate 4, pp. 51-53). A ventral view is given, and the rudiments consist of two minute tufts of hair, symmetrically placed on slight projections of the labium ("tige"), immediately posterior to the labella. These he calls "vestiges des palpes ?," adding a note of interrogation. I have not seen any preparation of T. italicus, but I cannot find any similar structure in Haematopata plavialis, or in any of the numerous drawings of Tabanus given in H. J. Hansen's 'Fabrica oris Dipterorum.' In Tabanus bromius and in T. sudeticus are tufts of hair on the ventral side of the labium, but no structures suggesting the rudiments of palpi.

r 'Modern Classification of Insects,' ii. p. 496. § 'Anatomy and Physiology of the Blowfly,' p. 131. || "Zur Anatomie und Physiologie des Rüssels von Musca," in Zeitschr. wiss. Zool. xxxix. (1883) pp. 683-719, tt. 40, 41.

¶ 'Mâchoires des Insectes' (Paris, 1897, 8vo, pp. 202). \*\* Kraepelin's ' Proboscis of Musca.' SECOND SERIES .- ZOOLOGY, VOL. IX. 30

labial palps." Meinert \*, of Copenhagen, has done much work on the trophi throughout the order. He has drawn, in a most admirable manner, the mouth-parts of the various families, but has passed over the large group of the Anthomyiidæ, considering it typified by the Muscidæ. According to Dr. Sharp  $\dagger$ , Meinert (who writes in Danish) considers that not only the appendages to a head-segment, but also part of the body of the segment, may be used in the construction of the mouth-organs.

II. J. Hansen<sup>‡</sup>, also of Copenhagen, has published beautiful drawings of the mouthparts. His work is in Danish, with a Latin explanation of the plates. His studies were mostly confined to the Orthorrhapha, *Tabanus* being elaborately treated. A novel and unsatisfactory terminology is to be found both in this and in Meinert's work.



Trophi of Blatta. The lettering as in Plates 8 and 9, as explained on page 229.

In the order Hemiptera the rostrum is considered homologous with the proboscis in Diptera. Those morphologists who have derived the labella in Diptera from the labial palpi have included the rostrum in their theory. In 1901, Dr. N. Leon §, a professor at the University of Jassy, in Roumania, found rudimentary labial palpi on the rostra of several aquatic Hemiptera.

I shall now endeavour to homologize the proboscis of Musca with the typical trophi of Blatta, as that has an intimate connection with the labial and maxillary palpi. The

- \* 'Trophi Dipterorum' (Kjöbenhavn, 1881, 4to). † 'Cambridge Natural History,' Insects, part п. р. 444.
- ‡ 'Fabrica oris Dipterorum,' 1883. § 'Recherches morphologiques sur les pièces labiales des Hydrocores.'

observations I have made mostly confirm the ideas of Savigny. Speaking of the mouthparts in Insecta he says: "the organ is the same, the use alone is modified or changed"\*. His nomenclature of the palpi in the Muscidæ must be excepted from this statement. Of all the morphologists known to me, Robineau-Desvoidy alone calls these labial. Dr. Lowne † thus quotes him:—The base of the labrum "is enveloped by the base of the labium, of which the palpi are always present."

Before proceeding further, it may be as well to say that I use the terminology, much the same as that of Kirby and Spence, given in C. O. Waterhouse's ‡ essay on the "Submentum," to which I wish to express my obligations.

In this investigation I have been guided by the following facts :---

1. Mandibles.-In the Tabanidæ, which have all the mouth-parts present except the labial palpi, the proboscis or labium has tracheated labella, and is so like in appearance and position that there can be no doubt of its homology with the proboscis in the Muscidæ. If a labium of Hæmatopota pluvialis has the soft parts dissolved away and is mounted with pressure (and I may remark, for the sake of brevity, that all the parts referred to later have been treated in this manner, unless expressly stated to the contrary), and is examined with the higher powers of the microscope, it will be seen that the dorsal surface has no chitinous structure, the necessary stiffening being afforded by a chitinous plate on the ventral side, the mentum (Pl. 8. fig. 1). I have examined Tabanus sudeticus and T. bromius, and have found the labium identical in this respect with H. pluvialis. It is, however, as well to mention that Chrysops cæcutiens, which has a very elongated labium, has chitinous structure on the dorsal side, while still retaining the mandibles. But this species, judging from the length of the labium, is a later and more specialized type than Tabanus, and the chitinous plate followed as a consequence of increased length requiring more "stiffening." It may generally be assumed, though not on conclusive evidence, that the archaic types in Diptera were furnished with a short labium and that extreme length is a case of specialization. A fairly obvious example is found in Siphona.

We may then say that *Tabanus*, having the mandibles present, has no chitinous structure on the dorsal side of the labium.

When we compare the corresponding parts in the Syrphidæ and the Empidæ, families in which the mandibles have disappeared, though the maxillæ are present, we find wellmarked chitinous rods on the dorsal side. We may reasonably presume that the mandibles are soldered into the dorsal surface of the labium. This view is held by Professor Packard, and has general acceptance with little or no opposition (Pl. 8. figs. 2, 3).

2. If we examine *Calliphora* we find a similar chitinous structure on the dorsal side of the labium. Dissection shows that the parts readily separate into two lateral rods with a broad central plate (Pl. 8. fig. 7).

In Eristalis tenax, E. arbustorum, and Syrphus balteatus these rods are different in

‡ 'The Labium and Submentum in certain Mandibulate Insects' (London, 1895, Svo, pp. 12, 4 col. pls.).

<sup>\* &#</sup>x27; Mémoires sur les Animaux sans Vertèbres,' Bouche, p. 11.

<sup>† &#</sup>x27;Anatomy and Physiology of the Blowfly,' p. 130.

shape and are continued along the sides of the main tracheæ. The central plate seems to be detached, but that the parts are homologous with those in *Calliphora* (Pl. 8. fig. 7) is evident.

3. Maxillæ.—Again examining Calliphora we find that, in addition to the mandibles, the maxillæ, which are present in the Syrphidæ and Empidæ, have disappeared. But if the base of the labium is dissected, the cardines of the maxillæ will be found embedded, and working the labrum as levers (Pl. 8. fig. 4). That these are cardines of the maxillæ may be proved by comparing the parts with those in *Eristalis* and *Helophilus* (Pl. 8. figs. 3, 5, & 6). A comparison with *Culex pipiens* only strengthens this proposition (Pl. 9. fig. 24) \*.

We also find the palpi in a different position. In *Calliphora* they are above and posterior to the base of the labrum; in *Empis* and *Eristalis* they are in a more anterior position and firmly attached to the cardines of the maxillæ (Pl. 8. figs. 2, 3, & 4)<sup>†</sup>. A dissection of the maxillæ in *Helophilus pendulus* and *Eristalis tenax* shows the palpi attached to the maxillæ by a membrane, which has at its extremity a chitinous plate, which is probably the palpifer. The bases of the palpi connect with the maxillæ just before they emerge from the enclosing membrane of the labium. There are well-marked ridges halfway down the maxillæ that indicate the boundary of the cardo. The laciniæ continue, the galæ having aborted. The palpifer shows only on the palpus, being pulled apart from the maxilla (Pl. 8. figs. 5 & 6). Further, I have dissected the maxillæ in *Culex pipiens*,  $\mathfrak{P}$  (Pl. 9. fig. 24), in *Tabanus bromius*, *T. sudeticus*, *Chrysops cæcutiens*, *Asilus crabroniformis*, and a species of *Simulium*, all species with a nearly complete armature, and I find that invariably the palpus is firmly attached to the stipes and cardo of the maxilla.

4. Labium.—The palpi in the Muscidæ are in quite a different position, attached to the membrane of the labium; at their bases in *Calliphora* are plates of chitin and rows of two or three bristles. The palpi have no connection with the levers of the labrum, which, as we have seen, are the cardines of the maxillæ in *Eristalis*. They are therefore *labial* and not maxillary palpi, and have worked round from a lower part of the labium to the upper. The chitinous plates and rows of bristles in *Calliphora* have their analogies in a great number of related species. In some the chitin is evident, in others it has almost disappeared, but the row of bristles is very constant, and can be seen in all the species possessing labial palpi that I have examined. It is fairly obvious that these parts represent the palpiger.

5. A dissection of the trophi of *Culex pipiens* throws some light on the subject under discussion. In both sexes the labium is simply a chitinous sheath for the lancets. In its paired and segmented flaps may be seen the homologies of the labella.

The cardines and stipites of the maxillæ are present, having much the same appearance as in the Muscidæ, and a palpifer can be traced supporting the three-jointed palpus (Pl. 9. figs. 23 & 24).

<sup>\*</sup> See note on page 229.

<sup>†</sup> The stipes and cardo are so soldered together that it is not possible, in the majority of cases, to define them. The palpifers are attached to the stipites and not the cardines.

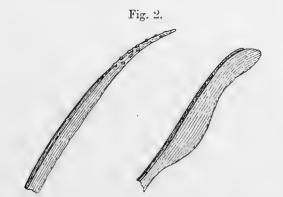
In the female the maxillæ, mandibles, hypopharynx, and labrum are very beautiful weapons. In the male the lancets are obviously atrophying, and they can only with difficulty be dissected out from the enclosing labium. Here is seen the process, which has been completed in the Syrphidæ and Empidæ, actually proceeding, or suddenly halted in a stage of the process.

In the males the cardines of the maxillæ hinge on to the maxillary palpi, which, in this sex, are very long and highly developed (Pl. 9. figs. 25, 26, and text-fig. 2).

Summary.—In the Muscidæ the mandibles are embedded in the dorsal side of the labium. The maxillary palpi, galeæ, and laciniæ are aborted, but the cardines remain. The palpi present are labial, and the palpigers are represented by chitinous plates with two or three setæ springing from or near them.

In the Syrphidæ and Empidæ the mandibles are similarly placed, but the maxillæ are represented by the laciniæ, the palpi, cardines, stipites, and palpifers. The labial palpi are aborted.

Rule.—A rule can be formulated :— The maxillary palpi when present in Diptera are always in contact with the upper part of the cardines, the stipites.



Extremities of maxilla and mandible of Culex pipiens, Q.

Rudimentary Maxillary Palpi.—I was fortunate in discovering a number of species, in the Anthomyiidæ, Muscidæ, and other families of the Cyclorrhapha, with four palpi which afford useful clues to the surrounding parts. They appear in different stages of atrophy, from a fairly developed organ to a rudiment of a few hairs. Some examples were described in a paper read at the meeting of the Royal Microscopical Society on June 18th, 1902, and since published in the Journal of that Society \*. These palpi enable us to indicate the position of the maxillæ with certainty, and, by proving the other pair to be labial, establish the proposition that the whole organ is the labium.

We have now the mandibles, the maxillæ and palpi, the labium and palpi, and the mentum clearly defined.

Paraglossæ, Ligulæ.-We now come to the parts of the labium, the paraglossæ and

\* Journ. Roy. Micr. Soc. 1902, p. 412. "Undescribed Palpi on the Proboscis of some Dipterous Flies, with Remarks on the Mouth-parts in several Families." ligulæ. In the Muscidæ, Tabanidæ, Syrphidæ, and other families we find, at the extremity of the labium, two paired organs, the labella and the transverse chitinous levers that support them. They are in the situation where they might be expected to be found, and I have little doubt represent—the labella the paraglossæ, and the transverse levers the ligulæ (Pl. 8. figs. 4, 8; Pl. 9. fig. 17, &c.). In the paraglossæ of *Culex* (Pl. 9. fig. 23) I have seen two strengthening rods, which confirm me in the above homology. They only appear on dissection and are not shown in the figure. In species of *Empis*, such as *E. chioptera* (Pl. 8. fig. 2), and in *Siphona geniculata*, the ligulæ have aborted.

Teeth.—The large majority of species in the Muscidæ, from Tachina down to Scatophaga, have an armature of teeth at the bases of the false tracheæ. These may be traced, through such specialized species as Stomoxys and Glossina, and may even be found in a most minute size in some of the species of the parasitic Hippobosca. They are arranged in symmetrical crescents, and are so close to both the mandibles and the ligulæ that they might possibly be parts of those organs; but the simpler hypothesis that they are outgrowths from the paraglossæ is probably the correct one. Some light is thrown on this point by the very exceptional dentition shown in Ephydra (Pl. 9. fig. 21). Here each of the pseudotracheæ is furnished along its whole course with many short chitinous teeth disposed at regular intervals.

Labrum, Lingua, and Mentum.—All morphologists seem agreed that the lancet-case corresponds with the labrum, and the hypopharynx with the lingua. The homology of the ventral plate on the labium with the mentum is fairly clear (Pl. 8. fig. 4).

Submentum.—The submentum is possibly membranous, but it may be the "fulcrum." This part is described as the chitinized walls of the pharynx, but a long tracheated tube is easily dissected out from the trophi of all the species I know, and seems to be the true pharynx. There is so little to guide that this point must remain doubtful; allowing this, we thus have the parts complete.

Summary.—The proboscis in Diptera may be regarded as homologous with the trophi of the typical insect mouth. In the Muscidæ it has been modified into a rod-like organ, enclosed in a thin membrane, and capable of extension and retraction. It is mainly formed of the labium, and has the labial palpi well developed and placed near chitinous ridges, which are the palpigers. The palpi have worked round from the under to the upper side—or, taking the usual position of the labium into account, from a posterior to an anterior position, where it is obvious that they would be of greater service to the insect.

The proboscis has two symmetrical tracheated flaps at the extremity, which represent the paraglossæ. The teeth, which are often present, may be considered outgrowths of the paraglossæ. The transverse chitinous levers which expand the labella are the ligulæ. Mr. Waterhouse shows ('Labium and Submentum') that the paraglossæ have a tendency to enlarge at the expense of the ligulæ, and this has occurred in the Muscidæ.

The labium has absorbed into its structure the mandibles and maxillæ on the dorsal side, and the mentum, and possibly the submentum, on the ventral side.

The mandibles act as supports and assist in working the labella.

The upper parts of the maxillæ, which are present in *Syrphus*, have aborted, leaving the cardines and stipites, which find use as levers, acting on the labrum and hypopharynx. The maxillary palpi have mostly aborted, but in many species they are present in a more or less rudimentary state. When the maxillary palpi are present, they are based on structures homologous with the palpifers. These are attached to the stipites. The palpi are situated at proportionally the same distance from the bases of the cardines as the palpi in the Syrphidæ and the Empidæ (Pl. 8. figs. 3, 5, 6; & Pl. 9. fig. 17). The proboscis has, on its dorsal surface, a lancet-case, the labrum, which acts as a sheath for the hypopharynx, which homologizes with the lingua.

At the base of the hypopharynx, and continuing it, is a tube, the pharynx; this is sometimes tracheated, and is well marked in this state in *Calliphora* and *Stomoxys*. This tube curves upwards under the base of the labrum.

The proboscis in the Syrphidæ and the Empidæ corresponds with that in *Musca*, except that, in their case, the labial palpi have aborted, and the laciniæ of the maxillæ and maxillary palpi are present.

*Rudimentary Maxillary Palpi.*—I shall now give a short description of the rudimentary maxillary palpi in a few species, figuring various forms.

Family ANTHOMYIIDÆ, subfamily *Mydæinæ*.—*Polietes lardaria*, Fabr. Palpi pyramidal in form, strongly haired, short pointed projection at extremity of stipes, palpifer marked; base  $\frac{1}{275}$  in., length  $\frac{1}{200}$  in. (Pl. 8. fig. 13.)

Same family and subfamily.—*Hyetodesia lucorum*, Zett. Very elongated, strongly haired, long blunt projection at extremity of stipes, palpifer marked; base  $\frac{1}{1122}$  in., length  $\frac{1}{257}$  in. (Pl. 8. fig. 16.)

Same family and subfamily.—*Hyetodesia perdita*, Meig. Acutely conical, well haired, no projection, palpifer indistinct; base  $\frac{1}{900}$  in., length  $\frac{1}{300}$  in. (Pl. 8. fig. 10.)

Same family and subfamily.—*Mydea impuncta*, Fallen. Broad at the base; base not haired; tapers off with a curve, where it is thickly haired; stipes broadens very much at end; palpifer indistinct; base  $\frac{1}{600}$  in., length  $\frac{1}{222}$  in. (Pl. 8. fig. 9.)

Same family and subfamily.—*Hydrotea dentipes*, Fabr. Short and thick; thickly haired, blunt projection of stipes; base  $\frac{1}{600}$  in., length  $\frac{1}{360}$  in. (Pl. 8. fig. 15.)

Same family and subfamily.—*Ophyra leucostoma*, Wied. Broad at the base, short and stout, thickly haired, palpifer distinct; base  $\frac{1}{450}$  in., length  $\frac{1}{400}$  in. The cardines are very strong in this species. (Pl. 8. fig. 14.)

Same family, subfamily Homalomyiinæ.—Homalomyia canicularis, Linn. Very small, conical in shape; base  $\frac{1}{1800}$  in., length  $\frac{1}{838}$  in. (Pl. 9. fig. 28.)

Family MUSCIDE.—Cyrtoneura stabulans, Fallen. Tubular and short; stipes projects, well haired; palpifer fairly distinct; base  $\frac{1}{600}$  in., length  $\frac{1}{450}$  in. (Pl. 8. fig. 11.)

In a very rudimentary form I have found the palpi in a number of species. They have all very much the same appearance, so that a separate description would be superfluous. I have figured four species. In most cases only a few hairs remain, but in *Lasiops* I have found quite a tuft.

Family ANTHOMYIIDE.	Subfamily Homalomyiine.
Subfamily Anthomyiinæ.	Azelia Macquarti, Stäg.
Hylemyia cardui, Meig. (Pl. 9. fig. 27).	
H. pullula, Zett. (very small).	Family SARCOPHAGIDE.
Lasiops ctenoctema, Kow.	Myiocera curinifrons, Fallen.
Anthomyia radicum (Linn.).	Family Muscins.
A. pluvialis (Linn.).	•
A. sulciventris, Zett.	Graphomyia maculata, Scop. (Pl. 9. fig. 31).
Phorbia floccosa ?, Macq.	Musca domestica, Linn. (Pl. 8. fig. 12).
Pegomyia bicolor, Wied. (Pl. 9. fig. 29).	M. corvina, Fabr.

Acalyptrate Muscidæ.—In a number of species in the Acalyptrate Muscidæ the palpi are quite fully developed, but, on account of the small size of the flies, are very difficult to make out. The maxillæ, when present in Diptera as hitherto observed, have only the laciniæ and palpi present, the galæ having aborted. Such a state of things is seen in the Culicidæ, Simulidæ, Tabanidæ, and Asilidæ. In a small and common species of Ephydra (Pl. 9. figs. 21 & 22) I found a maxilla which has all the parts represented. This species has also the remarkable dentition previously alluded to.

In *Balioptera combinata*, Linn. (Pl. 9. fig. 18), an arrangement is seen differing from those already mentioned, but there are several species that follow this type. It is difficult to say whether the palpi or the laciniæ are aborted. Comparing this species with the Syrphidæ one is inclined to think that the palpi are absent.

In Nemopoda cylindrica, Fabr. (Pl. 9. fig. 19), maxillary palpi can be made out, but the cardines are so faintly chitinized that their presence can only be suspected. In the nearly related Sepsis cynipsea the cardines and stipites are exceedingly short.

In Sphærocera subsultans, Fabr., the four palpi are found in a more developed state than any hitherto met with (Pl. 9. fig. 20.)

In the figure a dorsal view is given of the parts, showing the fulcrum, the mentum through the transparent membrane, and the labrum above it. I have examined several species of this family, but have only found similar palpi in *Borborus suillorum*, Hal. In *Limosina lugubris*, Hal., *L. sylvatica*, Meig., *L. fuscipennis*, Hal., and *Sphæroceru denticulata*, Meig., the palpi were of much the same type as in *B. combinata* (Pl. 9. fig. 18).

Archaic Type.—The varying armature and shape of the trophi in Diptera suggest a speculation as to archaic types.

I. The labium was probably short as in Tipula and has gradually elongated. The labial palpi have remained at or near their original distance from the head, but have worked round to the upper part so as to be of service. Where this has not occurred (1) they have aborted as in the Syrphidæ, Empidæ, Bombylidæ, Asilidæ, Tabanidæ, and Culicidæ; (2) or they have followed the labella down, as in *Dilophus* (Pl. 8. fig. 8).

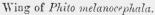
Siphona geniculata is an example of the extreme development caused by the advantages gained by elongation. In this species many parts usually present on the labella, teeth, and transverse expanding levers (ligulæ) have aborted, and no traces of the maxillary palpi are to be seen. From this we may infer that this type is more specialized, and consequently less archaic, than *Ophyra leucostoma* (Pl. 9. fig. 17), which has an abnormally short labium, the maxillary palpi well marked, and the parts on the labella very evident.

II. Pubescent Eyes.—All the flies in the Cyclorrhapha with pubescent eyes that I have examined, either have the maxillary palpi only, or possess rudiments of them, e. g., Syrphidæ, Polietes, Hyetodesia, Hydrotea occulta. Some species of Phoridæ are apparently an exception; it is, however, very doubtful whether this family is in its proper division.

III. Venation of Wings (text-figs. 3 & 4).—The rudimentary palpi seem to follow the venation of the wings in a curious manner. The cell formed by the 3rd and 4th longitudinal veins (subapical or 1st posterior cell) is open in the Anthomyiidæ, begins to close in Cyrtoneura stabulans, is nearly closed in Musca domestica, and is quite closed in Phito melanocephala. The palpi gradually diminish through these species till no sign is left in P. melanocephala.



Wing of Polietes lardaria.



IV. Tegulæ.-The tegulæ also seem correlated :--

- (1) When all the palpi are well developed, as in Sphærocera subsultans, the subapical cell of the wing is open, the tegulæ are absent.
- (2) When the palpi are more or less rudimentary, as in the Anthomyiidæ, the cell still remains open, but the tegulæ are well marked.
- (3) When the palpi are rudimentary, as in *Cyrtoneura stabulans*, the cell begins to close and the tegulæ increase in size.
- (4) When the palpi are very rudimentary, as in *Musca domestica*, the cell is still more closed, the tegulæ remain large.
- (5) When no trace of the palpi can be seen, as in *Calliphora*, the cell is still more closed, the tegulæ remain large.
- (6) In *Phito* and *Melanophora* the tegulæ are still more developed, no trace of palpi can be seen; the 4th longitudinal or median vein has closed the 1st posterior cell so much that it has left the margin.
- (7) In *Æstrus* the mouth-parts are rudimentary, the venation has left the lower part of the wing, and the tegulæ are at their largest development.

Working on the above data, a fly may be imagined with hairy eyes, a plumose arista, a venation approximating to that in the Anthomyiidæ, mandibles fused into the labium, which would be short and stout; maxillæ also absorbed, but with both palpi well SECOND SERIES.—ZOOLOGY, VOL. IX. 31 developed, and the tegulæ small or absent. This might be an ancestral or primitive type of the Muscidæ.

*Polietes* and *Hyetodesia* would only differ from this insect by less developed maxillary palpi, a longer labium, and larger tegulæ. *Ophyra leucostoma*, while retaining the short labium, has lost the plumose arista, the hairy eyes, and retains fairly large rudiments of the palpi. *Cyrtoneura* has also lost the hairy eyes, developed a slightly longer labium, but retains the plumose arista and fairly large rudiments of the palpi.

In *Hydrotea* the palpi are present, but the plumose arista has gone. Some species retain the short labium, and others have lost the pubescence on the eyes. Finally, we come to the little *Lasiops*, with hairy eyes and only rudiments of the maxillary palpi.

My diagram is drawn up on this system—that is, as the species lose primitive characters they become more recent; and it would be tedious to trace the matter further, as a glance at the scheme will make my meaning clearer than any written explanation. (Plate 10.)

Classification.—It will be seen that this arrangement shows what excellent natural groups the species of the Anthomyiidæ and the Muscidæ have been divided into, and how one character more, the rudimentary palpi, follows the order in which the genera have been placed. It is well marked in the subfamily Mydæinæ, dwindles in the Anthomyiinæ and Homalomyiinæ, disappears in the Cœnosiinæ, and no trace is found in the nearly related *Scatophaga*.

In this paper I have endeavoured to avoid a controversial attitude, but it must be obvious that if the conclusions I have arrived at are *correct*, the contrary must be the case with the works of several theorists, and that the generally accepted dogma that the palpi in Diptera are homologous and maxillary can no longer stand. 'Therefore it will probably be urged by some (and, looking at the subject from their point of view, I admit quite fairly) that my methods are out of date, and that comparative anatomy must give way to a minute sectional study of the insect from the ovum, through the metamorphoses, to the imago state. To this I answer that this method, so apparently promising and conclusive, when applied to the trophi of Diptera, is discounted by its results. Either it is a tool of such complexity and nicety that no observer has hitherto used it correctly, or the facts observed have not been properly weighed and understood.

Since the preceding pages were written, Professor V. L. Kellogg has published a paper which lends valuable aid to my contention as to comparative anatomy and ontogenetic study, when applied to the homologization of the mouth-parts of Diptera \*.

If the presence of labial and maxillary palpi in Diptera is admitted, and I cannot see how, unless my facts are traversed, this can be denied, such speculations as the derivation of the labella from the fusion of the labial palpi or from the *first* maxillæ cannot be entertained, though my investigations quite agree with the theory that the labium is a modified double maxilla, derived from the second pair of jaws.

\* "The Development and Homologies of the Mouth-parts of Insects," The American Naturalist, vol. xxxvi. (Sept. 1902), pp. 683-706.

## NOTE.—The Homology of the Cardines.

It has been objected that the homology of the levers of the labrum in the Muscidæ (the "apodemes" of Dr. Benjamin Lowne) with the cardines of the maxillæ is not quite clear. As this is of vital importance to my theory, I have enlarged my argument and summarized it as follows :—

- 1. In Vespa and Apis the cardines are on the same plan as in Musca. They are generally admitted to be the "hinges" of the "posts" supporting the palpifers and other parts. If these are cardines here, so must they be in Diptera.
- 2. It may be urged that the fact that the levers are enclosed is against the theory that they are cardines. This objection has no weight. The cardines being the lowest part, they would (if there were any tendency in that direction) be the first part to be embedded.
- 3. In *Culex*,  $\mathfrak{P}$ , the levers are undoubtedly cardines, the four-jointed palpi are affixed to them, and though the palpifer is differentiated, I have failed to see the point where the stipes and cardines fuse.
- 4. In *Eristalis* and *Helophilus* parts of the maxillæ are present with palpi. It is impossible to deny the homology of the posterior ends with the apodemes. Therefore as these parts bear the palpi, they must be in some part the stipites; and as similar parts in *Vespa* and *Apis* are admitted to be the cardines, in *Eristalis* and *Helophilus* they must be the fusion of the stipites and cardines, which applies equally to the Muscidæ.
- 5. It may be suggested that in the Muscidæ the levers are so obviously necessary to work the labrum and hypopharynx that they would specially evolve. To this it may be answered that the levers are present in *Culex*. In the female they hinge on to the blades of the maxillæ; in the male they work the long palpi characteristic of that sex. So in Diptera we know of three uses of the cardines, showing there exists a tendency to utilize this part.
- 6. In the small *Ephydra* figured (which, judging from a determination of Mr. Piffard, is *Hydrellia griseola*, Fallen), in the same places as the apodemes are also found complicated organs, which are evidently the complete maxillæ.
- 7. The negative proof—if they are not cardines, what are they?

### EXPLANATION OF THE PLATES.

The lettering applies to all the figures.

a, labium.	k, stipes.
b, paraglossa.	m, cardo.
c, ligula.	n, maxillary palpus.
d, labial palpus.	o, palpifer.
e, palpiger.	p, mentum.
f, mandible.	r, submentum.
g, maxilla.	s, labrum.
h, galea.	t, hypopharynx or lingua
i, lacinia.	

### ON THE LABIAL AND MAXILLARY PALPI IN DIPTERA.

### PLATE 8.

- Fig. 1. Labium of *Tabanus* (*Hæmatopota pluvialis*), lateral view. The remaining parts (the mandibles, maxillæ, max. palpi, labrum, and hypopharynx) have been removed.
  - 2. Head of Empis chioptera.
  - 3. Proboscis of Eristalis tenax, lateral view.
  - 4. ", Calliphora erythrocephala, lateral view.
  - 5. Dissection of the maxilla and palpus of Helophilus pendulus.

6. ", ", *Eristalis tenax*.

- 7. Dissection of the dorsal plate on the labium of *Calliphora erythrocephala*, showing the embedded mandibles. The lower end shows a portion of the pharynx, dorsal view.
- 8. Labium of Dilophus albipennis, ventral view.
- 9. Maxillary palpus of *Mydea impuncta*. Only the anterior end of the stipes is shown, with a lateral view. This applies to all the figures of palpi on these Plates.

10. Maxillary palpus of Hyetodesia perdita.

11. ,, ,, Cyrtoneura stabulans.

12. Rudiment of maxillary palpus, Musca domestica.

13. Maxillary palpus of Polietes lardaria.

	14.	22	22	Ophyra	leucostoma.
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- 15. ,, ,, Hydrotea dentipes.
- 16. ", ", Hyetodesia lucorum.

#### PLATE 9.

Fig. 17. Proboscis of Ophyra leucostoma, dorsal view.

- 18. " Balioptera combinata, lateral view.
- 19. ,, Nemopoda cylindrica, lateral view.
- 20. ", Sphærocera subsultans, dorsal view.
- 21. ,, a species of Ephydra (Hydrellia griseola, Fallen?).
- 22. Maxilla of same, more highly magnified.
- 23. Part of the labium of Culex pipiens,  $\mathcal{Q}$ , showing the labella, dorsal view.
- 24. Dissection of the cardo, stipes, palpifer, and palpus of the maxilla of Culex pipiens, 2.
- 25. Extremity of the labrum of *Culex pipiens*, S. This has affinities with the labrum in some species of the Syrphidæ.
- 26. Extremity of the labrum of C. pipiens,  $\varphi$ , showing the higher organization of the female.
- 27. Rudiment of maxillary palpus, Hylemyia cardui.
- 28. ", ", Homalomyia canicularis.
- 29. ", ", ", Pegomyia bicolor.
- 30. End of stipes, Phito melanocephala.
- 31. Rudiment of maxillary palpus, Graphomyia maculata.

### PLATE 10.

Diagram showing a speculative arrangement of genera and species, placed as they recede from a hypothetical primitive form.

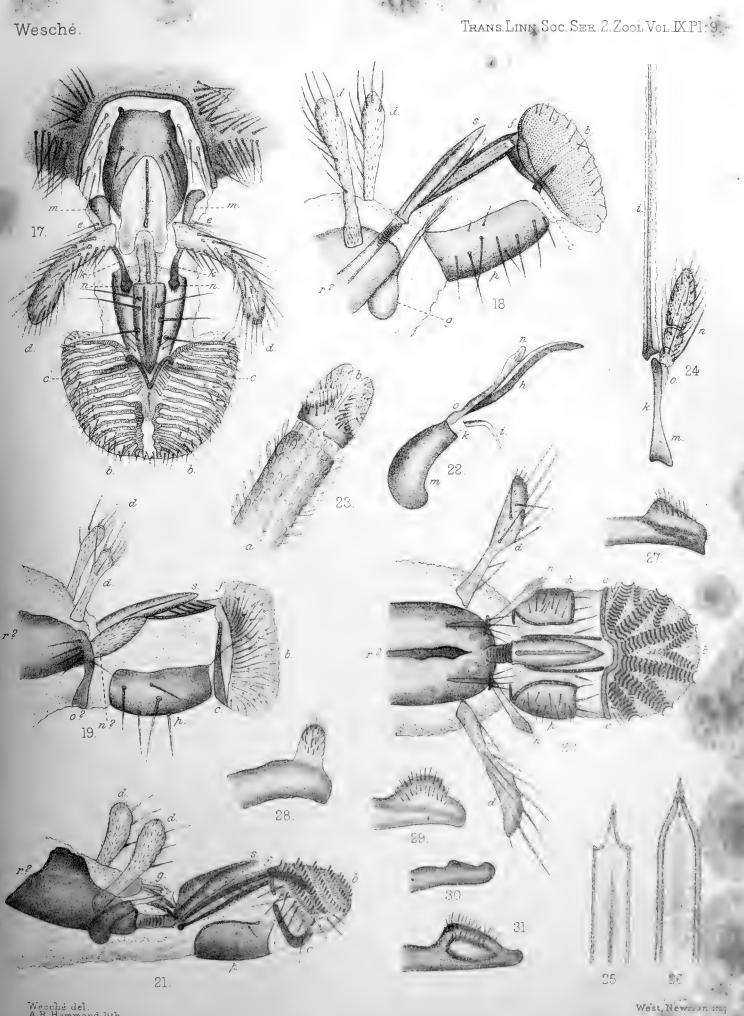
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PALPI IN DIPTERA.



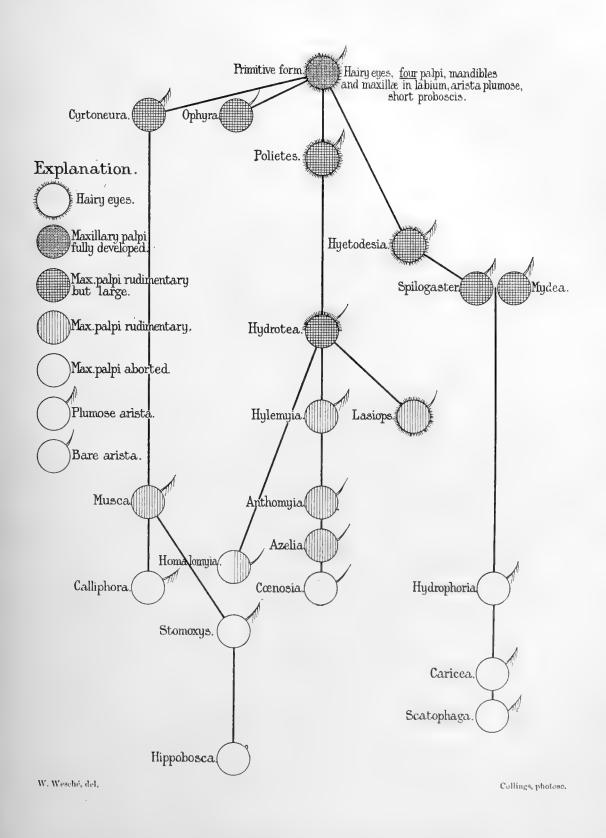


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PALPI IN DIPTERA.



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HYPOTHETIC ARRANGEMENT OF GENERA OF MUSCIDÆ.

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# [231]

V. On the Anatomy and Development of Comys infelix, Embleton, a Hymenopterous Parasite of Lecanium hemisphæricum. By ALICE L. EMBLETON, B.Sc., 1851 Exhibition Science Research Scholar; Associate of the University of Wales (Cardiff College). (Communicated by Dr. DAVID SHARP, F.R.S., F.L.S.)

## (Plates 11 & 12.)

### Read 4th June, 1903.

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## I. INTRODUCTION.

THE subject treated of in this paper is of interest both to the biologist and to the Comys infelix is a very small Hymenopterous fly belonging to the family economist. Chalcididæ, the members of which have long been recognized as beneficial from an economic point of view, inasmuch as they are great destroyers of the Coccid pests that are so inimical to cultivation in all parts of the world. Biologically this species of Hymenoptera claims attention by virtue of its remarkable life-history, the early stages of which are passed inside a scale-insect, while the imagines, male and female, lead a free life after emergence from the Coccid. In spite of their two-fold importance, little is known about these insects, and their life-histories remain obscure. Recently Bugnion (9) has published the results of his researches on the development, anatomy, and habits of Encyrtus fuscicollis, a form allied to Comys infelix, though with very different habits. He mentioned the fact that many embryos of this species were to be found enclosed in a capsule, or tube, in the interior of the host-a caterpillar, but he did not thoroughly elucidate the matter. Since Bugnion's paper was published, Marchal (39, 40, 41) has discovered that his species (now called Ageniaspis fuscicollis, Dalm.) offers in its development an example of the phenomenon so rare in zoology, and of extreme interest from a philosophical point of view, of dissociation of the embryo. In an early stage of the development, the embryo breaks up and forms from fifty to a hundred embryos. The development of this insect is being studied by this accomplished French savant, and we anticipate most interesting results. He suggests that the species of Ageniaspis afford SECOND SERIES .- ZOOLOGY, VOL. IX. 32

examples of chronic segregation, the individuals being separated in the times of their appearance in conformity with the habits of the species of which they are parasites. No morphological differences have yet been detected between the "seasonal races" in this case.

Apart from the investigations of these two naturalists, there has been, within the last few years, work done on the *Encyrtinæ* by the American school of entomology, especially by Dr. L. O. Howard and Dr. Ashmead, but their studies have not been directed to investigation of the ontogeny.

I propose, therefore, in this paper to record the results obtained after work for eighteen months on the Chalcid, *Comys infelix*; from the nature of the case there are necessarily some points which are left obscure.

As the species I am dealing with has at present only been characterized by a few diagnostic words, it may perhaps be well here to give very briefly the distinguishing features serving to identify it among other species of the genus—especially to distinguish it from *Comys bicolor*, which it resembles to some extent. At first I took it to be that species, but further investigation pointed to the conclusion that I was dealing with a new species. I submitted it to Dr. L. O. Howard, who confirmed my opinion, as did also Mr. P. Cameron and Mr. R. Newstead.

COMYS INFELIX, Embleton (Trans. Entom. Soc. London, 1902, ii. pp. 219-229).

A small fly, 2 mm. in length, 3.75 mm. across the outstretched wings. Colour extensively black, but variegated, the head and thorax dark brown, abdomen black; the coxæ of the first legs are silvery white, the other parts fuscous and the tarsi black ; tibial spur normal; in the second legs the coxæ are black, the femora white shading to black, the tibiæ being expanded at the distal ends, and bearing a long, powerful spur; the third legs have white coxæ, brown femora, and dark brown tibiæ with a normal spur, the tarsi begin white and then shade to black at the tip; the tarsi are all five-jointed. The antennæ are black, club-like at the tips, compressed in the female, but subcylindrical in the male; there are cleven segments, all more or less clothed in fine hair; the funicle is six-jointed, while the pedicel is shorter than the next segments. Between and rather behind the two large dark eyes are three ocelli. The scutum is raised and triangular, bearing an apical tuft of long dark setw, directed backwards. The fore wing is mottled in blackish fuscous patches. The abdomen is short, and united to the thorax by an inconspicuous petiole; laterally the abdominal segments become "looped up" over a small oval hinged plate on which are four long setæ. The ovipositor, almost entirely hidden, is composed of two large expanded chitinous plates, and a central sting made up of two pointed rods.

## II. NATURAL HISTORY.

(a) *Classification.*—The creature belongs to the subfamily *Encyrtinæ*, according to Howard in Comstock's report (10). The distinguishing characters of the Chalcididæ as given there are as follows:—Tarsi five-jointed; middle tibiæ with a very stout spur at

the tip. The *Encyrtinæ* come under this family and are distinguished from the *Aphelininæ* by the fact that the antennæ are more than eight-jointed. It is perhaps best to quote the more detailed diagnosis of the distinguishing characters of the *Encyrtinæ* as given in

Comstock's report : "Subfamily Encyrtine.- Tarsi five-jointed; middle tibiæ somewhat dilated towards the tip, and furnished with a long stout spur; antennæ more than 8- usually 11- or 10jointed. Parapsides of the mesoscutum not separated by furrows; mesothorax prominent, broad in the middle; vertex with an acute occipital margin; abdomen usually short and sessile. The members of this tribe are small active Chalcids, which, while by no means confined to Coccids as hosts, still are much more often parasitic on insects of this family than upon those of any other. Dr. Mayr (42), in his paper upon the European Encyrtinæ, tabulates the species according to their hosts, and we may briefly condense by saying that one species is parasitic upon an Hymenopterous insect, two upon Coleoptera, four upon Lepidopterous eggs, sixteen upon Lepidopterous larvæ, four upon Diptera, while forty species are parasitic upon Hemiptera, of which thirty-nine infest bark-lice, the remaining one being found upon two species of Aphides. Ratzeburg (46) mentioned two species of Encyrtinæ parasitic upon Hymenoptera, four on Coleoptera, four on Diptera, twelve upon Lepidoptera, and no less than twenty-five upon Hemiptera. Even these facts, however, cannot be taken as fairly indicating the proportion of these insects which are parasitic upon the Coccidæ, since the latter family has heretofore been so little studied in comparison with other groups, that doubtless many of its parasites have never been reared. When as much biological work shall have been done upon it as, for instance, upon any one of the families of Lepidoptera, we may expect to find that the proportion of *Encyrtinæ* parasitic upon insects of other families will become dwarfed by comparison."

"Genus Comys, Förster (19, 20, 21).—Antennæ rather long, eleven-jointed; funicle six-jointed; pedicel slightly shorter than the succeeding joints, from joint three the joints of the flagellum gradually decrease in length, with the female they become more and more compressed towards the tip of the club, with the male remaining subcylindrical. Head and face coarsely punctured. Mesoscutum without silvery white hair. Scutellum three-cornered, with a somewhat rounded tip, near which is a tuft of erect, long, stiff dark hairs. Ovipositor entirely, or almost entirely, hidden. Fore wings brownish on the distal half, the nearly clear basal half having a brownish cross streak; marginal vein shorter than stigmal; post-marginal and stigmal long. Males very similar to females, antennal characters giving the only absolute distinction; wings sometimes clear, and sometimes brownish as with females."

(b) Mode of Occurrence, &c.—Comys infelix was first noticed in August, 1901, on an Asplenium fern parasitized by Lecanium hemisphæricum \* var. filicum, and by Chionaspis aspidistræ, Signoret. I observed that Comys infelix emerged from the Lecanium, with

<sup>\*</sup> I notice that some of the most recent writers (in 1902) have called this Coccid Saissetia hemisphærica. I have not been able to discover why this alteration has been effected, if it is so, for the name Saissetia was used in Mollusca in 1900, and is therefore preoccupied.

which the fronds of the fern were covered; a small round hole was left in the dorsal shield of the scale as the only indication of its destruction by the fly; neither then nor since have I found more than one fly emerge from one host or victim. From the small white *Chionaspis* a very minute fly hatched out in abundance; it is apparently *Aspidiotiphagus citrinus*, Howard ('35 mm. in length), but I have not at present been able to continue the work on this species.

I soon discovered that the same kind of fly existed in the *Lecanium* when this occurred on other ferns—viz., *Aspidium falcatum*, *Asplenium* spp., *Pteris* spp. (?): usually the *Pteris* was most abundantly stocked with the scale; it also occurs on *Beaumontia*.

It is an interesting fact that the flies hatched out all through the year, though in fewer numbers in the winter, but appearing in great profusion in spring and early summer; similarly the earliest larval stages were most common in late summer and early autumn, but it was always possible to obtain the different stages all the year round. This continuity of production may merely be the result of the artificial conditions under which the insects live, for the palms and ferns which their hosts inhabit are all hothouse varieties experiencing fairly constant conditions as regards food-supply, warmth, and moisture, whereas in a state of nature they might be subject to seasonal changes. I have never found the parasite on ferns growing out of doors, and the *Lecanium* itself is considered to be exclusively a greenhouse species in Europe and America.

The females are much more common than the males, which appear comparatively rarely, and then only in small numbers; so far, I have found them in the spring and early summer. I shall subsequently mention that this disproportion of the sexes in *Comys infelix* is very great, perhaps a thousand females to one male: this is the only circumstance I have noticed that suggests the natural time of emergence, which, if this may be relied on, is the first warm weather of spring. It was at this period, too, that the females were produced in greatest numbers; the sporadic appearance of other examples is therefore quite probably due to the unnatural conditions of existence as stated above. The male is so rare that I have had but little opportunity of observing it, and owing to this rarity my remarks may be considered to apply only to the female except when the other sex is specially mentioned. During the time when the flies were so abundant, I kept them under cages with flowering *Genista* plants and some parasitized ferns. They were always most active in the direct sunshine, and in the first week of March, when I had a cage of them in the sun, I observed pairing to take place for the first time; subsequently I observed it repeatedly.

I was not fortunate enough to observe oviposition, but I will quote an account given by Mr. R. Newstead (43 a) (which he has kindly placed at my disposal) of the occurrence in an allied form—*Blastothrix sericea*, Dal. "On the 17th of October, 1901, after long and careful watching, I observed for the first time one of the chalcidid parasites in the act of laying eggs in the body of a coccid. When first seen, the parasite was running swiftly from place to place, evidently searching for a suitable host; its antennæ were bent downwards almost at right angles to the long scape forming their basal half, and were moved up and down rapidly and alternately, the tips each time touching the path of the insect as it progressed. Many coccids were examined, and, when a suitable one was found, the parasite turned its head towards the anterior extremity of the coccid, and, resting with all its feet upon the body of the latter, inserted its ovipositor into the centre of the thoracic area; it then slowly moved its abdomen up and down, and apparently laid its eggs in the puncture; the parasite then withdrew its ovipositor, and, turning round abruptly, feeling its way again with its antennæ, seized with its jaws the lips of the wound made by its ovipositor, and distinctly closed them upon it and apparently pressed the edges together; finally it passed the palpi over the wound, and then left the coccid to its fate."

These insects do not—as is the case with so many species—seek the light; on the contrary they prefer the shadow. I tested this many times by having them in a glass vessel, of which one half was illuminated and the other half shaded; they always left the light for the darkened end. This behaviour is all the more unexpected seeing that in the sunlight their activity was always so marked, but it may be that they were resting and therefore preferred to be in the dark. For the most part, they sit inactive on the plant on which they are bred; they seldom offer to leave it, flying but rarely and then only under the stimulus of strong sunshine; such flights are short, never exceeding the distance between one fern-frond and the next. Their most usual mode of locomotion is walking at a relatively rapid rate, supplemented by sudden jumps, effected doubtless by the powerful tibial spurs of the second legs; by this leap they often cover a distance of one or two feet. This rapid running movement gives them a certain likeness to ants, which they resemble curiously in colour and size, for their wings are carried folded flat upon the dorsal surface and are inconspicuous. The antennæ are constantly feeling and moving, as is also the case with ants, and at first sight this motion is sullicient to suggest the resemblance.

(c) Economic Aspects.—From an economic point of view Comys infelix is of signal importance inasmuch as it destroys one of our most injurious scale-insects. Coccidae attack a great many plants of commercial value and do immense damage; usually the horticulturist combats their ravages by means of spraying with insecticides, but the question of parasites is of the greatest importance. In a preliminary paper on the "Economic Importance of the Parasites of Coccida" (17), referring to C. infelia, I have said that "as far as I can judge from the facts that have come under my observation, I am led to rate very highly the value of these parasitic IIymenoptera as destroyers of Coccid pests. In the case of L. hemisphæricum, King's statement that it is one of the commonest pests in greenhouses applies to the district round Cambridge as well as to the United States, and the pest is satisfactorily controlled by the parasite. If the parasite is not found in other districts where the scale is injurious, it should be introduced there. Considerable difficulty has been experienced in the attempts to distribute the predaceous enemies, but in the case of the internal parasites, the task is much simpler, and success will be easier to attain, for it is only necessary to transmit a small plant bearing a few parasitized Coccidæ. From my work on this species I am led to believe that the Encyrtinæ are remarkably tenacious of life in their early stages." As regards the quarantine regulations that are so strictly enforced in many parts of the world, I

remarked that "the creatures may be imported on merchandise or by insects as well as on plants. Neither should it be forgotten, that if a pernicious scale be once introduced, then the parasites that may be contained in the scales are excluded. To avoid this, a knowledge of the marks by which parasitized scales can be distinguished from others, is really essential in the carrying out of the quarantine regulations" ... "it is of utmost importance that, previous to any attempt to destroy the Coccidæ, it should be ascertained whether internal parasites are present or not. If they are found in large proportion, then time should be allowed before any insecticide be used, so that the parasites may emerge from all those individuals containing them, so as to allow the beneficial creature to be perpetuated and increased. After the emergence of the flies, then the Coccidee, if any such there be, may be killed by using those insecticides which are especially adapted to the particular case." There seems, however, to be some difference of opinion on this subject of the importance of Hymenopterous parasites, but I find myself more and more convinced of the views expressed in the preliminary paper, because of the simple fact that having had this scale-insect under observation for a long time I can testify to the well-nigh total destruction of it by Comys infelix. I can readily understand the reluctance of those who have not had this advantage to admit the fact, when I recall that there may be a thousand scales on a plant, and that though nearly every one may be really parasitized and consequently utterly destroyed, there is nothing to reveal this. One must first understand the signs of parasitism in the scale before being able to appreciate the work done by the fly. In economic work of this description it is therefore of the utmost importance that the marks of parasitism should be recognized. I have shown a plant covered with parasitized Lecanium to people used to making biological observations, and they could not believe that the scales were parasitized and destroyed until they saw the fly actually emerge, and that although the parasitism was nearly complete.

It is necessary, in dealing with all insect pests, to use much vigilance and caution, but at the same time to combat them whenever they appear; but this can only effectually be through a proper knowledge of their habits and life-histories, for it is possible, as already stated, to do harm by destroying some beneficial creatures which live upon the pest. In countries which have been under cultivation for centuries a balance between the destructive and beneficial forces has been produced by adaptation, and in this way the destructive species are kept in check; it is therefore essential that care be taken not to remove any of the factors which help to maintain this necessary and delicate equilibrium. It is, at the same time, of utmost consequence that as soon as an injurious creature makes its appearance, it should be watched carefully; in the event of a species coming into the country, in the very early stages it may be dealt with successfully by resorting to hand picking, giving it, if possible, no chance to become established. An added danger to the introduction of an injurious species from another country, is the fact that in its native land it is accompanied by some enemy which keeps it in check; but when it sets up in the new home, it is free from this restraint and spreads enormously in consequence. In the case of parasites of injurious creatures it often happens that they can also be introduced with ease, if, for example, they happen to be beetles, flies, birds,

lizards, &c. It is a recognized method to reduce a pest by introducing some enemy from another country. This has been done in America against injurious scales, by introducing little Chalcid flies from Europe.

Thus the basis of economic entomology is life-history work, which has wider bearings than merely following and observing the different stages in the life-cycle of an insect, for all these separate pieces of work on life-histories contribute towards the solution of the great biological problems of distribution, adaptation to environment, parasitism, and even add to the data on the questions of heredity and variation\*. In order to arrive at any knowledge of how to control injurious insects, it is obvious we must first learn the facts of their life-histories, together with a knowledge of the distribution, food, enemies, climatic needs, &c., until its limitations can be outlined with approximate correctness then any steps taken to deal with it will probably be successful. This subject is at present warmly debated in various parts of the world, and some contend that in the long run it is better to trust to Nature than to extensive artificial operations. My contention is, that we may only trust to Nature when we have obtained a knowledge that will warrant us in so doing, and that will probably enable us to restore natural conditions when they have been abruptly infringed.

Since my paper, above referred to, was published, Professor Antonio Berlese, of the R. Scuola di Agricoltura, at Portici, has taken up this question and published two important papers on the method of Economic Zoology; and as he takes the same view of the subject as I have done, I hope he may be successful in his effort to attract greater attention to the economic importance of the parasites of Insects.

## III. DEVELOPMENT, AND STRUCTURE IN EARLY STAGES.

## $(\alpha)$ EGG.

I have examined the ovaries of a large number of the flies immediately after their emergence from the scales: though I cannot  $\ddagger$  say how long the specimens had been in the image condition inside the host, I found the eggs were present in the tubes in an already advanced stage of development (Pl. 11. figs. 2-5). It usually happened that the ovaries became crushed so that the eggs were most of them free. I have not been able to decide definitely whether the different stages of growth of the eggs are connected with different positions in the egg-tubes; but probably it is so, the egg nearest the oviduct in each tube being the most advanced. Except those in the very earliest stages, the eggs had the appearance of two masses of yolk connected by an isthmus; it is clear that this isthmus ultimately becomes the appendage of the perfected egg, which, as will be seen

\* A German economic entomologist, Dr. L. Reh, of Hamburg, is at present engaged in enlightening public opinion as to the value of knowledge of this sort.

<sup>†</sup> The reason why I am unable to say when the image condition is reached, is because the creature is inside the Coccid, and to expose it is to destroy it, and so no individual case can be traced. This difficulty will always be met with, and is insurmountable. From external signs it is possible to tell roughly when the creature pupates, because then it turns black, and this can be detected through the shell of the Coccid. But there is no such clue to the time when the image condition is assumed.

from Plate 11. figs. 6, 7, 8, is of a very remarkable form. It was difficult to decide in certain cases whether this neck was or was not equally connected with both masses; if so, it certainly soon becomes the exclusive property of the mass that will become the egg. There is a considerable difference in the two masses, more especially as regards the contents. The future egg-mass is almost oblong in shape, while the other portion is spherical and smaller; the granules in the former are larger and more concentrated than in the latter. It is a fact of interest and of some significance that the two masses or parts of the egg always respond in strikingly different ways to various staining reagents; for instance, when treated with methyl green in acetic acid and mounted in dilute glycerine, the true egg-mass and isthmus show a clear green-blue colour, while the other mass is purple. I observed that this stain behaved with similar distinction in other cells belonging to different parts of the body, the nuclei presenting the same colour as the egg-mass, and the cytoplasm of the cells the same as the yolk-mass. I could find no nucleus in the egg.

In the earliest stages the egg is an oval body containing coarse granules; this stage is followed by one in which a slight constriction is observable in the middle; this gets more and more marked until the condition of two masses connected by a fine isthmus is assumed. All these stages are found within a membranous covering (Pl. 11. figs. 2-5). In the latest stages a curious structure is present on the neck part of this dumbbellshaped egg; it is a valve-like projection, pointing towards the yolk-body like a lip. There is still a connection between the two masses (Pl. 11. figs. 6-9), but where this lip is situated there is an appearance of fine papillation or striation on the wall of the tube. At the distal end of the yolk-mass there is evidence of some thickening of the wall, but I cannot find any definite structural peculiarity beyond this. This dumbbell-shaped condition measures '35 mm.

I also examined flies which I had kept alive for a week or two on flowering plants, and in them I found eggs as stalked bodies; that is, the yolk-mass had disappeared, and left only the true egg-mass with the isthmus appearing as a stalk. This appendage ends as a curious forked apparatus, representing the valve or lip present on the connecting tube in an earlier stage. The papillated appearance is now more conspicuous; in the neck of the stalk, at the point where it forks, there is a plug of protoplasmic matter (Pl. 11. fig. 7). From this stage, though I could not observe the act of oviposition, I traced the egg to its destination in the body of the scale, where it is always situated on the right side of the anus (if one looks at it dorsally, towards the head). The form of the egg now is identical with that when last seen in the fly; it measures 25 mm., and always has the plug of matter in the stalk. In older Coccids, where the young larva is present, then the tail of the larva is seen to be capped with the remains of the stalked egg-case, the body of the egg having split into two when the larva emerged. This stalk measures .05 mm.

To summarize the processes I have described, I may say that the mass of matter from which an egg is developed becomes constricted in the middle until it finally assumes a dumbbell form; *i. e.*, two masses are connected by an isthmus. In this condition, changes between the two masses take place by means of the isthmus, as the result of

which, one mass becomes predominant and forms the egg; a portion of the isthmus remains attached to the egg as its stalk or appendage.

It is desirable to call attention to this, as I am not aware that any form of oogenesis quite similar to this has been described. I may add that, when I had made only a few observations, I thought it probable that the original mass of formative material divided into two, and that we might find ourselves in the presence of a condition suggesting an initial stage of dissociation of the embryo, but I was soon convinced that this was not the case. The fact that chemical stains and reagents acted differently on the two masses is of importance, indicating an essential dissimilarity in the nature of the two halves.

## (b) LARVA.

In tracing the early life-history of the fly a serious practical difficulty is met with, inasmuch as it is impossible to follow the same individual through the different stages, for to be able to observe it in the scale it must be exposed, and thus killed. In this way there is no certainty regarding the exact continuity of the observations; I have endeavoured to obviate this as much as possible by examining a great number of the parasitized scales in all stages of growth and at all times of the year; even so, I am sorry to say that there are some links missing from the chain.

General points.—In preparing these larvæ for the microscope, the best results were obtained with those which had been removed from the Coccid, and then suspended on a watch-glass in the vapour of osmic acid over the mouth of a bottle containing a '5 per cent. solution. In a minute or two the larvæ look brown; they are then washed carefully in water and mounted in glycerine. Others were mounted in Canada balsam, but in these preparations some shrinkage always occurred. Some I stained with boraxor alum-carmine, but the osmic acid preparations possessed many advantages. This applies also to the later stages in the metamorphosis before the pupal stage is reached, when the creature becomes black and chitinous.

# i. First observed Stage. (Plate 11. figs. 10, 11, 12, 13.)

*External form.*—I refer to this as the first "observed" stage, because it is probable that the larva immediately on hatching may be different from the youngest specimens I have succeeded in finding; the hypermetamorphosis may be greater even than that which I shall describe.

The larva of the fly is found in the younger Coccidæ as a soft white tapering maggot '75 mm. in length; the head is not differentiated in any conspicuous way from the rest of the body, the anterior end being merely bluntly rounded. Behind what may be called the "oral segment" are thirteen segments, including the bifurcated tail-segment; this segment is a most unusual structure, for the body terminates in two long tapering tails, each with a tracheal trunk continuing to its tip, suggesting that this is an adaptation subserving respiration. These delicate prolongations are always embedded near the anus of the host, and very frequently are capped with the old egg-case. The question of the respiratory significance of this apparatus will be discussed later.

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Tracheal system — The main tracheæ run in two lines parallel with the sides of the body; being full of air, they can be seen plainly through the semitransparent bodywalls; anteriorly they are connected by a transverse commissure in the second segment behind the head; there is also a posterior connection.

Bugnion (9) states that there are nine pairs of stigmata in the larva of *Encyrtus fusci*collis, occurring in the segments two to ten. Reinhard (47) has counted the same number in *Pteromalinæ* larvæ (*Decatoma, Callimone, Eupelmus, Pteromalus*). Laboulbène (35) describes also nine in the larva of *Pimpla Fairmairei*; but Ratzeburg (46), in the larva of *Anomalon circumflexum*, a parasite of *Bombyx*, found no stigmata at all, which he says is due to the fact that the larva lives inside the caterpillar. In the larva of *Comys infelix* at this stage I have been unable to detect any stigmata, though I have employed many methods in preparing the larvæ for the microscope, but always with negative results. Possibly the tail-apparatus takes the place of stigmata, for it is a most remarkable arrangement, and suggests a parallel with the metapneustic tracheal systems of some Dipterous larvæ in which there exist only a terminal pair of spiracles. In some metapneustic Dipterous larvæ a pair of anterior spiracles appear later; this is then called an amphipneustic larva. The arrangement in which the normal stigmata are present is called peripneustic.

Alimentary system.—In the bluntly rounded anterior end there is a circular mouth with a soft rim or lip (Pl. 11. fig. 11); inside there are two chitinous mandibles, each being a simple tooth or claw, one of which overlaps the other; these mandibles possess a powerful muscular apparatus. From the mouth, the alimentary canal runs to the tail; immediately behind the mouth there is a funnel-shaped pharynx, leading through an œsophagus to the stomach, in about the third segment. On either side of the stomach is a gland, probably possessing a salivary function (Pl. 11. fig. 13); these glands open into the pharynx. The alimentary tract is straight, apart from the stomach, which is sac-like and fills the larger part of the body-cavity, and contains fat-globules and other dark-coloured granules; it looks darker than the rest of the body, which is white, and, under a high power of the microscope, is seen to be granular. There is a short intestine behind the stomach, but at this stage it is not connected with the anus.

## ii. Second Stage.

*External form.*—The body now measures 1.75 mm. As the two-tailed larva grows its contents get more and more aggregated into ball-like masses. The body becomes rounder and thicker, while the tails atrophy (Pl. 11. fig. 13), till the stage is reached (fig. 14) in which the posterior end is rounded, but the two tracheal trunks are still visible projecting out of the body as withered ends not yet quite cast off.

Tracheal system.—Apart from the difference in the tail-apparatus, the two main tracheæ remain unaltered except for the fact that in each segment they give off a group of secondary branches. In this stage I have found the anterior and posterior commissures still present; in front of the anterior connective the main trunks continue, ultimately ramifying in the head; behind the posterior commissure the trunks are continued, finally projecting out of the body as withered atrophied remains of the tailapparatus (Pl. 11. fig. 14). Between these two transverse connectives are eight pairs of side branches, more marked than the finer anastomosing branches of tracheæ that, as stated, are given off in each segment. Of these eight pairs of conspicuous side branches, the first and last have each a definite spiracle, but the six pairs between have no spiracles, or else they are so small as to be unfunctional. This is an interesting condition between the peripneustic and the amphipneustic arrangements.

Alimentary system.—The mouth and mandibles show no alteration, and the alimentary canal is unchanged except that its contents are more marked in colour and quantity, and that the communication with the anus is now probably established. The coloured refringent granules in the stomach are most noticeable.

### iii. Third Stage.

• External form.—The larva now has become more swollen and measures just over 3 mm. in length (Pl. 11. fig. 15), and it is only very occasionally one finds traces of the tail-tracheæ outside the body.

Imaginal discs.—It is now possible to discern in outline the early rudiments of the future organs of the imago: these rudiments Weismann called "imaginal discs"; Künckel d'Herculais (34) called them "histoblasts," and Miall refers to them as "imaginal folds." Gradually they assume a form (Pl. 11. fig. 15) in which the antennæ can be seen as a pair of plate-like bodies near the mouth. Behind and almost above these is a pair of circular discs from which the eyes will arise. The buds which will ultimately form the buccal folds are also discernible. The leg-rudiments (Pl. 11. fig. 15,  $l.^{1-3}$ ) come behind the eyes, and on the outer margin the wing-rudiments are plainly traceable. Nearer the posterior end of the body are two oval masses of cells, representing the future sexual glands (Pl. 11. fig. 15, s.g.)—ovaries or testes; and following closely on these are three pairs of bud-like bodies, which are the rudiments of the sting (Pl. 11. fig. 15,  $st.^{1-3}$ ).

Tracheal system.—The tracheal trunks still have a lateral course, connected by an anterior and posterior transverse commissure. The stigmata are as in the preceding stage, but in connection with each of the four spiracles described as functional in that instar, there is an apparatus by which intercommunication is apparently set up between the respiratory systems of the host and parasite (Pl. 11. fig. 15). From each of these four spiracles there is a double tracheal tube running out into the host's body; these two branches become subdivided and ramify in the host-tissue, and by this means, it seems, the parasite obtains its air-supply. Whether these ramifying tracheæ originate from the tracheal system of the Coccid host, or from that of the parasite for whose benefit we may presume they are functioning, is quite obscure. If the former be the correct interpretation, we must conclude that the host develops a respiratory system for the benefit of the parasite itself, we have to deal with the remarkable fact that they constitute a tracheal system entirely outside of the creature to which they belong. Bugnion says that in

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*Encyrtus fuscicollis* the tracheæ of the host ramify on the tube containing the parasite, and serve for respiration of the young *Encyrtus*. The only other case I can find bearing on this point, is that described in 1837 by Dufour, of *Andrena aterrima* and a parasitic Dipterous larva\*. Dufour claims that two of the host's tracheæ grow into the body of the larva, which is thus supplied with air; but there seems some doubt about the interrelationship in this case.

As this instar passes into the next, the posterior pair of external tracheæ become marked by the appearance of three red-brown plate-like structures on each side of the body of the larva (Pl. 11. figs. 16, 17, 18, pl.); they are situated at the point where the radiating external tracheæ are united with the body-wall. These curious plates are present in the pupal condition, but are left behind when the pupal skin is cast.

Thus we see, in summarizing the facts recorded above, that in the larval condition respiration is at first carried on by means of a bifurcated tail-apparatus in which the two lateral tracheal trunks are continued; in this condition there are no spiracles, but later on the two tapering tails atrophy, and spiracles are developed. This condition is superseded by an arrangement of tracheæ ramifying outside the parasite, in the body of the host; there are now 8 pairs of stigmata, and the posterior pair of radiating tracheæ arise in the 9th segment behind the head.

Before the next (or prepupal) instar is reached, a process of histolysis takes place by which the internal organs are completely broken down, to be built up into the pupal tissue by means of a process of histogenesis, or regeneration.

In this instar, or at any rate during the later period of its existence, the larva appears to possess a membranous coat, or sheath. It is to a membrane of some kind or other that Bugnion refers in the passage quoted above as to the respiration of the larva of Encyrtus fuscicollis: he states that the embryos are all in one long common capsule, and he is of opinion that this is a product of the egg; but the case differs so widely from that of Comys infelix, that his facts cannot be of much service in making a parallel argument. As to the nature and origin of this sheath in Comys infelix, I am quite in doubt. Subsequently, as we shall see in the next instar, there exists a well-defined and ample membranous sheath, but whether the membrane observed in the third instar is really the same as that found later, or not, I cannot say with any certainty; no actual ecdysis has, however, been observed, and I think it is probable that the sheath is a larval skin retained on account of the respiratory apparatus attached to it externally. The question is complicated by the appearance in the next (or prepupal) instar, at the base of this respiratory apparatus, of additional structures in the form of certain oval red plates (Pl. 11. figs. 16, 17, 18, pl.), which appear to be applied to the sides of the body at the spot where the tracheæ radiate out. If these were developed outside an old skin, it would be a very remarkable fact: I have alluded to the possibility that these respiratory structures are really formed by the host, and in that case there would be no difficulty in understanding that they undergo further development even on the separated skin of the parasite.

\* Cf. Cambridge Natural History, Insects, ii. (D. Sharp), p. 26, fig. 13.

I have been unable to settle this question, for in order to do so with any finality it would be necessary to find the creature at the exact time when the change is taking place, and this would entail the examination of a vast number of individuals, and as cach examination involves a careful dissection of the small host first, the time required would be considerable.

It is at this point in its life-history that the creature turns completely round inside its host.

# iv. Prepupal Stage. (Plate 11. figs. 16, 17.)

External form.---A great change has taken place between this and the preceding condition, transforming the larva into the prepupa, or pseudonymph. In this instar the creature is still creamy-white, like the larval forms already described; it is, however, enclosed in a membrane (Pl. 11. figs. 17, 18, m.), which is probably the remains of the original larval cuticle, and the parasite is now head to tail in the Coccid, instead of head to head as was the case in the larval condition; its dorsal surface is now closely pressed to the inside of the dorsal surface of its host, whose body it now almost completely fills. 'The appendages, &c., of the imago body are well defined, though still imperfectly developed in this instar (Pl. 11. fig. 17). The head is differentiated from the rest of the body, the antennæ and eyes being clearly outlined, while the thoracic region has become more rounded. The rudiments of the legs and wings are folded across the ventral surface, and the segmentation of the abdomen is distinct, so that the creature now exhibits very definitely the form of the perfect insect. Internally, the organs have undergone less change as a result of the histolysis and subsequent regeneration. Packard (44, p. 67) has called this form the semipupa, and Siebold's term pseudonymph applies to the same instar; the nymphal form is attained after an ecdysis.

Tracheal system.—There are in this instar four large stigmata—three situated in the thoracic region and one in the abdominal segments, with six smaller abdominal stigmata which may not be functional, for only traces of the first five can be seen in the imago, and the seventh has entirely disappeared, or has fused with the sixth to form the large functional spiracle which is so conspicuous.

Situated on each side of the abdomen there are three oval red plates (Pl. 11. figs. 16, 17, 18, pl.), referred to above. These appear to be connected in some way with the respiratory function of the creature, for they are placed at the base of the large forked tracheal tube, which at that point effects its union with the body, or, in other words, branches out of the body at that point, to ramify over the membrane which encloses the insect. This membrane has been discussed when the preceding instar was being considered. Each of these curious plates is an oblong body applied closely to the outside wall of the abdomen; under a high power of the microscope, one of these plates is seen to contain red globules, of different sizes. It is not easy to determine what the function of these structures can be, but I suggest that they have some connection with respiration, seeing the radiating tracheæ arise at the same place as these anomalous plates. Nothing of this nature has been recorded by Bugnion as occurring in *Encyrtus ruficollis*, nor can I find elsewhere any statement bearing on these curious structures.

#### MISS A. L. EMBLETON ON THE ANATOMY

### v. Pupa. (Plate 11. fig. 18.)

External form.—The pupa measures 2.25 mm. in length. The earliest pupal form is not of a uniform black colour, the dorsal surface alone being black. The fully formed pupa is, however, completely black and chitinous, though still enveloped by the cuticular membrane whose origin has been already discussed. The first organs to assume their final colour are the eyes and ocelli, which early become charged with dark red-brown pigment, at a period when the rest of the body is creamy-white; gradually the colour deepens all over the thorax and abdomen, though the head, apart from the eyes and ocelli, remains almost transparent for a considerable time. When the body has become uniformly black, the creature is in an inert, passive condition, unlike the preceding larval stages, in which slow movements from side to side take place as a result of external stimulus. But after a time this black, inert pupa becomes the perfect insect, and breaks through the enveloping membrane (Pl. 11. fig. 18, m.) and the old pupal cast skin, and with its mandibles cuts a small round hole in the dorsal shell of the Coccid, and escapes, to lead its free existence.

Tracheal system.—The abdominal plates (fig. 18, pl.) and the radiating tracheæ are still present, but when the imago emerges they are left behind with the old sheathing membrane. The pair of tracheæ which radiate out from the head region never develop these oval red plates at their bases; it may be that these plates are more connected with excretion than respiration. The nymphal respiratory arrangements are apparently very transitory.

In order to obtain, if possible, more detailed and exact knowledge of the larva and pupa while still within the host, I cut the undissected host into a series of sections with the microtome. To do this I tried various methods for softening and cleaning the chitin, but the most successful results were obtained when I employed eau de Javelle or eau de Labarraque, as suggested by Looss. The chitin in this way was rendered transparent and permeable to reagents. I first hardened the specimens, and then left them in 25 per cent. eau de Javelle for 18 to 24 hours, afterwards washing out thoroughly with water. They were then dehydrated, embedded in paraffin, and good sections were obtained; sometimes I stained, before embedding, with alum-carmine or picro-carmine (five to six days), but usually I found it best to stain the sections when on the slide.

But though the sections were good, there was little or nothing to be made out by this method of investigation, which was not seen better in macroscopic dissections; except, of course, histology, but that I have been content to omit.

# IV. ANATOMY OF IMAGO, Q.

(a) Measurements.—Length (without antennæ) 2.5 mm.; length of thorax .9 mm.; width of head .75 mm.; width of thorax .74 mm.; width of abdomen .74 mm.; length of antennæ 1.25 mm.; extent of fore wing 1.5 mm.; extent of hind wing 1.25 mm.; width of fore wing .62 mm.

(b) Antennæ (Pl. 11. figs. 19, 20; Pl. 12. fig. 21).-The antennæ are relatively long

and club-like, composed of eleven segments, the funicle being six-jointed, while the pedicel is shorter than the succeeding segments. From the third segment, the joints which go to make up the flagellum decrease in length, but increase in width and become, in the female, compressed towards the tip; in the male they remain almost cylindrical. Except for the pedicel the whole organ is clothed with fine black hair. The antenna is light brown at its base, shading to black in the flagellum.

(c) *Head* (Pl. 12. figs. 26, 27).—The surface of the head and face is curiously sculptured and punctured; it is golden-brown, almost black beneath the eyes, which are very dark and composed of fine facets devoid of setæ. Between, and slightly behind, the eyes are three ocelli, the two basal being nearer the true eyes than they are to one another.

(d) Mouth-parts.—The maxillary palpi are the most conspicuous parts, being black and projecting laterally. The maxilla (Pl. 12. fig. 24) consists of a stout tooth made up of three joints, the second bearing the palp on its outer surface and a small club-like organ on its inner surface; there is next a broad flattened part of two halves; the palp comprises four pieces, and ends in a curious club-like structure with long setæ on its inner face and tip. The *lower lip* can be seen as a median structure below the mandibles (Pl. 12. figs. 22, 23); laterally it has a foliaceous setose apparatus united basally by a triangular membrane, to which is attached a labial palp on either side; this is made up of three segments. The mandibles are very simple, curved, plate-like organs, with setæ; they are approximately triangular in outline, the apices curving inwards, the bases being just above the maxillary palpi (figs. 22, 25). Overhanging the whole mouth-apparatus is an upper lip, with a setose edge (fig. 22, u.l.).

(e) Thorax.—Except for the shining black collar (Pl. 12. fig. 29, c.) the thorax is yellow with conspicuous darker patches of pigment and black hairs. The pronotum (Pl. 12. fig. 29, pr.) is almost circular; laterally it carries the small dark tegulæ. Behind the pronotum is the raised scutellum (fig. 29, sc.), a triangular area with the apex pointing backwards, and terminating in a tuft of long stiff black hairs, arising apparently in two longitudinal rows. The mesonotum and metanotum are black and glossy, the former serving as attachment for the fore wings, and the latter for the hind wings and third legs (Pl. 12. fig. 28). The thoracic spiracles are arranged in three pairs (Pl. 12. fig. 29, st.<sup>1-3</sup>); the mesothoracic are in a suture, only seen by looking from the side; the metathoracic are conspicuous (figs. 28, 29).

(f) Fore wing (Pl. 12. figs. 19, 20).—The wings are mottled with black fuscous areas, and are covered with fine hairs, forming a fringe round the distal margin. At the base of the short incurving vein is a group of dark setæ, with a second group just behind. From the description of the genus as given in Comstock's report, quoted above, and from my figures, it will be easy to see the disposition of the wing-veins.

(g) *Hind wing* (Pl. 12. figs. 19, 28).—These wings are smaller and more delicate than the fore wings, and are not mottled, being uniformly transparent and clothed with fine short hairs.

(h) First legs (Pl. 12. fig. 31).—The coxæ are silvery white, while the femora are dark, separated from the coxæ by two trochanters; the tibiæ are slender and fuscous,

the spur being no longer than the first tarsal joint; the *tarsi* comprise five segments, the last being the *claw*, made up of two hooked down-curving setæ. The whole leg is covered with short dark hairs.

(i) Second legs (Pl. 12. fig. 30).—These differ from the first only in colour and in the length of the tibial spur. The coxæ are black, the two trochanters rather paler, while the femora are almost white; the tibiæ are yellow, and dilated distally; the spur is long and powerful, and by its means the creature performs the characteristic hopping movements; in preserved specimens the second legs project beyond the third (Pl. 12. figs. 19, 20, 30).

(j) *Third legs* (Pl. 12. fig. 28).—The small rounded *coxæ* are silvery white, the *femora* are brown and the *tibiæ* black, while the *tarsi* are almost white, the tip of the claw being black. The spur is of normal size, as in the first leg.

(k) Abdomen (Pl. 12. figs. 32, 33, 34, 35, 36, 37).—The abdomen is of a deep glossy black, with numerous long dark hairs, and ventrally a soft down of short hairs. There are seven segments succeeding the petiole. The structure of the exoskeleton of the abdomen in the perfect insect is not easily ascertained, for there are many obscure points, and it was only after dissecting a great number of specimens that I was able to arrive at even an approximately correct knowledge in this matter. After trying many methods, I found that the most satisfactory specimens were those that had been macerating for a day or two in water, until they were quite soft and greatly distended; in such preparations the black abdominal plates stand clear of each other with the swollen white internal tissue showing between : this was most useful, for in such a condition one could clearly and unmistakably make out the relative positions of the parts before dissection. Another advantage is that the pieces of the exoskeleton can be removed one by one if great care be used, and the whole series put together again on a slide and mounted in Canada balsam (Pl. 12. figs. 34, 35, 36, 37). An alternative method, which often proved very helpful, was to leave the flies in 10 per cent. (or 5 per cent.) KOH for 24 hours, when all the soft parts are destroyed, the chitinous parts remaining uninjured and in a condition in which they can be easily separated from one another; when properly washed, dehydrated, cleaned, and mounted in Canada balsam, the structure is seen to even better advantage than in the former method, for the chitin has become, to some Nevertheless, the difficulty always remains that curved and extent, transparent. rounded pieces of the armature must be flattened when mounted, rendering some distortion unavoidable. This difficulty is met with chiefly in the matter of obtaining a correct interpretation of the structures which go to make up the petiole (figs. 34, 35, 36, 37). This has a dorsal and a ventral face, each composed of two small chitinous plates, of which the dorsal pair is much the thicker and stronger, being always conspicuous in mounted preparations, while the ventral pieces need careful search before they are In these flattened mounted specimens, the dorsal factors of the petiole discovered. appear as a dark mass situated between the side wing-like parts of the abdominal plate immediately behind the petiole (figs. 34-37). In life these two lateral flaps of the abdominal plate curve round the abdomen to the antero-ventral face, leaving the petiole standing out in front; its dorsal elements also curve round, forming a sort of short tube,

the remaining (ventral) face of which is completed by the ventral pieces of the peticle. This dark basal portion of the petiole-ring is made up of two separate elements, meeting in the middle line, where they are very narrow; at the sides they are much deeper (Pl. 12. fig. 36), so that, in outline, the two together are cup-like in mounted specimens, with an almost straight base resting on the segment behind the petiole; the two sides are prolonged to form blunt points, which articulate with the propodium and make a concavity between, filled by a pallid membrane, like a semicircle between two horns. The (anterior) rim of this semicircle is a clear strong chitinous band. The chitin of these parts is smooth, and devoid of surface reticulations such as mark the abdominal Ventrally (Pl. 12. figs. 36, 37) the structure of the petiole is very similar plates. to that seen on the dorsal side, but the chitin of which these parts are composed is thin and reticulated, making them obscure and difficult to detect. Another difficulty too in investigating the ventral structures arises from the fact that these almost transparent parts often remain attached to the metathorax, and so get lost. But with careful manipulation it is seen that they are borne between two lateral horn-like projec-tions of the segment abutting on the petiole, and that their anterior edge is not concave as in the dorsal region, but straight or slightly convex. The two strong outstanding points from the ventral abdominal segment apparently form the articulation, and in the natural position would point towards the dorsal surface on the face that meets the thorax; they would not point up and forward, as is necessarily the case when the parts are flattened-out under a cover-glass. This petiole, therefore, differs greatly from what prevails in either the Aculeate Hymenoptera or the Ichneumonidæ. Dorsally, behind, the petiole there are seven separate plates (figs. 34, 36). Each plate, except the last, is made up of a median area connecting two lateral flaps. In the first of these (and what must be looked upon as the true second segment), the lateral parts are broad and wing-like, their function being to fold round the anterior face of the abdomen, curving towards the ventral surface; this segment bears no trace of a spiracle.

The 2nd, 3rd, 4th, and 5th plates form a progressive series, each with an atrophied spiracle. The flaps are bent back more in each segment (Pl. 12. figs. 34, 36) until in the 6th this curvature reaches its maximum, for the side parts are very slender until near the tips, where they expand. At this point there is the only functional spiracle in the abdomen: it is a large circular orifice (Pl. 12. fig. 40) surrounded by a chitinous ring; in the clear centre can be seen a tongue-like structure; the large trachea can be traced running from this spiracle into the body. The median part of the seventh plate is slender and deeply concave in front. The last dorsal plate has no lateral expansions; at its points on either side is situated a remarkable organ, which, for want of a better term, I refer to as the "tactile plate"; it is over this that the preceding plates have been looped, as it were (figs. 33, 34, 36, 39). This organ consists of a pear-shaped plate (figs. 42, 43) placed transversely to the length of the body, the pointed end being on the inner side; the plane of the plate is at right angles to the dorsal surface. The plate itself consists of a membrane stretched over a loop-like ring of chitin and supplied strongly with nerves; at its pointed inner end there is a solid chitinous rod, which, in the natural position of parts, points forwards at right angles to the length of the oval plate;

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this rod is almost the same length as the plate, to which it is attached by a hinged joint, as may easily be proved by moving the rod to and fro on the plate-rim. The plate itself carries four long setæ, the two inner being the biggest, and the outer the smallest. It is hard to say what is the function of this curious apparatus. I have watched the living insect walking about for hours on a fern-frond, hoping to get some clue as to the use of this "tactile plate"; I have examined its structure microscopically, but cannot be certain of its function. In life, the long hairs were always standing out conspicuously from the side of the abdomen, and occasionally it seemed they were brought into a more erect and bristling attitude, but beyond that I observed nothing.

Turning now to the ventral elements of the abdominal exoskeleton, it is found that there are six large segments (Pl. 12. figs. 32, 35). Behind these there are two small subcircular pieces, one on each side of the base of the sting, and two large pieces still further behind these, nearer the middle line close to the apex of the ovipositor; probably these are the vestiges of the seventh and eighth segments. The ventral plates are almost all alike, except that the one adjoining the petiole has the two horns pointing forwards (*cf.* petiole). The others all have the lateral parts rounded at the ends, and the surfaces are reticulated and bear fine hairs, becoming more numerous on the posterior segments. The last of the ventral series of plates covers the ovipositor, which is almost entirely hidden in life, though sometimes in a lateral view the tip may be seen protruding slightly (fig. 33).

I find but little information in books as to the structure of the abdomen of Chalcididæ. More attention has been given to the external anatomy of the Aculeata, but the structure of the abdomen in *Comys infelix* is so different from that of the Aculeates that the homologies of some of the parts are still an enigma to me. Bugnion, who dealt with the anatomy of a form allied to *Comys infelix*, left the difficult points of the morphology untouched; and he is also silent as to some of the important points of simple anatomy of this part of the body.

Ovipositor (Pl. 12. fig. 41).—The ovipositor or sting has been largely studied in the Aculeata, but I can find little information about it in the Chalcididæ. Certain portions of this organ in *Comys infelix* are so different anatomically from the sting of the Aculeates that it appears at first sight almost hopeless to homologize the two by mere comparison, and it is necessary to thoroughly understand the development to arrive at really permanent results. As regards this a preliminary difficulty exists: it is now generally admitted that the sting of the Aculeates is developed from appendages situate in the pupa on the eleventh and twelfth body-segments, the segments themselves being subsequently very highly modified to form parts of the complex apparatus. Bugnion has figured the ovipositor of *Encyrtus fuscicollis*, and it agrees largely with what I find to exist in *Comys infelix*; he also figures the buds of the appendages in the larva, and shows that they arise in three different segments, viz., the three in front of the anal segment. If this is correct, great caution is necessary in comparing a sting formed by appendages of three segments with a sting that is developed from appendages of two segments only. I have no information to give on this point in *Comys*, and shall therefore briefly describe the structures I have figured.

The ovipositor is furnished on either side with two large expanded chitinous plates; these are held together anteriorly by a three-cornered nodule of chitin (Pl. 12. fig. 41). Of these two pairs of plates, the inner is the larger; each half carries a fringe of short bristles round the distal border. The outer edge of this plate is strengthened by a thickening of the chitin; this thickening leaves the margin and turns into the middle of the plate before it reaches the extremity. Where these two inner plates articulate with the triangular nodule, there arises a curved rod which runs round and back, meeting its fellow of the opposite side in the middle line; these two curved bars end near the extremities of the inner plates, and they form the pointed stinging-apparatus of the ovipositor. A little below the level of the articulating nodules, these two curved rods converge together and are embraced by a thin membranous sheath; at this point the enveloping sheath expands into a pair of oval claspers or clamps, through which the rods of the sting run. The membrane is continued on as a covering or director to the stingpoints. At first I was uncertain as to whether these rods were separate from the membranous sheath or not, but later on I found it was possible to dissect them out as perfectly free structures, grooved to the tip from the point where they become swathed in the sheath.

As regards the origin of the parts of the ovipositor-or sting-in Hymenoptera, there seems to exist a considerable amount of confusion in the literature on the subject; the point on which I find authors disagree is as to whether the three pairs of buds (or imaginal discs) present in the larval condition belong to two segments or to three. Bugnion says they arise in three different segments representing three pairs of appendages, and he figures them accordingly; he says: "la tarière (gorgeret, stylets et valves), représentant également trois paires d'appendices, dérive de six petits disques qui se montrent dans la seconde moitié de la période larvaire, de chaque côté de la ligne médiane, à la face inférieure des trois derniers segments."... "J'ai observé moimême la formation des six disques de l'armure génitale chez les larves d'Encyrtus, la transformation de la partie centrale de ces organes en petits bourgeons digitiformes, puis la division des deux bourgeons intermédiaires en quatre (?), mais il ne m'a pas été possible de suivre leur développement ultérieur." He seems to be in some doubt as to the division of the median pair into two pairs of buds. Kraepelin (33), in Apis mellifica, states that in the earliest instar " an der Bauchseite der drei vorletzten Segmente findet man um diese Zeit je ein Paar länglich runder Wülste, welche, von Tracheen umsponnen und augenscheinlich der Hypodermis entstammt, man nach Weissmann's Definition als Imaginalscheiben zu bezeichnen das Recht hat."..." Bald zeigen diese Wülste weitere Differenzirungen, namentlich die des dreizehnten Segmentes. An letzteren gewahrt man nach kurzer Zeit eine Längstheilung, derart dass jeder Wulst nunmehr aus zwei nebeneinander liegenden cylindrischen Zapfen besteht, deren basale Theile unter sich wie mit dem correspondirenden Wulst der andern Seite verbunden sind. Die Wucherungen des zwölften Segmentes sind zu länglichen, gekrümmten Zapfen geworden, während die des elften Ringes zwei rundiche mit je einem langen Faden in Verbindung stehende Blasen repläsentiren."

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But Dewitz (16) also worked at the development of the sting in *Apis mellifica*, and he asserts that the three pairs of sting-rudiments arise from two segments, and his figures show this very unmistakably. He says: "auf der Bauchseite der beiden vorletzten Segmente, dem 11. und 12., sicht man die erste Anlage des Stachels als 6 kleine Wärzchen, von deren 4 dem vorletzten, 2 dem drittletzten Leibesringe angehören. Die beiden letzteren krümmen sich bei ihrem späteren Wachsthum mit den Spitzen nach den Seiten und sie sowohl, als auch die 4 übrigen liegen unmittelbar unter der Oberhaut in kleinen Höhlungen." He finds the development is similar in *Locusta viridissima*, and also in *Vespa vulgaris*, of which he remarks : "die beiden vorletzten Segmente, das 11. und 12. hinter dem Kopfe zeigen wieder die 6 Stachelwärzchen in kleinen Vertiefungen unter der Oberhaut liegend, welche ebenfalls aus Imaginalscheiben entstanden sind."

Janet (31), too, supports the view that the parts of the sting arise in two, and not in three segments: his remarks apply to *Myrmica rubra* and are as follows: "sur le 11<sup>e</sup> anneau il y a deux appendices qui sont les rudiments des stylets. Sur le 12<sup>e</sup> anneau nous voyons le rudiment de la glande à venin, deux appendices qui se souderont plus tard en une pièce unique impaire et donneront le gorgeret et, enfin, sur les côtés du gorgeret, deux appendices qui deviendront les valves protectrices de l'aiguillon." His figure shows this very clearly.

Packard (44) quotes these writers, but seems to be unaware of any discrepancy; he reproduces the figures of the development of the sting in *Bombus*, as given by Dewitz, showing that only two segments are involved, but he says, "as shown, then, by our observations and those of Dewitz, the rudiments of the ovipositor consist of three pairs of tubercles, arising, as Kraepelin and also Bugnion have shown, from three pairs of imaginal discs, situated respectively on the seventh, eighth, and ninth uromeres, or at least on the three penultimate segments of tubercles, but that they arise in *two*, and not in *three*, segments, there being two pairs in the posterior segment.

Regarding the ultimate fate of the sting-buds, Kraepelin remarks that the parts arising from the first of the three pairs that he admits to be present go to form the oviduct and passages; but it is very difficult to suppose that the external buds figured by Bugnion on the corresponding segment could become transformed in such a manner, for it would involve a complicated process of invagination.

I have been unable to find anything further relating to the development of the sting in Hymenoptera; Zander's (66, 67) papers are on the morphology of the adult structures, and do not consider the larval condition. One of the most recent papers (Anglas, 1) on the metamorphosis of the wasp does not deal with the sting origins at all.

# V. ANATOMY OF IMAGO, J. (Plate 12, figs. 44, 45.)

The male of this species differs in several respects from the female. It is smaller than the largest females, being about the same size as the smaller specimens; it looks somewhat longer than it is in reality on account of the fact that the wings, when folded on the back, extend a short distance beyond the end of the body; this is true for the hind wings as well as for the fore wings.

In colour, the male fly differs considerably from the female. The body is entirely black, except several white joints of the legs. The thorax and head are dull black, and not golden brown as in the female. The antennæ are completely black, and do not end in a club-like dilatation, for the component segments are almost equal in size. The antennæ of the male fly can also be distinguished from those of the female by the fact that they possess a conspicuous covering of fine black hairs, relatively long; the elbow, too, is not so strongly marked as in the female antenna. When the male is looked at from the side, it is seen that the antennæ are arched upwards and forwards, the tips curving down again.

The wings are, proportionately, much larger than in the female; they differ also in not possessing the shaded fuscous patches so noticeable in the other sex; they are, on the contrary, of a shining iridescent colour, having an almost metallic appearance. The group of hairs so marked on the surface of the female fore wings, is absent in the male, in which the entire surface of the wing is covered with a soft down of fine hairs.

The legs are similar to those of the female, the second pair being furnished with the large tibial spur so characteristic of the species.

The abdomen is relatively smaller than that of the female, but, as regards the arrangement of the segments and of the curious lateral plates, the form is identical. The reproductive apparatus differs entirely from that seen in the female. In the natural condition, there is a small pointed process projecting from the tip of the body, on either side of which can be seen a little wing-like organ. When dissected out, the male organs are found to be composed of a central hollow piece, or penis (Pl. 12. fig. 45, p., h.), in which run the ducts communicating with the glands. On each side there is a jointed, hooked rod, ending in three sharp teeth. Outside these parts, laterally, there is another rod-like organ, which ends in a long spike, or seta. The tip of the penis has curious little papillæ, which are the openings of the ducts leading from the gonads.

Note.—While performing the work recorded above, I have been fortunate in having the valuable help of Dr. D. Sharp, who has, with constant generosity, given me the benefit of his knowledge and experience; I am, therefore, only too happy to take this opportunity of acknowledging, with gratitude, the essential service he has rendered.

Balfour Laboratory, Cambridge, May 14th, 1903.

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## VII. EXPLANATION OF THE PLATES.

### PLATE 11.

- Fig. 1. Portion of fern-frond attacked by Lecanium hemisphæricum var. filicum, the Coccid being parasitized by Comys infelix.
- Figs. 2, 3, 4, 5. Early stages in the development of the egg within the egg-tubes of Comys infelix.
- Fig. 6. Fully formed egg previous to the disunion of the two parts, showing the valve-like apparatus on the connecting neck. A=true egg-mass; B=yolk-mass.
  - 7. Egg after losing the yolk-mass; the valve-apparatus is retained as a bifurcated foot to the stalk which is plugged with a quantity of protoplasmic matter. Egg-cases like this are found in the host's body, and are often seen capping the tail of the larva.
  - 8. Valve-apparatus more highly magnified.
  - 9. Egg before the separation of the two masses, drawn on  $\frac{1}{2}$  mm. scale. Length =:35 mm.; length of stalk after separation =:05 mm.
  - 10. First observed larva with the bifurcated tail. Length = 75 mm.
  - 11. Mouth and mandibles of first larva, with buccal glands. 12. Posterior segments of same.
  - 13. Larva just before the second instar, in which the tails are atrophying.
  - 14. Second instar in which the tails remain only as withered ends of the tracheæ.  $sp.^{1-2}$ =spiracles.
  - 15. Third instar showing imaginal discs.  $l_{\cdot}^{1-3} = \text{leg-buds}$ ;  $st_{\cdot}^{1-3} = \text{sting-buds}$ ; s.g. = sexual glands.
  - 16. Prepupa in situ in the host (h.). (The insect is represented in an inverted position.)
  - 17. Prepupa removed from host but still in its sheathing membrane (m.). pl.=oval red plates.
  - 18. Pupa in membrane. Length =2.25 mm.
  - 19. Comys infelix,  $\Im$ , dorsal view. Length = 2.5 mm. 20. The same, ventral view.

### PLATE 12.

Fig. 21. Ventral view of head.

- 22. Mouth-parts in situ. u.l.=upper lip; md.=mandible; p.=maxillary palpi.
- 23. Labial palpi. 24. Maxilla and palp (p.).
- 25. Mandible, drawn on scale of  $\frac{1}{20}$  mm. Length = 18 mm.
- 26. Surface of face, with two ocelli and part of an eye. 27. Surface of the eye.
- 28. Hind wings, 3rd legs, and 3rd thoracic spiracles (sp.<sup>3</sup>).
- 29. Dorsal view of thorax. c.=collar;  $sp.^{1-3}=\text{spiracles}$ ; pr.=pronotum; t.=tegulæ; sc.= scutellum.
- 30. Second leg with tibial spur.
- 31. First legs with thoracic segment of attachment.
- 32. Ventral view of abdomen of specimen distended with water, showing relative positions of parts.
- 33. Lateral view of abdomen as seen in life, showing sting.
- 34. Dorsal plates of abdomen and petiole.
- 35. Ventral plates of abdomen flattened, showing petiole and sting.
- 36. Dorsal plates and petiole, flattened.
- 37. First ventral plate and petiole.
- 38. End view of the tip of the abdomen, showing the arrangement of the plates round the anus.
- 39. Tactile plate, in situ.
- 40. Large functional spiracle on the 7th dorsal plate.
- 41. Sting-apparatus.

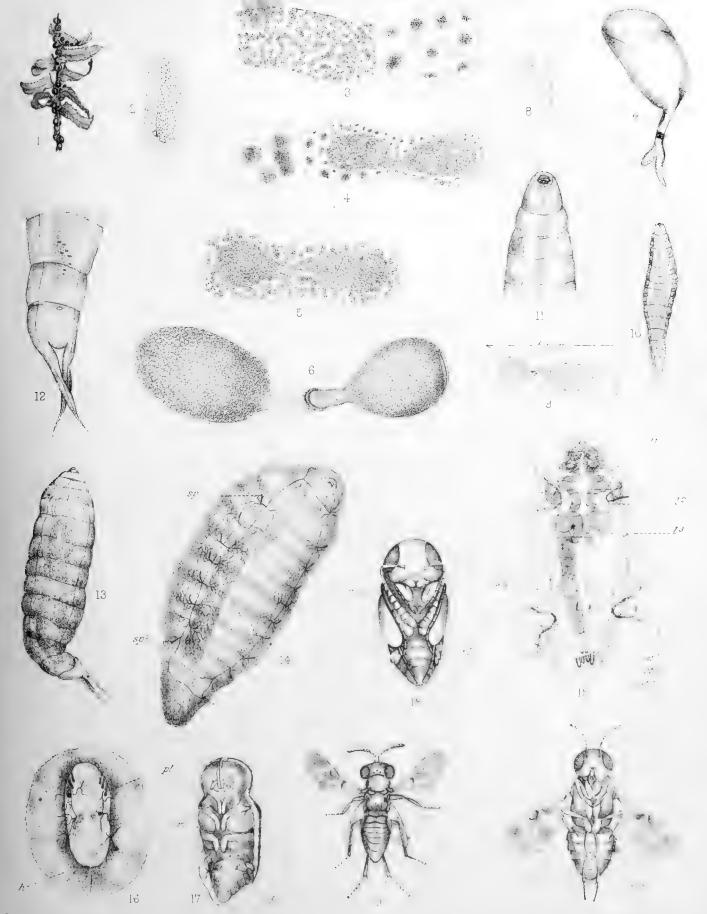
Figs. 42, 43. Tactile plate and hinge.

Fig. 44. Comys infelix, 3, dorsal view.

45. ,, ,, skeletal parts of the reproductive organs. p.= penis; h.= hooks.

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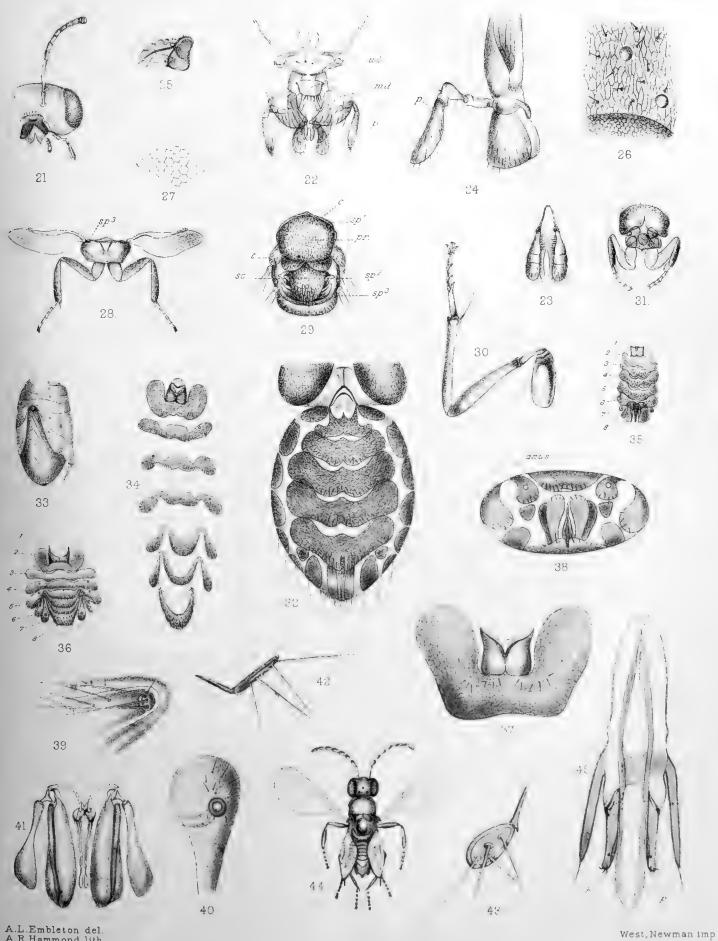


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VI. Littoral Polychæta from the Cape of Good Hope. By ARTHUR WILLEY, D.Sc., F.R.S., Colombo Museum, Ceylon. (Communicated by Dr. W. G. RIDEWOOD, F.L.S.)

## (Plates 13 & 14.)

#### Read 3rd December, 1903.

THE Annelids here described were collected by Mr. W. F. Purcell in the years 1896 and 1900, with the co-operation of Messrs. G. H. Glasson and R. M. Lightfoot. The collection was sent, by arrangement, from the South African Museum to the British (Natural History) Museum, and intrusted to me for examination. Most of the specimens were preserved in an alcoholic solution of corrosive sublimate, and, in many cases, care had been taken to procure the extrusion of the proboscides, which is a matter of importance in the systematic study of errant Annelids.

There is a pronounced Mediterranean and Northern element in the Annelid fauna of the Cape, a feature which has already been noted by Dr. von Marenzeller \*, and, indeed, it would appear that the geographical distribution of marine Annelids is primarily determined by thermal considerations. Many species are eurythermal, and hence cosmopolitan or pan-oceanic; where this is not the case, we frequently meet with instances of discontinuous distribution, the areas of distribution being separated by thermal barriers. The only terrestrial barriers of first importance are the Isthmus of Suez and the Isthmus of Panama, and that these have not always prevented the inter-oceanic exchange of types is clear from the fact that the Annelid fauna of the Indo-Pacific region may be said to be composed of an assemblage of endemic, Caribbean, and Mediterranean constituents.

The following are the species dealt with in this paper :----

- 1. Euphrosyne capensis, Kinberg.
- 2. Lepidonotus clava semitectus, Stimpson.
- 3. Polynoe scolopendrina, Savigny.
- 4. Hemilepidia erythrotænia, Schmarda.
- 5. Parmenis capensis, sp. n.
- 6. Sthenelais fuliginosa capensis, Claparède.
- 7. Eulalia capensis, Schmarda.
- 8. Phyllodoce sp.?
- 9. Glycera convoluta africana, Keferstein.
- 10. Neanthes latipalpa, Schmarda.
- 11. capensis, sp. n.
- 12. Mastigonereis operta (Stimpson).
- 13. Perinereis mendax (Stimpson).
- 14. Platynereis striata (Schmarda).

- 15. Eriphyle capensis, Kinberg.
- 16. Marphysa sanguinea hæmasoma (Montagu).
- 17. capensis (Schmarda).
- 18. Purcellana, sp. n.
- 19. Lysidice capensis, Grube.
- 20. Maclovia iricolor capensis (Montagu).
- 21. Lumbriconereis coccinea, Renier.
- 22. nardonis, Grube.
- 23. capensis, Grube.
- 24. Cirratulus atrocollaris, Grube.
- 25. tentaculatus meridionalis (Montagu).
- 26. --- capensis, Schmarda.
- 27. Flabelligera luctator, Stimpson.
- 28. Lipobranchus capensis, sp. u.

\* Marenzeller, E. von, "Polychäten der Angra Pequena-Bucht," Zool. Jahrb. Syst. Bd. iii. pp. 1-24 (1888).
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I am greatly indebted to Prof. F. Jeffrey Bell for his kindness in looking over the proofs of this paper.

1. EUPHROSYNE CAPENSIS, Kinberg. (Plate 13. figs. 1-3.)

Euphrosyne capensis, Kinberg, 1857, Öfv. Ak. Förh. Stockholm, 1858, p. 14; Grube, 1867, 'Novara' Exped, Anneliden, p. 6; McIntosh, 1885, 'Challenger' Polychæta, Reports, vol. xii. part 34,

p. 1; Marenzeller, 1888, Polychäten der Angra Pequena-Bucht, p. 1.

Euphrosyne polybranchia, Schmarda, 1861, Neue wirbellose Thiere, ii. p. 136.

The identity of Schmarda's species with Kinberg's *E. capensis* was first established by Prof. McIntosh.

The collection contains seven examples taken "between tide-marks among rocks, St. James, False Bay," and "among roots of sea-bamboo off Woodstock and Salt River beaches." The colour of the living worms is stated to have been brick-red.

The largest specimen has 64 segments, a length of 64 mm., and width of 15 mm. Others with 54 segments measured 20–22 mm. in length, and one with 52 segments measured 46.5 mm. in length, showing that there is no fixed correlation between the total length and the number of segments.

The anterior pair of eyes is placed upon the ventral side of the head (fig. 1), and on either side of them there is a minute parophthalmic tentacle which has not hitherto been described. With strong reflected light they are easily seen under a low power, more clearly in some specimens than in others (fig. 2).

The cephalic caruncle occupies the median dorsal area of the first seven segments (fig. 3).

2. LEPIDONOTUS CLAVA SEMITECTUS, Stimpson. (Plate 13. fig. 4.)

Lepidonotus semitectus, Stimpson, "New Marine Invertebrates," Proc. Acad. Philad. vii. 1855, p. 393; Marenzeller, 1888, Polychäten der Angra Pequena-Bucht, p. 3.

The very numerous examples of this species contained in the collection present a varying aspect, differing in colour from mottled dark brown or black to mottled scarlet on the elytra. They represent the Cape community of the Mediterranean and British species, *Lepidonotus clava* (Montagu). The remaining synonymy is given by Marenzeller. The above trinomial designation of the species requires some explanation. It seems there is no real specific distinction between the Cape and the northern forms. The worms in this collection are topotypes of Stimpson's *L. semitectus*, and the word *semitectus* is merely employed here to denote this fact. Their colour-mean, average dimensions, and periodicity probably diverge more or less from those of the northern members of the species. If Stimpson had employed a geographical epithet for the trivial name of his specimens, it would have better suited our purpose, because the typical *L. clava* is also "semitectus" in respect of the elytra; but as he did not, I retain his term with the view of recognizing his rights and avoiding a controversy concerning priority.

The opposed scales sometimes touch in the middle line, leaving uncovered diamond-

shaped patches (presenting a white nucleus surrounded by reddish-brown pigment) along the middle of the back; successive scales also meet each other sometimes, but not always. The scales are orbicular, margin unfringed, often reddish in colour, with pale outer border.

The length of the *tentaculum impar* varies, and this may be due either to normal variation or to regeneration after injury. In one specimen the median cephalic tentacle was thick and white, and only half the length of the paired antennæ, though there was no sign of abnormality beyond the absence of pigment. In another the tentaculum was barely longer than the antennæ and rather stouter. In a third the tentaculum was half as long again as the antennæ, as long as the palps, and, like the latter, terminating in a flagelliform appendix (flagellum).

A moderately large specimen showed 26 segments, and measured about 22 mm. in length, with width of 10 mm. over the setæ, 8 mm. without the setæ.

One tube contained forty-one specimens taken between tide-marks amongst rocks, St. James, False Bay. In another there were six examples, taken amongst roots of sea-bamboo off Woodstock beach, Table Bay, in 8-10 feet of water.

The elytra are tuberculate on the surface, with plain margins. The papillæ of the palps are disposed in six longitudinal rows.

3. POLYNOE SCOLOPENDRINA, Savigny. (Plate 13. fig. 5 and fig. 25.)

Hemilepidia tuberculata, Schmarda, Neue wirbellose Thiere, Bd. i. 2, 1861, p. 149.

Polynoe attenuata, McIntosh, 1885, 'Challenger' Polychæta, Reports, vol. xii. part 34, p. 120; cf. Marenzeller, 1888, Polychäten der Angra Pequena-Bucht, p. 5.

Schmarda's *Hemilepidia tuberculata* cannot, in my experience, be specifically distinguished from *Polynoe scolopendrina* (Savigny)\*.

Segments about 110; length 70 mm.; width without setæ 6.5 mm., with setæ 9 mm. The dorsal tubercles, of which there are a median row and a lateral row on each side of the dorsum, commence about the 20th segment. The ventral (nephridial) papillæ are large, visible without the use of a lens. Dorsal cirri alternate with the elytra in anterior region of body, becoming consecutive behind the last elytron. *Cirri anales* 2, stout, subulate, with filiform tip.

The elytral formula is the same as for *Hemilepidia erythrotania*, namely, 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 26, 29, 32, always counting the segment which carries the tentacular cirri, *i. e.* the buccal segment, as the first segment of the trunk.

Locality. Amongst roots of sea-bamboo off Woodstock beach, Table Bay, ten specimens. The elytra of the first pair are round and larger than the succeeding oval scales. The anterior eyes occupy the frontal peaks.

A specimen in another tube, from St. James, False Bay, presented a pale flaceid appearance.

\* Of. Baron de Saint-Joseph, "Les Annélides . . . de Dinard," Ann. Sci. Nat. (7) v. 1888, p. 183; and McIntosh, W. C., 'British Annelids,' Ray Society Mon. 1900, p. 390.

 $35^*$ 

4. HEMILEPIDIA ERYTHROTÆNIA, Schmarda. (Plate 13. fig. 6 and fig. 26.)

Hemilepidia erythrotania, Schmarda, 1861, Neue wirbellose Thiere, ii. p. 150; Marenzeller, 1888, Polychäten der Angra Pequena-Bucht, p. 4.

This polymeric Polynoid has, so far as I am aware, only been recorded from the Cape region, and constitutes one of the features of the South African Annelid fauna. *Euphrosyne capensis* is another characteristic component of this fauna.

The pigmentation of the elytra consists of a broad sharply defined black area at the mesial borders, which just meet in the middle line. The rest of the surface of the elytra is colourless, except for a small dark spot over the scars.

The principal character by which it differs from the type of *Polynoe scolopendrina* is in the curved tip of the ventral setæ, which is smooth in *H. erythrotænia* and bidentate in *P. scolopendrina*.

Locality. Amongst roots of sea-bamboo off Woodstock beach, Table Bay.

The tentaculum and antennæ, especially the latter, are beset with small squamiform papillæ. The dorsal surface of the body is devoid of tubercles.

5. PARMENIS CAPENSIS, sp. n. (Plate 13. figs. 7 & 8 and figs. 27-29.)

In the diagnosis of his genus *Parmenis*, Malmgren \* includes the following characters :—" Elytra, paria 15, totum dorsum imbricatum tegentia. Setæ rami superioris seriatim transverse spinulosæ, breviores et crassiores quam setæ rami inferioris. Hæ infra apicem glabrum bifidum vel profunde bidentatum, dente superiore apice curvato."

In the definition of the species *P. Ljungmani* an error has crept into the text, the dorsal setæ being described as "paullum *tenuiores* quam setæ rami inferioris" instead of "paullum *crassiores*."

The Cape specimens which I refer to this group have 15 pairs of elytra and as many as 39 segments, the last 6 segments uncovered, as happens also in *Lagisca*. The elytra of the first pair are circular and very much smaller than the succeeding elytra, which have an ovate form with long diameter placed obliquely with reference to the longitudinal axis of the body. The outer and posterior borders of the elytra are fimbriated, apparently differing in this respect from the northern type, which is described as having elytra "margine glabro."

The anal cirri resemble the dorsal cirri in length and form, and, like these, are densely fringed † with elongate papillæ.

The pigment of the elytra is sparse, with an interrupted submarginal tract of neutral tint and a scar-patch.

The dorsal fascicle of setæ is cespitose; the setæ are numerous and much shorter, though only a little thicker, than the ventral.

The ventral setæ are strongly bidentate.

The posterior elytra, more especially the penultimate, are noticeable on account of their larger size.

Locality. Amongst roots of sea-bamboo off Woodstock beach, Table Bay.

\* Malmgren, A. J., 'Annulata Polychæta,' 1867, p. 11.

† The term "ciliated " is commonly employed in a special sense to describe this condition.

#### 6. STHENELAIS FULIGINOSA CAPENSIS.

I can find no distinctive character in what I take to be the Cape representative of the Mediterranean *Sthenelais fuliginosa*, Claparède \*.

The length is 28 mm., width (including setæ) 4 mm., width of ventral surface without parapodia 1.5 mm. Segments between 70 and 80 in number.

Locality. One specimen found amongst roots of sea-bamboo (arborescent Fucus) off Woodstock beach, Table Bay, in 8-10 feet of water.

## 7. EULALIA CAPENSIS, Schmarda.

Eulalia capensis, Schmarda, 1861, Neue wirbellose Thiere, ii. p. 86; McIntosh, 1885, 'Challenger' Polychæta, Reports, vol. xii. part 34, p. 168; Marenzeller, op. cit. 1888, p. 5.

Tentaculum impar between, and slightly in advance of, the large eyes, longer than the frontal antennæ. Cirri tentaculares 8, arranged in the following manner on the first three segments:—I  $\frac{2}{0}$ , II  $\frac{2}{2}$ , III  $\frac{2}{\text{cirri ventrales}}$ . Proboscis crowned with 17–19 marginal papillæ and densely beset with papillæ over the surface, except in its posterior portion. Length 8 mm., width 3.5 mm. over all; length of papillose portion of proboscis 15 mm.

As indicated in the formula for the tentacular cirri, the third segment carries the fourth tentacular cirrus above and a *cirrus ventralis foliaceus* below, on each side.

Locality. Ten specimens from a depth of 8-10 feet off Woodstock beach, Table Bay. Colour during life, green.

## 8. PHYLLODOCE sp.

In the absence of information concerning the structure of the proboscis, I refrain from giving a definite name to three specimens of *Phyllodoce* dredged at a depth of 10 feet in Table Bay on a mud bottom. Like *Eulalia capensis*, the colour in the fresh condition was green. There are upwards of 172 segments; length 40.5 mm.; width without setæ 1.5 mm., with setæ 2 mm. The specimens had all lost the proboscis.

The head is rotund, not longer than broad, sometimes narrower in front; its posterior margin, near which the eyes are placed, is entire.

The tentacular cirri are disposed as in *Carobia* $\dagger$ ; they are short and stout, their length not exceeding the width of the body.

The character of the proboscis is absolutely essential to the definition of species of *Phyllodoce* and its subgenera *Anaitis* and *Carobia*.

† Of. Marenzeller, op. cit. (Adriat. Annel.) 1874, p. 426; and same author, 1879, "Südjapanische Annel.," Denkschr. Ak. Wien, xli. (2nd Abth.) p. 127.

<sup>\*</sup> Cf. Marenzeller, "Zur Kenntniss der adriatischen Anneliden," SB. Ak. Wien, i. Abth. Bd. lxix. 1874, p. 421.

9. GLYCERA CONVOLUTA AFRICANA.

Glycera convoluta, Keferstein, 1862, Zeitschr. wiss. Zool. xii. p. 106; Grube, 1869, Jahresber. Schles. Ges. Breslau, 1870, pp. 59 & 63; Grube, 1877, Monatsber. Akad. Berlin, p. 510 (Table Bay, 50 fathoms); de Saint-Joseph, Ann. Sci. Nat. (sér. 7) xvii. 1894, p. 27.

Glycera africana, Arwidsson, 1898, Bergens Mus. Aarbog, no. xi. p. 21 (no locality).

From the description which Dr. Arwidsson gives of G. africana in his recent studies on the Glyceridæ and Goniadidæ, I am unable to recognize its distinctness from Keferstein's G. convoluta, and the author makes no mention of the fact that the latter species was recorded by Grube from Table Bay among the Annelids obtained during the cruise of S.M.S. 'Gazelle.' Keferstein pointed out that the species of the genus Glycera fall into two sections, according to the presence or absence of gills. The present species belongs to the gill-bearing section, and is distinguished by its biannulate body-segments and by the rounded truncated character of the ventral portion of the bifid posterior lip of the parapodium. The simple unbranched branchiæ, absent from about a score of segments in the anterior region, attain their greatest dimensions in the mid-region of the body. There are upwards of 140 segments; length 32 mm.

Locality. Two specimens found in the mud on the mud-banks in the lagoon at the mouth of the Knysna River; one example dredged on mud-bottom in Table Bay at a depth of 10 feet.

10. NEANTHES LATIPALPA TYPICA. (Plate 13. fig. 9 and Plate 14. figs. 1-2 a, b.)

Nereis latipalpa, Schmarda, 1861, Neue wirbellose Thiere, ii. p. 104.

Neanthes latipalpa, Kinberg, 1865, Öfv. Ak. Förh. p. 171; Marenzeller, 1888, Polychäten der Angra Pequena-Bucht, p. 6.

Schmarda committed an undoubted indiscretion in applying the same specific name to two different Nereids from the Cape, *N. latipalpa* and *Mastigonereis latipalpa*, and introduced a further element of confusion by making one and the same figure (Taf. xxxi. fig. 244) do duty for the two species.

The principal character of the species is afforded by the paragnaths of the order VI, which constitute a monostich of large triangular teeth about 23 in number, confluent across the middle line, so that the group V cannot easily be separated, and is therefore to be regarded as quasi-existent. In Kinberg's original specimen, which I have had the opportunity of examining, there were 23 teeth in the row—11 on each side and 1 in the centre.

The first specimen in the collection of the South African Museum which I looked at had the same number of teeth in the groups V + VI as in Kinberg's type. But the number is subject to considerable variation, both in different individuals and on the two sides of the same individual, ranging on either side from 8 to 15. The paragnaths of order I may be represented by a single tooth or by two or three, placed, as usual in this group, one behind the other. The teeth of group VI may be flattened and linear instead of erect and conical.

The feet are approximately equal throughout the length of the trunk (*pedes æquales*), and the dorsal cirrus is equal to or rather less than the length of the dorsal ligule.

The head is long, and the eyes are placed at the corners of a wide trapezium.

The paragnaths of the distal or maxillary division of the proboscis are much smaller and feebler than those of the proximal or oral division.

Length 95 mm.; width in front (gradually tapering backwards) is 4 mm. without the feet, 6 mm. inclusive measurement.

Locality. Forty-one atokous specimens taken among rocks at Green Point, Table Bay, in November 1896; twelve epitokous examples taken in the mud on the mudbanks of the Knysna lagoon.

In the structure of the parapodia and their armature this species apparently does not differ from Grube's *Nereis brevicirris* \* from St. Paul, but with regard to the arrangement of paragnaths, there is, in the latter species, a group of three teeth of the order V placed in a triangle behind the confluent monostich of VI. In spite of this apparent difference, which is not great in view of the frequency of meristic variations and of the common occurrence of supernumerary teeth, I think Grube's species would be more suitably entitled *Neanthes latipalpa brevicirris*.

Another representative of the same specific group was collected in Ceylon by Mr. L. A. Borradaile, who has added the specimen to the material of the British Museum.

11. NEANTHES CAPENSIS, sp. n. (Plate 13. fig. 10 and Plate 14. figs. 9 & 10.)

A number of small Nereids taken in company with *Platynereis striata* off Woodstock beach have all groups of paragraths represented in the proboscis by conical sclerites, and therefore belong to Kinberg's genus *Neanthes*.

The third pair of tentacular cirri stretch over 4-8 segments. There is a faint moniliform pattern along the centre of the back over the dorsal vessel, which serves to distinguish them, when the proboscis is not exserted, from *Platynereis striata*. The ligules of the feet are rounded in front and become conical behind.

An incomplete specimen had 63 segments; length 31 mm., width over all 3.5 mm. The length of the antennæ seems to vary somewhat from about half the length of the prostomium to more than half this length.

The paragnaths of group VI are disposed in an acervus, and the species therefore falls into line with N. acuminata, Ehlers, and N. crucifera, Grube.

12. MASTIGONEREIS OPERTA. (Plate 13. figs. 11 & 12 and Plate 14. figs. 7-8 a, b.)

Nereis operta, Stimpson, 1855, Proc. Acad. Philad. vii. p. 392.

Mastigonereis latipalpa, Schmarda, 1861, Neue wirbellose Thiere, ii.

Mastigonereis retrodentata (Quatrefages, 1865, Hist. Nat. Annel. i. p. 557); cf. Marenzeller, 1888, Polychäten der Angra Pequena-Bucht, p. 7.

The collection comprises atokous and epitokous forms, with transitions from one condition to the other. The occurrence of epitoky is a fact of great bionomic interest, but from a strictly systematic standpoint an epitokous Annelid, although it has achieved its highest development, is of no more practical use for diagnosis than the same worm in the atokous condition. That is to say, the substitution of reniform setae

\* Grube, A. E., "Anneliden," Novara-Reise, Zool. Bd. ii. (Vienna, 1867), p. 19, Taf. ii. fig. 2.

for normal setæ and the development of the natatory membranes (ligular lobes) on the parapodia add no useful character to the definition of a particular species. This is a rather curious fact. In an epitokous worm the anterior region of the body retains on the whole its normal specific character, but in the modified posterior region the specific features are concealed below the profusion of secondary natatory appendages of the feet, although the characteristic form of cirri and ligules is retained and can be recognized by careful examination below the mask of epitoky.

An atokous example measured 93 mm. in length, 8 mm. in width (including the feet), and possessed 114 setigerous segments. An epitokous female was nearly 140 mm. long.

Locality. Six atokous specimens taken amongst seaweed off Woodstock beach in August 1896, and seven epitokous specimens from the same locality collected in December 1900.

13. PERINEREIS MENDAX (Stimpson). (Plate 13. fig. 13 and Plate 14. figs. 3-6.)

Nereis mendax, Stimpson, Proc. Acad. Philad. vii. p. 392 (1855).

Mastigonereis podocirra, Schmarda, 1861, Neue wirbellose Thiere, ii. p. 108; Marenzeller, 1888, Polychäten der Angra Pequena-Bucht, p. 7.

Nereis Stimpsonis, Grube, 1867, 'Novara ' Exped., Anneliden, p. 18, Taf. i. fig. 8.

Kinberg's genus *Perinereis* is determined by the character of the paragnaths of order VI, which occur as one or two linear or broadly conical or arcuate chitinous sclerites on each side of the median group V. I have examined the types of Kinberg's genera of Nereidæ by special arrangement between the authorities of the British Museum (Natural History) and the Royal Museum at Stockholm, and am bound to say that I am not clear as to the distinct generic properties of *Perinereis*, *Paranereis*, and *Pseudonereis*\*.

Very numerous examples of this species were taken between tide-marks at St. James, False Bay, and two specimens from Woodstock, Table Bay. They are described as living "in holes between the barnacles &c. on the upper sides of rocks exposed at low tide."

14. PLATYNEREIS STRIATA (Schmarda). (Plate 13. fig. 14 and Plate 14. figs. 11 & 12.)

Platynereis striata (Schmarda), see Kinberg, 1865, "Annulata nova, Nereidum dispositio nova," Öfv. K. Vet.-Akad. Förh. 1865, Stockholm, 1866, p. 177.

The length of the antennæ is equal to that of the prostomium. The third pair of tentacular cirri stretch over 10-14 segments. There are about 80 segments in all; length about 52 mm.; width without feet 3 mm., with feet 5 mm.

The dorsal cirrus is about twice the length of the dorsal ligule, and this proportion does not appreciably alter through the length of the body.

The paragnaths have the form of minute granulations characteristic of the genus *Platynereis*, which has priority over Malmgren's genus *Leontis*. The groups VII+VIII

<sup>\*</sup> The *Pseudonereis anomala* of Gravier ("Contribution à l'étude des Annélides ... de la Mer rouge," Arch. Mus. Paris, (8) xi. 1900, pl. xii. figs. 50-52) is not a *Pseudonereis* in Kinberg's sense. I have seen specimens of it from Karachi, and think it is worthy of subgeneric rank at least, unless it be regarded as a *Nereis* s. str.

are represented on the ventral side of the oral division of the proboscis by five distichous or tristichous acervuli; the sides of the proboscis are unarmed, so that there is a long interval between these ventral acervuli and the group VI. Group V is unrepresented.

Numerous examples taken among roots of sea-bamboo off Woodstock beach, Table Bay, at a depth of 8–10 feet.

15. ERIPHYLE CAPENSIS, Kinberg.

Eriphyle capensis, Kinberg, 1864, "Annulata nova," Öfv. Ak. Förh. Stockholm, p. 561. See Marenzeller, 1888, Polychäten der Angra Pequena-Bucht, p. 7, ubi syn.

According to Dr. von Marenzeller, this species is distinct from E. aphroditois by the structure of the falciform and scalprate setw. I have not succeeded in convincing myself on this point, and incline towards the trinomial designation E. aphroditois capensis.

In the collection of the South African Museum there is a specimen, 304.8 mm. long, with diameter of 13 mm., taken "between tide-marks amongst rocks, St. James, False Bay." The colour when the worm was alive is stated to have been brick-red.

The branchiæ occur as simple filaments on the 8th, 9th, 10th, and 11th setigers, 12-pinnate on the 12th setiger, rising in succeeding segments to a maximum of about 14 pinnæ.

16. MARPHYSA SANGUINEA HÆMASOMA. (Plate 13. fig. 15.)

Marphysa sanguinea (Montagu), cf. Marenzeller, 1888, op. cit. p. 11.

I cannot detect any essential difference between Marphysa hæmasoma, Quatrefages (Hist. Nat. Annel. i. 1865, p. 334), and the European M. sanguinea, except a difference of size.

One small specimen was taken between tide-marks at St. James, False Bay.

The compound setæ are spinigerous; the branchiæ commence on the 17th segment, and occur as simple filaments through 7 segments.

17. MARPHYSA CAPENSIS (Schmarda). (Plate 13. fig. 16.)

Marphysa capensis (Schmarda), 1861, Neue wirbellose Thiere, ii. p. 126.

Numerous specimens taken among roots of sea-bamboo off Woodstock beach, Table Bay. In one specimen, 125 mm. in length, the branchiæ commence on the 22nd segment, the first half-dozen being simple filaments. There are about 35 posterior segments without branchiæ. Width of body measured over the ventral cirri S mm., tapering gradually behind. Compound sette falcigerous. Jaws:--II r. 4, l. 3, large teeth only at anterior end of the long jaw-piece; III l. 4; IV l. 3, r. 6; V 1--1.

In another specimen the branchize commence simple on the 15th foot, becoming biramous on the 24th and triramous on the 25th foot.

18. MARPHYSA PURCELLANA, sp. n. (Plate 13. fig. 17.)

This interesting species is closely related to *M. adenensis*, Gravier ("Contribution à l'étude des Annélides Polychètes de la Mer rouge," Arch. Mus. Paris, (4) ii. fasc. 2, SECOND SERIES.—ZOOLOGY, VOL. IX. 36

1900, p. 270, pl. xi. figs. 91–92), and my own inclination is to adhere to the trinomial system by the designation *Marphysa adenensis Purcellana*.

It differs from M. adenensis in that the prostomium is broader than long and its frontal border is emarginate; the median antenna is the shortest, shorter than the prostomium.

The branchiæ are pinnate and the compound setæ falcigerous, these being the principal characters which relate it to *M. adenensis*.

The pinnate branchiæ occur on segments 10-30. The feet are low. There are 136 segments (in the specimens examined), followed by an apparently regenerated tail-end of about 10 segments, terminated by two slender anal cirri, at the base of which are two quite short cirri. The total length is about 95 mm., and the width in the branchial region 5 mm.

This species, in common with M. adenensis, differs from M. Belli in the form of the set and branchiæ, but resembles it in a striking manner in the localization of the branchiæ \*.

I have much pleasure in dedicating this species to Mr. W. F. Purcell, by whom it was collected.

19. Lysidice capensis, Grube. (Plate 13. fig. 18)

Lysidice capensis, Grube, 1867, 'Novara' Exped., Annel. p. 12, Taf. i. fig. 4.

Five examples of this species were taken between tide-marks at St. James, False Bay.

20. MACLOVIA IRICOLOR CAPENSIS. (Plate 13. figs. 19 & 20.)

One specimen taken among roots of sea-bamboo off Woodstock beach, Table Bay. It consists of 215 segments, incomplete behind, 102 mm. long, 3 mm. wide. The dorsal cirræ are evanescent, but the setæ which enter them are present. It can hardly be separated specifically from  $\mathcal{M}$ . *iricolor* (Montagu)  $\dagger$ , differing only in size, so far as I can ascertain from the alcoholic material. Another specimen comes from St. James, False Bay.

21. LUMBRICONEREIS CCCCINEA, Renier. (Plate 13. fig. 21 and Plate 14. fig. 13.)

See Ehlers, Borstenwürmer, 1868, p. 389.

A tube contained 28 Lumbriconereids from St. James, False Bay. Most of them appeared to belong to this species, which is characterized by the breadth of the anterior end, and especially by the subglobular prostomium. Compound falciform setæ (in the specimen examined) occurred in the first 13 setigerous segments, simple hamate setæ thereafter. Simple limbate capillary setæ occurred in the first 28 setigers, and on one side I found them again cropping up in segments 41, 42, and 43. This shows (what I have often observed before) that the distribution of the various forms of setæ in the Lumbriconereidæ is subject to considerable variation.

A specimen of 70 mm. had 100 setigerous segments.

\* Compare also Eunice stragulum, Grube (Philippine Annelida, 1878, p. 163).

† Cf. Willey, A., "On Maclovia iricolor (Montagu)," J. Mar. Biol. Assoc. (n. s) vi. pp. 98-100.

12.1

# 22. LUMBRICONEREIS NARDONIS, Grube. (Plate 13. fig. 22.)

See Ehlers, Borstenwürmer, 1868, p. 381.

It is with some hesitation that I assign a specimen found in the same tube with the preceding to this species. It is difficult to distinguish Lumbriconereidæ, as a rule, from one another. Almost the only difference (the only one which I can recognize) between L. coccinea and L. nardonis relates to the form of the prostomium, which is subglobular in the former and subconical in the latter.

Capillary setæ occur in the first 46 segments, up to 7 in a fascicle.

The two species L. coccinea and L. nardonis are associated together in the Adriatic, and it would seem that this is also the case in Table Bay, though further observations are required in confirmation of this statement.

## 23. LUMBRICONEREIS CAPENSIS, Grube.

Lumbriconereis capensis, Grube, "Fortsetzung . . . über Eunicea : II. Lumbriconereidæ," Jahresber. Schles. Ges. 1878 (Jhrg. 56), Breslau, 1879, p. 95.

Probably synonymous with L cavifrons, Grube ('Novara' Exped., Annel. 1867, p. 13); it cannot be distinguished satisfactorily from L.  $D\ddot{u}beni$ , Kinberg, 1864.

Six specimens from St. James, False Bay. One was much slenderer than the rest, having 300 segments, head conical, capillary setæ in about 60 segments. Another shorter specimen had capillary setæ (frequently 3 in a foot) in about 36 segments. No compound setæ.

Another specimen (125 segments, incomplete behind) had simple curved limbate setae in the first 50 setigerous segments, thereafter the hamate limbate setae. Prostomium rather longer than three succeeding segments, ovate.

## 24. CIRRATULUS ATROCOLLARIS, Grube.

Cirratulus atrocollaris, Grube, "Annel. Gazelle," Monatsber. Akad. Berlin, 1877, p. 536.

Body round, smooth, and short; segments over 200, crowded and short; there is a half-collar of black pigment on the third segment below; length nearly 40 mm.; ventral aciculæ no stronger than the dorsal, slightly curved; aciculæ absent from about 30 anterior segments; most of the curved ends of the aciculæ are broken off; the setae are excessively brittle; branchiæ in paired acervi.

Twelve specimens "in mud on mud-banks in the Knysna Lagoon," a large salt-water lagoon formed by the sea entering the mouth of the Knysna River.

## 25. CIRRATULUS TENTACULATUS MERIDIONALIS.

Cf. Marenzeller, Polychäten der Angra Pequena-Bucht, 1888, p. 16.

Ventral aciculæ commence at the 46th segment (52nd, Marenz.), the dorsal after the 100th (184th, Marenz.); anterior branchial filaments numerous, forming a continuous transverse acervus; length 70 mm., width 2.5-3 mm.

Twenty-one examples between tide-marks amongst rocks at Sea Point, Table Bay.

26. CIRRATULA CAPENSIS, Schmarda.

Cirratulus capensis, Schmarda, 1861, Neue wirbellose Thiere, ii. p. 56; McIntosh, 1885, 'Challenger' Polychæta, vol. xii. p. 383; Marenzeller, 1888, Polychäten der Angra Pequena-Bucht.

Segments 1st-3rd achætous, 4th-28th with capillary setæ only, 29th ventral aciculæ commence, 41st dorsal aciculæ commence; on the dorsum of segments 6 and 7 on each side an acervus of about 20 branchial filaments with slender insertions and thickened extremities; then for about 20-25 segments branchiæ occur in each segment, afterwards becoming more and more irregular, reappearing in greater numbers and with more dorsad insertion towards the posterior end; ventral aciculæ 5, sometimes 3, in a fascicle; a few capillary setæ occur throughout the length of the body in the ventral fascicles; the ventral aciculæ are stout and strongly curved; dorsal aciculæ slender and nearly straight; eye-spots on sides of head; length 114 mm., width 5-8 mm.; colour in life, orange.

Numerous examples off Woodstock beach, Table Bay.

27. FLABELLIGERA LUCTATOR, Stimpson.

Cf. Marenzeller, 1888, op. cit. p. 15.

Large pro-eminent brown hooks (*festucæ*), one to each segment, with one in reserve; setæ of flabellum numerous; dorsal surface convex, smooth, about 46 segments without the flabellum, attenuate behind; length 33 mm., maximum width nearly 5 mm.

I cannot properly distinguish this species from the northern *F. affinis*, M. Sars. It is evidently the Cape form of the species, and I think the name should read *F. affinis luctator*. Of course, *F. affinis capensis* would be the more appropriate designation, but it would probably introduce confusion, as the name *luctator* has been applied to the Cape members of this race of Flabelligeridæ.

Seven specimens among roots of sea-bamboo off Woodstock beach; five specimens from St. James, False Bay.

28. LIPOBRANCHUS CAPENSIS, sp. n. (Plate 13. figs. 23 & 24 and Plate 14. fig. 14.)

A single specimen of a small black Scalibregmid with white transverse head was collected between tide-marks amongst rocks at St. James, False Bay, by Mr. W. F. Purcell.

I submitted this worm to Dr. J. H. Ashworth \*, who pronounced it to be unlike any of the Scalibregmidæ known to him.

There are 4 fascicles of setæ in all segments commencing immediately behind the head; setæ of two kinds—simple, smooth, capillary setæ and furcate setæ; a fringe of papillæ surrounds the terminal anus; branchiæ absent; more than 60 segments.

The collection also contains a Capitellid (tube No. 87) from roots of sea-bamboo off Woodstock beach, which I was unable to identify.

\* Ashworth, J. H., "The Anatomy of Scalibregma inflatum, Rathke," Quart. Journ. Micr. Sci. vol. xlv. pp. 237-309 ; see p. 297, on the family Scalibregmidæ.

## EXPLANATION OF THE PLATES.

## PLATE 13.

- Fig. 1. Euphrosyne capensis. Anterior end from below, showing the tori buccales.  $\times 8$ .
  - 2. Same. Ventral surface of prostomium, enlarged to show the anterior pair of eyes, with the minute parophthalmic tentacles.
  - 3. Same. Anterior end from above, showing the caruncle.  $\times$  8.
  - 4. Lepidonotus clava semitectus. Anterior end from above; the first two pairs of elytra have been removed.  $\times 8$ .
  - 5. Polynoe scolopendrina. Anterior end from above.  $\times 8$ .
  - 6. Hemilepidia erythrotænia. Anterior end from above.  $\times 8$ .
  - 7. Parmensis capensis. Anterior end from above.  $\times$  8.
  - 8. Same. Head from the right side.
  - 9. Neanthes latipalpa. Anterior end from above.  $\times 4$ .
  - 10. Neanthes capensis. Anterior end from above.  $\times 8$ .
  - 11. Mastigonereis operta. Anterior end from above; in the extruded pharynx the paragnaths of group V are irregular; the tentacular cirri are rather abnormal.  $\times 4$ .
  - 12. Same. Epitokous phase; eyes enlarged and contiguous.  $\times$  4.
  - 13. Perinereis mendax. Anterior end from above.  $\times$  4.
  - 14. Platynereis striata. Anterior end from above.  $\times$  8.
  - 15. Marphysa sanguinea hæmasoma. Anterior end from above.  $\times$  3.
  - 16. Marphysa capensis. Anterior end from above.  $\times 2$ .
  - 17. Marphysa Purcellana. Anterior end from above.  $\times$  3.
  - 18. Lysidice capensis. Anterior end from above.  $\times$  2.
  - 19. Maclovia iricolor capensis. Anterior end from above. × 4.
  - 20. Same. In a state of protraction.  $\times$  4.
  - 21. Lumbriconereis coccinea. Anterior end from above. × 4.
  - 22. Lumbriconereis nardonis. Anterior end from above.  $\times$  4.
  - 23. Lipobranchus capensis. Anterior end from above.  $\times$  15.
  - 24. Same. Anterior end from below.  $\times$  15.
  - 25. Polynoe scolopendrina. Ventral setæ : A, superior ; C, inferior.  $\times$  130.
  - 26. Hemilepidia erythrotænia. Corresponding setæ. × 130.
  - 27. Parmenis capensis. Foot from an elytra-bearing segment.  $\times$  20.
  - 28. Same. Tip of a ventral seta.
  - 29. Same. Portion of an elytron.

#### PLATE 14.

Fig. 1. Neanthes latipalpa. Eighth foot of right side.  $\times$  26.

2. Same. Seventy-third foot of right side.  $\times$  26.

Figs. 2 a & b. Details of ventral setæ.

N.B.—The few sette represented in the feet are designed to illustrate the distribution of the homogomph and heterogomph varieties.

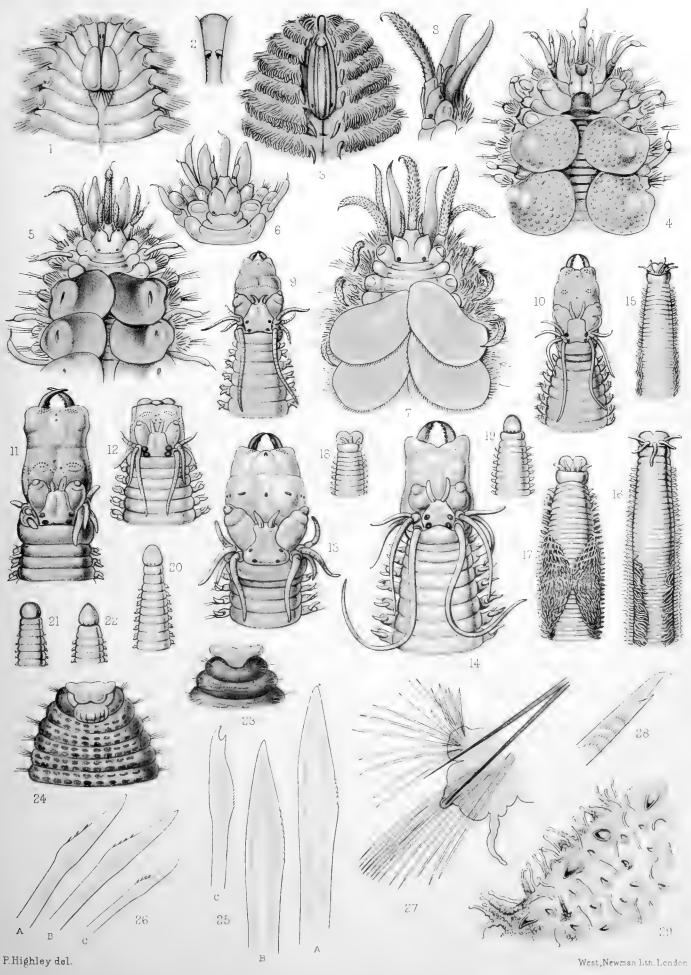
Fig. 3. Perinereis mendax. Thirty-ninth foot of right side during commencing epitoky. × 24. SECOND SERIES.—ZOOLOGY, VOL. IX. 37

- Figs. 4, 5, & 6. *Perinereis mendax*. Eleventh, sixty-second, and seventy-eighth parapodia respectively of the right side of an atokous individual. × 24.
  - 7 & 8. Mastigonereis operta. Thirty-eighth and eighty-fourth feet respectively of the right side.  $\times$  24.
  - 8 a & b. Details of setæ.
  - 9 & 10. Neanthes capensis. Twelfth and fifty-seventh feet of right side, with details of setæ.  $\times$  55.
  - 11 & 12. Platynereis striata. Twelfth and seventieth feet of right side. × 40.

11 a & 12 a. Details of setæ.

Fig. 13. Lumbriconereis coccinea. Compound ventral setæ from the sixth foot of right side.

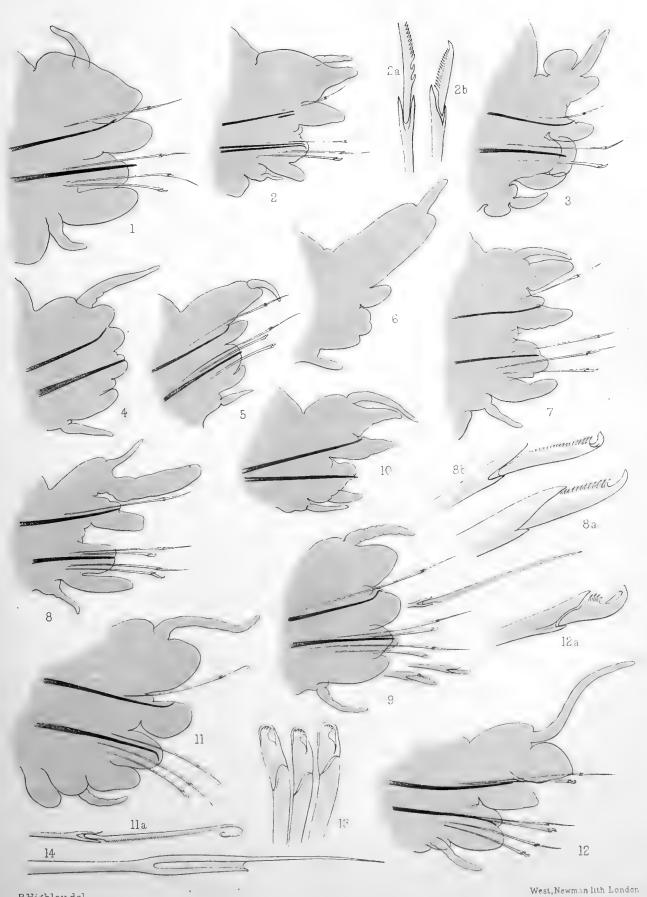
14. Lipobranchus capensis. Furcate seta. × 350.



CAPE POLYCHÆTA.



Willey.



P.Highley del.

CAPE POLYCHÆTA.



# VII. On the Evolution of Topographical Relations among the Docoglossa. By H. J. FLEURE, D.Sc., Fellow of the University of Wales. (Communicated by Professor W. A. HERDMAN, F.R.S., F.L.S.)

## (Plates 15–17.)

#### Read 17th December, 1903.

THE researches, the results of which are here described, were pursued in the laboratories of the University College of Wales, Aberystwyth, and owe a great deal to the kind encouragement and stimulating advice of my friend, Professor Ainsworth Davis. Prof. Yves Delage was so good as to allow me to work in the Lacaze-Duthiers Laboratory at Roscoff during the summer of 1902, and I have to thank him for affording me the possibility of collecting material and observing the habits of the animals studied. I must also thank my friend Mr. H. N. Adair for very valuable help in improving and finishing the sketches which accompany this paper.

## Part I.—The common Ancestor of the Prosobranch Gastropods.

The Docoglossa form a well-marked group, having many characteristic features possessed by all the members. Such features include the oval foot, the horseshoeshaped shell-muscle, the general characters of the visceral hump, the position and form of pericardium and heart, the characters of the kidney, and the disposition of the gonad. These features, therefore, seem to have been acquired before the members of the group diverged amongst themselves, and it is thus of special interest to trace their history from an origin somewhat farther back than their latest common ancestor. The group retains several very primitive Gastropod characters, such as the close approach to external symmetry, the symmetry of the shell-muscle, the strong labial commissure, and the two kidneys each possessing excretory tissue and each communicating with the pericardium. This allows the conclusion that Docoglossa branched off from near the base of the Gastropod stem, and it is therefore best to take as starting-point the latest common ancestor of the Prosobranch Gastropods.

The present account of this hypothetical form is based upon inferences drawn from a direct study of the detailed anatomy of various Docoglossa—*Emarginula*, *Fissurella*, *Haliotis*, *Scissurella*, and *Trochus*. I have also utilized, as far as possible, the results of the work of Pelsencer, Haller, Boutan, Thiele, and Woodward on various archaic Gastropods. The form described is for convenience referred to as the Prostreptoneure. This name is selected because the form is supposed to have already undergone that torsion of the branchial region and visceral hump which characterizes the Prosobranchs, and therefore to have possessed the twisted visceral loop of the nervous system.

It is, however, possible that the Gastropods had begun to diverge among themselves second series.—ZOOLOGY, VOL. IX. 38

before that process was complete, and the Prostreptoneure is to be regarded as a general type of what were probably a few closely related forms.

The Prostreptoneure was probably far more symmetrical externally than many of its descendants. This view is supported by the following considerations :--

- 1. The Docoglossa remain symmetrical throughout development, and at an early stage Haliotis has a symmetrical pair of shell-muscles (Boutan). The earliest post-torsional condition of the shell-muscle is almost certainly a paired one, and that of Scissurella, which shows this condition, may be primitive.
- 2. Among the earliest Gastropod fossils we find many feebly spiral shells which are almost or quite symmetrical. Among the oldest Gastropod fossils also is the large order of the Bellerophontidæ, which usually possess symmetrical shells.
- 3. The remains of symmetry, both external and internal, are far more marked among the more primitive than among the more specialized Prosobranchs.

The torsion, however, had so profoundly disturbed internal symmetry that the retention of complete external symmetry is improbable.

It is therefore supposed that the shell of the Prostreptoneure was nearly, but not quite, symmetrical and possessed a moderately-developed spiral, coiling in or near the sagittal plane. In the anterior edge of the shell there was a sinus or slit, which was situated in the median plane or somewhat to the right.

The Foot was fairly long and primarily useful for creeping over rocks and on seaweeds. It probably possessed a broad, and possibly bilobed, front edge, an adaptation to the habit of creeping upon the surface of the water. This breadth may have also permitted swimming-movements to a moderate extent. There was a moderately developed operculum on the postero-dorsal surface of the foot.

The approach to external symmetry indicates, perhaps, a certain ability to move through water, probably by swimming and surface-creeping. It is also adapted to the circumstances of a life on floating seaweeds, but the Prostreptoneure was more probably a shore-living form, perhaps favouring among other places the rock-pools. The marked asymmetry of *Pleurotomaria*, the Trochidæ, and typical Monotocards seems to have been developed as a further specialization to a creeping habit.

The Alimentary Canal was in the form of a U with some amount of extra coiling on the distal limb of the U. This can be inferred with some certainty, as a gut of that type occurs in *Pleurotomaria*, *Haliotis*, many species of *Trochus*, and various Tænioglossa, and it also characterizes the Cephalopoda. The general disposition of the gut will be further discussed in dealing with the consolidation of the Docoglossan visceral hump (see Pl. 15. fig. 6).

Within the lips the lining epithelium of the mouth was cuticularized, and there must have been a pair of lateral projections bearing extra strong cuticle which formed the jawplates. These jaw-plates were probably united by a median dorsal piece, but the arch with the strong front edge seen, for example, in the Patellidæ is perhaps a specialization, though it certainly resembles the upper jaw of Cephalopods, as Thiele has remarked. It is certain that the Docoglossan odontophore has been greatly specialized during

the evolution of the group, and one can consider the relations in Pleurotomaria as

corresponding more closely to those of the Prostreptoneure. There were certainly one pair of buccal glands and probably a pair of dorso-lateral pouches in the buccal cavity. Farther back occurred valves, probably dorsal and ventral, and behind them a pair of lateral æsophageal pouches opened into the gut-cavity. In this region the appearance of the gut in transverse section would be that of a very wide cavity with a pair of dorsal longitudinal infoldings and a median ventral infolding forking into two towards its free edge (Pl. 17. fig. 22*a*). The æsophagus reached back (Pl. 15. fig. 6) as far as the bend of the U, and was followed by the stomach, the region in which the digestive secretions were intimately mixed with the food.

With the Stomach communicated the spiral cæcum, the great digestive gland, and probably a crystalline style-sac.

The Digestive Gland in Cephalopods, *i. e.* pre-torsional forms, consists of a pair of compact lobes; but the torsion must have considerably altered the disposition of such a massive organ, which could not change its position without affecting the external form of the animal. It was probably squeezed out during the torsion and development of the visceral hump, so that it afterwards filled the interstices between the gut and the bodywall. It is doubtful whether any trace of the original paired condition remained in the Prostreptoneure. The ducts of the digestive gland opened into a groove in the stomachwall, and this groove was, as in *Haliotis*, continued into the cavity of the spinal cæcum. This, and the fact that the ducts of the digestive gland in Cephalopoda open into the spiral cæcum direct, suggests that one function of that outgrowth is to provide a temporary store when necessary for the copious secretion of the digestive gland. In that case the loss of the stomach (Pl. 15. fig. 8), and the consequent improbability of wastage of the secretion due to its flowing on too far in the intestine.

A crystalline style-sac is well known among Lamellibranchs; it also occurs in *Nautilus*, and Moore and Randles have found it in various Architænioglossa. It may therefore have occurred in the Prostreptoneure. This structure must not be confounded with the spiral cæcum, as they occur together in various forms, as Moore and Randles have shown.

A rectal gland may have been present.

The Nervous System has been studied in such detail by Lacaze-Duthiers, Bouvier, Haller, Woodward, Pelseneer, Thiele, and others that its probable primitive Gastropod condition is in the main a matter of general knowledge and agreement. It is not therefore necessary to describe it in detail here.

Controversy has arisen more especially with regard to the innervation of the epipodium and the evolution of pleural centres. The first question seems to be practically settled in favour of the view, advanced by Huxley, Pelsencer, and Haller, that the epipodium is a pedal organ, and that the ventral ganglionic cords of *Pleurotomaria*, *Haliotis*, &c. are to be called "Pedal Cords." On this point, however, Thiele maintains another opinion; but the matter does not directly concern the Docoglossa, and it can therefore be passed over without further comment.

The pleural centres were certainly imperfectly developed in the Prostreptoneure, and the lateral portions of the circumœsophageal ring were divided into two connectives on either side, as is the case in the Docoglossa—*Pleurotomaria, Haliotis, &c.* From the outer one of these two connectives on either side arose the nerves of the mantle-region and the connectives which form the visceral loop. In *Haliotis* the points of origin are very near that end of the connective which abuts upon the posterior part of the ring, and Thiele holds this to be the primitive condition. In *Pleurotomaria* the points of origin are farther forwards, and Woodward believes this type to be primitive, especially as among the Trochidæ and Haliotidæ there is a tendency for the pleural centre to mount up to the visceral nerve, a specialization along a peculiar line. Among the Docoglossa the imperfectly developed pleural centres are not in such close connection with the pedal cords as in *Haliotis*, but they also show the tendency for the pleural centre to mount up the visceral nerve, and perhaps therefore on the whole support Woodward's view, as they are beyond dispute very early Gastropod forms. The pallial nerves were most probably not concentrated into a single trunk (*Woodward*). Scissurella resembles the Docoglossa, and therefore *Pleurotomaria* rather than *Haliotis*, and so seems to support Woodward's view. The nervous system in general thus seems to have resembled that of *Pleurotomaria* and the Docoglossa, and in many details, such as the nerve-supply of the slit-region, that of *Haliotis*. The visceral loop was certainly smaller than in *Haliotis* and nearer the median plane than in that form or the Docoglossa.

The Circulatory System (Pl. 16. fig. 16 a) no doubt resembled in general features that of the Fissurellidæ, and to a less extent that of *Scissurella*, *Haliotis*, and *Pleurotomaria*. The ventricle was developed around the rectum, and gave rise to an aorta at its posterior end. This aorta sent a blood-channel (visceral artery) to the upper part of the visceral hump, and then went forward to the head to open into a sinus surrounding the cushion of the odontophore. Thence the blood streamed into the lower part of the visceral hump through a sinus surrounding the radular sac, and another connection led the flow of blood into the paired longitudinal sinuses surrounding the pedal nerve-cords. The course of the aorta in *Haliotis*, where, on its way towards the head, it surrounds the radular sac, is certainly a specialization.

The Respiratory System included a pair of subequal ctenidia in a median or nearly median anterior branchial cavity, whose roof contained a pair of mucous glands. In *Pleurotomaria* and *Haliotis* we find a secondary elongation of the ctenidia and hypertrophy of the mucous glands. The right ctenidium and corresponding mucous gland and osphradium were smaller than the corresponding organs of the other side.

There were certainly two kidneys, right and left of the rectum and pericardium. The right kidney was functionally by far the more important of the two and possessed several intervisceral lobes, showing a structure resembling that in *Haliotis* and *Trochus*. A right reno-pericardial pore has been found in practically all the archaic Gastropods, and therefore must have been present in the Prostreptoneure.

The condition of the left kidney is not so easy to ascertain. This organ is very small among the Docoglossa, but possesses some amount of excretory tissue and retains the reno-pericardial canal (Pl. 17. fig. 24). Among the Fissurellidæ it is reduced almost to vanishing-point. In *Pleurotomaria*, *Haliotis*, and the Trochidæ, on the other hand, it is large, and forms the papillary sac, lying practically in the mantle-roof in front of the pericardium; it seems to possess a pericardial canal in these forms also. Lankester and Pelseneer have therefore homologized the left kidney of these Rhipidoglossa with the single kidney of Monotocards, and their view has been supported by the ontogenetical work of Erlanger, which was, however, confined to the rather specialized Paludina. The difficulties in the way of this view have been well urged by Perrier, who found that the papillary sac is no longer an organ for the excretion of nitrogenous waste, but, quite on the other hand, a builder of reserve material. Another of his arguments was that the left kidney of these forms is represented by the nephridial gland of the Monotocards. Woodward has supported Perrier's view in a tentative fashion, but the most recent work inclines in favour of the older opinion. In particular, Miss Drummond has confirmed Erlanger's ontogenetic work, and Thiele has described a structure in Trochus cinerarius which resembles the nephridial gland and is here an outgrowth of the left kidney, as that of Monotocards is an outgrowth of their single kidney. The difficulty remains that it seems almost impossible to derive the Monotocard kidney from an organ specialized in another direction, such as is the case with the left kidney of Trochus and even of Pleurotomaria. We should therefore, apparently, have to derive the Monotocards from forms more primitive than Trochus or Pleurotomaria, in which the left kidney had not yet acquired the special epithelium and the highly peculiar circulatory arrangements of a papillary sac.

However this may be, it would seem to correspond best with the facts were we to endow the Prostreptoneure with a left kidney, more compact and much smaller than the right, but still retaining ordinary excretory epithelium. The Prostreptoneure possessed a single gonad whose duct led either into the pericardium or, more probably, into the reno-pericardial canal of the large right kidney, as is the case, at any rate, in *Haliotis* and *Trochus*.

At the end of this account of the hypothetical ancestor of the Prosobranchs it seems important to urge that no attempt is made to derive that group from the Docoglossa, which are certainly highly specialized on lines of their own. It is only supposed that the Docoglossa diverged from a very primitive Prosobranch stock, and thus, though the divergence may be considerable, the group is an important one in connection with the problems of Gastropod phylogeny.

The difference between the view here developed and that brought forward by Thiele touches the extent of the external asymmetry of the ancestral form. Thiele, influenced by the paired ctenidia and the many other admittedly primitive characters of *Pleurotomaria* and *Haliotis*, would imagine an ancestor somewhere intermediate between the two, not so high as the former, but not so distinctly flattened as the latter. It possessed a paired arrangement of the shell-muscle, but the spiral was already very distinctly asymmetric.

Such a view appears to me to connect too closely the development of the torsion and that of the conical spiral hump. In a previous essay (22) I have endeavoured to clear up one or two difficulties in connection with the former process, and to show more especially why the torsion was essentially a forward and upward movement of the

branchial cavity along the right side. The main argument there employed is that the pretorsional right etenidium and left kidney and gonad, the gonad probably earliest of all, acquired predominance in their respective functions. This gonad is the important one already in the Cephalopods, and its predominance would probably ensure a predominance of the kidney which it used as an excurrent channel. The gill of that side would therefore be more liable to get soiled than its fellow, which latter would acquire greater importance. In such a condition, movement (that is, selection of variations of position) of the branchial cavity up the right side would enhance the advantage of this ctenidium, and therefore increase the efficiency of respiration. This had previously been diminished through the development of the visceral hump above the posteriorly placed branchial cavity.

It seems to me that the paired shell-muscle is a post-torsional, or almost post-torsional, development which may have helped to set the branchial cavity in a completely forward position. Such a shell-muscle corresponds to a fairly symmetrical shell, and the embryological and palæontological facts, though too scanty to be of the first importance, seem to support the view here advanced, that the Prostreptoneure had not advanced far in the direction of external asymmetry. There is also nothing in connection with the torsion-process as just sketched out which in any adequate fashion accounts for or involves the development of the typical asymmetric spiral. This last development can be understood on other grounds, which will now be discussed, though it may first be said that the difference between Thiele's opinion of the Prostreptoneure and that advanced here is by no means fundamental, as a *Haliotis* not yet flattened would be very much like Pl. 15. fig. 3, in which, it is freely admitted, the amount of asymmetry may be somewhat under-estimated.

As the Prostreptoneure seems to have possessed an operculum, it must have been able to protect itself from unfavourable circumstances by retracting the delicate parts more or less into the shell. It is probable that variations of reduction of the left shellmuscle accumulated very early among the Gastropods, in consequence of the increased freedom this would give to the incoming stream bathing the more important ctenidium. Disappearance of this muscle and inward motion of the area of insertion of its fellow would facilitate complete retraction, there being now only one fixed point some distance in, instead of two comparatively near the edge of the shell. With the loss of the left shell-muscle, the left side of the shell and visceral mass lost their support, and we may suppose them to have sagged, especially as a median spiral meant a centre of gravity high above the foot and consequent unstable equilibrium, as the shell had by this time grown considerably in length to increase the efficiency of retraction. Finally, the shell has wound around its point of support, and so lodged a maximum length of cavity in a minimum space and retained the centre of gravity as low as possible. Such a course of evolution seems to correspond to the facts so far as they are known, and obviates the necessity of connecting the extreme external asymmetry of Pleurotomaria and Trochus with the torsion, and of ascribing it to the Prostreptoneure. The conical spiral is therefore correlated with the creeping habit, and contrasts with the symmetry of the Docoglossa adapted to an adhesive habit.

#### TOPOGRAPHICAL RELATIONS AMONG THE DOCOGLOSSA.

## Part II.—THE DOCOGLOSSA. FOOT AND EDGE OF SHELL.

The present attempt to sketch the evolution of topographical relations among the Docoglossa is based upon a detailed study of Acmæa virginea, A. testudinalis, A. corticata, and A. fragilis, Patina pellucida, a species of Nacella, and Patella vulgata, P. cærulea, and P. ornata. I have also had the advantage of Haller's notes on Acmæa galathea (he uses the name Scutellina galathea), Lottia viridula, Scurria, Nacella, Ancistromesus, and Patella magellanica. The chief types of structure within the group are therefore taken into consideration, so there seems reason to hope that the course of evolution here sketched out offers, at any rate, a basis for constructive criticism.

The Docoglossa exemplify the adaptation of the Prostreptoneure to a life more especially in exposed parts of the tidal zone, coupled with the adoption of the method of adhesion for protection. In the specialization to the adhesive habit is involved the loss of the imperfectly developed method of protection by retraction, *i. e.* the reduction of the operculum, and the cessation of evolution on the lines above sketched out for *Pleurotomaria* and the Trochidæ. For efficient adhesion there should be an adhesive surface broad in proportion to the height of the adherent body, a shell capable of being pulled down and held down symmetrically, and a shape which would give the least possible purchase to the waves.

The Foot, already broad in front, was shortened by loss of the tail-process adapted for a creeping habit, and was further broadened into an oval—a change which hastened the disappearance of the habit of retraction. The animal probably possessed symmetrically disposed shell-muscles, but if that symmetry had previously been disturbed, it was now re-established.

The Edge of the Shell now grew downwards and outwards, ever enlarging the rim so as to form a complete cap for the animal. Stages of such a development have been seen and figured by Boutan (5). It then became necessary to be able to pull down the shell into contact with the rock or other surface by a force operating as symmetrically as possible and as directly as possible at every point. Backward marginal extension of the paired shell-muscles secured this to a large extent, and had the advantage that it gave the greatest possible moment to the downward force. Ultimately, the extensions met behind and gave the horseshoe form to the shell-muscle, forming at the same time a wall around the soft viscera within (Pl. 15. figs. 3-7).

The fibres of the shell-muscle went down into the foot, the outer ones almost vertically, so as to hold the shell-edge down, the inner ones obliquely, so that they exerted a downward and inward pull on the shell-edge. The inner oblique fibres, which very greatly strengthen adhesion, seem to characterize more especially the Cyclobranchs.

The horseshoe (marginal) shell-muscle of the Docoglossa contrasts with the central muscle of the Haliotidæ, which pulls the roof-like shell down into close contact with the contracted animal, without, however, bringing the shell-edge down against the rock. A cap-shaped shell, which it was possible to draw down against the rock at every point, must have imprisoned the epipodium within a narrow space and led to selection of

variations of reduction of the latter. The mantle-edge, always near the shell-edge, would also, under the circumstances, perform most efficiently that function of giving the animal an impression of its immediate surroundings which had been the *raison d'être* of the epipodium. We therefore understand the reduction of the epipodium and the development of sensory structures on the mantle-skirt. The edge of the latter was already occupied by shell-secreting glands, so the sensory zone was differentiated ventral to this.

No trace of the epipodium exists among Monobranchs, but a lateral glandular streak occurs along the sides of the foot in *Patina*, among the Nacellidæ, and in very young specimens of *Patella*. This structure has been homologized with the epipodium by Pelseneer, but the homology is denied by Haller because of the non-development of the streak among the Monobranchs, which he considers to be the ancestral group. Thiele, too, denies the homology, though he looks upon the Cyclobranchs as the more primitive group; his opinion rests on the view, which he alone adopts, that the epipodium is no part of the foot, but rather the equivalent of the "Notaum" of Chitonidæ, the organ which surrounds and secretes the shell-plates, and is by other specialists homologized with the mantle of Gastropods. In any case, there is no doubt that the epipodium has been very much reduced among the Docoglossa, and this is all that concerns us at this stage.

As the adaptation of the shell-edge to the form of the underlying surface became important, and the available space was limited by competition of barnacles, algæ, &c., the possession of a "home" became a valuable consideration. Since the animals still crept about to some extent, residence on one spot necessitated the evolution of the "Homing-Power" which is such a well-known and remarkable feature of Patella. The sensory arrangements which make homing possible have been the subject of discussion, and Lloyd Morgan has credited the cephalic tentacles with this function. Ainsworth Davis has, however, found that Patella homes after excision of the cephalic tentacles, and he ascribes the homing faculty to the pallial tentacles. In his favour is to be said that the mantle-tentacles become differentiated among the Docoglossa (Pl. 17. fig. 21 a-c), they are undeveloped in Acmæa virginea, small and fairly equal in A. testudinalis, and very numerous in Patella and most Cyclobranchs, where they are divided into large and small tentacles. The concomitant development suggests correlation, which is also otherwise probable; too much stress must, however, not be laid on this, as the pallial gills have also developed concomitantly with them, and the mantle-tentacles may be correlated with protection of these latter from unfavourable influences.

Cyclobranchs often possess a depressed scar, in regard to which I agree with those observers who think it due to wear and tear, shuffling of the foot, &c. The edge is the deepest part of the scar, no doubt as a result of friction with the shell-edge. This depressed edge of the scar possesses a special biological value, for it places the shelledge, the animal's vulnerable point, in a groove from which it is all the more difficult to dislodge it.

As Haller and others have stated, the eyes have degenerated, because the head always remains under the shadow of the protecting shell.

# Part III.—THE VISCERAL HUMP OF THE DOCOGLOSSA. INTRODUCTORY.

With the shortening of the foot the mass of the visceral hump would come to lie quite behind it—that is, with its weight operating against the force of adhesion. In such a condition of the spiral, too, the waves would have great power. Variations of growth would therefore be selected, in which the extension of the shell-edge was especially marked in the posterior region. In this way the spiral or its remains would acquire a position over the posterior part of the shell-mouth, and a continuance of the process gives the condition in very young Acmææ (Pl. 15. fig. 2). Later, even this vestige of the spiral disappears, and the well-known Docoglossan cone-like shell remains; the disappearance has undoubtedly increased efficiency of adhesion. The cone-shaped shell is highly advantageous under the conditions of life, for a large part of the pressure of the waves glances off without appreciable effect, and another part by striking downwards only strengthens the resistance to removal.

As the shell-rim grew backwards, a space remained above the broadening foot which became occupied by the posterior part of the contents of the spiral. The contents of the apical region of the spiral, now fairly far forwards, settled down in the upper part of the cone (figs. 3-5)—that is, above the contents of the base of the spiral. This may be called the first stage of the process of consolidation of the viscera. Its occurrence is inferred partly from the topographical relations of organs to be considered later, and partly from a consideration of Boutan's figures of embryos of Acmaa.

It is of interest to note that enlargement of the shell-rim, so that the spiral no longer extends beyond it, is also found among the Bellerophontidæ (fig. 1).

## Part IV .--- BRANCHIAL CAVITY AND HEART.

The slit in the anterior edge of the shell weakened the force of attachment, and natural selection operated to bring about its disappearance, though this reduced the efficiency of the branchial cavity. The settling of the viscera as just described also reduced its efficiency by pressing on the cavity from behind. The apical viscera accommodated themselves on the right side (fig. 7), as the left ctenidium was by far the more important of the two, and free space for it was therefore a necessity. This rendered the right ctenidium still more inefficient, and it disappeared, the anus and excretory openings meanwhile shifting to the place it left vacant (Pl. 17. figs. 19 & 20).

The respiratory arrangements have been discussed by Dall, and are the bases of the modern classification of the Docoglossa. These are, therefore, relatively well known, and need not be described at length on this occasion.

Pressure of the viscera reduced the branchial cavity, and led to selection of variations whereby the position of the remaining etenidium became oblique, and a greater length could be sheltered in the cavity, while a larger surface was thus turned to the incoming stream. Considerations of space meanwhile led to the reduction of the mucous glands, and these two changes greatly increased the chances of damage to the ctenidium due to excrement. These disadvantages, together with the pressure on the branchial cavity, its imperfect currents, and the frequent prolonged exposure to air, brought about the

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ultimate disappearance of the left ctenidium. In *Acmæa fragilis*, Miss Willcox found a muscular strengthening of the excurrent channel of the large right kidney and described it as a penis, a description which raises special difficulties and is highly improbable. In the light of the above considerations, it is, however, easy to explain the development of muscularity as an attempt to force excrete beyond the limits of the gill.

Haller has shown that, even before the loss of the left ctenidium, the development of respiratory outgrowths occurs along the ventral surface of the mantle-skirt. With the loss of ctenidial respiration among the Cyclobranchs, this process is carried much further and a circle of gills appears on the mantle-skirt which—in *Ancistromesus*, for example—are even branched.

The roof of the branchial cavity in Cyclobranchs is thin and honeycombed with bloodspaces, so that it probably serves for the breathing of damp air among those forms which live high up the shore.

With the loss of the right ctenidium, the right auricle of the heart was reduced, and variations in the position of the heart were selected which did away with the now purposeless curves in the blood-stream. This involved the shifting of the heart towards the left, so that the auricle lay directly behind the remaining ctenidium. The ventricle would then turn to the left, so as to lie behind the auricle, and its previously antero-posterior axis would run obliquely backwards from right to left (Pl. 16. fig. 16 a-c). The communication between ventricle and aorta shifted at the same time to a position directly behind the auriculo-ventricular aperture. The pressure of the consolidating viscera meanwhile reduced the size of the pericardium, and the presence of the rectum became rather an obstruction than a support, so that we find complete separation of the two, the rectum running parallel to the ventricle, but just outside the pericardium.

A feature of the Docoglossan heart is that the ventricle is united to the dorsal wall of the pericardium along its morphological longitudinal axis, *i. e.* along a line going obliquely backwards from right to left (figs. 17 & 18, *Meso.*). It is accepted that the pericardium arises as a pair of sacs, one on each side of the rectum, and that the ventricle of the heart develops in the musculature of the partition-wall between them, either above, around, or below the rectum. The remains of the partition are "mesocardia," but they usually disappear in Gastropods. The connection between ventricle and pericardial wall in *Patella* may be such a mesocardium, possibly a secondarily persistent embryonic character: figs. 18 *a* and *b* show this condition as seen in section of *Acmæa* and of *Patella*. A mesocardium occurs in *Chiton*, and it is quite possible that it was also present in the Prostreptoneure.

The Docoglossa possess a special intrapericardial "Bulbus Aortæ" separated from the ventricle by a valvular aperture. It is a development of the base of the aorta, and is relatively strongly muscular, especially on the side against the ventricle. Its specialization is probably due to the fact that the two arterial streams diverge in opposite directions, both of which are at 90° to the direction of the blood-stream through the ventricle. This curve could not be straightened out as the others had been, and, as an alternative, extra muscular tissue has been developed at the basis of the aorta which is included within the pericardial cavity. The change from ctenidial respiration to respiration by the pallial gills and the roof of the branchial cavity has led to dwindling of the efferent ctenidial vein and strengthening of the pallial vein which joins it (Pl. 16. figs. 16 & 17). Small vessels from the roof of the branchial cavity have become connected with the auricle direct (fig. 17), instead of with the efferent ctenidial or the pallial vein.

Part V.-CONSOLIDATION OF THE VISCERAL MASS. FIRST AND SECOND STAGES.

With regard to the consolidation of the viscera, it has been argued in preceding paragraphs :—

- 1. That the contents of the ancestral spiral visceral hump settled in the space left free between the broadening foot and the conical shell, and that the contents of the upper part of the spiral were laid down with apex forwards over those of the basal part (Pl. 15. fig. 4).
- 2. That the apical viscera settled to the right, as the left side was occupied by the ctenidium, which was still important.
- 3. That the pericardium moved to the left side after the disappearance of the right ctenidium, and pulled the rectum with it for some distance.
- 4. That the anus and excretory openings moved to the right to the space left free by the disappearance of the right ctenidium.

In this way the rectum became connected with the upper portion of the viscera and connected them with the pericardial region.

The steps in the process of consolidation of the visceral mass are inferred largely from a study of the topography of the included organs. For the sake of brevity and clearness, however, the stages of consolidation will first be described, and then will follow an account of their effects on the mutual relations of the different organs.

The reduction of height was an important consideration for the Docoglossa, and this led to the settling of the high visceral mass with its "upper" and "lower" parts side by side. The apical viscera lay to the right, and the remainder of the upper region was affected by the shift of the pericardium to the left, so that it followed and came to lie along a line going obliquely backward from right to left (Pl. 15. fig. 7). The lower portion therefore settled on the right side in the posterior region, and led forwards to the left beneath the pericardium and so on to the median anterior head. The lower viscera thus crossed beneath the upper just about beneath the last remains of the spiral, and it is possible that the coincidence of position is evidence of correlation between these changes. This stage is represented in fig. 7, and may be called the second stage of the consolidation of the viscera.

The general concentration made the apical viscera squeeze under the branchial cavity, and this pushed the lower viscera in this plane towards the left (curve Q). A special pressure was also exerted from behind (Z, fig. 7) as the antero-posterior axis shortened, and this pressure helped to reduce the branchial and pericardial cavities. It is interesting to note that Haller found a more spacious pericardium in Acmae galathea, which seems to be very primitive, than in other forms. Another effect was that the pericardium was pushed forwards, and we notice that the posterior boundary of the pericardium is more oblique in the, on the whole, more primitive Acmaa than in the more specialized *Patella* (Pl. 17. figs. 19 & 20). These pressures from behind, and from the right as the apical viscera settled beneath the branchial cavity, may be referred to as the third stage of the process of consolidation.

Owing to the special circumstances of dearth of free space for the lengthening gut, the topographical relations of the intestinal coils are of value in tracing out the history of the consolidation.

The gut of the Prostreptoneure has already been mentioned, and its probable disposition was as follows :—

- 1. It was essentially a U-tube with extra coiling on the intestinal limb of the U. The rectum ran through the pericardium (figs. 6 & 16).
- 2. The parts of the gut were :
  - (A) The Fore-gut making the proximal limb of the U.
  - (B) The Stomach and the beginning of the intestine. This ran forwards, perhaps above A.
  - (C) The middle regions of the intestine which probably lay near B proximally and near D distally.
  - (D) The terminal part of the intestine which came forwards through the pericardium.

One of the first changes among the Docoglossa was the lengthening of the wide stomach-region, *i. e.* the first part of B, and it is permissible to suppose that this extension would be dorsalwards where space was freer. It is permissible to correlate this lengthening with the special difficulty of digesting the food, which consists mainly of small tough Algæ &c. growing on exposed rocks, or, in the case of many species of Acmæa, of calcareous coralline Algæ.

After the first stage of consolidation of the viscera, it is therefore probable that B lay more or less in the upper part of the visceral mass, A, C, and D as before. The loops B-C and C-D were certainly lengthening and the lengthening parts of B and C and of C and D would probably keep together.

In the second stage of consolidation of the visceral mass, region A would go with the lower part of the viscera, and would thereafter lie along a line going back from the median anterior position towards the right. B, going with the upper viscera, would make a dorsal loop from its junction with A round the back and left side and behind the pericardium towards the right anterior corner. C, as before, would lie at first near B and further on near D. D would be pulled out towards the left as the pericardium shifted in that direction; it would therefore run back from the anus, behind the pericardium to the left side, and would meet C at the back (see Pl. 15. fig. 8).

A gut practically of this type has been figured by Haller for Acmaa galathea (fig. 9) and for Lottia viridula, and the preceding paragraphs on the disposition of the gut aim at tracing its previous evolution. They are admittedly hypothetical, but are inserted for the sake of completeness. Their correctness hardly affects the value of subsequent deductions, as it would have been easy to take Acmaa galathea as our starting-point, and derive the other types of gut from its actual arrangements.

It would be possible to describe the second stage of the process of consolidation by saying that the posterior portion of the high visceral hump laid itself down on its left side (Pl. 15. fig. 7). In such a process the fore-gut, whose front end was fixed, must have undergone a counter-clockwise torsion approaching 90°. The torsion of the visceral hump through 180°, to which all Gastropods have been subjected, had already had its effect on the fore-gut. The total twist on this organ in the Docoglossa therefore should approach 270°. As Amaudrut, Willcox, Robert, Woodward, and others have shown, the cross-section of the gullet allows us to infer the amount of torsion to which it has been subjected. This is possible because of the presence of a primitively dorsal pair of longitudinal folds and a ventral subdivided fold opposite them. In the Docoglossa these folds stretch very far back, and a series of sections allows us to trace them round (Pl. 17. figs. 22 & 23) till the dorsal pair, having passed the mid-ventral line, mount far up the right wall. The maximum torsion traceable in Acmæa (fig. 23) seems to be about 250°, but it is as much as 300° in Patella. This correspondence with theory is good evidence for the second stage of the consolidation-process above mentioned, and further evidence is obtainable from the nervous system.

In the Prostreptoneure, as in primitive Gastropods generally, the visceral loop of the nervous system is in intimate relation with the fore-gut. As the latter moved to the right, it must have pressed the visceral loop before it, and, since we find that loop on the right side in all Docoglossa, this may be quoted as evidence of the second stage of the consolidation.

The extra  $30^{\circ}$  of torsion in *Patella* and the separation of gut and visceral loop must be dealt with later.

## Part VI.—CONSOLIDATION OF THE VISCERAL MASS. LATER STAGES.

In Acmæa virginea, testudinalis, corticata, and fragilis the gut is arranged practically as in Haller's types, but with two differences of detail (Pl. 16. fig. 11). The limb A is placed as if it had been pushed back from the right anterior corner, and the arrangement of the junction of B and C points to the same inference. This is what is here and above described as the third stage of the process of consolidation, a squeezing-in of the viscera of the apical region in the right anterior corner-it is continued farther in pursuance of the process of general concentration. At the same time, the viscera of this region exerted a pressure on the fore-gut in the ventral region to the left, and thus gave it a curve to the left (Q, fig. 11). The junction of regions B and C now formed a loop L, which characterizes most of the remaining Docoglossa and which may be double (fig. 11). Changes in the head-region carried this process of inpushing from the right anterior corner still further, and may be referred to as the fourth stage of consolidation. The food of the Docoglossa must be raked up from hard rocky or tough algal surfaces, and in correlation with this the odontophore has grown relatively to the other parts and differentiated in various ways so as to secure firmness and exact symmetrical adjustment. A further fact is that the buccal glands increased markedly in mass, many forms possessing two pairs. The acinous mass of the gland also shifted back from the wall of the buccal cavity, thus increasing the free space above the radula, and accumulated

on the anterior surface of the visceral hump. These two causes further increased the backward pressure (X).

As region A of the gut moved backwards and inwards, the visceral loop of the nervous system, moored probably by its osphradial and rectal nerves, remained on the right and was in this way separated from the gut. Its very reduced size among so many of the Docoglossa is probably a consequence of this separation. The gut of the Cyclobranch *Ancistromesus*, according to Haller's figure (Pl. 15. fig. 10), shows the effect of the first two stages of consolidation and of the others to some extent, but particularly of a fifth stage. A fairly proximal part of region C, apparently situated previously on the right side, has been pushed in over the dorsal surface of the direction of the pressure on it. The pressure in question was due to the concentration of the shell-muscle on either side, but it took effect mainly on the right (Y), as the pericardium on the left was hardly susceptible of further compression. The part of region C which has spread on the dorsal surface of the visceral hump is referred to in later paragraphs as loop M; it characterizes the group of the Cyclobranchs. The position of the loop C-D dorsal to B in *Ancistromesus*, instead of at its left side in other types, is not a difference of theoretical importance.

In Patella vulgata (Pl. 16. figs. 12 & 13) are seen the effects of all the processes thus far enumreated.

Regions  $\mathcal{A}$  and  $\mathcal{B}$  and loop  $\mathcal{L}$  are fundamentally as in  $\mathcal{A}cmaa$  testudinalis, save that  $\mathcal{A}$  is pushed still farther back from the right anterior region, to which it is now distinctly concave, forming the curve  $Q_1$ . This is to be understood as a further effect of pressure in processes 3-5. It is probable that this pressure has also increased the torsion of the fore-gut, and so accounts for the extra 30° of torsion beyond the 270° whose origin has already been traced.

Processes 3 and 4 seem to have had the additional effect of pushing back a loop N on the ventral surface of the visceral mass, as usual from the right anterior corner. Process 5 accounts for the loop M on the dorsal surface of the mass, as in *Ancistromesus*.

Patella cærulea (Pl. 16. figs. 14 & 15) is particularly interesting in that of itself it makes us infer process 5. The junction of A and B and that of C and D are pushed in from the right over the dorsal surface, and this process is also evidenced in the same way by P. radians and P. ornata. In the two latter forms loop N is not apparently developed. In Patina pellucida the gut resembles that of Patella cærulea, save that the junctions mentioned are even more strongly pushed in over the dorsal surface, and the loop M is for this reason pressed to the left; loop N is, however, not developed.

In the Nacellidæ we find very marked elongation of the gut, but it is arranged as in *Patina*, save that loop M has its two hind limbs close to one another, and they run round the left side to the back in close contact with B. The inpushing from the right is very marked, and may account for this change, which, however, may be due to a close connection between M and B or M and the loops C-D at an early stage. At all events, there is no fundamental difference between Nacella and Patina in this respect.

In *Scurria* the Docoglossan gut attains its greatest length, but even here it only shows local lengthening of what is fundamentally a Nacellid gut.

## TOPOGRAPHICAL RELATIONS AMONG THE DOCOGLOSSA.

We therefore see that the Docoglossan gut is arranged on what is fundamentally a single type complicated by progressive lengthening in a confined space.

From the disposition of the parts of the gut and of the various organs of the hump it has thus been possible to infer the course of the process of consolidation of the visceral hump. This has been described as consisting of five stages, which, though necessarily separately discussed, must be understood to have acted in part simultaneously.

## Part VII.-SUMMARY OF DOCOGLOSSAN EVOLUTION.

Other processes enumerated contributed to the development of the Docoglossan characters, so that the evolution of the group may be summarized as follows :---

- I. The foot shortened and broadened into its characteristic oval shape, and the tailprocess disappeared. This caused a forward pressure on the viscera, which is discussed in dealing with the third stage of the consolidation-process (IV. 3, below).
- II. The shell-edge grew downwards and outwards, giving the cone-like form. Growth was particularly marked along the posterior edge, and in this way the apex came to lie far forwards. Correlated with this are the reduction of the epipodium, the sensory differentiation of the mantle-edge, the degeneration of the eyes, and the evolution of the horseshoe shell-muscle.
- III. The changes in II. reduced the efficiency of the branchial cavity, which was already impaired by the loss of the slit. As a result, we find alteration of the position of the Monobranch ctenidium, and complete disappearance of the ctenidia in Cyclobranchs. In both groups the mantle-skirt becomes an important respiratory organ, and in the latter group a circle of pallial gills is developed. Concomitant changes occurred in the heart, which moved to the left side.
- IV. Consolidation of the viscera. This has been described in five stages :---
  - 1. The contents of the spiral settled down in the space above the broadened foot. The viscera of the base of the spire went from front to back ventrally, and those of the apical region from the back to a right anterior position dorsally.
  - 2. The viscera further consclidated so as to reduce height. The upper parts of the mass, together with the rectum, drew to the left as the pericardium (III.) moved thither, and thus came to lie along a line going obliquely backwards from the right anterior corner to the left side. The lower viscera, on the other hand, arranged themselves along a line going forwards from the right side to the head. They crossed under the upper viscera about beneath the apex of the cone.
  - 3. The shortening of the antero-posterior axis caused pressure forwards on the viscera and pericardium. The apical viscera were at the same time squeezed in under the branchial cavity, and exercised a pressure backwards from the right anterior corner.
  - 4. The growth of the buccal mass and the increase of the salivary glands increased the backward pressure just mentioned.
  - 5. The concentration of the shell-muscle led to inpushing of the viscera, and the effects are visible particularly on the right side.

and an and

## Part VIII.—APPENDIX TO EVOLUTIONARY SKETCH.

It now remains to deal with various details of the group's evolution that would have appeared to be digressions had they been treated in the discussion of the main scheme.

The Buccal Mass has been specialized in important points, whose bionomical correlatives must be briefly mentioned, though a detailed discussion would not be profitable without comparison throughout with other primitive Gastropods. The specialization is on different lines in *Acmæa* and *Patella*, thus supporting the view that Cyclobranchs and Monobranchs have diverged from a common ancestor rather than evolved one from the other.

The odontophore of the Prostreptoneure showed in transverse section a V-form, which was modified among the Docoglossa as an adaptation to efficiency of raking. The cartilage-pieces drew close together and altered so as to fill the groove, the remains of which are more conspicuous in Acmæa than in *Patella*. The teeth of the radula have become strong and specialized hooks or claws, and the differentiated median tooth has been reduced or has become similar to the others, as a specialized median piece would scatter rather than rake in.

In species of Acmaa, which in several cases feed on calcarcous Algæ, the cartilages of either side have fused, giving a much enhanced firmness.

Among the Patellidæ, on the other hand, we find general growth, increase of the number of muscles, and differentiation of extra cartilages to which muscles are attached, and which thus increase the possibilities of adjustment.

Reference has already been made to the jaws, the buccal glands, and the lost spiral cæcum of the stomach. It is noticeable that the æsophageal pouches of the Docoglossa do not show the marked glandular development which characterizes these organs in *Haliotis*, &c., and, perhaps in correlation with this, the valves are reduced which in the latter prevent food from returning to the buccal cavity when it is in these pouches. The œsophagus or crop has become very much more complex within the group. Within the limits of the Docoglossa the nervous system has not greatly altered. The changes in the visceral loop have already been mentioned. The anterior ends of the pedal commissures are far wider apart in Acmæidæ and Nacellidæ than in Patellidæ. The latter show therefore a concentration perhaps correlated with the increased efficiency of adhesion which undoubtedly characterizes them. The figures of the Docoglossan nervous systems due to Bouvier, Pelseneer, Haller, and Miss Willcox are so widely distributed in text-books that I have thought their reproduction in connection with this paper unnecessary.

Thiele has observed various special patches of sensory epithelium whose phylogenetic importance is not yet determined, so I pass them by and give merely a reference to pages 326 and 327 of his recent paper (46).

The necessity for compactness of the viscera explains the development by the Docoglossan right kidney of superficial lobes around the visceral hump superseding the intervisceral lobes of the kidney of the ancestral form. The only intervisceral lobe which remains is the small subrectal one into which the reno-pericardial canal opens.

As the pericardium turned to the left and forwards, the left kidney was pushed before it into the roof of the branchial cavity; it was also pulled with its excretory aperture to the right and its Docoglossan position (Pl. 17. figs. 19, 20, & 24) is thus accounted for. The reno-pericardial canals have already been correctly described by Goodrich and Pelseneer, and it only remains to be said that their elongation, as evidenced by the position of their renal apertures far from the pericardium (fig. 24), is a consequence of the pushing of the excurrent apertures to the right and of the pericardium to the left. If the spacerelations in my sections (fig. 24) do not exactly correspond with those shown in the drawings of other workers, I would ascribe this to individual variation and variation with age, which undoubtedly occurs.

The molluscan gonad shows an extreme adaptability of position, and, considering the special pressure on the right, it is natural that it should usually occur on the left among the Docoglossa.

## Part IX.—Affinities of the Docoglossa.

The affinities of the Docoglossa amongst themselves have been discussed by Pelseneer, Dall, Haller, and Thiele. It is now generally admitted that the Lepetidæ are specialized forms adapted to a deep-sea life, though, in the retention of the median tooth of the radula and of vestiges of the spiral, they show primitive features. They may be a basal offshoot, but, as it is at any rate certain that the other groups are not descended from them, I have ventured to omit them from the foregoing evolutionary sketch.

Pelseneer, Dall, and Haller all think that the Cyclobranchs have descended from Monobranch-like forms, but Thiele disputes this because :---

- (a) The ctenidium of *Acmæa* has, according to him, no homology with that of other Gastropods—it is a new development.
- (b) The Cyclobranchs show equal remains of both ctenidia (in the osphradia and neighbouring tissue).
- (c) Dall and Haller have described rudiments of mantle-gills among the Monobranchs, and believe these to be very early stages in the evolution of the Cyclobranch gill-wreath. Thiele, however, sees in them disappearing vestiges.

The conclusion (a) above seems to me to be quite unjustifiable on the grounds given that the ctenidium is oblique and free except at the basis in Acmaa, attached and free only at the apex in other Gastropods; that ctenidium and osphradium are not so nearly connected as in *Haliotis*, &c.; that the structure of the Acmaan gill is simpler than that of others; and that the efferent ctenidial vein joins the great mantle-vein.

This last is to be expected, as the great mantle-vein is undoubtedly a development of the veins from the mantle which join the efferent branchial vein even in *Haliotis*. The simplicity of structure is easily understood when we believe that the Acmæan gill is a structure arrested in an early stage of degeneration, and the other two characters do not seem to me to be of morphological importance. I therefore accept the general opinion that the ctenidium of Acmæa is the left ctenidium of the Prostreptoneure, probably in a somewhat degenerate condition. Perhaps Haller has made the evolution of Cyclobranchs from Monobranchs appear too direct, but if we rather suppose, as

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I think he means, that both groups have descended from a common ancestor nearer the Monobranchs, Thiele's difficulty about the ctenidial vestiges disappears. It is easy to understand that along one line of development both ctenidia were early reduced, while along the other the reduction of one was arrested, so that it persisted in a probably slightly degenerate state. The respiratory importance of the branchial roof in Patellidæ explains the maintenance of the osphradial sensory structures.

This view of the affinities of the subgroups, which is, I think, in full accord with Pelseneer's opinion, is also supported by the presence of probable vestiges of the epipodium among the Cyclobranchs; the common ancestor would have retained this ancestral organ to some extent. The odontophore also shows that the two orders have diverged along somewhat different lines. The account given here of the consolidation of the viscera shows, I think, that the Monobranchs are the more primitive group, but that the ancestor of both may be supposed to have been intermediate between Acmæa galalhea, for example, and Ancistromesus.

The affinities of the Docoglossa with other forms are difficult to trace on account of the antiquity of the group. The Haliotidæ, Pleurotomaria, and the Trochidæ have evolved far along other lines, especially as regards the shell-muscle, the branchial cavity, the visceral loop of the nervous system, the disposition of the visceral hump and its contents, the heart and pericardium, and the kidneys. Scissurella is certainly somewhat more like the Docoglossa in external features in some species and in the condition of the branchial cavity, but it is in other respects nearer the Haliotidæ &c. The Fissurellidæ have the same form of the shell-muscle and the condition of the kidneys is similar to that among the Docoglossa, but it is probable that among them the complete external symmetry is secondary. They have, besides, evolved on lines of reduction of the shell and unique specialization of the branchial cavity, while the process of consolidation of the viscera was also probably very different. It is possible that the Docoglossa may be connected with the Bellerophontacea, which possessed symmetric shells that in some cases show a tendency towards expansion of the rim, analogous to that which has had such far-reaching effects among the Docoglossa. This is, however, quite problematic, owing to our very limited knowledge of the palæozoic Gastropods. We are only justified in hinting that the Docoglossa and Bellerophontacea are two of the earliest offshoots from the Gastropod stem.

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### EXPLANATION OF THE PLATES.

## (Hyp.=Hypothetical.)

#### PLATE 15.

- Fig. 1. Shell of Bellerophon expansus. Wenlock Limestone, Dudley.
  - 2. Shell of embryo Acmæa showing vestige of spiral.
  - 3. The hypothetical Prostreptoneurc, seen from the right side, the shell being supposed to be removed.
- Figs. 4 & 5. Stages illustrating the transition to a Docoglossan type.
- Fig. 6. A supposed dissection of the Prostreptoneurc, from the left side. The gut and pericardium are shown as embedded in the general mass of the remaining organs of the body; details of the latter are omitted for the sake of simplicity.
  - 7. Schematic diagram showing the settling-down of the viscera in the pro-Docoglossa in the second stage of consolidation of the visceral mass.
  - 8. The gut at the hypothetical stage represented in fig. 7. The rectum is only dotted in.

(The letter Q in figs. 8-10 should be deleted.)

- 9. The gut of Acmæa galathea. After Haller.
- 10. The gut of Ancistromesus. After Haller.

### **PLATE 16.**

Fig. 11. The gut of Acmæa virginea, A. testudinalis, or A. corticata.

Figs. 12 & 13. The proximal and distal portions of the gut in Patella vulgata.

Figs. 14 & 15. The proximal and distal portions of the gut in Patella cærulea.

Fig. 16 a. The heart and pericardium of the hypothetical Prostreptoneure.

- 16 b & c. Hypothetical diagrams illustrating the transition to the condition in the primitive Docoglossa.
- 17 a. The heart of Lottia viridula. After Haller.
- 17 b. The heart of Patella vulgata.
- 18 a. Oblique section through the pericardium of Acmæa.

### **PLATE 17.**

Fig. 18 b. Oblique section through the pericardium of Patella.

- 19. Dorsal view of Acmæa testudinalis after the removal of the shell, the pigmented epithelium, and the roof of the branchial cavity.
- 20. Corresponding view of Patella vulgata.
- 21 a, b, & c. A portion of the mantle-edge in Acmæa testudinalis, A. virginea, and P. vulgata respectively.
- 22 a-f. A series of transverse sections through region A of the gut of Patella vulgata, showing merely the longitudinal folds.
- 23. A corresponding diagram, showing the maximum torsion observed in Acmæa virginea.
- 24. A transverse section showing the renal communications of the reno-pericardial canals in *Patella*.

#### Reference Letters used in the Plates.

A. = Fore-gut or special secretory region.

An. = Anus.

- Ant.Ao. = Anterior aorta.
  - Ao. = Intrapericardial "Bulbus Aortæ" in fig. 18.
  - $B_{\cdot}$  = Wide region of absorption and admixture of secretions in gut.
  - B.Gl. = Buccal glands.
  - Br.C. = Branchial cavity.
    - $C_{\cdot} =$  Intestinal region of gut.
    - Ct. = Ctenidium.
    - D. = Terminal region of intestine.
- D.F.G. = Folds which are dorsal in the gullet-wall.
  - $E_{\cdot} = E_{ye}$ .
  - EP. = Epipodium.
    - F. = Foot.
- Gl.M. = Glands of mantle-edge.
- G.M.T. =Greater mantle-tentacle.
- G.M.V. =Great mantle-vein.
  - H.P. = Great digestive gland.
  - K.B. = Boundary between the two kidneys in fig. 24.
    - L = Special wide loop of intestine (region C) which immediately follows region B in Acmaa, Patella, &c.
- L.Au. = Left auricle.
- L.Ct.V. = Left efferent ctenidial vein.

L.K. = Left kidney.

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L.K.Ap. = Aperture of post-torsional left kidney,

L-M. = Junction of loops L and M of the intestine.

L.M.T. = Lesser mantle-tentacle.

L.R.P. = Reno-pericardial canal of the left kidney (renal pore).

 $M_{\cdot}$  = Dorsal intestinal loops characteristic for Cyclobranchs.

M - L = Junction of loops L and M of the intestine.

Meso. = Connection between ventricle and dorsal wall of pericardium.

Mt. = Mantle-skirt.

M.Tent. = Mantle-tentacle.

 $N_{\cdot}$  = Ventrally-placed loop of intestine following loop M in Patella vulgata.

N.R.V. = Veins from nuchal roof.

Oes.P. = Lateral cosophageal pouches.

- Op. = Operculum.
- $Osph_{\cdot} = Osphradium.$

 $P_{\cdot} = Pericardium_{\cdot}$ 

Post.A. = Posterior a orta.

Pr. and arrows indicate direction of pressure of viscera on pericardium.

P.Z. = Pigment-zone.

- Q (curve) indicates the part of region A of the gut which is pushed to the left by pressure from the right anterior corner.
- $Q_1$  indicates the part of region A of the gut which is pushed inwards and backwards by pressure from the right anterior corner.
  - $R_{\cdot} = \text{Rectum}.$

R.Au. =Right auricle.

R.Ct.V. = Right efferent ctenidial vein.

R.K. = Right kidney.

R.K.Ap. = Papilla and aperture of post-torsional right kidney.

R.R.P. = Reno-pericardial pore of the right kidney.

S.M. = Shell-muscle.

Sp.C. = Spiral cæcum.

- St. = Slit in mantle.
- T. = Cephalic tentacle.

V. (upper & lower) = Upper and lower parts of the consolidating visceral mass.

V.F.G. = Folds which are ventral in the gullet-wall.

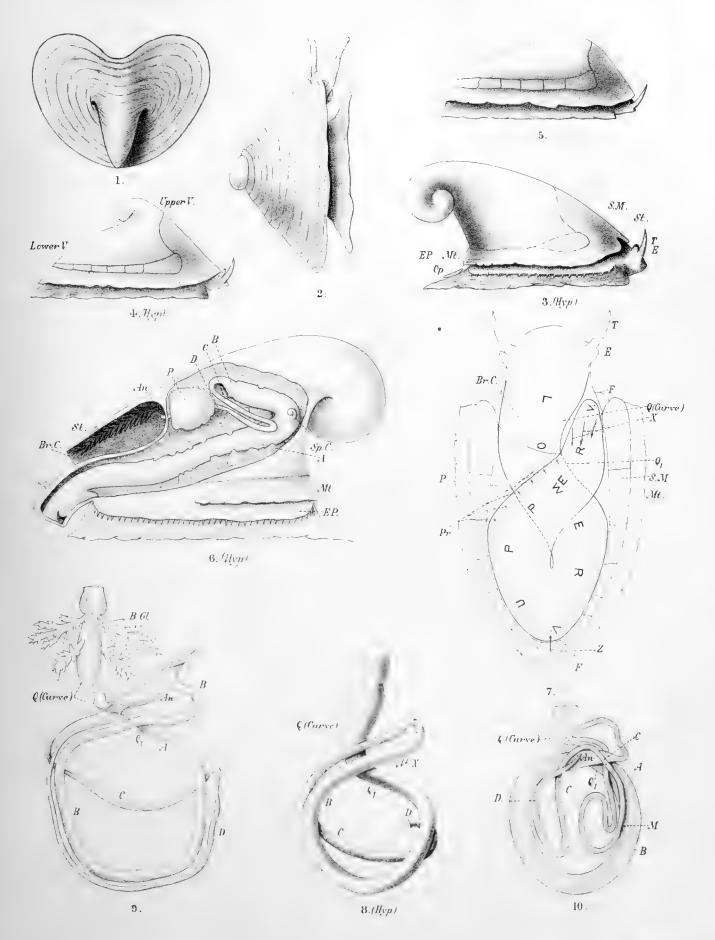
Vn. = Ventricle.

X and 3 arrows indicate pressure obliquely backwards from the right anterior corner of the visceral mass causing curve  $Q_1$ .

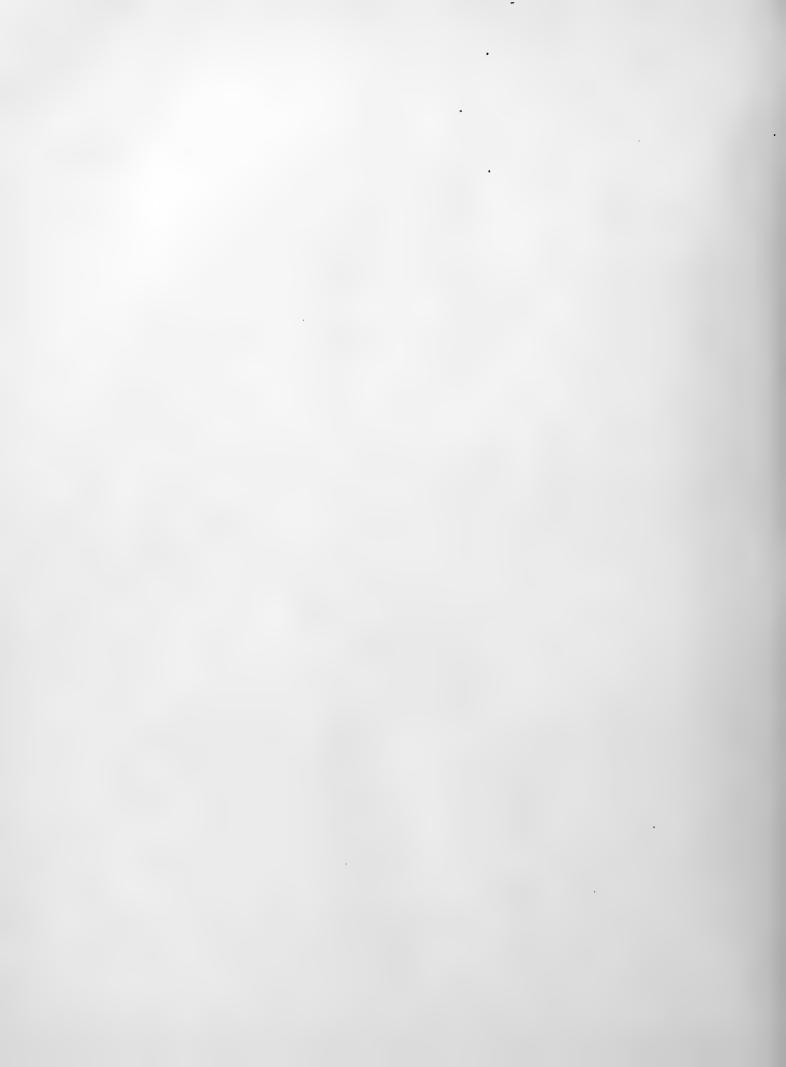
Y and 2 arrows indicate pressure inwards from the right side of the visceral hump.

Z and 1 arrow indicate pressure forwards at the back of the visceral hump.

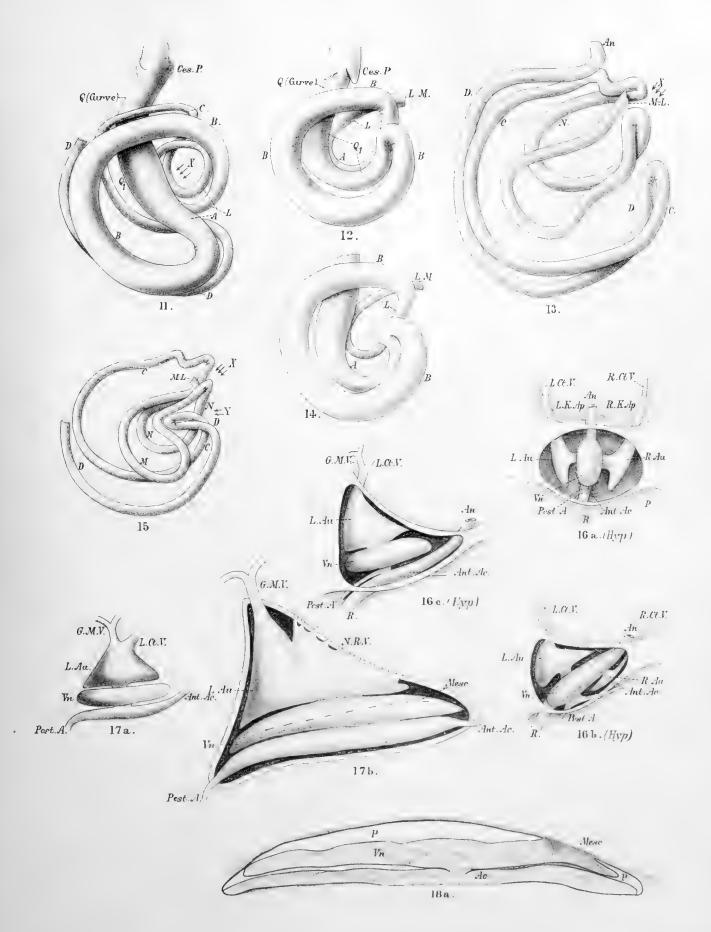
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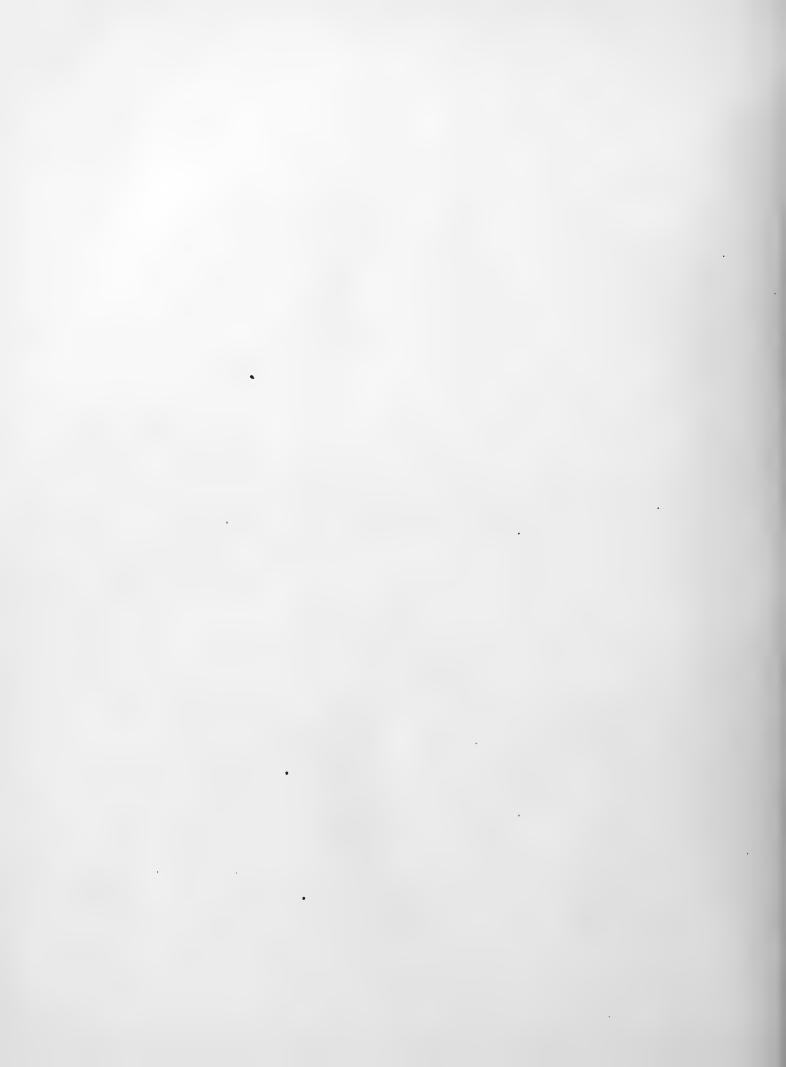
ANATOMY OF THE DOCOGLOSSA.

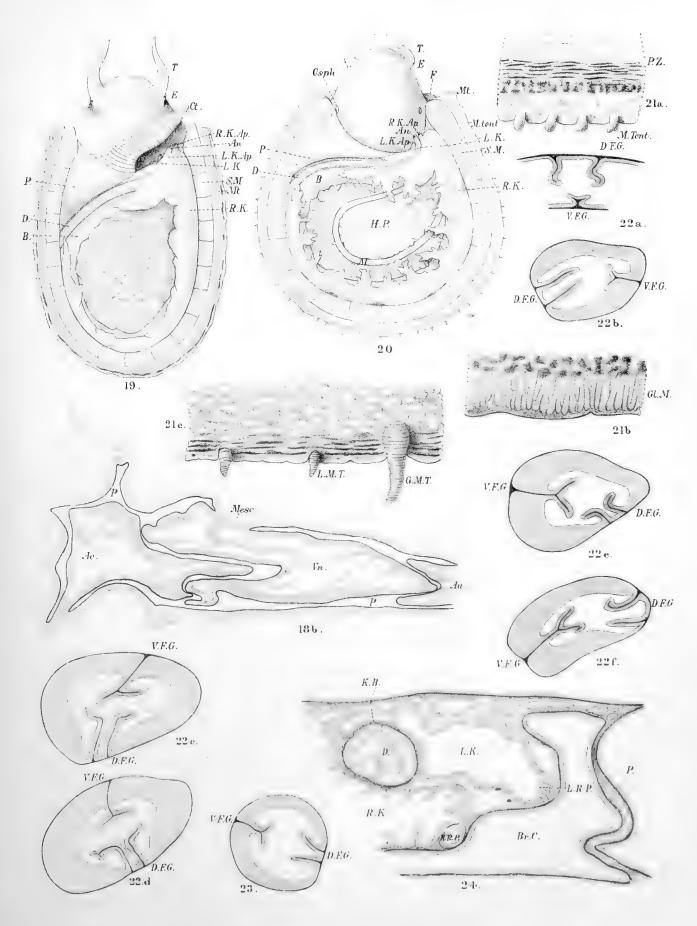


Fleure.



ANATOMY OF THE DOCOGLOSSA.





ANATOMY OF THE DOCOGLOSSA.



## [ 291 ]

VIII. On some Species of the Genus Palæmon, Fabr., from Tahiti, Shanghai, New Guinea, and West Africa. By Dr. J. G. DE MAN, of Ierseke (Holland). (Communicated by the Rev. T. R. R. STEBBING, M.A., F.R.S., Sec.L.S.)

### (Plates 18-20.)

Read 3rd March, 1904.

**THE** following Report contains the description of some species of the genus *Palæmon*, Fabr., several of which were sent to me for examination by Prof. F. Jeffrey Bell, of the British Museum (Natural History), whereas the others, belonging to my private collection, were gathered in fresh water at Catumbella, near Benguella, by Mr. P. Kamerman, the same gentleman to whom I am also indebted for the interesting Brachyura from Angola described four years ago in Mémoires Soc. Zool. de France, 1900, pp. 31-65, pls. i., ii. One species from Catumbella has not previously been observed in West Africa, and may even eventually prove to be new to science; another, from Cameroon, unfortunately represented by only one specimen, seems to be the rare *P. Foai*, Cout., the exact habitat of which is still unknown; and finally a remarkable hitherto unknown character of *P. asperulus*, v. Martens, was observed, namely, that some segments of the abdomen are carinated.

The following species are described :---

Palæmon (Eupalæmon) lar, Fabr. Palæmon (Parapalæmon?) asperulus, v. Martens. Palæmon (Macrobrachium) latimanus, v. Martens. Palæmon (Eupalæmon) macrobrachion, Herklots. Palæmon (Eupalæmon) Foai, Cout. Palæmon (Macrobrachium) jamaicensis (Herbst), var. Vollenhovenii, Herklots.
Palæmon (Macrobrachium) Olfersii, Wiegm.
Palæmon (Macrobrachium?) sp.

#### A.—INDO-PACIFIC SPECIES.

#### PALEMON (EUPALEMON) LAR, Fabr. (Plate 18. fig. 1.)

Confer: Spence Bate, Report on the 'Challenger' Macrura, 1888, p. 789, pl. 129. fig. 1; de Man, Notes from the Leyden Museum, i. 1879, p. 168 (sub nomine *Pal. ornati*, Oliv.), and in Max Weber, Zoolog. Ergebn. Reise Niederl. Ost-Indien, ii. 1892, p. 445, and Abhandlungen der Senckenbergischen Naturf. Gesellschaft, Bd. xxv. Heft iii. 1902, p. 774.

Four adult males from fresh water at Tahiti. British Museum (Natural History). The tooth-formulæ and the measurements of the legs of the second pair are indicated in the Table. These specimens closely resemble the figure quoted from the 'Challenger' Report. The rather slender rostrum is as long as or somewhat longer than the peduncles SECOND SERIES.—ZOOLOGY, VOL. IX. 42 of the upper antennæ, though not reaching to the end of the scaphocerites; the upper margin is slightly convex above the eyes, and its distal half is more or less turned upward. The third tooth is situated just above the orbital margin; in three specimens this tooth is as long as the second, and both are longer than the others, but in the male No. 4 these teeth are not longer than the rest.

The telson of No. 1 and No. 2 ends in a short median acute tooth (fig. 1); the inner of the two spines on each side is three times as long as the outer, and overreaches the median tooth by its distal half. In the two other specimens the median tooth and the spines are more or less worn off. In these four specimens the second legs are of about equal size; in all the slender fingers are gaping, just as in the figure quoted, in consequence of the strong development of the teeth with which they are armed, and they are also somewhat curved inward. The dactylus is regularly curved towards the tip and usually a little shorter than the immobile finger; the latter is provided with a conical tooth at a fourth of its length from the articulation and with a smaller one between this tooth and the proximal end of the finger. The dactylus bears also a conical and compressed tooth at a third of its length from the articulation, which is not smaller than the tooth of the other finger, and between this tooth and the articulation is seen four or five much smaller obtuse teeth; sometimes, however, the latter are more or less rudimentary.

The second legs are of a fine dark purple colour, darkest on the fingers, which appear almost black; the articulation of the fingers is beautiful orange-red, as also the articulation between carpus and palm, and the fingers are marked with pale spots, as in the figure in the 'Challenger' Report. The dorsal surface of cephalothorax and abdomen and the posterior margin of the upper teeth of the rostrum have also a purple colour, though paler than that of the second legs, being more cherry-red. As regards their colour, our specimens apparently agree with those from the River Papeuriri in Tahiti, described in the Report on the 'Challenger' Macrura.

An adult male and an adult female from Patani, on the island of Halmahera, are now before me (vide de Man, in Abhandl. Senckenb. Naturf. Gesellschaft, xxv. Heft 3, 1902, p. 777). In these specimens the cephalothorax and the abdomen are not adorned with the beautiful purple colour observed on the specimens from Tahiti, and the three posterior pairs of legs are longer and more slender. So, e. g., in the adult male from the River Tobelo, that is 115 mm. long, the meropodites of the fifth pair are 16 mm. long, and, measured on their outer side, in the middle 1.6 mm. broad; the carpopodites are 10.5 mm. long, and 1.6 mm. broad at the distal end; the propodites have a length of 17 mm. and are 0.96 mm. broad in the middle, the terminal joints finally are 4.5 mm. long. In our male (No.4), however, of exactly the same size, the meropodites of the fifth pair are 14 mm. long and 1.85 mm. broad in the middle; the carpopodites are 8 mm. long and 1.6 mm. broad at the distal end; the propodites are 8 mm. long and 1.6 mm. broad at the distal end; the propodites are 15 mm. long and 1.12 mm. broad in the middle, the terminal joints finally are 3.5 mm. long.

The Tahiti species may therefore be regarded as a local variety, for which I propose the name spectabilis, because it is certainly identical with P. spectabilis, Heller, from the same island.

	1. ♂·		2. ♂•		3. ♂•		4. ♂.	
Length of the animal	125		118		116		110	
Length of the whole leg	155	145	153	147	122	116	138	135
Length of the merus	30	29	28.5	28	24	23	27	26.5
Width of the merus at the distal end	5.4	5.2	5	5	4.5	4.5	4.75	4.75
Length of the carpus	27	26	27	26	21	21	25	25
Width of the carpus at the distal end	5.5	5	5.5	5.25	4.7	5 4.75	5	5
Length of the palm	42	37	43	40	33	30	37	36
Breadth of the palm in the middle	5.75	4.75	5.33	5.25	4.7	5 4.5	5.25	5
Thickness of the palm in the middle	5	4.25	4.5	4.5	4.2	54	4.5	4.5
Length of the fingers	30.5	27	29	28	23.5	21.5	26.5	25
Length of the whole hand	72.5	64	72	68	56.5	51.5	63.5	61
Formula of the rostrum	2 9 3		2 9 3		2 8 3		$\frac{2}{7}$	

Measurements in millimetres.

PALÆMON (PARAPALÆMON?) ASPERULUS, v. Martens. (Plate 18. figs. 2-8.) Palæmon asperulus, v. Martens, Archiv Naturg. xxxiv. Jahrg. 1868, p. 43, Taf. 1. fig. 5. Palæmon asperulus, Ortmann, Zool. Jahrb., Syst. v. p. 708.

One young female from South Hu-peh, China. British Museum (Natural History).

Though *P. asperulus* was described a third of a century ago, it has apparently never been observed since that time, and, so far as I am aware, no mention of this species has been made since 1868, except by Dr. Ortmann, who, however, did not have any specimens at his disposal. We must therefore regret that only one young female has been collected, for, according to von Martens, *P. asperulus* is a common species in the fish-market of Shanghai.

Our female is 47 mm. long from tip of rostrum to the extremity of the telson, quite young therefore, this species attaining, indeed, a length of 83 mm. The rostrum (fig. 2) is *short* and reaches to the distal end of the antennulary peduncles; it is lanceolate, and appears very slightly arcuate above the eyes. The upper margin bears 10 equal teeth, the first of which is placed just twice as far from the posterior as from the anterior margin of the cephalothorax. This first tooth stands a little farther from the second than the following teeth, that are equidistant and reach to the tip of the rostrum. The under edge bears 3 teeth, which are smaller than those of the upper margin; the first is situated just below the seventh tooth of the latter, and these teeth have also about the same length and extend to near the tip. The rostrum has a stout shape and that part which is situated above the lateral crest appears, in the middle of the rostrum, as high as that below it. Three teeth are on the cephalothorax, the fourth is situated just before the orbital margin.

Von Martens describes the rostrum as being as long as the scaphocerites (l. c. p. 34), but in his figure it does not reach so far; this figure, however, is inaccurately drawn, for the lateral spines of the cephalothorax have been forgotten altogether.

The hepatic spine is a little smaller than the antennal, and is situated posterior to and somewhat below the latter.

The cephalothorax is covered, though not closely, with very small spinules, which are only 0.04 mm. long. The abdomen is finely punctate. The first segment (Pl. 18. fig. 3) presents a remarkable form, which has not hitherto been observed in any species of this genus, the dorsal part of it being distinctly tricarinate by three, not very sharp, longitudinal carinæ, that reach from the anterior to the posterior margin of the segment. The two lateral carinæ converge very slightly backwards, and the upper surface is concave between the median crest and each lateral one; even on the outer side of each lateral carina the surface appears a little concave, though a second lateral crest does not exist. Though the second segment is not at all carinate, its surface appears, however, on each side of the median line, near the posterior margin, very slightly concave. The third and fourth segments are rounded above, but the fifth is distinctly carinate in the median line of the dorsal surface, though only along the posterior half; on each side of the crest the surface appears a little concave. The telson tapers rather strongly towards the posterior extremity (fig. 4), that ends in a sharp acute median tooth, which is shorter than the internal of the two spines on each side of it. The upper surface of the telson is roughened by minute spinules, which are still smaller than those of the cephalothorax. The anterior pair of spines on the upper surface is a little farther from the anterior end of the telson than from the posterior extremity; it is, of course, very seldom that a third spine occurs on the left side, close to the anterior one.

The short filament of the upper antennæ is united for a very short distance with the outer one, this distance being only one-third of the length of the third joint of the peduncle. The external footjaws project half their terminal joint beyond the peduncles of the outer antennæ. The legs of the first pair overreach the scaphocerites by the length of their hands: the fingers are just as long as the palm. The carpus, which is somewhat thickened as usual at its distal end, is 5.5 mm. long, the hands are 3.6 mm. long; so that the carpus is only once and a half as long as the hand (fig. 5).

The legs of the second pair (fig. 6) are equal and rather feeble; they project a fourth of their wrist beyond the scaphocerites. Measured along its upper margin, the merus appears  $5\cdot 2$  mm. long; this joint is almost cylindrical and thickens but very slightly anteriorly, so that it is  $1\cdot 6$  mm. thick at the distal end. The carpus, which is  $6\cdot 4$  mm. long, is distinctly somewhat longer than the merus : von Martens says that both joints are equally long, but in his figure the merus appears distinctly shorter. The carpus also thickens gradually towards the distal end, and is, moreover, slightly compressed; in consequence of this, the distal extremity appears  $1\cdot 9$  mm. broad looked at from above, but only  $1\cdot 65$  mm. when it is measured at the outer side (fig. 7).

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The carpus bears on its outer side a longitudinal ridge along its whole length, and this ridge is continued for a short distance, about 1.5 mm., along the outer margin of the palm. Both merus and carpus bear, moreover, on their upper surface an impressed longitudinal line, which runs in the same direction from the distal end of the ischium to that of the carpus (fig. 6). The hand is 13 mm. long, the palm measures 7.5 mm., the fingers 5.5 mm.; the palm is thus somewhat longer than the carpus and the fingers, and the proportion between palm and fingers also conforms to the original description, according to which their proportion should be as 3:2. The lateral margins of the palm, which is 2 mm. broad in the middle, are parallel with each other, so that its upper surface presents the same breadth almost along its whole length; the palm is 1.5 mm. thick in the middle, so that it appears a little compressed in the proportion of 4:3. The fingers shut close together and are somewhat curved inward, so that the inner margin of the hand runs very slightly concave; the fingers are also a little broader than thick and they have the same breadth to near their acute tips. Each finger bears a sharp cutting-edge, at the proximal end of which is seen a small conical tooth; the dactylus bears, moreover, a second tooth between it and the articulation, so that the tooth of the immobile finger is situated just between the two of the dactylus. One observes on each side of the cutting-edge the usual short hairs as in other species, and on the upper and lower surface of the fingers small tufts of short hairs, which are somewhat longer near the tips, but otherwise the fingers are quite smooth. The straight inner border of the palm is beset with very small spinules, 0.12 mm. long, visible only by means of a magnifying-glass; still smaller ones are seen on the outer margin; the lower surface of the palm bears also a few microscopical spinules, but the upper is nearly smooth. The palm is also a little hairy; the hairs are short, fine, and widely separate. The other joints of these legs are everywhere covered with similar small spinules and similar short The second legs are 32 mm. long, measuring just two-thirds the length of fine hairs. the animal; they have a pale flesh-colour.

The three posterior pairs of legs are *short and stout*. Those of the third pair reach nearly to the end of the antennal scales, the two others are but little shorter. The meropodites of the third pair (fig. 8) are 5.33 mm. long, measured along their upper margin, and 1 mm. thick on their outer side; the propodites are 5 mm. long and 0.72 mm. broad in the middle, the terminal joints finally are 1.9 mm. long. The meropodites of these legs are thus *five*, the strongly compressed propodites *serven* times as long as broad on their outer side, and the terminal joints are little longer than a third of the propodites. The propodites are armed with nine mobile spines along the posterior margin of their upper and lower surfaces; these spines measure 0.32-0.38 mm., and are about half as long as these joints are broad. The propodites are a little hairy on their upper and on their lower surface, as also along their anterior margin, but are otherwise smooth; the other joints are also a little hairy and almost smooth, though a few microscopical spinules may be distinguished under the microscope.

**Palamon asperulus should very likely be referred to the subgenus** Parapalamon. **Those species with which** P. asperulus is most closely allied are P. (Parapalamon) javanicus from Java and Sumatra, Palæmon (Parapalæmon) Horstii, de Man, from Celebes, and P. (Eupalæmon) elegans, de Man, from Java. A female with eggs of P. javanicus, Heller, described by myself in the 'Notes from the Leyden Museum,' i. 1879, p. 181, is now before me, and also type specimens of P. elegans from Buitenzorg. The female of P. Horstii is still unknown, so that the type specimens of this species were not required.

The female of P. elegans differs at first sight from our female of P. asperulus by the legs being much more slender and by the slender carpus of the second legs being distinctly longer than the palm; the abdomen is not carinate, and there are other differences.

The abdomen of P. javanicus is also rounded, without a trace of the longitudinal carinæ that are characteristic of the Chinese species. In the female of P. javanicus all the legs are, moreover, more slender. The carpus of the first pair is twice as long as the hands. In the second legs, which are also considerably more slender than those of P. asperulus, the palm appears in the right leg just as long as, but in the left distinctly shorter than, the carpus.

The legs of P. (*Parapalæmon*) Horstii are short and stout, and evidently bear a close resemblance to those of P. asperulus; but if my figures of the second legs of the male (in Max Weber's 'Decapoden des Indischen Archipels,' 1892, Taf. 27. fig. 39) are compared with the figure of P. asperulus in von Martens's paper, there can be little doubt that the species are different. The rostrum closely agrees in both species, but in that of P. Horstii there are four teeth on the cephalothorax.

P. (Parapalæmon) asperulus, v. Martens, has hitherto only been observed at Shanghai.

PALEMON (MACROBRACHIUM) LATIMANUS, v. Martens. (Plate 18. figs. 9-12.)

Palæmon latimanus, von Martens, Archiv Naturg. Bd. xxxiv. 1868, p. 44.

Palæmon latimanus, de Man, Archiv Naturg. Jahrg. liii. 1888, p. 557; and in Max Weber's Zoolog. Ergebn. Reise Niederl. Ost-Indien, ii. 1892, p. 477, Taf. 28. fig. 45; and in Abhandl. Senckenbergischen Naturf. Gesells. Bd. xxv. Heft 3, 1902, p. 780.

Palæmon (Macrobrachium) latimanus, Nobili, Annali Museo Civico Genova, Ser. 2, vol. xx. (xl.) 1900, p. 485, figs. 3 a-c & 4.

Palamon latimanus, Schenkel, in Verhandl. Naturf. Gesells. Basel, Bd. xiii. Heft 3, p. 512 (1902).

Five adult males and one young female from Dinawa, Owen Stanley Range, 120 miles inland from Yule Island, at an altitude of 4000 feet.

In the third of my papers quoted above I supposed that the two male specimens from Celebes, 107 mm. and 103 mm. long, were adult, because they were even a little longer than the type specimen described by von Martens, which measured 97 mm. The five adult males from Dinawa, which are all about the same size, are, however, still *considerably larger*, for they measure from tip of rostrum to the end of the telson 130– 140 mm. Specimens of this size have never been examined, so far as I am aware. Unfortunately, however, they have all lost the legs of the second pair, but one second leg is lying loose in the bottle.

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In the large males the rostrum extends to the middle of the terminal joint of the antennulary peduncles, or to the end of it; it closely resembles the figure published by Nobili of the type specimen of von Martens, but in some specimens the upper margin is more strongly inclined downward. In these five individuals the upper margin bears five, the lower two teeth, and in all the first two teeth stand on the cephalothorax. In two males the second tooth of the upper margin is just as long as the following two together (fig. 10), but in the others it is but little longer than the third tooth (fig. 9). In Nobili's figure of the type the second tooth of the lower margin is as far from the first tooth as from the tip, but in the Dinawa males the two teeth stand close together and the second is considerably farther from the tip than from the first tooth. In the young female which is 75 mm. long the rostrum is 5 mm. longer than the peduncles, and it is armed above with 6, below with 3 teeth ; two stand again on the cephalothorax, the second is but little larger than the following, and the foremost tooth is still a little farther from the tip than the length of the fifth and of the sixth tooth taken together. The three teeth of the under margin are smaller than those of the upper; the third reaches to the distal end of the penultimate joint of the upper peduncles.

Only in one single male (fig. 11) the extremity of the telson ends in a short acute median tooth; the inner of the two spines on each side is twice as long as the outer and extends beyond the median tooth a third of its length. In the other specimens the extremity of the telson is more or less worn off, and in the female this segment is wanting.

In these adult males the outer footjaws project the distal fourth of their penultimate joints beyond the peduncles of the outer antennæ. The legs of the first pair extend a third or a fourth of their wrist beyond the scaphocerites. The fingers are just as long as or a little longer than the palm, and the carpus is once and a half as long as the hand.

Only in one male, which has a length of 130 mm., the first four joints of the right leg of the second pair are still present; the merus, which is 23 mm. long, extends 2 mm. beyond the scaphocerites.

The large left leg of the second pair, which lies loose in the bottle (fig. 12), is 152 mm. long, and is consequently somewhat longer than the animal, for it no doubt belonged to one of the five males. It closely agrees with Nobili's figure of the type, but the palm is comparatively longer and the dactylus appears a little longer than the immobile finger. Measured along the outer margin, the merus appears to be 33 mm. long; looked at from above the proximal extremity that articulates with the ischium, it appears to be 5 mm., the distal end, however, 8 mm. broad. The carpus is 22 mm. long and measures, in conformity with the original description, two-thirds of the merus; viewed from above its proximal extremity, it appears 3.75 mm. broad, and its greatest width, at a fourth of the whole length from the distal end, measures 10 mm. The hand, measured along the outer margin, appears to be 71 mm. long, the palm 42.5 mm., the fingers 28.5; the palm is twice as long as the carpus, and the fingers are a little shorter than the merus. The palm is, in the middle of its length, 11 mm. broad and 7.75 mm. thick, being compressed in the proportion of 1:1.4; in the type specimen - -

figured by Nobili this proportion is as 1:1.22 or as 1:1.23 (vide de Man, in Max Weber's 'Decapoden des Indischen Archipels,' p. 479). This difference depends, no doubt, upon the difference of age, or is perhaps individual. In a male specimen from Minahassa the palm of the left leg was 25 mm. long, 10.5 mm. broad, and 8.5 mm. thick; though the palm was a little less broad than in the leg that I am describing, it was, however, somewhat thicker, so that the proportion was as 1:1.23 (de Man, in Kükenthal's 'Decapoda,' 1902, p. 783). The palm is thus four times as long as broad; in the type figured in the 'Annali del Museo Civico di Genova' the palm appears three times as long as broad, but the type specimen is much younger, being only 97 mm. long, and the leg that is figured measures only 85 mm. The fingers of our specimen shut close together, and the dactylus is almost 1.5 mm. longer than the immobile finger. At the end of a short black-coloured cutting-edge, which extends almost along a third of the length of the finger from the tip, is seen a small conical tooth, and another of the same size stands in the middle between this tooth and the articulation; between this second tooth and the articulation the finger presents two smaller teeth, and between this second tooth and that at the end of the cutting-edge are seven small teeth that gradually decrease in size distally. The black-coloured cutting-edge of the immobile finger is somewhat longer, extending along two-fifths of its length, and it presents a conical tooth at its proximal end; between the latter and close to the articulation this finger carries fifteen small teeth, of which two or three in the middle are a little larger than the others. The dactylus, however, carries only ten teeth between the cutting-edge and the articulation. The number of these teeth apparently increases with the age; in a young male from the island of Rotti, 50 mm. long, each finger bore only nine teeth between the tooth at the end of the cutting-edge and the articulation (de Man, in Max Weber's 'Decapoden des Indischen Archipels,' 1892, p. 480). The whole leg is covered with small spinules. On the outer margin of the merus they are less numerous than elsewhere; but on the outer, and in a less degree also on the inner, side of the carpus these spinules are more crowded than on the upper and lower surface of this joint. The outer margins of the palm and of the dactylus are closely beset with these spinules, but their number gradually decreases towards the inner margin of the palm, and on the upper as also on the lower surface of both fingers they are few in number. The spinules on the inner margin of the immobile finger are very slightly larger than those on the inner margin of the palm and than the crowded spinules on the outer margin of the dactylus. This leg has a reddish colour, but on the inner side of merus and carpus it is marbled with black, as are also the distal extremities of the red-coloured fingers.

The three posterior legs are stout. Those of the third pair project a third or a fourth of the length of their carpopodites beyond the scaphocerites; the fourth pair is somewhat shorter; and the fifth legs extend scarcely beyond the middle of the antennal scales. The meropodite of the fifth legs of one of the adult males from Dinawa is 17 mm. long and 2.75 mm. thick in the middle; the carpus, measured to the articulation with the propodite, appears 10.5 mm. long and 2.66 mm. thick on its outer side; the propodite is 18 mm. long and 1.75 mm. broad in the middle, and the dactylopodite measures 5 mm.

In all the specimens of P. latimanus that I have examined anteriorly, the upper

margin of the rostrum was armed with 10, 9, rarely 8 teeth, which reached to the tip, and Nobili describes also 8 or 9 teeth for specimens from the Mentawei Islands; in seven individuals from Celebes, recently described by Schenkel, three were armed with 9, the four others with 7, 8, 11, and 12 teeth. The type specimen from the island of Samar finally had a rostrum armed with 6 teeth on the upper margin. We may consequently conclude that the number of these teeth is subject to much variation, and there are perhaps local varieties in which it is constantly larger. The male specimen from North Halmahera, 74 mm. long, that I have described in the third of the papers quoted (p. 782), is lying before me. The meropodites of the fifth pair are 9 mm. long and 1·33 mm. broad on their outer side; the carpopodites are 5 mm. long and 1·2 mm. thick at the distal end; the propodites are 10 mm. long and 0·85 mm. broad in the middle; the dactylopodites finally are 2·75 mm. long. The three posterior legs are thus comparatively *a little less stout* in proportion to their length than those of the adult specimens from Dinawa.

Palæmon (Macrobrachium) latimanus has hitherto been recorded from the following localities:—Mentawei Islands (Nobili); Flores (de M.); Rotti (de M.); Timor (de M.);
Amboina (de M.); Halmahera (de M.); Celebes (de M., Schenkel); Samar (von Martens);
Fiji Islands (Ortmann). Fresh water.

#### B.—SPECIES FROM WEST AFRICA.

PALEMON (EUPALEMON) MACROBRACHION, Herklots. (Plates 18. and 19. figs. 13-29.)

Palemon macrobrachion, Herklots, Additamenta ad Faunam Carcinologicam Africæ Occidentalis, L. B., 1851, p. 15.

Palæmon macrobrachion, de Man, in Notes from the Leyden Museum, i. 1879, p. 177.

Confer: Carl W. S. Aurivillius, 'Krustaceen aus dem Kamerun-Gebiete,' in Bihang till K. Svenska Vet.-Akad. Handlingar, Bd. xxiv. Afd. iv. No. 1, 1898, p. 19.

The following collection is lying before me :-

One male of medium size, obtained by Messrs. Büttikofer and Sala in 1881 in Liberia. (Leyden Museum.)

One adult male and one somewhat younger female without eggs, from the River Prah, South of Ashantee, West Africa. (British Museum, Natural History.)

Nine specimens of medium size  $(1 \circ, 8 \circ)$  from the Congo Coast, probably from Ambriz.

About 300 young and very young specimens, half of which have unfortunately lost their legs of the second pair, from fresh water at Catumbella, near Benguella; presented to me, together with the Congo specimens, by my cousin, Mr. P. Kamerman.

Dr. Aurivillius, who has also studied a large number of specimens of this species collected in Cameroon, was led to the conclusion that *P. macrobrachion* ought to be identified with *P. acanthurus*, Wiegm.; and he is followed in this opinion by Miss Rathbun in Proc. U.S. National Museum, xxii. 1900, p. 315. The identity of both species appears very probable also to me: nevertheless I prefer to describe the SECOND SERIES.—ZOOLOGY, VOL. IX. 43 African specimens still provisionally under the name given to them by Herklots, because neither Aurivillius nor myself was enabled to study also American individuals of *Palæmon acanthurus*. It may be possible, indeed, that slight differences exist between the two species, differences that have been overlooked in the published descriptions, and we must consider that von Martens, who examined American specimens of *P. acanthurus* together with one from Sierra Leone, was unable to decide whether the latter specimen was to be referred or not to *P. acanthurus* (vide Archiv f. Naturg. xxxv. Jahrg. 1869, p. 30).

The rostrum of the male specimen \* from Liberia, the cephalothorax of which is closely covered with minute spinules, differs rather much from all the other specimens in the large collection lying before me. In the first place, it is but little longer than the peduncles of the internal antennæ, much shorter than the scaphocerites, and it extends straight forward, being not at all upturned at the extremity (Pl. 18. fig. 13). The 11 teeth of the upper margin extend to the tip, there being no smooth interspace separating one or two apical teeth from the preceding. The first two stand on the carapace and are somewhat more distant from one another than the others. One observes 5 teeth along the distal half of the lower margin, the first of which is situated just below the seventh tooth of the upper border.

The right leg of the second pair is almost once and a half as long as the animal, the left is but 4 mm. shorter. As regards the length and the shape of the joints, these legs fully agree with that of the adult male from the River Prah described below, and the same conformity is observed as regards the number, the form, and the arrangement of the spinules with which the joints are beset. Each finger is armed with a small conical tooth, but between this tooth and the articulation there are only two or three smaller teeth; both fingers of each leg are thickly covered with a woolly felt. The three posterior legs are comparatively just as long as in the adult male from the River Prah and agree also in the other characters; the meropodites of the legs of the third pair are 11.5 mm. long and, in the middle, 1.66 mm. broad.

The rostrum of the adult male (Table, No. 2) from the River Prah is broken off, only the three posterior teeth of the upper margin are still present; two of them are on the carapace, the third just above the orbital margin. The cephalothorax is somewhat roughened anteriorly, especially on the sides, by microscopical spinules, only visible by means of a magnifying-glass. They exist also on the telson. In my first description of *P. macrobrachion* (*l. c.* 1879) the carapace is said to be smooth. The anterior pair of spinules on the upper surface of the telson is situated exactly in the middle, the posterior pair just half-way between the anterior and the extremity. The latter ends in an acute median tooth in the middle, on either side of which are inserted the two usual spines; the internal spines extend considerably beyond the median tooth.

The inner or shorter of the two outer flagella of the upper antennæ are 20 mm. long from their extremity to the end of the peduncle, being slightly longer than the latter;

<sup>\*</sup> For the measurements of the body and of the second legs, as also for the toothing of the rostrum, I refer to the Table on p. 321, where the dimensions of 38 specimens are given. The joints of the second legs have been measured along their outer margin.

they are united for a fifth of their length with the outer flagella and are slightly serrated.

The external maxillipedes extend a third of their terminal joint beyond the peduncle of the lower antennæ. The legs of the first pair, which are 42 mm. long, project with little more than their hands beyond the tip of the antennal scales. The slender carpus is 18 mm. long, and 1:33 mm. thick at the distal end; it is almost three times as long as the chela, which is 6:66 mm. long and the fingers of which are slightly longer than the palm. Only one leg (fig. 14) of the second pair is still present; this leg is a little longer than the animal. The merus extends for about a third of its length beyond the antennal scales; it is straight and thickens slightly to a little behind its distal end, its greatest width being 6:5 mm.; this joint appears consequently five times as long as thick. The carpus is one-fourth longer than the preceding joint; it is slender and thickens slightly and rather regularly towards the distal end, its diameter being here about one-eighth of the whole length. The carpus is, however, not quite straight, but very slightly curved, so that the inner margin appears a little concave, the outer very slightly convex. The palm has about the same length as the merus and is as much shorter than the carpus as the latter. The almost quite straight palm is cylindrical, presenting over its whole length a diameter of 4 mm., so that this joint is 8 times as long as thick. The fingers, which are thickly covered with a woolly felt, quite close together; the immobile finger is armed with a small conical tooth, about 0.75 mm. high, at one-third of its length from the articulation, and between this tooth and the articulation seven or eight smaller teeth are observed, placed in a longitudinal row. The dactylus carries likewise a small conical tooth, 1.5 mm. beyond that of the immobile finger, and between it and the articulation five or six smaller teeth. The inner and the inferior sides of merus, carpus, and palm are covered with slender spinules, those on each side are somewhat larger and arranged here more

The following legs are stout, a little hairy, and thickly covered, except on the lateral parts, with minute spinules; the legs are, however, partly broken and incomplete. The propodites of the third pair reach almost to the end of the scaphocerites; the carpus of the following pair reaches to the cornea of the eyes, that of the fifth pair finally extends to the anterior margin of the cephalothorax. The meropodites of the legs of the third pair are 17 mm. long and 2.5 mm. thick in the middle.

The cephalothorax of the female from the River Prah is smooth. The upper margin of the rostrum (fig. 15) is straight till a little beyond the middle, then it curves very slightly upwards, reaching to the end of the scales. It is armed above with 9 basal teeth, the first two are on the carapace, the third just above its anterior margin, and the ninth tooth reaches almost to the distal end of the peduncles of the inner antennæ; finally with two small *apical* teeth close to the tip, the posterior of which is separated by a smooth interspace, which is 5 mm. long, from the foremost tooth of the basal portion. The first and the second teeth are twice as distant from each other as the second is from the third, and the three or four foremost teeth of the basal portion increase very slightly

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in length. The convex inferior margin carries 5 teeth, the first of which is situated below the seventh of the upper margin, the fifth just opposite the middle of the smooth interspace. The two portions into which the rostrum is divided by the lateral crest are equally high.

The outer footjaws project beyond the peduncles of the lower antennæ by a third of their terminal joint. The legs of the first pair extend by half their hand beyond the antennal scales ; the slender carpus, 11.5 mm. long, is two and a half times as long as the chela, which measures 4.5 mm., and the fingers of which are somewhat longer than the palm. Only the right leg of the second pair is still present (fig. 16). It is considerably feebler than that of the male and reaches with the distal third of the carpus beyond the antennal scales. The carpus, 2 mm. thick at the distal end, is 1.25 mm. thick at the extremity. The fingers shut together and are thickly covered with felt; the palm is 1.9 mm broad when looked at from above, but only 1.7 mm. in the middle when the lateral side is measured, so that it is not exactly cylindrical. The spinules with which the joints are covered are comparatively much smaller than in the adult male, but their arrangement is the same. The hand is a little longer than the carpus, and the carpus is much longer than the merus. The following three legs are somewhat less stout than those of the adult male and their joints are almost smooth ; those of the fifth pair reach to the end of the scaphocerites; the two other pairs, which have about the same length, are a little shorter. The meropodites of the third pair are 10.5 mm. long and, in the middle, 1.33 mm. thick.

The situation of Boutry, where the type specimens of Herklots were obtained, is in the immediate vicinity of the River Prah, for Boutry is situated close to Dixcove, and that place is not far distant from the mouth of the river.

The cephalothorax of the only male from the Congo Coast is almost smooth. The slender rostrum (Pl. 19. fig. 17), which projects about 1 mm. beyond the antennal scales, is not straight, for the distal half curves somewhat upward and the upper margin is very slightly arcuate above the eyes. The basal portion carries 9 teeth, three of which are on the cephalothorax, and the ninth tooth reaches to the distal end of the penultimate joint of the antennular peduncles; then follows a smooth interspace, 5 mm. long, finally two smaller apical teeth close to the extremity. The first and the second teeth are a little more distant from each other than the following. The inferior margin is provided with 6 teeth, the first immediately before the eyes, the following increase in length, and the sixth is situated below the penultimate apical tooth of the upper margin. The rostrum resembles that of the female from the River Prah, but is more strongly turned upward and has a more slender form. The first legs overreach the scales only by the length of their fingers; the carpus is 7.5 mm., the hand 3.66 mm. long.

Though this specimen is but little smaller than the male from Liberia, the legs of the second pair are *considerably shorter*, and have the same form and length as in the females. This fact, however, is often observed in the males of this genus. As regards the measurements of the right leg, I refer to the Table; they nearly agree with those of the female from the River Prah. The whole leg is somewhat shorter than the animal and fully agrees in its other characters with that female. I will only add that the merus

reaches as far forward as the peduncle of the upper antennæ, and that the palm is 2.1 mm. broad looked at from above and 1.9 mm. in the middle measured on the outer side. The fingers are already covered with the characteristic woolly pubescence. The left leg is only 30 mm. long and almost quite smooth. The following legs are also smooth; those of the fifth pair reach to the end of the antennal scales.

Five of the eight females from the Congo Coast are provided with eggs; the largest of these five is 80 mm., the shortest 58 mm. long from the tip of the rostrum to the end of the telson. The cephalothorax is smooth. The rostrum (fig. 18) agrees, in its general characters and outer appearance, with that of the female from the River Prah and in all it curves more or less upward at the distal end; the teeth-formulæ are given in the Table. In all eight females 8, 9, or 10 teeth of the basal portion are separated by a smooth interspace from one or two, rarely three apical teeth, and these apical teeth are on the carapace and the lower margin is armed with 4, 5, or 6 teeth.

In the larger specimens the fingers of the first pair project beyond the antennal scales, in the smallest one these legs are just as long as the scaphocerites. The legs of the They are generally second pair agree with those of the female from the River Prah. equal, half as long or little more than half as long as the animal. In the largest female, which is 80 mm. long, these legs project a fourth of their carpus beyond the antennal scales; in another (No. 7), which has almost the same size, the second legs (Pl. 18. fig. 19) are just as long as the scaphocerites. In the former specimen the carpus is 12 mm. long, and 1.5 mm. thick at the distal end, in the other these numbers are 10 mm. and 1.6 mm.; so that the carpus of No. 5 appears somewhat slenderer than in the other. In two females the carpus is a little shorter than the hands, but in the others these joints have about the same length; the fingers, which in all are covered with a feltlike pubescence, though the tips are generally devoid of it, are usually a little shorter than the palm. The fingers carry about the same teeth as in the male, but they are fewer in number and smaller. So, e. g., in the female (No. 6) the dactylus (figs. 20-22) carries an obtuse tooth at one-third of its length from the articulation and behind it four other teeth, which are also obtuse, a little smaller and of unequal size. The immobile finger is also armed with an obtuse tooth at the end of its cutting-edge, and this edge is a little longer than on the other finger; between this tooth and the articulation are seen six smaller teeth, also of unequal size. Looked at from above the palm presents the same breadth along its whole length, but viewed from the lateral side, palm and fingers slightly decrease in height or thickness and the fingers taper gradually towards their tip. In the largest female (No. 5) the upper surface of the palm is 1.5 mm. broad, but looked at from the outer side the palm appears 1.4 mm. thick at its proximal end, 1.3 in the middle, and 1.1 at the base of the fingers. Fine short hairs are distributed on the joints, and as regards the distribution and size of the small spinules on their inner and lower surface, these Congo specimens fully agree with the female from the River Prah. So, e. g., the spinules on the inner margin of the carpus of the leg figured (fig. 20) are rather slender and 0.25-0.27 mm. long (fig. 21); similar spinules occur on the inner margin of the palm; those on the inner margin of the merus are, however, a little shorter and thicker. The spinules on the outer margin of the joints are much thinner and feebler. The three posterior legs agree also with those of that female. In the largest female (No. 5) the legs of the fifth pair exceed the antennal scales by the length of their dactylopodites; the two preceding pairs are a little shorter, extending only to the end of the scales. Their joints have a smooth, shining surface.

The numerous specimens from Catumbella, 28 of which have been measured, are almost all very young, and the few of somewhat larger size are, however, younger than the Congo individuals described above. The largest specimen is a male, measuring 60 mm. (No. 11 of the Table). The cephalothorax is apparently still smooth. The rostrum (Pl. 19. fig. 23), which extends to the end of the scales and curves very slightly upwards at the extremity, makes a rare exception to nearly all the other individuals: there are, for instance, no apical teeth on the upper margin; the 10 teeth of the upper margin, the third of which is situated just in front of the anterior margin of the cephalothorax, reach to the distal end of the antennulary peduncles; and the space between the tenth tooth and the apex, 2.75 mm. long, is slightly convex, without apical teeth. The first legs overreach the antennal scales by half the palm; the carpus is 7.5 mm., the hand 3.5 mm. long. The left leg of the second pair (the right is wanting) measures two-thirds the length of the animal, and projects almost with two-thirds of the carpus beyond the Though this specimen is but little shorter than the Congo male antennal scales. described above, this leg, however, is much shorter, less stout, and the surface of the joints is almost smooth, the spinules being less distinctly developed; the measurements, however, present the same proportions, and the fingers are already covered with the woolly pubescence characteristic of this species. The other legs agree with those of that male, the fifth pair reaching to the end of the scales.

In the other specimens the rostrum, which is as long as the scales or projects very little (0.5-1.5 mm.) beyond them, is generally more or less turned upwards at the distal end (fig. 24); it is usually armed above with 8, 9, or 10 teeth on the basal portion and with one or two apical teeth, separated by a smooth interspace from the preceding; and when two apical teeth are present, then they are situated close together near the tip of the rostrum or at some distance from one another. The lower margin is armed with 4, 5, or So, e. g., in a male specimen that is 37 mm. long, the rostrum, the formula of 6 teeth. which is  $\frac{10+2}{4}$  and the slender distal end of which curves a little upward, projects slightly beyond the scales for half a millimetre, as in many other individuals. The first legs reach to the end of the antennal scales, and those of the second pair, that are just half as long as the animal, overreach the antennal scales by the whole length of their hand. In another male of exactly the same length the first legs are just as long as in the preceding specimen, but those of the second pair project a fourth of their carpus beyond the scaphocerites; the legs of the third pair reach as far forward as the terminal spine of the lateral margin of the scales.

In the largest female (No. 22), which is 58 mm. long, the first legs project only by half the length of their fingers beyond the distal end of the antennal scales; the chelæ, in which the fingers are distinctly longer than the palm, are just half as long as the slender carpus. The legs of the second pair (Pl. 18. fig. 25 and Pl. 19. fig. 26) are little

more than half as long as the animal, and project beyond the distal end of the scales by a third part of their carpus. The chelæ are also slender and somewhat shorter than the preceding joint; the fingers, already slightly publicated, are a little shorter than the palm. The palm is 1 mm. broad above, and its breadth remains the same along its whole length, but it narrows slightly towards the base of the fingers when the lateral side is looked at: the palm is 0.75 mm. high in the middle, so that it is but slightly compressed, namely in the proportion of 4:3. The second legs are nearly smooth and the fingers are marked with small red spots. The third and fourth legs reach almost to the end of the scales.

In younger females, which are 35 mm. long, the first legs reach as far forward as the lateral terminal spine of the scales; the second legs, half as long as the animal, project with only their chelæ beyond the distal end of the scales. This is also the case in still younger individuals, though sometimes the wrist projects a little beyond the scales. Now it should be remarked that the carpus of the second legs has generally in these younger specimens from Catumbella a somewhat slenderer form than in the older individuals from the Congo Coast, as will be found by comparing in the Table the proportion between the length of this joint and its thickness at the distal end in different individuals.

As regards the teeth of the fingers in these Catumbella individuals, the following may be remarked:—Each finger is provided with a cutting-edge, at the end of which stands an obtuse tooth, and between this tooth and the articulation are seen a few other teeth. So, *e. g.*, in a male specimen that is 35 mm. long, the dactylus carries two rounded teeth between the tooth at the end of the cutting-edge and the articulation, but on the immobile finger there are here no teeth at all.

Of another male (No. 20), which is 29 mm. long, one of the equal second legs is represented in fig. 27, and the teeth of its fingers in fig. 28 of Pl. 19. The cutting-edge of the dactylus extends along two-thirds of its length, that of the immobile finger is a little longer. The obtuse tooth at the end of the cutting-edge of the dactylus is a little smaller than that of the other finger. Between that tooth and the articulation on the dactylus two obtuse teeth of equal size are seen, as large as the distal tooth; on the immobile finger, however, three much lower teeth, also of equal size, but considerably smaller than the tooth at the end of the cutting-edge.

In the largest female (No. 22), which has a length of 58 mm., the dactylus is armed with four, the immobile finger with two teeth between the obtuse tooth at the end of the cutting-edge and the articulation; all are smaller than the distal teeth, and those of the dactylus are of somewhat unequal size (Pl. 19. fig. 26). In another female, which is 33 mm. long, there are but two small teeth on each finger between the tooth at the end of the cutting-edge and the articulation; in another, 30 mm. long, three, and in this individual the middle of the three teeth on the dactylus appears double. In both females the cutting-edge of the dactylus is a little shorter than that of the immobile finger. In a fourth young female, 25 mm. long (No. 38), the teeth of the fingers are shown in Pl. 19. fig. 29. The obtuse tooth at the end of the cutting-edge is situated on the dactylus at one-third of its length from the articulation, and behind it there exists still only one, situated about twice as far from the articulation as from the distal tooth and of about the same size. Just in the middle between both teeth one sees the distal tooth of the immobile finger, which is as large as that of the dactylus; posterior to it this finger carries still two low teeth that are a little smaller.

Palamon (Eupalamon) sundaicus, Heller, from the Java Sea, is perhaps the most closely allied form. One of the four female specimens which I described a few years ago is lying before me (vide Zool. Jahrb., Syst. ix. 1897, p. 779, Taf. 37. fig. 71). It is 75 mm. long, and its size is thus about the same as that of the macrobrachion specimens from the Congo. The rostrum has about the same form and characters, but it arises almost in the middle of the cephalothorax; the distance of the first tooth from the posterior margin of the cephalothorax is indeed *twice* as great as its distance from the anterior margin; in P. macrobrachion, however, five to eight times as far, so that in the African species this tooth is situated much nearer to the orbital margin. In P. sundaicus the two spines on the sides of the cephalothorax are situated about in the same horizontal line, but the hepatic spine of P. macrobrachion is situated much lower. The legs of the second pair much resemble each other in both species; but the fingers are smooth, not covered with the woolly pubescence characteristic of the West-African form, and their toothing is different, the dactylus being armed with only two teeth, the immobile finger with only one. The second legs are, moreover, otherwise coloured. The other legs present also a great conformity in both species. According to Max Weber, P. sundaicus inhabits the coast of Natal (Max Weber, Zool. Jahrb., Syst. x. 1897, p. 165).

Palæmon (Eupalæmon) macrobrachion, Herklots, inhabits the rivers of West Africa from Liberia to Benguella.

# PALEMON (EUPALEMON) FOAI, Coutière. (Plate 19. figs. 30-37.)

# Palamon (Eupalamon) Foai, nov. sp., Coutière, Bull. Muséum d'Hist. nat. Paris, 1902, No. 7, p. 517.

One single male, collected in the River Kribi, 25 miles from the coast of Cameroon, West Africa. This specimen belongs to the British Museum.

This species, certainly different from *P. (Eupalæmon) macrobrachion*, Herklots, is apparently related to *Palæmon paucidens*, Hilgd., a species discovered at Adeli, near Bismarckburg, Togo Country, described by Hilgendorf in Sitzungsber. Gesellschaft Naturf. Freunde, Berlin, 1893, No. 5, p. 155. As Coutière does not compare his species with *P. paucidens*, it will be done in the course of this description.

Our specimen is 8 cm. long from the tip of the rostrum to the end of the telson; Coutière's largest specimen was 70.5 mm. long. The cephalothorax is smooth. The rostrum is stout and projects *straight forward* exactly to the end of the antennal scales; it is armed above with six, below with two teeth. The rostrum arises on the anterior half of the cephalothorax; the distance of the first tooth from the anterior margin of the cephalothorax is just one-fourth the whole length of the upper surface from the posterior to the anterior margin. The upper margin is *very slightly* convex above the eyes, but in *P. paucidens* the rostrum, which is armed above with 7-8, below with 1-2 teeth, and scarcely extends beyond the distal end of the antennulary peduncles, has been described as high, foliaceous (" blattförmig"), and short. Just as in the species

from Togo Country, however, only one tooth is situated posterior to the orbital margin, the second standing already before it. The second tooth is the longest of all, for the distance of its tip from that of the first, 5.5 mm. long, measures just one-third the distance of the tip of the first tooth from the posterior margin of the cephalothorax. The two following teeth are shorter than the second, 3 mm. long, and the fifth and the sixth, each a little more than 2.5 mm. long, are again a little shorter than the two preceding; the sixth is 2 mm. distant from the tip of the rostrum. The teeth of the upper margin are all rather small. In the middle of the free portion of the rostrum, immediately posterior to the point of the fourth tooth, that part which is situated above the lateral crest is but very little higher than that below it; the rostrum is not at all high. In the middle of the rostrum the lower margin appears slightly convex; the two teeth are still smaller than those of the upper margin and are situated, about as in P. paucidens, on the anterior half of the inferior margin. The first is situated a little beyond the middle of the fifth tooth of the upper margin, the second just behind the middle of the sixth; the distance of the second tooth from the tip of the rostrum is twice as long as the length of that tooth and twice as long as the distance of the sixth tooth of the upper margin from the tip. The hepatic spine is situated below and posterior to the antennal one, exactly below the first tooth of the rostrum. Our specimen also agrees with Hilgendorf's description in this character, that the two pairs of spinules on the upper surface of the telson are situated more backward than in P. macrobrachion, as is represented in my figures. The telson (figs. 31 & 32), which is 11 mm. long and 4 mm. broad at base, ends in an acute median tooth, with two spines on each side as usual, the inner of which extends beyond the median tooth, about as in P. macrobrachion. The anterior pair of spinules on the upper surface is situated 6 mm. from the anterior end of the telson, immediately behind the middle; it is 2.25 mm. distant from the posterior pair, and the latter 2.75 mm. from the tip of the median tooth at the end of the segment. In P. macrobrachion, however, the first pair of spinules is situated just before the middle of the telson. The eyepeduncles are a little longer than broad. The short flagellum of the upper antennæ, which is distinctly serrated and 12.5 mm. long, is united only for a sixth of its length with the outer one, and is scarcely longer than their peduncle.

The outer footjaws reach two-thirds of their terminal joint beyond the distal end of the peduncles of the outer antennæ. The legs of the first pair (fig. 33) project a fourth of their wrist beyond the distal end of the antennal scales. The slender carpus is 11.5 mm. long and 0.9 mm. thick at the distal end; the hands are half as long as the wrist and the fingers are just as long as the palm.

Unfortunately, one of the second legs is lost; the other, 75 mm. long, has almost the same length as the body. It is a *rather feeble* leg in proportion to the size of this specimen; but I have shown in the description of *P. macrobrachion* that the length and the size of the second legs differ sometimes very much in different specimens: compare, *e. g.*, in the Table on p. 321 the male (No. 1) from Liberia and that from the Congo (No. 4). The second leg (fig. 34) of our specimen from the River Kribi much resembles that of *P. macrobrachion* as regards the proportion of the length of the joints, but it differs at first sight *in the absence of the woolly felt* with which the SECOND SERIES.—ZOOLOGY, VOL. IX.

fingers are covered in the last-named species. The merus is 14.5 mm. long, the carpus 18 mm., the hand 25.25 mm., viz. the palm 16 mm., the fingers 9.25 mm. Just as in Palæmon macrobrachion, the carpus is distinctly longer than the merus and shorter than the whole hand; it is also a little longer than the palm and almost twice as long as the fingers. The latter measure little more than one-third the length of the whole hand. The slender merus thickens gradually and regularly towards the distal end, and, being here 2:4 mm. broad, this joint appears just six times as long as the thickness at the distal end. The merus of *P. macrobrachion* thickens not so regularly towards the distal extremity. The slender carpus widens likewise regularly towards its distal extremity, and, being here 2.5 mm. broad, this joint appears just seven times as long as thick at the distal end. The hand closely resembles that of the male of P. macrobrachion from Liberia described p. 303. Viewed from above, the palm appears 2.2 mm. broad, and presents the same breadth along its whole length; in a lateral view, just as in P. macrobrachion, the breadth slightly decreases towards the base of the fingers, and in the middle of its length the palm is 1.9 mm. thick. The palm is not quite cylindrical, but very nearly so, and it is a little less broad than the distal end of the carpus. Just as in the male from Liberia, the fingers are a little curved inwards, so that the inner margin of the hand is slightly concave. The fingers shut close together. The dactylus appears at its base a little broader or thicker than the other finger, and tapers regularly towards the tip; it is armed with a small conical tooth just at a third of its length from the articulation, and between it and the latter there are still two other similar teeth. The immobile finger likewise carries a tooth, a little nearer to the articulation than in the other finger, and also two other teeth between the articulation and the distal tooth. Between the distal tooth and the tip a sharp cutting-edge is seen on each finger. The joints are covered with small spinules which on the upper outer side are smaller and less numerous than elsewhere; on the outer border of the palm they are arranged in a longitudinal row, but they are here a little smaller than on the inner margin. These spinules occur also on the fingers. The joints of this leg are very slightly hairy; the hairs, however, are very short and fine, and the leg has a reddish colour. In the larger leg of the second pair of P. paucidens from Togo Country, the merus was 11.3 mm. long, the carpus 11.5 mm., the palm 15.5 mm., and the fingers 9.6 mm.; merus and carpus were thus shorter than in our specimen, especially the carpus, which was scarcely longer than the preceding joint.

In the species described by Hilgendorf the fingers were each armed, beside with the basal teeth, with seven spines ("Dornen"), standing on both sides of the cutting-edge; these spines are wholly wanting in our species from the River Kribi.

The three posterior legs of our specimen resemble those of P. macrobrachion; they are, however, a little stouter. Those of the third pair project, by little more than their terminal joints, beyond the scaphocerites, those of the two other pairs only by half their dactylopodites. The meropodites of the fifth pair are 11.5 mm. long and 1.04 thick, measured on the outer side; the carpopodites are 6.5 mm. long and 1.5 mm. thick at the distal end; the propodites are exactly as long as the meropodites and 0.7 mm. broad in the middle; the terminal joints are 3.1 mm. long. In a female specimen of *Palæmon macrobrachion* from Congo of about the same size, being 78 mm. long, the legs of the fifth pair have the following measurements:—The meropodites are 9.5 mm. long and 0.86 mm. thick in the middle; the carpus is 6 mm. long and 0.82 mm. thick at the distal end; the propodites are 11.5 mm. long and 0.5 mm. broad in the middle, the terminal joints finally are 3.2 mm. long. In *P. macrobrachion* the propodites of these legs are thus distinctly longer than the meropodites and, like the carpopodites, a little more slender than in the male from the River Kribi. The three posterior legs of the male from the River Kribi are covered with scattered microscopical spinules, especially on their upper margin. Hilgendorf has not described the three posterior legs of *P. paucidens*.

[For note received since this paper was in type, see p. 327.—SEC.L.S.]

# PALÆMON (MACROBRACHIUM) JAMAICENSIS (Herbst), var. VOLLENHOVENII, Herklots. (Plates 19. and 20. figs. 38-53.)

Palæmon Vollenhovenii, Herklots, in Tijdschrift voor Entomologie, i. 1858, p. 96; de Man, in Notes from the Leyden Museum, i. 1879, p. 178.

Palæmon jamaicensis (? Herbst), Benedict, in Proc. U.S. National Museum, vol. xvi. 1893, p. 540.

Palæmon jamaicensis, Herbst, var. Vollenhovenii, Aurivillius, in Bihang till K. Sv. Vet.-Akad. Handl., Bd. xxiv. Afd. iv. No. 1, 1898, p. 16, Taf. 2. figs. 1-5.

The following collection is lying before me \* :--

One adult male from Liberia. (Leyden Museum.)

Three nearly adult males and two young females, from the River Prah, Ashantee. (British Museum.)

190 specimens of different size, collected in the river at Catumbella, near Benguella. (Private collection.)

Some time ago Dr. Ortmann, who was enabled to compare adult males of this species from Cameroon with American specimens of P. jamaicensis (Herbst), finally concluded that the African form was quite identical with the American type (Ortmann, 'Os Camarões da agua doce da America do Sul,' S. Paulo, 1897, p. 209). Aurivillius, however, who compared ten specimens from Cameroon with one adult individual from Central America, is inclined to regard the African form as *a variety* of P. jamaicensis; and I like to follow him provisionally in this opinion, because no American specimens are at my disposal. Nevertheless, I suppose that fresh descriptions of the African form will still be welcome.

The largest specimen of all lying before me is the male from Liberia. The rostrum (fig. 38), closely resembling that which has been figured by Aurivillius (l. c. fig. 1), reaches to the end of the peduncles of the upper antennæ, and is armed above with 16 teeth, a number already observed by that Swedish naturalist; they are equidistant, but the first

<sup>\*</sup> The measurements of the body and of the second legs are indicated in the Table (p. 322), also the formulæ of the rostrum. The joints of the second legs are measured on their upper surface, the merus, e. g., up to the distal end of the upper margin of the ischium. Nos. 4 and 5 are the Congo specimens described in my paper of 1879.

is slightly more distant from the second than the others, and the distance of the foremost tooth from the tip is a little longer than the interspace between the preceding teeth. Five teeth are on the cephalothorax. The rostrum is slightly convex above the eyes and its distal half is directed downward.

In young individuals of this species (fig. 39) the posterior extremity of the telson ends in an *acute* triangular point, and of the two spines on each side the inner larger one reaches beyond the acute extremity; the anterior pair of spinules is situated immediately behind the middle. In older individuals, however, the telson extremity is usually more or less worn off, and it is therefore quite erroneous to describe it as largely rounded, as H. Milne-Edwards and Ortmann have done (Ortmann, in Zool. Jahrb., Syst. v. 1891, p. 729, Taf. 47. fig. 7). In the male from Liberia the extremity of the telson appears still triangular, but the acute point is already worn off.

The outer footjaws of this specimen are just as long as the peduncles of the upper antennæ, overreaching those of the lower antennæ by their terminal joint.

The legs of the first pair extend for half their carpus beyond the scaphocerites; and the hands, which are 11.5 mm. long, and in which the fingers appear a little shorter than the palm, are slightly more than half as long as the wrist, which measures 20.5 mm.

The larger leg (fig. 40) of the second pair is situated on the left side. The merus reaches almost to the end of the antennal scales. The carpus, which is 10 mm. broad at its distal extremity, is not shorter than the merus when the upper surface is measured; and an individual of about the same size, in which both joints were also equally long, has been described by Aurivillius from Cameroon (l. c. p. 17). The hand, a little more than half as long as the body, is somewhat more than three times as long as the carpus, and the palm appears almost twice as long as this joint. The palm, somewhat more than three times as long as broad, is a little broader than the carpus and a little less thick than broad, viz. 11.5 mm. thick and 12.5 mm. broad. The fingers, a sixth shorter than the palm, are armed each with a conical tooth, that on the immobile finger is somewhat larger and situated somewhat closer to the articulation than on the dactylus; between this tooth and the articulation the dactylus carries in addition three small obtuse teeth, the immobile finger only one. The fingers are slightly curved inward, and leave therefore a narrow interspace between them when closed. The whole leg is closely beset with small acute denticles, which are larger and less numerous on the inner side. The right leg fully agrees with the other, but the carpus is a little shorter than the merus, the fingers are almost as long as the palm, and the teeth with which they are armed are considerably smaller.

The legs of the third pair reach as far as the scaphocerites, those of the fourth as far as the external maxillipedes, and the legs of the last pair extend to the end of the peduncles of the outer antennæ. The meropodites of the fifth pair are 16 mm. long and 2.25 mm. thick, measured on their lateral side; the carpopodites 9 mm. long and 2.25 mm. thick at their distal end; the propodites 15 mm. long and 1.4 mm. thick in the middle, measured on their outer side.

The three males from the River Prah are about the same size as that from Liberia;

in all the rostrum is broken off, and this is also the case with the legs ! A larger leg of the second pair, lying loose in the bottle, belongs very likely to the male No. 2 that still bears its shorter left leg. This loose leg (No. 2, r) closely resembles the larger leg of the male from Liberia, but the fingers are a little longer in proportion to the palm, and the large tooth of each finger is somewhat more distant from the articulation. The palm, 11 mm. broad, is 9.5 mm. thick in the middle. The other, shorter leg fully agrees with the shorter leg of the male from Liberia, which in this specimen is borne on the right side.

In the female No. 3, from the River Prah, the rostrum, slightly arcuate above the eyes, reaches almost to the end of the antennal scales, and resembles that of the male from Liberia. The last two joints of the outer footjaws, the right leg of the second pair, and the three posterior legs are wanting. The merus of the left leg reaches to the middle of the antennal scales; the carpus, 9 mm. long, is 3.25 mm. broad at the distal end. The inner margin of the chela is concave, the palm is 3.75 mm. broad and 3 mm. thick in the middle, and the fingers, that shut close together, are only armed with minute teeth near the articulation, and are as long as the palm. The other female has lost its legs.

Such a large and fine collection as that of the 190 specimens from the river at Catumbella has most probably never been at the disposal of any naturalist. Unfortunately, in half of them the legs of the second pair are wanting.

The teeth-formulæ of the rostrum of 22 males and as many females (that are all provided with the legs of the second pair, so that they certainly belong to this species) are the following :---

*Males.*—One specimen  $\frac{11}{4}$ ; five specimens  $\frac{12}{3}$ ; six specimens  $\frac{12}{4}$ ; one specimen  $\frac{12}{6}$ ; one specimen  $\frac{13}{3}$ ; one specimen  $\frac{13}{4}$ ; one specimen  $\frac{13}{5}$ ; one specimen  $\frac{14}{3}$ ; two specimens  $\frac{14}{4}$ ; one specimen  $\frac{15}{5}$ .

In one specimen the upper margin bears 11 teeth, in twelve 12, in three 13, in four 14, in one 15, and in one 18. The lower margin is armed in seven individuals with 3 teeth, in eleven with 4, in two with 5, and in two with 6.

*Females.*—Six specimens  $\frac{12}{3}$ ; six specimens  $\frac{12}{4}$ ; one specimen  $\frac{13}{3}$ ; six specimens  $\frac{13}{4}$ ; three specimens  $\frac{14}{4}$ .

In twelve specimens 12 teeth on the upper margin, in seven 13, in three 14. The lower margin is armed in seven females with 3, and in fifteen with 4 teeth.

In the males the number of teeth on the upper margin varies from 11 to 18, the most frequent number is 12; the teeth of the lower margin vary from 3 to 6, the usual number is 4. In the females the upper teeth vary from 12 to 14, the lower from 3 to 4; the usual number of the former is 12, of the latter 4, exactly as in the males.

In twenty-three specimens 4 teeth are on the cephalothorax, in four 5, and in two 3; in ten specimens the fourth tooth stands just above the orbital margin, in five the fifth.

In not a single one of the 190 specimens from Catumbella is the rostrum limited to the length of the antennulary peduncles; in the larger individuals (fig. 41) it generally reaches

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more or less beyond these peduncles, though still not extending to the tip of the scales; but in the numerous specimens of smaller size, the quite young ones, the rostrum usually extends to the extremity of the scales, and even rarely a little beyond them. It has the same form as in the specimens from Liberia and from the River Prah that have been described above, and it agrees also with the figures in the paper of Aurivillius (*l. c.* figs. 1 & 2). The upper margin is *slightly convex* above the eyes, and the distal half is directed *downward*, but the acute tip is generally somewhat *turned upward*; the rostrum is slender, tapers gradually to a point, and the part situated above the lateral crest is scarcely higher than that below it.

In the largest male but one (No. 7) the outer footjaws project with their terminal joint beyond the peduncles of the lower antennæ, just as in the adult male from Liberia; in quite young individuals they overreach these peduncles about three-fourths of the terminal joint. The legs of the first pair project beyond the antennal scales for half their wrist; this joint is 14 mm. long; the hands are 7.34 mm. long, and the fingers are very slightly shorter than the palm. Only the left leg (fig. 42) of the second pair is present, and this leg is apparently the larger one. The merus reaches as far forward as the antennal scales. When this leg is compared with the larger leg of the male from Liberia, or with the described larger leg of the specimen from the River Prah, the joints appear less stout, being somewhat less broad or thick in proportion to their length. The merus and the carpus are equally long; the former is 5.25 mm. thick, and the diameter of the carpus at its distal extremity, measured above, is 6 mm. broad. The palm is nearly as long as that of the larger leg from the River Prah, viz. 35 mm., but only 8 mm. broad instead of 11 mm.; the palm is 6 mm. thick in the middle. The spinules on the inner side of the palm are somewhat larger than in the individuals from Liberia and the River Prah. The fingers are a little shorter in proportion to the palm, and their tips are less abruptly curved inward than in the specimens from Upper Guinea; the teeth are typically developed, so that the fingers leave an interspace between them. The legs of the third pair project for half their terminal joints beyond the end of the scaphocerites, those of the fourth reach to the end of the peduncles of the internal antennæ, and the last pair is but very little shorter. These legs are thus a little shorter than in the adult male from Liberia, but this may depend upon age; for the rest, they agree in other characters.

In the male No. 8 the rostrum is slightly upturned at its distal end and reaches to the end of the antennal scales. The right leg is the larger (fig. 43), but it is considerably smaller than in the specimen just described; the fingers are but little shorter than the palm and shut close together, as the teeth are still quite small. The dactylus bears two small teeth between the articulation and the distal tooth; likewise the immobile finger. The second legs appear quite as slender as in the preceding individual. The merus of the right leg is 3.5 mm. broad, the carpus 4.25 at its distal end, and the palm is 4.5 mm. thick in the middle.

In the largest male (No. 6) the legs of the second pair are rather feeble and short, when compared with the two males already described. In both legs (fig. 45) the carpus reaches to the distal end of the scales, and the right leg is but 3 mm. longer than the

left. The palm of the right leg is 3.5 mm. broad and 3 mm. thick in the middle; the carpus, which has a length of 10.5 mm., is 3.6 mm. thick at the distal end, so that in this specimen the palm appears not broader than the carpus. The dactylus carries *five* small teeth of equal size between the tooth at the end of the cutting-edge and the articulation; on the index, however, only one obtuse tooth is seen behind that at the extremity of the cutting-edge. All these teeth are very small and of equal size, so that the fingers shut close together. This specimen is evidently an individual variety, in the same way as *Palæmon vagus*, Heller, is a variety of the well-known Indian *P. lar*.

In the male No. 12 the rostrum fully resembles that of the male No. 8 described above; it reaches to the end of the scales, but there are only 11 teeth on the upper and 3 on the lower margin; three teeth stand on the cephalothorax. The outer footjaws project for four-fifths of their terminal joint beyond the peduncles of the lower antennæ. The carpus of the first legs is 7 mm. long, and projects for two-fifths of its length beyond the distal end of the scales; the hand, 3.75 mm. long, is little more than half as long as the carpus, and fingers and palm have the same length. The left leg of the second pair is the larger, projecting for a third of the carpus beyond the scaphocerites. The merus is distinctly longer than the carpus and 1.4 mm. thick at the distal end; the carpus is 1.8 mm. thick at its distal extremity. The palm is 2.25 mm. broad and 1.8 mm. thick in the middle.

In the quite young male (No. 16) the rostrum (Pl. 20. fig. 46) reaches, as in most young individuals, to the end of the scales, and four teeth stand on the cephalothorax. The outer footjaws project for three-fifths of their terminal joint beyond the peduncles of the external antennæ. The carpus of the legs of the first pair, 5.3 mm. long, extends for one-fifth of its length beyond the scaphocerites; and the hand, 3 mm. long, is again a little more than half as long as the wrist. The larger leg of the second pair is the left one (Pl. 19. fig. 47); the carpus extends for a fourth of its length beyond the scales; the merus is 8 mm., the carpus 1.16 mm. thick, at their distal extremities. The palm is 1.42 mm. broad and 1.31 mm. thick in the middle. The immobile finger (Pl. 20. fig. 48) bears one, the dactylus two obtuse teeth between the conical tooth at the end of the cutting-edge and the articulation. The legs of the third pair reach to the end of the scales, the two following are somewhat shorter.

In the largest female but one from Catumbella, 84 mm. long, which bears no eggs, the rostrum (fig. 49) reaches midway between the distal end of the antennulary peduacles and that of the scales. It fully resembles that of the preceding specimens from the same locality: the fifth tooth stands just above the orbital margin, the upper margin is slightly convex above the eyes and the tip is somewhat turned upwards; the third tooth of the lower margin reaches to the middle of the terminal joint of the antennulary peduacles. The outer footjaws extend almost for the whole terminal joint beyond the extremity of the peduacles of the outer antennae. The carpus of the first legs is 13 mm. long, and projects for half its length beyond the antennal scales; the hand is 7 mm. long. The left leg (fig. 50) of the second pair is considerably larger than the right (fig. 51). The merus is 3 mm., the carpus 3.4 mm. thick, at their distal ends, and the latter projects for half its length beyond the end of the scales; the palm, slightly longer than the

fingers, is 4.5 mm. broad and 3.5 mm. thick in the middle. The fingers shut close together; the dactylus is armed with two small teeth, the immobile finger with one besides the tooth at the extremity of the cutting-edge.

In the young female No. 23 finally the rostrum reaches to the end of the scaphocerites and agrees with the other specimens. The outer footjaws project for two-thirds of their terminal joint beyond the lower peduncles, and the legs of the first pair for a fourth of the carpus beyond the distal end of the scales. The larger leg of the second pair is the left (fig. 52), measuring just two-thirds of the body. The merus is 1 mm., the carpus 1.33 mm. broad, at their distal ends, and the latter projects for a third of its length beyond the antennal scales. The palm is 1.52 mm. broad and 1.27 mm. thick in the middle; as usual, the dactylus (fig. 53) is provided with two, the index with one small tooth behind the distal tooth at the end of the cutting-edge. The legs of the third pair reach to the extremity of the scaphocerites.

The larger leg of the second pair of the large male (No. 7) from Catumbella has a pale yellowish-green colour; the carpus appears on the inner, the palm on its outer side dark green, and the fingers are also dark green to their tips, but they show a yellowish-red tinge at their proximal ends and at their articulation. In the other specimens these legs are of a pale flesh-colour, reaching to the base of the fingers; the latter are dark bluish coloured, often with pale tips.

It is, indeed, a pity that in Liberia and in the River Prah no younger specimens have been collected or at Catumbella individuals of larger size, for then it would have been possible to decide whether the more slender appearance of the second legs of the Angola specimens is caused by their younger age or not; in the latter case the Angola form would be a distinct, new variety of Palæmon jamaicensis. Benedict has already observed (l. c.) that specimens from the Quanza River at Cunga are "a little more slender" than others from Old Providence, West Indies. If further researches should prove this to be really the case, I propose for this variety the name angolensis.

PALÆMON (MACROBRACHIUM) OLFERSII, Wiegm. (Plate 20. figs. 54-74.)

- Palæmon Olfersii, Wiegmann, in Archiv für Naturg. Jahrg. 2, vol. i. 1836, p. 150; Greeff, in Sitzungsber. Gesells. zur Beförderung ges. Naturw. Marburg, 1882, No. 2, p. 30; Ortmann, in Revista do Museu Paulista, No. ii. 1897, p. 212, Est. i. figs. 10 & 11; Aurivillius, l. c. p. 23.
- Palæmon spinimanus, H. Milne-Edwards, Hist. Nat. Crust. ii. p. 399; von Martens, in Archiv für Naturg. 1869, p. 26, Taf. ii. fig. 3.

Bithynis Olfersii, Rathbun, The Brachyura and Macrura of Porto Rico, Washington, 1901, p. 124.

One adult male from the River Prah, Ashantee. (British Museum.)

60 young specimens, a third of which are males, from the river at Catumbella, near Benguella. (Private collection.)

The adult male from the River Prah is 58 mm. long from the tip of the rostrum to the end of the telson. The rostrum (fig. 54) reaches almost to the end of the antennulary peduncles, is slightly directed downward, and armed above with 16, below with 5 teeth; the upper teeth are equal, small, equidistant, and five are on the cephalothorax. The telson tapers rather much towards the triangular pointed extremity and the anterior pair of spinules is situated just before the middle. The outer footjaws are as long as the rostrum, reaching almost for their whole terminal joint beyond the peduncles of the external antennæ. A third part of the carpus of the first pair of legs, that is 8.5 mm. long, extends beyond the antennal scales, and the hands are 4.5 mm. long.

The right leg of the second pair is wanting, the left has been figured (fig. 55). Measured along its upper or outer margin, the merus appears 12 mm. long and 6 mm. thick in the middle, the carpus 13.5 mm. long and 5.25 mm. thick in the middle; the palm is 17 mm. long, just half as broad (8.5 mm.). and 5.8 mm. thick in the middle, the fingers finally are 12.5 mm. long. The upper and inner sides of the palm are covered with felt and with scattered soft longer hairs; along the inner margin of the palm long, slightly curved, acute spines are seen, which gradually grow smaller on the index towards the tip. A second row of spines occurs on the upper surface of the palm near and parallel with that on the inner margin, and a few spines stand also on the upper and on the lower surface of the immobile finger at its base; a row of much shorter and more numerous spines is found along the arcuate outer margin of the palm, and both upper and lower surface of palm and fingers are beset with similar short spinules. The merus, strongly swollen in the middle, bears acute, slightly curved spines on its inner surface, as also the carpus, and these spines are arranged more or less distinctly in three or four longitudinal rows. Similar, though shorter, spines stand all round the carpus; on the outer side, however, of the merus they are very short and small, so that the surface appears here almost smooth, even under a feeble magnifying-glass. The fingers are armed with small rounded teeth along the whole length of their inner margins, 15 or 16 on the immobile and 12 or 13 on the other finger, with short hairs on each side of them. The meropodites of the fifth pair are 7.5 mm. long and 1.2 mm. broad in the middle on their outer side.

The numerous specimens that have been gathered in the river at Catumbella by Mr. P. Kamerman, and presented by him to my collection, are all young and many are of very small size. The rostrum is rather variable as regards its form and the number of teeth with which its margins are armed, as is proved by the following descriptions and a glance at the Table of measurements. A short apical part of the rostrum armed with one or two apical teeth, which are somewhat more distant from the preceding than these are from each other, is constantly distinguishable; and this apical part is generally more or less turned upward. As regards the legs of the second pair, I wish to remark that the palm appears less enlarged, when compared with the adult individual from the River Prah, and also that the preceding joints present a more slender form than in the adult. There can, however, be no doubt that these specimens are really the young of P. Olfersii.

The large male (No. 3 of the Table) is 42 mm. long from the tip of the rostrum to the end of the telson. The rostrum, slightly convex above the eyes (fig. 56), reaches almost to the distal end of the scaphocerites and is armed above with 14 teeth, of which 5 stand on the cephalothorax; the foremost tooth is smaller than the penultimate and situated nearer to the apex than to that tooth. The lower margin of the rostrum is armed with 5 teeth on its distal half. The telson tapers strongly towards the posterior extremity, which is long-pointed (fig.57); the inner of the two spines on each side reaches considerably

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beyond the acute tip. The anterior pair of spinules on the upper surface is situated just before the middle of the telson. The external maxillipedes extend for their terminal joint beyond the distal end of the lower peduncles. The carpus (fig. 58) of the first legs, 5.33 mm. long, projects for little more than the hands beyond the antennal scales, and the hands are 3 mm. long. The left leg (fig. 59) of the second pair is considerably stronger and longer than the right, and extends beyond the antennal scales for three-fourths of the carpus. This leg, 36.5 mm. long, is little shorter than the body, merus and carpus are subequal in length, and the chela is about twice as long as the carpus. Merus and carpus are swollen, the former in the middle, the latter nearer the distal extremity; both joints resemble those of the adult male from the River Prah. The hand also agrees with it, but the palm is less enlarged in proportion to its thickness and the fingers are still closer together. Along the inner margin of the hand is seen a longitudinal row of rather strong spines which gradually decrease in length towards the tip of the fingers, and on the upper surface of palm and fingers spinules occur similar to those on the adult leg from the River Prah, with the soft flexible hairs and the felt also similar. The inner margins of the fingers (fig. 60) are armed along their whole length with small obtuse teeth, fourteen or fifteen in number; on each finger, however, the third or fourth is conical, acute, and a little larger than the others.

The other leg (fig. 61) is much shorter and projects for nearly the whole hand beyond the antennal scales. The chela is twice as long as the carpus. The palm is very little broader than the carpus and distinctly shorter than the fingers, that shut close together. Both fingers (fig. 62) bear a sharp cutting-edge, at the end of which one observes an obtuse conical tooth. On the dactylus this edge extends along three-fourths of the finger; on the immobile finger it is a little longer; posterior to the tooth at the end of the cuttingedge the mobile finger is armed with three somewhat smaller, obtuse, equidistant teeth, the index with four that are still smaller.

In another male (No. 5) of about the same size the rostrum reaches to the end of the scaphocerites; it is very slightly arcuate above, the distal end somewhat turned upward and  $\frac{16+1}{4}$  dentate. The first ten or eleven teeth stand much nearer to one another than the following, and the sixth tooth is placed just above the orbital margin. The right leg of the second pair is little shorter than the animal and almost once and a half as long as the left. At a third of its length from the articulation the immobile finger of this larger leg is armed with a conical tooth and posterior to it with four very small ones; between the conical tooth and the tip of the finger one observes ten or eleven rounded teeth which gradually decrease in size towards the tip, and the first of which is but little larger than the four teeth near the articulation. The dactylus bears a similar conical tooth, larger than the others and a little farther from the articulation than on the immobile finger; posterior to it there are only three, which are, however, slightly larger than the four of the index, and between this tooth and the tip of the finger ten or eleven small rounded teeth are seen, which again decrease in size. The fingers of the smaller chela are provided with a cutting-edge, at the end of which stands a tooth and between it and the articulation three or four smaller teeth.

In another young male (No. 7), which has a length of 36 mm., and that as regards its

other characters agrees with the preceding, the right leg is lost, but the left (fig. 63) differs from them by the palm being considerably shorter than the fingers and by the fingers being much more curved and leaving a wide interspace between them, filled up with hairs. This leg is the shorter one, because the still present coxopodite of the other leg is much larger; and in this case it is no doubt that leg which in de Saussure's figure of Palæmon Faustinus is seen on the right side (de Saussure, 'Mémoires pour servir à l'Histoire Naturelle du Mexique, etc.' 1° livr. Crustacés, 1858, pl. iv. fig. 30). Each finger bears a cutting-edge with a tooth at the end of it; and between this tooth and the articulation the dactylus is armed with two somewhat smaller teeth, the immobile finger with four that are still smaller than those of the dactylus (fig. 64).

This phenomenon, that the fingers of the smaller leg gape in some individuals, the interspace being then filled up with hair, but closed together in others, has already been described for other species, e. g. for Palæmon (Eupalæmon) endehensis, de M., which occurs in fresh water of the island of Flores (de Man, 'Decapoden des Indischen Archipels,' 1892, p. 465, Taf. xxvii. fig. 42).

The rostrum of the male (No. 8) that is 34 mm. long is a little (0.75 mm.) longer than the scaphocerites, and agrees with the other specimens. The outer footjaws project for half their terminal joint beyond the distal end of the lower peduncles, and the legs of the first pair extend beyond the scaphocerites by the length of their fingers. The left leg (fig. 65) of the second pair projects with the whole hand, the right leg with the fingers, beyond the distal end of the antennal scales. The inner margin of the palm of the larger leg is armed with ten large spines that are 0.16 mm. long, *i. e.* one-seventh of the breadth of the palm; five or six spines occur along the inner margin of the immobile finger. Each finger bears a sharp cutting-edge that extends along two-thirds of the daetylus and almost along three-fourths of the immobile finger; at the end of each cutting-edge stands a small obtuse tooth. Between this tooth and the articulation (fig. 66) there are on each finger still four other teeth of about the same size. The fingers of the other leg agree with them, but they are armed with only three low teeth between the tooth at the end of the cutting-edge and the articulation.

In the youngest male (No. 9) that has been measured, which is 27 mm. long, the rostrum is still a little longer than the dorsal surface of the cephalothorax, and projects  $l\frac{1}{2}$  mm. beyond the distal end of the scaphocerites. The slightly convex basal part reaches to the end of the antennulary peduncles, and the apical part is slightly turned upward; there are three teeth on the cephalothorax, the fourth standing immediately before the orbital margin. The legs of the first pair reach to the end of the antennal scales. The second legs are equal and project for almost their whole hand beyond the scaphocerites. The carpus is just a little longer than the merus and shorter than the hand. The tooth at the end of the cutting-edge stands on the dactylus at about one-third of its length from the articulation, and there are three similar teeth between the latter and that tooth; on the immobile finger the cutting-edge reaches a little farther, and here also three low teeth are found posterior to it.

In the largest female (No. 10), which is 41 mm. long, the apical part of the rostrum (fig. 67) is rather much turned upward and reaches slightly beyond the antennal scales;

the basal part is, as usual, very slightly arcuate. Two-thirds of the terminal joint of the external maxillipedes extend beyond the peduncles of the external antennæ. The legs of the first pair extend beyond the scaphocerites for the distal fifth of their wrist. The carpus is 5 mm. long, and 0.52 mm. thick at the distal end; the hand is 2.72 mm. long, the palm measuring 1.56 mm., the fingers 1.16 mm., and the palm is 0.56 mm. broad. The larger leg of the second pair (fig. 68) extends almost with half the carpus beyond the scales, the shorter leg with only the hand. The cutting-edge (fig. 69) of the immobile finger extends along three-fourths of its length, but it is somewhat shorter on the dactylus; the dactylus bears three low and obtuse teeth of equal size posterior to the somewhat larger conical tooth at the extremity of the cutting-edge; on the immobile finger, however, the inner margin runs somewhat irregularly between the distal tooth and the articulation, but distinct teeth are not distinguishable. The fingers of the shorter leg (fig. 70) present the same characters, but the teeth at the extremity of the cutting-edges are rudimentary. The legs of the third pair overreach the scaphocerites with half their dactylopodites.

Though the Catumbella specimens are all young or even very young, still there is one ora-bearing female amongst them. This specimen is 40 mm. long; the eggs are very numerous, about 0.5 mm. long and a little less broad. The rostrum, which reaches to the end of the scales, is very slightly arcuate above the eyes, and the acute tip is somewhat turned upward. The upper margin is armed with 16 acute teeth besides the two apical ones; the fifth tooth stands just above the orbital margin, and the two apical teeth, of which the anterior is much the smallest, are situated on that distal part which is slightly turned upward. The posterior apical tooth is a little more distant from the preceding than the latter are from one another. The inferior margin bears five teeth.

The chelæ of the first pair of legs extend beyond the distal end of the scaphocerites; they are 2.66 mm. long, the carpus 4.5 mm. Only the right leg of the second pair is present, the carpus reaches almost to the end of the antennal scales. The carpus is, as usual, little longer than the merus and than the palm; the fingers, that shut close together, are provided with the usual cutting-edge and a small tooth at the end of it. The dactylus bears, moreover, three small teeth between that tooth and the articulation, the immobile finger also has traces of teeth. This leg is somewhat hairy, and there are a few spinules along the inner margin of the joints, but for the rest it is smooth; it resembles the smaller leg of the described young males, but it appears to be more slender.

The legs of the third pair reach to the end of the antennal scales, the following are hardly shorter. The meropodites of the fifth pair are 4.8 mm. long, the propodites 5 mm.; the former are 0.64 mm., the latter 0.42 mm. broad in the middle.

In the younger female (No. 13), which is 31 mm. long, the legs of the first pair project with their fingers beyond the antennal scales. Those of the second pair are equal and overreach the antennal scales with one-fifth of their carpus. The tooth at the end of the cutting-edge stands, on the immobile finger of the right hand, at a little more than one-fourth of its length from the articulation, and between both one observes three smaller teeth of equal size; the cutting-edge of the dactylus is somewhat shorter, and posterior to it only two teeth are recognizable, one of which is conical, the other low and rounded. The other hand agrees with that described.

In the youngest female (No. 17) finally, which is 21 mm. long, the apical part of the rostrum (fig. 71) is slightly turned upward and extends just a little beyond the antennal scales. The legs of the first pair reach to the distal end of the scaphocerites. The carpus is 2 mm. long, and 0.22 mm. thick at the distal end; the hand is 1.16 mm. long, the palm measuring 0.62 mm., the fingers 0.54 mm., and the palm is 0.25 mm. broad. The second legs (fig. 72) are almost equal and their wrists reach almost to the end of the scales, so that the fingers and two-thirds of the palm project beyond the scales. In both chelæ the cutting-edge of the immobile finger extends along about two-thirds of the finger, that of the dactylus is somewhat shorter; at the end of each cutting-edge there is a well-developed conical tooth and, between it and the articulation, on each finger two other teeth that are a little smaller, especially those of the immobile finger (fig. 73).

### PALEMON (MACROBRACHIUM?) sp. (Plate 20. figs. 75-80.)

One male and one egg-bearing female from Catumbella, near Benguella.

I describe first the female, because it is still provided with both legs of the second pair. The specimen is 46 mm. long from tip of rostrum to the end of the telson. The eggs are very numerous and small. The rostrum (fig. 75) is short, a little arcuate above the eyes, then inclined downward, but the apex is very slightly turned upward again; the rostrum extends a little beyond the distal end of the penultimate joint of the upper antennæ. It is armed above with 11 rather strong teeth, that reach the distal extremity, four of them standing on the cephalothorax, the fifth just above the orbital margin; the first tooth, a little more distant from the second than the following, is situated twice as far from the posterior margin of the cephalothorax as from the anterior. The lower margin bears two quite small teeth immediately in front of the eyes. The cephalothorax is smooth. The hepatic spine is smaller than the antennal one and situated behind and rather far below the latter. Both in the female and in the male the extremity of the telson (fig. 76) is triangular, but the acute tip itself is apparently worn off, so that the extremity appears to be truncate (fig. 77); on each side one observes the usual two spines, of which the inner reaches beyond the truncate tip. The anterior pair of spinules is situated just behind the middle. The outer footjaws project with their terminal joint beyond the peduncles of the external antennæ.

The legs of the first pair (fig. 78) extend with their chelæ beyond the distal end of the antennal scales; the carpus is 4.8 mm. long; the hands, the fingers of which are distinctly somewhat shorter than the palm, measure 3.5 mm. The carpus is 0.74 mm. thick at its distal end, this being almost one-sixth of its length, so that it has a rather stout shape.

The legs of the second pair are *equal* (fig. 79) and 28 mm. long, a little more than half the length of the body; they project for a small part of their carpus beyond the antennal scales. The merus of the left leg is 5 mm. long and 1.75 mm. thick anteriorly; the carpus is 4.75 mm. long and 2 mm. thick at the distal end; the palm is 5.5 mm. long,

2.25 mm. broad, and 1.66 mm. thick in the middle; the fingers finally are 5 mm. long. The palm is thus *very little* broader than the carpus. The fingers, about as long as the palm and as the merus, but a little longer than the carpus, shut close together; their inner margins (fig. 80) are provided with a sharp cutting-edge, and between it and the articulation each finger is beset with three or four very small teeth. The whole leg is covered with acute spinules, which on the inner margins of the joints are a little longer than elsewhere; the joints seem, moreover, to be covered with felt and are somewhat hairy.

Similar to the legs of the first pair, the three posterior pairs are stouter and less slender than those of the young males of P. Olfersii that have been described on p. 315. In the young male of this species, which has a length of 41 mm. (No. 5 of the Table), the meropodites \* of the third pair of legs (fig. 74) are 5 mm. long and 0.96 mm. broad in the middle, measured on their outer side, *i. e.*, five times as long as broad; the propodites are 4.4 mm. long and 0.54 mm. broad in the middle, a little more than eight times as long as broad. In our female (fig. 81), however, the meropodites of the third pair are 5.5 mm. long, but 1.4 mm. thick, so that they are only four times as long as broad, and the propodites, 4.6 mm. long and 0.7 mm. broad, are hardly seven times as long as broad. The legs of the third pair reach in the female to the end of the scaphocerites, those of the fourth pair are as long as the outer footjaws, and the last pair are still somewhat shorter. The three posterior legs are hairy along their upper and lower margins, but for the rest quite smooth.

The male, that unfortunately has lost its second legs, has exactly the same size as the female. The rostrum fully agrees with that of the female, bearing also 11 teeth above, but it reaches to the middle of the terminal joint of the upper antennæ, and there are three small teeth on the lower margin. The outer footjaws reach almost to the end of the scales, projecting a fifth part of the penultimate joint beyond the lower peduncles. The first legs overreach the antennal scales with half their carpus; this joint is 5.5 mm. long and 0.73 mm. thick at the distal end, so that it appears a little more elongate than in the female; the chelæ are 3.8 mm. long. The two following pairs of legs are wanting, those of the fourth pair reach almost to the end of the scales, the last pair is incomplete. I at first thought that the female was that of P. Olfersii, and that the legs of this species were much thicker in the female than in the male. This would, however, be quite an exceptional phenomenon, and this opinion was fully refuted by the examination of the male, in which the legs are just as stout and thick as in the female. It is therefore to be regretted that the second legs of the male are wanting. I have not succeeded in identifying this species with any yet known, but it bears apparently a great resemblance to P. (Macrobrachium) Iheringi, Ortm., from Brazil.

\* The joints are measured on their outer side, along their upper margin.

## FROM THE INDO-PACIFIC AND WEST AFRICA.

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", ", carpus	28	42	13.5	14.5	12	13.75	10	10.5	10-25	00	11.5	9.5	8.5	7	7.5	6.6	£.9	4.15	10
Diameter of the carpus at the distal end}	3.75	5.5	ଦା	ଦା	1.5	1.75	1.6	1.4	1.33	0-95	1.66	6.0	1	6.0		0.81	9.0	9F-0	0.5
Length of the hand	35.5	53.5	16	17.5	ei I	15.5	12.25	10.5	10.5	8-25	14	00 01	8.75	21.4	9.25	5.9	1. 1. 1.	3.8	3.63
», », palm	23	34	6	10	6.5	S.5	67.5	5.5	9	2. <del>†</del>	00	Ç.Ŧ	5	4.25	r0	3.4	5.4	C1	67
», s, fingers	12.5	19.5	2	7.5	5.5	1-	5.5	51	4.5	3-75	9	3.7	3.75	3.5	4.25	2.5	2.1	1.8	1.63
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Length of the animal	29	22	58	54	52	51	50	36	35	35	32	31	30	27.5	27	26	26	25	25
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Wholelength of the legs of the second pair	•	15	3.4	29.5		•	•	17	•	16.5	•	•	:	13	14	11.5	15	11.5	
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Diameter of the carpus at the distal end ]	FF-0	F-0	1	0.56	8-0 99	8.0	0.8	9-0-8	0.52	0.47	0-48	0+46	0-46	0.3S	61-0	0.37	0.37	0.32	0.36
Length of the hand	3.46	en 	9-25	5 7.83	33 7	6.65	5 6-5	4.18	Ŧ	3.65	3.64	3.27	3.52	ŝ	50 50 50	2.6	0	2.5	2.84
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" ingers	. 1.46	1.35	4-25	5 3.5	3	2.8	5.8	3 1-82	1.7	1.65	1.54	1-46	1.62	1.36	1-44	1.18	1.34	1.1	1-24
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Measurements in millimetres of Palæmon (Eupalæmon) macrobrachion, Merklots.

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$ \left\{ \begin{array}{cccccccccccccccccccccccccccccccccccc$	Breadth of the palm in the middle		1.65	1·3 1·4	<b>c</b> .1							2.4	1.75	2.25	9.1	2·1	-
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	Thickness of the palm in the middle		1.4 1.4			1.12	3.4			2.2	2.25	61	1.5	1.83	1.4	1.35	0.75
	Length of the fingers		6 6		10	4				6	9.5	6	2.2	8-25	5.2	5.25	3.5

Measurements in millimetres of Palæmon (Macrobrachium) jamaicensis (Herbst), var. Vollenhovenii, Herklots.

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## DR. J. G. DE MAN ON SPECIES OF PALÆMON

No. 1, Liberia; Nos. 2 and 3, River Prah; Nos. 4 and 5, Congo; Nos. 6-24, Catumbella.

## FROM THE INDO-PACIFIC AND WEST AFRICA.

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F	Formula of the rostrum	$\frac{16}{5}$	$\frac{4}{5}$	11	$\frac{4}{5}$	7,	$\frac{5}{4+1}$		$\frac{5}{4}$		49 - I (41	요 <u>년</u> ]4	broken.	12-21	$\frac{4}{5-2}$	3 14+ 6	$\frac{3}{6+2}$
216161 คียีว	Total length of the legs of the second pair. Length of the merus	$\begin{array}{c} 1. \\ 66. \\ 1. \\ 1. \\ 5. \\ 5. \\ 5. \\ 5. \\ 5. \\ 5$	28.5 5.7 5.5 5.5 5.5 5.7 5.7 5.7 5	28. x 29. x 4. x 20.	$\begin{array}{c} 36.1\\ 36.5\\ 152.65\\ 152.65\\ 252.55\\ 252$	233.x 233.x 4.1.1.5 5.5 5.5 5.5 5.5 5.5 5.5 5.5 5.5 5	$\begin{array}{c} \begin{array}{c} 233\\ 1 \\ 1 \\ 2 \\ 3 \\ 3 \\ 3 \\ 3 \\ 3 \\ 3 \\ 3 \\ 3 \\ 3$	$\begin{array}{c} 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 \\ 2 $	257. 1.4.5 5.1.1.4.5 5.1.1.4.5 5.1.1.2.5 5.1.5 5.1.5 5.1.5 5.1.5 5.1.5 5.1.5 5.1.5 5.1.5 5.1.5 5.5 5	$\begin{array}{c} 35\\ 35\\ 35\\ 35\\ 35\\ 35\\ 35\\ 35\\ 35\\ 35\\$		$\begin{array}{c} 29\\ 29\\ 5\\ 5\\ 5\cdot 5\\ 6\cdot 75\\ 2\cdot 5\\ 2\cdot$	င်္က ကို ကို ကို ကို ကို ကို ကို ကို ကို ကို ကို ကို ကို ကို	$\begin{array}{c} 1.\\ 19\\ 3.6\\ 0.74$	15 5 15 5 15 15 15 15 15 15 15 15 15 15 15 15 15	$\begin{array}{c} 1.\\ 2^{\circ}.56\\ 0.36\\ 0.44\end{array}$	$\begin{array}{c} 12.65\\ 12.65\\ 0.5\\ 0.5\\ 0.5\\ 0.5\\ 0.5\\ 0.5\\ 0.5\\ 0.$
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ынанан жын	Total longth of the legs of the second pair. Length of the merus	$\begin{array}{c} 26\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\ 2\\$	21 4 4 6.0 5.7 7.7 8 .0 8 .0 8 .0 8 .0 8 .0 8 .0 8	19.6 19.6 1.1 1.1 1.1 1.1 1.1 1.1 1.1 1.1 1.1 1		$\begin{array}{c} 1, 7, 5\\ 1, 7, 5\\ 3, 4\\ 2, 6\\ 2, 5\\$	$\begin{array}{c} 19\\ 13\\ 3.5\\ 0.8\\ 2.9\\ 1\\ 2.9\\ 2.9\\ 2.9\\ 1\\ 2.9\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\ 1\\$	$\begin{array}{c} 15.5\\ 15.5\\ 3.752\\ 0.52\\ 2.25\\ 144\\ 2.22\\ 2.22\\ 122\\ 2.22\\ 122\\ 122\\ 122\\ $	$\begin{array}{c} 15\\ 3.06\\ 3.06\\ 2.53\\ 2.53\\ 2.53\\ 2.16\\ 2.16\\ 2.16\\ 2.16\\ 1\end{array}$	$\begin{array}{c} 1.\\ 16.5\\ 3.2\\ 0.58\\ 0.74\\ 0.65\\ 2.34\\ 2.34\\ 2.34\\ 2.34\\ 2.34\\ \end{array}$	10 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	14.5 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0	$\begin{array}{c} 14\\ 2&2\\ 2&2&2\\ 2&2&2&2\\ 2&2&2&2&2\\ 2&2&2&2&$	$\begin{array}{c} 13.6\\ 12.6\\ 2.76\\ 2.76\\ 2.76\\ 2.76\\ 2.76\\ 2.76\\ 2.76\\ 1.9\\ 1.9\\ 1.9\\ 1.9\\ 1.9\\ 1.9\\ 1.9\\ 1.9$	$\begin{array}{c} 13.5\\ 2.7\\ 2.7\\ 3\\ 0.4\\ 3\\ 0.5\\ 3\\ 0.6\\ 1.86\\ 1.86\end{array}$	10014008000 10014008000 10014000 10014000 10014000 10014000	$1.4 \pm 0.038$

In the females, and in the males Nos. 7-9, the diameter of merus and carpus is measured at the distal extremity; in the other males, however, in the middle.

## TABLE OF THE WEST-AFRICAN SPECIES OF THE GENUS *PALÆMON*, FABR., CONTAINED IN THIS PAPER.

Miss Rathbun, in her instructive paper "The Decapod Crustaceans of West Africa" (Proc. U.S. National Museum, vol. xxii. 1900, p. 315), mentions four species of the genus *Palæmon* as inhabiting West Africa. Three species ought now to be added to them, viz., *P. (Eupalæmon) Foai*, Cout., another undetermined species of the same subgenus from the Upper Congo (Coutière, *op. cit.* p. 519), and finally the species from Catumbella belonging to the subgenus *Macrobrachium*, related to *P. Iheringi*, Ortm. Some principal characters of the five species described in this paper are the following :—

- A. Large chelipedc with palm cylindrical. (Subgenus Eupalæmon.)
  - a. Rostrum  $\frac{(8, \frac{2}{9}, \frac{2}{9}, \frac{3}{9}, \frac{10}{10}) + (1 \text{ or } 2)}{4, 5, \text{ or } 6}$  dentate.

Apical teeth of the upper margin usually present.

Anterior pair of spinules situated before the middle of the telson.

Carpus of second legs longer than merus, always longer than palm, fingers covered with felt.

P. macrobrachion, Herklots.

 $\beta$ . Rostrum  $\frac{6}{2}$  dentate, no apical teeth.

Anterior pair of spinules situated immediately behind the middle of the telson. Carpus of second legs longer than merus and longer than palm, fingers without felt.

P. Foai, Cout. (River Kribi.)

- B. Large chelipede with palm more or less compressed. (Subgenus Macrobrachium.)
  - $\gamma$ . Rostrum  $\frac{11-16}{3-6}$  dentate, no apical teeth.

Carpus of second legs about as long as merus or a little shorter, always shorter than palm. Three posterior legs slender.

P. jamaicensis, Herbst, var. Vollenhovenii, Herklots, and var. ? angolensis, de M.

δ. Rostrum  $\frac{(13-16) + (1 \text{ or } 2)}{4-7}$  dentate, apical teeth present.

Carpus of second legs about as long or slightly longer than merus, either a little longer or a little shorter than palm.

 $\epsilon$ . Rostrum  $\frac{11}{2}$  dentate, no apical teeth.

Carpus of second legs about as long as merus, but not longer than it, slightly shorter than palm. Posterior legs, also the others, thicker than those of the two preceding species.

Palæmon sp. (Catumbella.)

### EXPLANATION OF THE PLATES.

#### PLATE 18.

- Fig. 1. Palæmon (Eupalæmon) lar, Fabr. Extremity of the telson of the largest male, long 125 mm., × 6.
- Fig. 2. Palæmon (Parapalæmon?) asperulus, v. Martens. Lateral view of cephalothorax and rostrum of the young female, × 3.
  - 3. Abdomen of the same,  $\times$  3.
  - 4. Extremity of the telson,  $\times$  25.
  - 5. Right leg of the first pair,  $\times$  6.
  - 6. Right leg of the second pair, looked at from above,  $\times$  6.
  - 7. Lateral view of the carpus of the same leg, viewed from the outer side, the upper surface is situated on the left hand,  $\times 6$ .
  - 8. Right leg of the third pair,  $\times$  6.
- Fig. 9. Palæmon (Macrobrachium) latimanus, v. Martens. Lateral view of cephalothorax and rostrum of an adult male from Dinawa,  $\times 2$ .
  - 10. The same of another adult male,  $\times$  2.
  - 11. Extremity of the telson of an adult male,  $\times$  10.
  - 12. Left leg of the second pair of an adult male, viewed from above,  $\times 1\frac{1}{2}$ .
- Fig. 13. Palæmon (Eupalæmon) macrobrachion, Herklots. Lateral view of cephalothorax and rostrum of a male, long 70 mm., from Liberia, × 2.
  - 14. Right leg of the second pair of the adult male from the River Prah, viewed from above,  $\times 1\frac{1}{2}$ .
  - 15. Lateral view of cephalothorax and rostrum of the female from the River Prah,  $\times 2^*$ .
  - 16. Right leg of the second pair of same female, looked at from above,  $\times 2$ .
  - 19. Left leg of the second pair of the female (No. 27), long 76 mm., from the Congo Coast,  $\times$  2.
  - 20. Right leg of the second pair of the female (No. 6), long 78 mm., from the Congo Coast,  $\times$  2.
  - 21. Two spines of the inner margin of the carpus of this leg,  $\times$  25.
  - 22. Teeth of the fingers of this leg,  $\times$  25. The hairy felt has been omitted.
  - 25. Left leg of the second pair of the largest female, long 58 mm., from Catumbella,  $\times$  2.
  - 27. Right leg of the second pair of the male (No. 20), long 29 mm., from Catumbella,  $\times$  5.

#### PLATE 19.

- Fig. 17. Palæmon (Eupalæmon) macrobrachion, Herklots. Lateral view of cephalothorax and rostrum of the male (No. 4) from the Congo Coast, × 2.
  - 18. The same of the female (No. 7) from the same locality,  $\times 2$ .
  - 23. Lateral view of cephalothorax and rostrum of the largest male, long 60 mm., from Catumbella.  $\times$  2.
  - 24. The same of the largest female, long 58 mm., from the same locality,  $\times$  2.
  - 26. Teeth of the fingers of the left leg of the second pair of this female,  $\times$  25. The teeth of the dactylus are on the left hand.

\* Though this figure, as also fig. 18 of Plate 19, are quite accurate, their appearance is not natural, as they have been turned downward by the draughtsman, so that the rostrum runs horizontally forward and somewhat downward, instead of being turned slightly upward.

#### DR. J. G. DE MAN ON SPECIES OF PALÆMON

- Fig. 28. Teeth of the fingers of the right leg of the second pair of the male (No. 20), long 29 mm., from Catumbella,  $\times$  50.
  - 29. Teeth of the fingers of one of the legs of the second pair of the young female (No. 38), long 25 mm., from Catumbella,  $\times 50$ .
- Fig. 30. Palamon (*Eupalamon*) Foai, Cout., male, from the River Kribi. Lateral view of cephalothorax and rostrum,  $\times 2$ .
  - 31. Telson,  $\times$  3.
  - 32. Extremity of the telson,  $\times$  12.
  - 33. Leg of the first pair,  $\times$  2.
  - 34. Left leg of the second pair,  $\times$  2.
  - 35. Two spinules of the inner margin of the palm of the same leg,  $\times$  25.
  - 36. Two spinules of the longitudinal row on the outer margin of the palm, and six thinner ones near that row on the upper surface of the palm of the same leg,  $\times 25$ .
  - 37. Teeth of the fingers of the same leg,  $\times$  25. The teeth of the dactylus are on the left side.
- Fig. 38. Palæmon (Macrobrachium) jamaicensis (Herbst), var. Vollenhovenii, Herklots. Lateral view of cephalothorax and rostrum of the adult male from Liberia,  $\times 1\frac{1}{2}$ .
  - 39. Extremity of the telson of a young male (No. 14), long 41 mm., from Catumbella,  $\times$  25.
  - 40. Larger (left) leg of the second pair of the same male,  $\times 1\frac{1}{2}$ .
  - 41. Lateral view of cephalothorax and rostrum of the male (No. 7), long 90 mm., from Catumbella,  $\times$  2.
  - 42. Left leg of the second pair of the same male,  $\times 1\frac{1}{2}$ .
  - 43. Right leg of the second pair of the male (No. 8), long 80 mm., from Catumbella,  $\times 1\frac{1}{2}$ .
  - 44. Left leg of second pair of same male,  $\times 1\frac{1}{2}$ .
  - 45. Right leg of the second pair of the largest male (No. 6), long 96 mm., from Catumbella,  $\times 1\frac{1}{2}$ .
  - 47. Larger (left) leg of the second pair of the young male (No. 16), long 38 mm., from Catumbella, × 3.

#### **PLATE 20.**

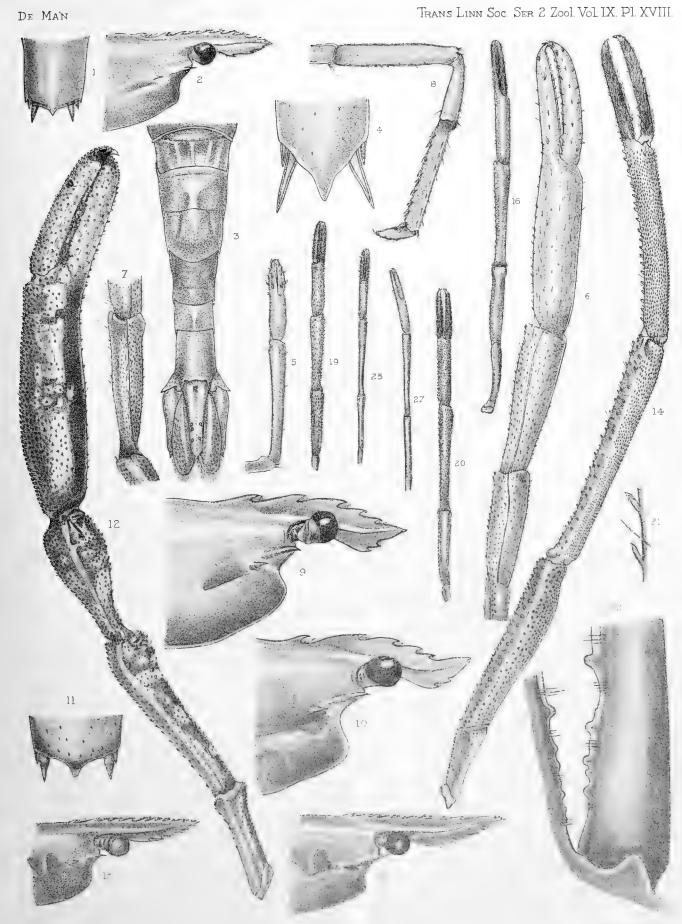
- Fig. 46. Palæmon (Macrobrachium) jamoicensis (Herbst), var. Vollenhovenii, Herklots. Lateral.view of cephalothorax and rostrum of the young male (No. 16), long 38 mm., from Catumbella, × 3.
  - 48. Teeth of the fingers of the larger (left) leg of the second pair of the same male,  $\times$  13.
  - 49. Lateral view of ccphalothorax and rostrum of the largest female but one from Catumbella (No. 18), long 84 mm.,  $\times$  2.
  - 50. Left leg of the second pair of the same female,  $\times 1\frac{1}{2}$ .
  - 51. Right leg of the second pair of the same female,  $\times 1\frac{1}{2}$ .
  - 52. Left leg of the second pair of the young female (No. 23), long 40 mm., from Catumbella,  $\times$  3.
  - 53. Teeth of the fingers of the same leg,  $\times$  13.
- Fig. 54. Palæmon (Macrobrachium) Olfersii, Wiegm. Lateral view of cephalothorax and rostrum of the adult male from the River Prah,  $\times$  3.
  - 55. Left leg of the second pair of the same male,  $\times 1\frac{1}{2}$ .
  - 56. Lateral view of cephalothorax and rostrum of the male (No. 3), long 42 mm., from Catumbella,  $\times$  3.
  - 57. Extremity of the telson of the same male,  $\times$  25.
  - 58. Left leg of the first pair of the same male,  $\times$  6.
  - 59. Larger (left) leg of the second pair of the same male,  $\times 2$ .
  - 60. Teeth of the fingers of the same leg,  $\times$  5.
  - 61. Right leg of the second pair of the same specimen,  $\times 2$ .
  - 62. Teeth of the fingers of the same leg,  $\times$  10.

- Fig. 63. Left leg of the second pair of the young male (No. 7), long 36 mm., from Catumbella,  $\times$  2.
  - 64. Teeth of the fingers of the same leg, enlarged.
  - 65. Left leg of the second pair of the young male (No. 8), long 34 mm.,  $\times$  3.
  - 66. Teeth of the fingers of the same leg,  $\times$  25.
  - 67. Lateral view of cephalothorax and rostrum of the largest female (No. 10), long 41 mm., from Catumbella,  $\times$  3.
  - 68. Left leg of the second pair of the same female,  $\times$  3.
  - 69. Teeth of the fingers of the same leg,  $\times$  25.
  - 70. Right leg of the second pair of the same female,  $\times$  3.
  - 71. Lateral view of cephalothorax and rostrum of the youngest female (No. 17), long 21 mm., from Catumbella,  $\times$  6.
  - 72. Right leg of the second pair of the same female,  $\times$  6.
  - 73. Teeth of the fingers of the same leg,  $\times$  25.
- 74. Right leg of the third pair of the male (No. 5), long 41 mm., from Catumbella,  $\times$  5.
- Fig. 75. Palæmon (Macrobrachium?) sp. Lateral view of cephalothorax and rostrum of the female from Catumbella,  $\times 3$ .
  - 76. Telson of the male,  $\times$  5.
  - 77. Extremity of the telson,  $\times$  25.
  - 78. Right leg of the first pair of the female,  $\times$  5.
  - 79. Left leg of the second pair of the female,  $\times$  3.
  - 80. Teeth of the fingers of the same leg,  $\times$  25.
  - 81. Right leg of the third pair of the female,  $\times$  5.

**Note received since the foregoing pages were in type :**—

The preceding description (pp. 306-309) agrees quite well with that of Coutière. Of the three specimens described by him, a male long 70.5 mm. and two somewhat younger females, the male had for its rostrum the formula  $\frac{1}{6}$ , the two females respectively  $\frac{1}{8}$  and  $\frac{1}{3}$ . In the male the carpus of both legs of the second pair was a little longer than in the specimen from the River Kribi, being once and a half as long as the merus, and the fingers of the larger left leg measured not quite one-third the length of the whole hand. The joints of these legs are described as smooth, except some sharp spinules on the lower border of the palm; when touched, the legs appeared, however, to be slightly scabrous. Coutière makes no mention of the characteristic position of the spines of the telson, and it is remarkable that he does not compare his species with *P. paucidens*, Hilgd.— 17th November, 1904. J. G. DE M.]





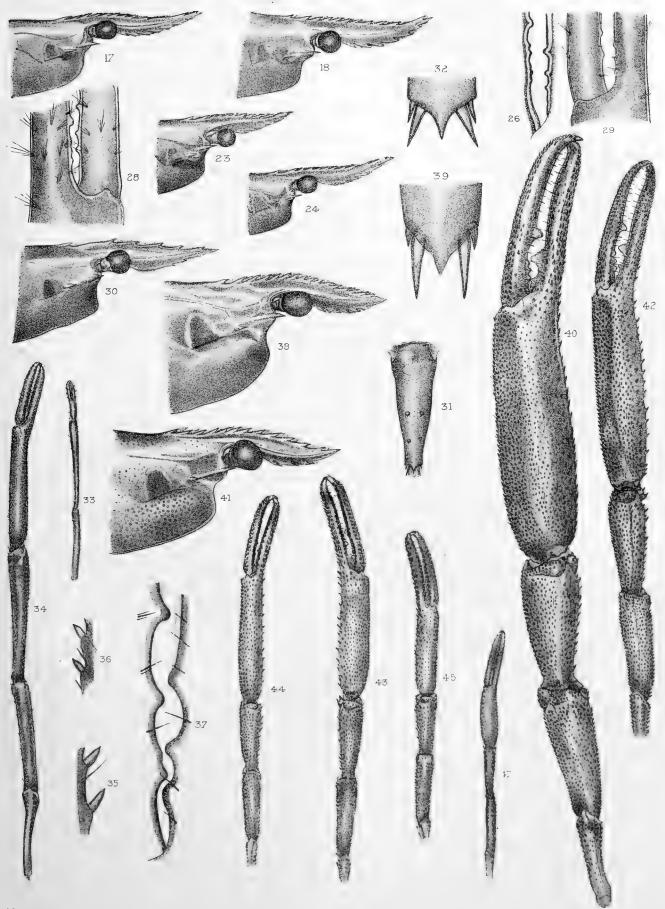
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SPECIES OF PALAEMON.

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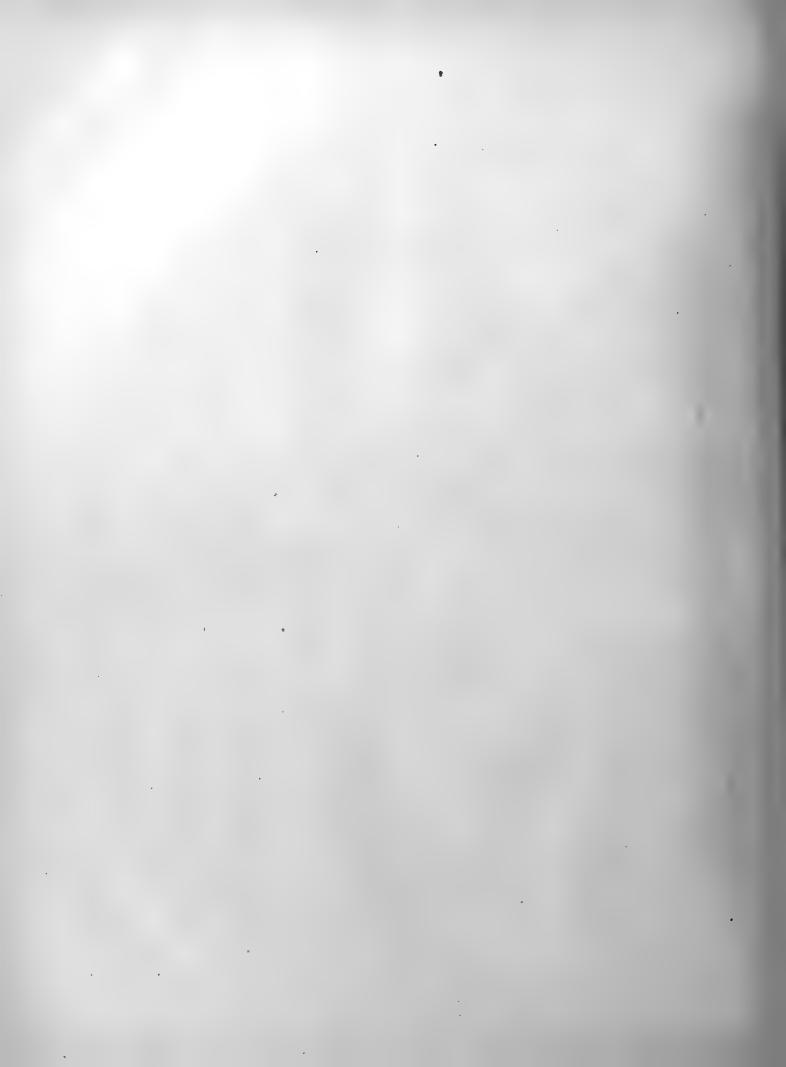


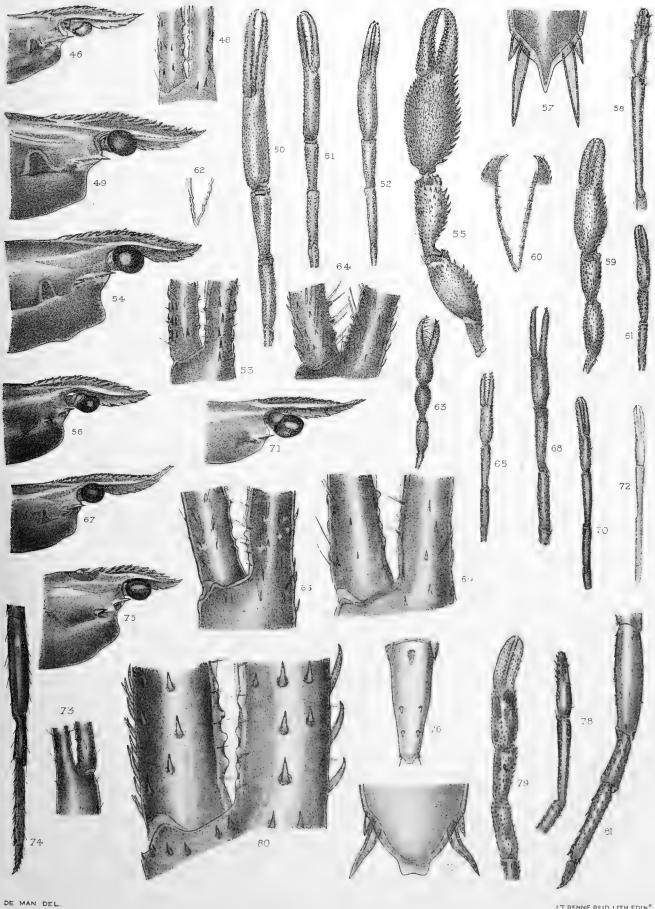
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SPECIES OF PALAEMON

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# IX. Observations on some undescribed or little-known Species of Hemiplera-Homoptera of the Family Membracidæ. By G. BOWDLER BUCKTON, F.R.S., F.L S.

### (Plates 21 & 22.)

Read 17th November, 1904.

THE efforts made during the last few years to systematize, in some natural manner, the Homopterous family of Membracidæ have met with varying success. The somewhat numerous species have hitherto engaged less attention from the entomologist than they deserve, though they constitute a remarkable group, in which diversity of form suggests problems and theories on the effects of environment, and mimicry also, which will exercise the patience of the experimentalist and the acumen of the biologist. The little interest shown may partly be ascribed to the comparatively small size of some species, which necessitates an appeal to the microscope so as to reveal their chief characteristics; yet many entomological collections contain undescribed examples of these Hemiptera which will repay the investigation into their distribution and life-history, &c.

An examination of a few examples not hitherto described—or, at least, not adequately so for identification—constitutes an excuse for offering some notes to the Linnean Society.

Another cause of the entomologist's indifference may be the fact that very few representatives of the family are known as denizens of Europe. Species are mostly exotic to England, and are at present most numerously represented on the continents of North and South America. The European species typified by Linnæus in *Centrotus cornutus* and the American in *Membracis foliacea* by Fabricius, are now expanded into several subfamilies and numerous genera.

The significance of their remarkable forms and their dependence on environment, also on their protective and aggressive mimicry, have been discussed by Prof. Poulton. To him and to the Rev. Canon Fowler, both Fellows of our Society, I am indebted for information as to the economics of the species and their persistence throughout the struggle for life.

Where the man of science can frame a tenable hypothesis he often produces more valuable fruit than the compiler of facts, however unanswerable these may be; but the work of the resolver of what appears to be a confusion into a consistent order has its value. On this footing I offer to the Linnean Society the present contribution. It is advanced as tentative, and must be so until our knowledge of the life-history of Membracidæ shall add to the bare facts now alone at our disposal.

The recently published memoirs by W. W. Fowler, in the 'Biologia Centrali-Americana' of Godman and Salvin \*, and my 'Monograph of the Membracidæ' †, may be consulted

\* Biol. Centr.-Amer., Rhynch.-Homop. (W. W. Fowler), vol. ii. (1894).

† Mon. Membracidæ (Buckton) (1903).

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as to related genera. In the last work an attempt has been made to classify the family as it is at present known.

The 'Biologia' above alluded to of course only deals with the American insects. Prof. Ign. Bolivar has obligingly forwarded to the writer specimens from the Musée d'Histoire Naturelle de Madrid, and the writer has also received examples of unnamed species from the Musée Belgique. These form the subjects of the present memoir.

### RHYNCHOTA-HOMOPTERA.

MEMBRACIS MICANS, sp. n. (Plate 21. fig. 1.)

Pronotum foliate and flattened laterally; metopidium rising perpendicularly above the eyes. Colour pale stramineous, shining like mica, with a pale brown fascia reaching from each shoulder to the thin upper edge, succeeded by two other interrupted fasciæ, the latter carried to the posterior end. Legs pale ochreous; fore legs slightly spatulate with brown claws. Tegmina hyaline with yellow neuration. Twelve specimens at my disposal were pretty constant in their colouring.

From the Belgian Museum. Collected by M. Van Voixem. Size  $9 \times 6$  millimetres.

MEMBRACIS VERGENS, sp. n. (Plate 21, fig. 2.)

Rather large. Colour a dull coal-black. Seen in profile, with a bright ochreous band which extends backwards from above the eyes on the metopidium to the dorsal edge; this forms a waving stripe on a black ground. Metopidium rather overhangs the head. Legs black and slightly spatulate.

Hab. Sta. Caterina.

Coll. Camilie, Van Voixem. Size  $12 \times 6$  millimetres.

HAMMA NODOSUM \* (genus et species nov.). (Plate 21. fig. 3.)

Pronotum turgid and prolonged into a knot-like sinuous process, furnished with numerous small spines. This serpentine appendage is continued free from the dorsum, and is nearly as long as the tegmina. These last are short, each furnished with a broad corrugated limbus and with a brown coarse neuration. Metopidium high and crested.

*H. nodosa* is of a concolorous shining coal-black. The tegmina are ochreous and diaphanous at the tips. Legs black, except the hind pair, which are rufous. The posterior process is contorted into segmental knots.

*Hab.* The Kameroons, W. Africa. Size  $4 \times 2$  millimetres. Allied to *Sphongophorus*.

MICROSCHEMA MUCRONATA, sp. n. (Plate 21. fig. 4.)

Larger. Pronotum rising perpendicularly from the frons into a pointed dorsal process, obtuse in the outline and continued as a straight line to the sharp posterior apex. Suprahumerals rather short and divergent. Colour bright red, with punctured dots.

\* "Aμμα, a knot.

The upper edge of pronotum broadly black at the summit, which shade is continued as a black line nearly to the apex of the tegmen. The tegmina ample and pointed at the tips, with a broad limbal edge and of a fine purple-brown colour, too dense to show the neuration. From pale sordid brown. Legs rather spatulate. Size  $15 \times 6$ millimetres.

Musée de Madrid.

### ACONOPHORA OBFUSCATA, sp. n. (Plate 21. fig. 5.)

Pronotum porrect, or projected forwards as a flat sharp horn, laminated at the edges. Colour dark fuscous and mottled. Pronotum carried to the posterior end, which terminates in a point nearly reaching to the tips of the tegmina. Legs rather long, with vellow tibiæ. Tegmina pale ochreous with a fuscous neuration.

This insect is somewhat like A. flavipes, but it is not so large and the given locality differs also.

Hab. Mexico. Size  $11 \times 4$  millimetres.

#### TRAGOPA TRIANGULATA. (Plate 21. fig. 6.)

General aspect scutiform. Pronotum, viewed from the dorsal aspect, Small. trapezoidal or four-sided. Tegmina short, much corrugated, and difficult to separate from the abdomen. Suprahumerals hardly visible, but by the frontal aspect rather auriculate, suggesting some affinity to Chelyoida \*. Eyes large and prominent. Legs short and robust. Colour sordid ochreous, with dark fuscous on the thorax and on the abdomen. Size  $4 \times 4$  millimetres.

Musée de Madrid.

### POPPEA SUCCINEA, sp. n. (Plate 21. fig. 7.)

Pale amber-yellow, rather transparent. Pronotum raised into bulbous tubercles, the posterior bulb of which forms two stout processes, somewhat similar to the suprahumeral horns. Eyes prominent. Tegmina hyaline, glistening, but corrugated, and with a broad limbus. The suprahumerals are divergent and united between the shoulders to a button. like scutellum, which joins the tuberculous dorsum.

This insect has a considerable resemblance to Poppea concinuat, but is larger and has more robust suprahumerals.

Hab. Mexico. Size  $9 \times 3$  millimetres. Musée de Madrid.

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ELECTROPHINA PACIFICATA (genus et species nov.). (Plate 21. fig. 8.)

Has some of the characters of a Ceresa, particularly in the neuration of the tegmina, which are remarkable for their length, viz. about twice that of the body, and also by the occurrence of conspicuous suprahumeral horns. These are barely visible in Ceresa.

\* Mon. Membracidæ, pl. 33. fig. 2, p. 156. † See Mon. Membracidæ, pl. 34. fig. 5.

*Electrophina pacificata* is a relatively large insect, almost concolorous yellow, with the pronotum slightly inflated and punctured. It is not laminated, or flat, as in *Ceresa*. A dull fuscous patch over the metopidium, a transverse stain on the pronotum, and a fuscous tint at the posterior horn, are the sole variegations of the yellow colour of the insect. The horn is free above the large abdomen. The tegmina show ovoid membranous cells which are bounded by pale fuscous nervures. Legs moderate in length and brown.

Hab. Coll. de Pacifico. Size  $13 \times 5$  millimetres. Musée de Madrid.

CERESA NITENS, sp. n. (Plate 21. fig. 9.)

Pronotum arcuate and flat, and ending in a sharp point. Abdomen large and ringed. Metopidium, when seen from the front, high and furnished with short suprahumerals. Legs short. Surface very shining, like corrugated talc; colour siennayellow or of an amber hue. Pronotum marked by a conspicuous brown or black transverse fascia. Tegmina slightly ferruginous, but with clear membranes. Legs ferruginous brown.

Hab. Chiriqui. Size  $9 \times 5$  millimetres. Musée de Madrid.

## ENTYLIA MŒSTA, sp. n. (Plate 21. fig. 11.)

Small. Metopidium, as seen from the front, rising into a pointed and punctured prominence, which appears broad and truncated by the profile view. Pronotum rises behind into a hump, which falls off to the posterior apex. Colour dingy ferruginous, with a pale carina on the procephalon and two other streaks down the hump. Tegmina short, with grey patches on the shoulders and corrugated grey on the tips. Legs stout.

*Hab.* Mexico. Size  $5 \times 3$  millimetres. Musée de Madrid.

# ENTYLIA FUSCODORSA, sp. n. (Plate 21. fig. 10.)

Larger than the last insect. The procephalon smaller and less truncated. Colour pale greenish yellow. Tegmina with deep punctures and brownish blotches between the venations, and with still larger blotches below the pronotal horn. The lower margin of the pronotum notched where it joins the metopidium. The dorsal hump is often, but not invariably, ferruginous brown. Tegmina olive-grey. Legs ferruginous. Size  $6 \times 4$  millimetres.

HYPSAUCHENIA JUGULATA, sp. n. (Plate 21. fig. 12.)

Dorsum with a yellow patch between the procephalic horn and the dorsal prominence. The long curved cephalic process has a yellow line on each side, which runs from the eye

to the summit. The fore legs obscurely spatulate, the other legs yellow. The general colour of the insect brownish black, more or less covered with a fine corrugated punctuation.

The species hitherto described are distributed over several islands of the Indian Ocean and the Philippines, but this is the first record of their occurrence in Sumatra.

Hab. Sumatra. Size  $8 \times 9$  millimetres.

Musée de Madrid.

OURANORTHUS PALUS \* (genus et species nov.). (Plate 22. fig. 1.)

Although this somewhat singular insect does not strictly conform to the diagnosis given by Fairmaire for his genus *Lamproptera*, I think provisionally it may be placed under that classification. The erect horn in the dorsum is single, not seen as "cornubus duobus," and is inserted at a right angle just above apex of the abdomen. Lanceolate in form, it is neither carinated nor glabrous. The metopidium rises above the eyes into a tumid hump, and then it proceeds nearly straight to the apex. Legs stout and slightly spatulate. Frons furnished with two short recurved suprahumerals. The colour fine yellow and the surface devoid of hairs. Tegmina yellow, with orange-coloured nervures.

Hab. Bangalore, India. Size  $8 \times 5$  millimetres. Musée de Madrid.

KLEIDOS PALMATUS, sp. n.

Tegmina sombre brown, but inclining to red at the tips. Posterior horn vomerate or like a plough-share, with fine servations on the lower edge. A slight tubercle occurs above the geniculate angle of the horn. In other respects it resembles *Kleidos vomeris* (figured in Mon. of the Membracidæ, pl. xlviii. fig. 2) and is the second example of that genus.

Hab. Zanzibar. Size  $9 \times 6$  millimetres. Kleidos vomeris occurs in Ceylon.

ANCHON STRIGATUM, sp. n. (Plate 22. fig. 3.)

Procephalon conical, with the summit divaricate or split into two leaves, which the insect appears to be able to close and open at will. The base of the cone has a white line which runs to the top of the same. Posterior horn ulnate and tapers to the end, without any dilation. There are no suprahumerals, or they may be represented only by obtuse points. Tegmina bright and of a shining yellow, but corrugated and stained with fuscous on the limbus, a spot on the costa, and a patch on the inferior edge. Tibiae yellow. Size  $9 \times 6$  millimetres.

This insect recalls Anchon albolinealum, but it is distinct. Hab. Cameroons, W. Africa.

\* oupa, tail; aropbiw, I erect.

ANCHON FUSCUM, sp. n. (Plate 22. fig. 2.)

Concolorous light brown, except at the tips of the tegmina, which are darker, and fuliginous near to the costa, and the legs obscurely ferruginous. The procephalon is without suprahumerals and the summit is divaricate, as in the last species. Posterior horn ulnate and sinuous. Size  $7 \times 5$  millimetres.

Hab. Cameroons, W. Africa.

TALOIPA TINCTORIA\* (genus et species nov.). (Plate 22. fig. 4.)

Small, robust. Concolorous black, except the tegmina. Suprahumerals short and square to the frons and to the metopidium. The posterior horn of the pronotum very short, and not equal to half the tegmen. Frons and face hirsute. Tegmina ochreous, but diaphanous, corrugated with a brown neuration. The base stained with a red suffused fascia, giving the wings a mottled tint.

Hab. Manila, Philippines; Bangalore. Size  $7 \times 4$  millimetres.

This insect has mixed characters of Centrotus and Otinotus, &c.

LEUCOTHORAX VILLOSA (genus et species nov.). (Plate 22. fig. 5.)

Large, robust. Posterior horn simple, but rather curved and shorter than the tegmina. Suprahumerals acute by the profile view, but truncated by the dorsal aspect. Colour dark shining brown, furnished with a broad white villous space on the thorax and at the wing-insertion. Two white spots on the dorsum. Legs strong, black, with yellow at the tips of the tibiæ and the tarsi. Membranes of the tegmina corrugated and shining, but the neuration is obscure.

This is a striking species, partly from its diverging horns and tomentose coating. Hab. Cameroons. Size  $12 \times 6$  millimetres. Musée de Madrid.

LEPTOCENTRUS IMPUNCTUS, sp. n. (Plate 22. fig. 6.)

Suprahumerals stout and recurved. Procephalic horn rather short, cylindrical, and distant from the abdomen. General colour dark brown, shining, with a tendency to show a white pilose spot on the pronotum. Tegmina long, with warm ferruginous and brown corrugations and nervures.

In the Madrid Museum there are several specimens of this species, which show slightly different sizes and also colouring, but they may be considered as identical.

Hab. Padautsin (?). Size  $10 \times 5$  millimetres.

IBICEPS RUFIPENNIS, sp. n. (Plate 22. fig. 8.)

Colour dark brown, nearly black. Metopidium rather high, with erect suprahumerals and a free cylindrical posterior horn which is longer than the abdomen. The tegmina brown, with a broad rufous or yellow spot occupying the apical area. This spot is more

\* τὰ λοιπὰ, the residue.

obvious in some examples than in others. There is also a greyish sheen spread over the basal portions of the wings.

Hab. Cameroons. Size  $8 \times 4$  millimetres.

OPHICENTRUS SERPENTARIUS, sp. n. (Plate 22. fig. 7.)

This species is characterized in great part by the sinuous form of the posterior process or horn. Although the examples given by Canon Fowler in the Biol. Centr.-Amer. are all American, this species from Africa and from Tasmania has its significance.

Colour dark brown, showing a slight grey public public method. Posterior horn stout, much gnarled and bent into a tapering curve shorter than the tegmina, which last are warm reddish fuscous with dark neuration and a corrugated limbus. Legs stout. Abdomen and the rest of the body dark brown.

Hab. Cameroons. Size  $8 \times 4$  millimetres.

Musée de Madrid.

There are other smaller specimens in the same Museum which have broad fuscous bands on the tegmina, and these as varieties may be designated *Ophicentrus minor* var., from the Cameroons.

POLOCENTRUS LABATUS, sp. n. (Plate 22. fig. 10.)

This genus is characterized by the clavate apex of the posterior horn, which is serrated below the clubbed extremity. The suprahumerals are short and obtuse by the profile aspect. Colour ochreous-orange, mottled with fuscous. Frons square and brown. Legs stout, flat, with yellow tibiæ. Tegmina with yellow cellules and with broad brown nervures.

The usual habitat of the genus appears to be Southern India, but this species is from Abyssinia.

Musée de Madrid. Size 8×4 millimetres.

POLOCENTRUS CAUDATUS, sp. n. (Plate 22. fig. 9.)

Suprahumerals shorter and more erect than in *P. lobatus*, and the tegmina not brocaded with brown but diaphanous. Colour uniformly bright ochreous yellow. Legs flattened and almost spatulate. The clavate apex of the posterior horn is large and serrated on the lower margin.

*Hab.* Natal. Size  $8 \times 5$  millimetres.

TRAPEZOIDA HIRSUTA (genus et species nov.). (Plate 22. fig. 11.)

The pronotum quite covers the scutellum and is domed in outline when seen from the side, but it has a somewhat four-sided outline from the dorsal aspect. The tegmina ample, broad, and longer than the posterior horn. Metopidium square, with short suprahumerals.

Frons covered with hairs. Eyes prominent. Legs with black femora and yellowfringed tibiæ. Colour uniformly dark fuscous, but with a yellow carina on each of the suprahumerals and two wide yellow fasciæ across the dorsum, leaving the apex black. The tegmina are dense and do not readily show the neuration.

Hab. Central America. Size  $7 \times 4$  millimetres.

Musée de Madrid.

Perhaps this insect might be included in the original genus *Centrotus*; yet it differs from Linnæus's typical *Centrotus cornutus*, which has been retained for reasons set forth in my 'Monograph of the Membracidæ,' p. 245.

There is no waste in the products of animal life, and it is a fact familiar to all observers that the effete excretion of one animal is often the food for another lower in the biological scale. The sweet secretions from many Homoptera are much sought for by ants and by the members of some insect families separate from them both in habit and classification. Thus we have Aphidæ, Cercopidæ, Fulgoridæ, and Membracidæ all laid under contribution for the pleasure or nourishment of different orders of insects. Whilst in the Aphidæ we find at least two discharging orifices or necturies for such excreta, Mr. E. Green has shown that in *Centrotus nectaris* of Ceylon the larvæ have but one duct, which is capable of extension like the tube of some telescopes.

The larvæ of another species are common at the Cape of Good Hope, probably belonging to the genus *Oxyrhachis*, which carry their single nectary erect from the apex of the abdomen. They also are visited by ants. Although the winged insect has not yet been ascertained, a figure of this curious larva or pupa may be added to the singular forms which represent the pupal and immature stages of the Membracidæ.

It may be remarked that these pupæ are incapable of flight, yet they have the rudiments of the tegmina much developed, and that they are very active in their movements. They possess eyes and antennæ.

Future observation will show, indeed, whether they are pupe or only arrested imagoes.

## Pupa. (Plate 22. fig. 12.)

Robust. Colour wholly black, except the eyes, which are large, prominent, and sordid ochreous. Metopidium continued into a single sharp and erect horn which slopes nearly straightly to the apex of the abdomen, where it rises into an erect coriaceous and conical nectary, wide at its base and tapering to its summit. This is perforated and forms the nectary or duct for ejaculation, just as in *Aphis*.

The wing-cases or rudimentary tegmina are short, pointed, and black, with traces of an obscure neuration. Legs very stout, rather flat, with coarse tarsi. Size  $5 \times 3$  millimetres.

These pupze are probably the immature forms of an Oxyrhachis which develops simultaneously in the month of January, at Wynberg, a suburb of Cape Town, Africa.

The fact that these pupe have only a single horn above the metopidium, instead of the double horn of *Oxyrhachis*, need present no difficulty when we consider the extraordinary shapes often assumed by certain insect organs which are not really homologues, though they may appear to be such. The legs of a larva need not be necessarily those of the corresponding imago which emerges from it.

### EXPLANATION OF THE PLATES.

#### PLATE 21.

- Fig. 1. Membracis micans. The imago has a glistening and talc-like surface. Size  $9 \times 6$  millimetres.
- Fig. 2. Membracis vergens. A large species remarkable for its dark hue and its broad ochreous streak. Size  $12 \times 6$  millimetres.
- Fig. 3. Hamma nodosa. Small, pronotum rugose and contorted into knots.
  - 3 a. The frons and metopidium. The sides are furnished with small spines. Size  $4 \times 2$ millimetres.
- Fig. 4. Microschema mucronata. Large, remarkable for its bright colour, and sharp apex to the dorsal edge of the pronotum.
  - 4 a. Frontal view of the frons and stemmata. Size  $12 \times 15$  millimetres.
- Fig. 5. Aconophora obfuscata. The imago shows a broad foliated summit of the porrect procephalon. 5 a. Front aspect of the procephalon as seen on edge. Size  $11 \times 4$  millimetres.
- Fig. 6. Tragopa triangulata. Small and robust in figure. The pronotum does not reach beyond one-half of the tegmina.
  - 6 a. Dorsal view. The pronotum forms an irregular triangle. The head is below the metopidium, which last has two lateral ear-like processes. Size  $4 \times 4$  millimetres.
- Fig. 7. Poppea succinea. This semitransparent insect has the pronotum more or less inflated into coriaceous bubbles which have acute points. Tegmina hyaline and blistered on the surface. 7 a. The dorsal aspect of the insect. Size  $9 \times 3$  millimetres.
- Fig. 8. Electrophina pacificata. The long wings and the extended suprahumeral horns are distinctive. 8 a. Frons and metopidium with horns. Size  $13 \times 5$  millimetres.
- Fig. 9. Ceresa nitens. Very glistening, amber-coloured, robust.
  - 9 a. Front view of same insect, with its high metopidium and short suprahumerals. Size  $9 \times 5$ millimetres.
- Fig. 10. Entylia fuscodorsa. Imago with truncated summit of the pronotum, punctured with fine dots within the sculptured carinæ. Size  $6 \times 4$  millimetres.
- Fig. 11. Entylia mæsta. Imago small, with greyish pubescence.
  - 11 a. Front aspect of the same showing the thin edge of the procephalon. Size  $5 \times 3$  millimetres.
- Fig. 12. Hypsauchemia jugulata. This specimen from Sumatra has lost the summit of its procephalon which, probably like the Indian species, was curved over the back. Size  $8 \times 9$  millimetres.

#### PLATE 22.

- Fig. 1. Ouranorthus palus. The winged insect is remarkable for the erect process proceeding from the caudal apex of the pronotum. Though allied, it certainly is not Lamproptera capreolus of Fairmaire.
  - $1 \alpha$ . The head, pronotum, and recurved suprahumeral horns of the same insect. Size  $8 \times 5$  millimetres.
- Fig. 2. Anchon fuscum. Allied to A. albolineatum, but it wants the white streak on the pronotum.
  - 2a. The front aspect clearly shows that the procephalon is cleft into broad plates or foliations. The insect is bright amber-coloured. Size  $7 \times 5$  millimetres.

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- Fig. 3. Anchon strigatum. The dorsal process is here free and ulnate. The procephalic point probably is cleft like that of the last-named species. Size  $9 \times 6$  millimetres.
- Fig. 4. *Taloipa tinctoria*. The pronotum here is obtuse, and it ends posteriorly in a blunt process shorter than the abdomen. The bright orange colour on the base of the tegmina may be noticed.
  - 4a. The hirsute frons with the square metopidium. Size  $7 \times 4$  millimetres.
- Fig. 5. Leucothorax villosa. Large, with truncated but short dorsal processes. The chest has a white villous coat.
  - 5 a. The dorsal view of the pronotum.
  - 5 b. The frontal aspect of the insect. Size  $12 \times 6$  millimetres.
- Fig. 6. Leptocentrus impunctus. Remarkable for its long tegmina. 6 a. The head and frons.
  - 6 b. The venation of the tegmen of the same. Size  $10 \times 5$  millimetres.
- Fig. 7. Ophicentrus serpentarius. The undulating form of the dorsal process has been used generically by Canon Fowler, and I do so tentatively, whilst the immediate cause of variation in secondary organs is sub judice.
  - 7 a. Frontal view of the insect. Size  $8 \times 4$  millimetres.
- Fig. 8. Ibiceps rufipennis. The Imago. Bright shining, warm brown. The grey on the tegmina as shown by this figure is only meant to represent the light glancing on the corrugations of the wing, and it is not due to any patches of grey colour. Its long pronotal horn is smooth, instead of rough as represented on the Plate.
  - 8 a. The head and front view of the pronotum. Size  $8 \times 4$  millimetres.
- Fig. 9. Polocentrus caudatus. The winged insect is somewhat remarkable from its short posterior horn, which, like the rest of this genus, is serrated below. Legs spatulate.
  - 9 a. Front view with the short suprahumerals. Size  $8 \times 5$  millimetres.
- Fig. 10. Polocentrus labatus. This insect is from Abyssinia, and has the characteristic serrated posterior horn.
  - 10 a. The front view with the dark frons and pointed suprahumerals.
  - 10 b. The tegmen with its dark fuscous venation which encloses the chief ochreous cellules. Size  $8 \times 4$  millimetres.
- Fig. 11. Trapezoida hirsuta. This insect from Central America has a square metopidium which is strongly hirsute. The dorsal view of the pronotum shows something of a lozenge shape.
  - 11 a. Head and frons of the same.
  - 11 b. Dorsal view of the insect. Size  $7 \times 4$  millimetres.
- Fig. 12. Larva of a Membracid, not uncommon in the neighbourhood of Cape Town, and at Wynberg, S. Africa, but the winged insect has not yet been determined. The erect caudal nectary discharges a liquid, probably of a saccharine nature, and gives the insect a grotesque appearance. Probably it is visited by Ants, as is known to be the case with the larva of *Centrotus* nectaris of Ceylon. Size 5 × 3 millimetres.

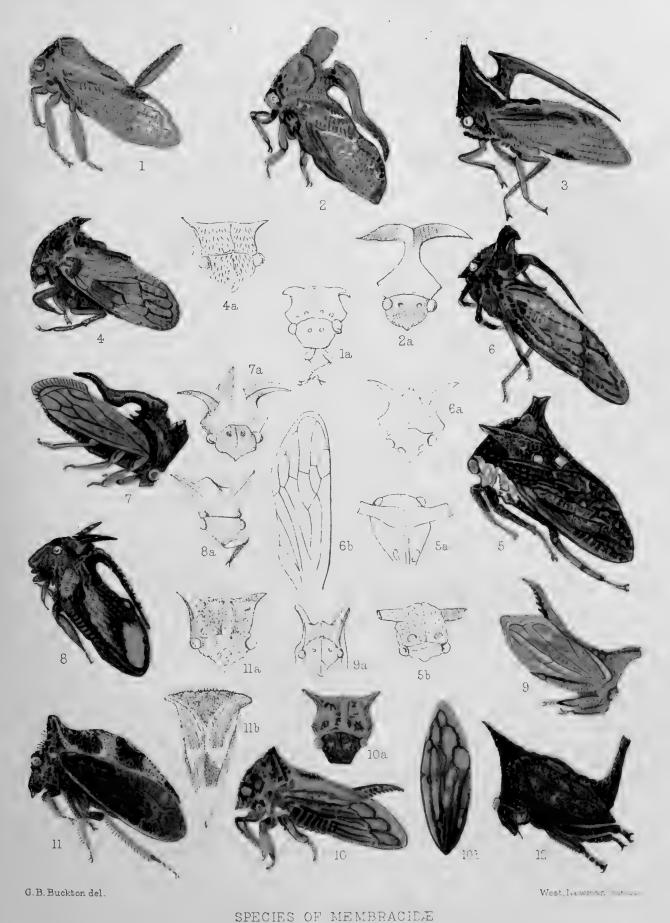


G.B.Buckton del

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SPECIES OF MEMBRACIDÆ







X. The Genitalia of both the Sexes in Diptera, and their Relation to the Armature of the Mouth. By WALTER WESCHÉ, F.R.M.S. (Communicated by JOHN HOPKINSON, Esq., F.L.S.)

#### (Plates 23-30.)

#### Read 21st June, 1906.

WHEN, five years ago, I made some dissections of the genitalia of the males in *Scatophaga lutaria*, Fabr. \*, and *S. stercoraria*, Linn., I was much hampered by the absence of any systematic nomenclature. Huxley, in his 'Anatomy of Invertebrated Animals,' passed by the genitalia of the male cockroach with a mere allusion to the complexity of the parts †.

L. Dufour ‡ in his, at all events, comprehensive review of the genitalia in Diptera, never attempts to grapple with the separate parts, contenting himself by saying: "L'armature copulatrice, receptacle de la verge, est une machine des plus compliqués, destinée à se porter hors un corps lors de l'union des sexes. Les nombreuses pièces plus ou moins symétriques, cornées ou coriacées qui la composent, combinent leur action, soit entre elles, soit avec les organes externes de la femelle pour consommer l'acte de la fécondation."

Packard is no help, either in his larger works, or in his small paper on the homologies of the ovipositor and the homologous parts in the male insect §.

Kirby and Spence classify the ovipositors, giving them some very unwieldy names, but make no analysis of the parts of the male  $\parallel$ ; an omission to be regretted, as they are, at the least, of equal interest, and in their way of equal symmetry and beauty, with the armature of the mouth-parts, though more difficult to dissect out.

But in a paper on the genus *Phronia* of the Mycetophilidæ by A. Dziedzicki ¶ I found a scheme of nomenclature for the external values of the genitalia of both sexes, but not for the complicated parts that are attached to the penis of the male, that combination being called the "appendix interna" or "adminiculum." The only careful and complete study of this part exists in Dr. B. Thompson Lowne's monograph on the Blow-fly \*\*; he has named all the parts as they exist in this insect, and given admirable figures of the male armature, drawn on a large scale, so as to be easy of comprehension. So with the material drawn from Dziedzicki, from Lowne, and a small contribution from Miall and Denny's 'Cockroach,' and my own resources, I am able to formulate a

\* Journal of Quekett Micr. Club, April 1903. + p. 350 (1877 edition).

‡ "Recherches anatomiques et physiologiques sur les Diptères," 1851, Mém. Prés. Ac. Sci. Paris, tome xi. p. 198.

§ Proc. Boston Soc. Nat. Hist., xi. 1868.

- || Description of plates 15 & 16, 1828 edition.
- ¶ Hor. Soc. Entom. Ross., tome xxiii. 1889.
- \*\* 'The Anatomy, Physiology, Morphology, and Development of the Blow-fly,' 1895.

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complete nomenclature for the genitalia of Diptera. Lately, F. du Rosille \* has demonstrated the value of a study of these organs, by distinguishing a number of species in the difficult *Sarcophaga* genus that have previously passed as *S. carnaria* (Linn.), by a comparison of the male armature.

There are two papers on the male genitalia of Lepidoptera by F. Buchanan White, M.D. †, and P. H. Gosse ‡; but these works are mainly engaged with the characters of the outer and visible parts, with the view of determining species. There is no attempt to dissect out the interior or to classify the armature; but, nevertheless, the papers have value, as they show, particularly in the beautiful drawings of Gosse, the endless variety of shape and contrivance that may characterize any portion of the male armature.

The male genitalia in Diptera always consist of a central tube, surrounded by more or less complicated appendages. All these parts are extremely variable in shape and in their relations to each other, but it will be seen that they homologize, though they undergo very remarkable transformations. For convenience they may be divided into four divisions :—(1) the posterior external valves; (2) the anterior external valves; (3) the penis and its appendages; (4) the interior organs.

(1) Posterior external values.—The posterior external values consist of the (a) Forcipes inferiores and the (b) Forcipes superiores.

(2) Anterior external values.—The anterior external values are the (c) Laminæ superiores.

(3) Penis and appendages.—In the third section are a number of organs beginning with (d) the part of the penis, usually a hyaline membrane, which is the orifice and continuation of the ejaculatory duct; (e) the theca or sheath, which has ramifications called by Lowne (f) the Paraphallus and (g) the Hypophallus; (h) the Spinus titillatorius, (i) the Forcipes interiores, (k) the Palpi genitalium, and (m) the Apodemes of the penis, often called, for the sake of distinction, the double apodeme.

(4) Interior organs.—The interior organs consist of (n) the Ductus ejaculatorius, (o) the Sacculus ejaculatorius, (p) the Ejaculatory apodeme, (r) the Vas deferens, (s) the Paragonia, (t) the Vasa efferentia, and (u) the Testes.

### (a) FORCIPES INFERIORES.

Structure.—These are a pair of more or less complicated hooks. They are on the dorsal side of the abdomen in the Muscidæ, but are laterally placed on the sides of paired processes, the forcipes superiores, which are even more dorsal still, being on the sides of the median line. Occasionally they have another hook articulated on to them and are sometimes hairy, but generally they are structurally strongly chitinized, with setæ and spines disposed in contact-areas.

Nomenclature.—They correspond with the valvulæ externæ of Lowne; they are also known as zygapophyses or claspers.

<sup>\*</sup> Mém. Soc. Linnéenne du Nord de la France, Amiens, 1905.

<sup>† &</sup>quot;On the Male Genital Armature in the European Rhopalocera," Trans. Linn. Soc., ser. II. Zool. vol. i. (1876).

<sup>‡ &</sup>quot;On the Clasping-Organs ancillary to Generation in certain Groups of the Lepidoptera," Trans. Linn. Soc., scr. II. Zool. vol. ii. (1882).

Cecidomyiidæ and Mycetophilidæ.—They are clearly present in the Cecidomyiidæ and the Mycetophilidæ. In the genus Sciara they are quite valvular in appearance, and are on the ventral side of the abdomen in their true inferior position (Pl. 23. fig. 1).

Bibio.—They are simple in Bibio and Scatopse (Pl. 23. figs. 5, 7).

Tipulidæ.—In the Tipulidæ they are remarkably developed. In *Tipula oleracea*, Linn., the part consists of two hooks and a plate, forming an extraordinarily complicated process (Pl. 24. fig. 25); the plate has a sense-organ, consisting of a number of socket-like depressions and enclosed in a chitinous ring. In each socket is a membranous bulb (Pl. 24. figs. 27, 28).

*Rhyphus.*—The part is complicated and strongly chitinized in *R. fenestralis*, Scop., hairy and smaller than the f. superiores in *R. punctatus*, Fabr.

Stratiomyiidæ.—In the Stratiomyiidæ, where the genitalia of the two sexes are exteriorly much alike, these parts are simple and quite on the ventral side; this is markedly so in *Chloromyia formosa*, Scop., and *Michrochrysa polita* (Linn.).

Tabanus.—In Tabanus bromius, Linn., two pairs of organs are found, and those on the ventral side I homologize with this part; they are normally bent at a right angle to the median line, an unusual position (Pl. 29. fig. 109).

Asilidæ.—In the Asilidæ they are smaller than the dorsal processes. In an undetermined Australian Asilid the part has a hook articulated to it (Pl. 24. fig. 36).

*Empide.*—In the Empidæ these parts are absent in E. stercorea, Linn., but are represented as relatively small in most of the genera.

Doliochopodidæ.—In the Dolichopodidæ, where the "so-called fan" is well-developed, this part appears to consist of two hyaline plates under the hypopygium (Pl. 25. fig. 43).

Syrphidæ.—They vary much in form in the Syrphidæ, but are not complicated; they are usually simpler and much less developed than those in Syritta pipiens (Linn.) (Pl. 25. fig. 54).

*Muscidæ*.—In the whole of the Muscidæ they are prominent on the dorsal side, and form useful specific characters; in *Glossina* at least four species can be differentiated from these organs alone (Pl. 26. figs. 61, 65; Pl. 27. figs. 76, 77, 79, 80).

*Muscidæ Acalyptratæ.*—They are also present in those families where, the female having developed a telescopic horny ovipositor, the penis has been modified into a long ribbon-like structure (Pl. 28. fig. 96).

Homology with the ovipositor.—In the majority of flies these organs are on the eighth segment of the abdomen, and correspond with the ventral egg-guides or values of the ovipositor, also on the eighth segment of the abdomen. This is very clear in *Chloromyia* formosa (Scop.). From their position, as Lowne points out \*, they "correspond with the inferior blades of the ovipositor in *Locusta*," or with the ventral values in *Tipula* oleracea †.

<sup>\*</sup> Note.—In my two earlier papers on Scatophaga and Glossina I have called these parts the Forcipes superiores, transposing the adjectives. As my studies had been confined to the Muscidæ, where these hooks are always more prominent, important, and articulated on the dorsal side of the hypopygium, this seemed the more reasonable nomenclature. Study of the other families and of the ovipositor has enabled me definitely to settle the homology of the part with that formulated by Dziedzicki.

<sup>+ &#</sup>x27;Blow-fly,' p. 732.

#### (b) Forcipes superiores or Valvulæ internæ.

*Structure.*—These so-called hooks are mostly (exceptions will be found in some Culicidæ and Tipulidæ) valves, which are generally covered with hair, or bulbous and palp-like in appearance, suggesting a sensory function.

Nomenclature.—Lowne is responsible for calling them valves, Dziedzicki for the first name.

Mycetophilidæ.-In Phronia and Sciara they are hairy bulbs (Pl. 23. fig. 1).

Bibionidæ.—In Scatopse notata (Linn.) they are large plates, quite overshadowing the usually more prominent forcipes inferiores (Pl. 23. fig. 7).

Culicidæ.—In the Culicidæ they are very elaborate; in Culex pipiens they are large and are fitted with modifications of setæ, several knife-like and one leaf-like, and have besides single large hooks articulated on to their extremities (Pl. 23. fig. 16). Anopheles cinereus has also a hook articulated to the forceps, but is in other respects simpler (Pl. 23. fig. 14).

Tipulidæ.—In the Tipulidæ they consist of large hairy plates as in Tipula oleracea (Pl. 24. fig. 22), of plates with an articulated hook as in Gynoplista bella, Westwood (Pl. 23. fig. 19), or a more foliaceous form as in Ptychoptera scutellaris, Meigen (Pl. 23. fig. 17).

Strationyida.—In the Strationyidae they are hairy and thinner in proportion to their length than in Sciara.

Tabanidæ.—They are represented by two hairy bulbs in Tabanus bromius, Linn. (Pl. 29. fig. 109).

Asilidæ.-They are relatively very large in the Asilidæ (Pl. 24. fig. 37).

*Empidæ*.—A very marked form is seen in *Empis stercorea*, Linn. As a rule it is much less developed in this family (Pl. 25. fig. 40).

Dolichopodida.—Of all the families in Diptera they are in most extraordinary development in the Dolichopodida. They form the fans that have earned this tribe the popular name of the "fan-tailed flies." They are in their greatest relative size in the genera *Dolichopus* and *Pacilobothrus* (Pl. 25. fig. 43).

Syrphidæ.—They are variable, but never very prominent, in the Syrphidæ. In *Eristalis tenax* (Linn.) they are represented by two small hairy processes between the larger forcipes inferiores, which in this case are much like the f. superiores in shape and structure; they are more developed in *Syrphus pipiens*, but still smaller than the f. inferiores (Pl. 25. fig. 55).

Muscidac.—They are hairy values in the Muscidac, which have the anus at their base and close over and protect the penis. Sometimes they are fused as in *Rutilia splendida* and *Olivieria lateralis*, Fabr. (Pl. 30. fig. 120), or absent as in *Glossina*\*, where they are represented by two rows of hair on either side of the median line.

Cordyluridæ.—In Norellia spinimana, Fallén, there is rather a characteristic armature (Pl. 28. fig. 91).

Use and Homology.—This part seems to act either as a protection to the genitalia or

\* "Genitalia of G. palpalis," W. Wesché in Journ. Quekett Micr. Club, no. 57 (Nov. 1905).

as a sensory organ. It homologizes with the superior values of the ovipositor in *Tipula* or with the paired values in *Musca*, possibly with Huxley's "podical plate" in *Periplaneta orientalis*, Linn.

# (c) LAMINÆ SUPERIORES.

Structure.—This part consists of paired processes, often of a separate plate on the anterior edge of the cavity containing the genitalia. Structurally it is strongly chitinized and often with hooked bristles, sometimes with bunches of hair; so far as my observations have gone, the plate is always without spiracles.

Nomenclature.—It is so called by Dziedzicki, who also names the segment on which the part rests the "Lamina basalis."

*Mycetophilidæ*.—It is well-marked in the genus *Phronia*, but seems absent in other genera of the Mycetophilidæ, nor can it be differentiated in the Culicidæ.

*Tipulidæ.*—It is obvious in *Tipula oleracea*, where the ventral edge of the abdomen opposite the forcipes is studded with a number of tubercles; but it does not seem developed in the Stratiomyiidæ, Tabanidæ, Asilidæ, Bombylidæ, Empidæ, Dolichopodidæ, or the Syrphidæ (Pl. 24. fig. 24).

Muscidæ.—In most of the Muscidæ it is very evident and varies with species. In Echinomyia fera (Linn.) and Phyto melanocephala, Meig., small plates with anterior clefts are found. In Sarcophaga it is very marked, often having long hairy lateral processes on the anterior edge, though in the nearly related Sarcophila latifrons, Fall., it is hardly perceptible. In Musca domestica, Linu., two marked lateral processes project, but in Stomoxys calcitrans (Linn.) and Pollenia rudis, Fabr., only cleft hairy plates represent the part. It can be differentiated, but is not prominent, in Calliphora erythrocephala, Meig.

In *Glossina*, where the whole of the last segment is turned in under the abdomen, the forcipes inferiores rest against an arched horny band which represents this part; but in *G. morsitans*, Westw., where the whole ventral surface consists of a coriaceous membrane without any chitinous plates, there is in the usual situation of this part a lunule of chitin with strong short bristles thickly spread over it; this is absent in *G. palpalis*, Des.

It has soft-haired, bulbous tubercles, small in size, in *Morellia hortorum*, Fall., and *Hyetodesia obscurata*, Meig. In *Hydrotæa*, where the legs have many contrivances for holding the female, it is but little developed. The most striking elaboration of the part that I am acquainted with is on the abdomen of a small undetermined fly of the genus *Anthomyia* that was common inside the houses in Maryborough, Queensland; on this insect are two pectinated arms, articulated on to the segment opposite the genitalia (Pl. 26. fig. 66).

Sepsidæ.—In an undetermined species of Nemopoda from Jersey this part is much developed; on it are two pairs of hairy prominences, a pair of membranous tubercles, somewhat like palpi in structure, and a pair of barbs (Pl. 29, fig. 103).

Cordyluridæ.—In Scatophaga litorea, Fall., and Norellia spinimana are characteristic developments of this part (Pl. 27. fig. 87; Pl. 28. fig. 97).

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Use.—From the situation of the part, the number of spines and hooks usually found on the organ, it is obviously used in holding the female.

Homologies with oripositor.—It appears to homologize with the ventral portion of the fourth segment of the abdomen of the female, counting the last segment of the ovipositor, that bearing the values or egg-guides, as the first. Properly speaking, the first segment of the abdomen is that next the thorax, but, as the number of the segments is variable, the only way of comparing the genitalia of the sexes with exactness is to count that bearing the values as the first segment.

## (d) The Extremity of the Penis.

Structure.—This part has to be differentiated from the theca or cover, therefore for the present purpose I shall regard it as the orifice of the ejaculatory duct. It is mostly a delicate flexible hyaline membrane with characteristic triangular, more or less chitinous plates often forming part of the structure, or it may be a free, transparent chitinous tube as in the Tipulidæ.

Mycetophilidæ.—In Sciara thomæ (Linn.) it is difficult to make out, but appears to be a structureless hyaline stile (Pl. 23. fig. 1).

Bibionidæ.—In Bibio hortulanus (Linn.) and B. marci (Linn.) it appears as a plate, with the edges bent over, which do not meet but are covered by a delicate membrane. It has the appearance of the organ as seen in some Coleoptera (*Dermestes*). In Scatopse notata it is membranous, and with the character of the whole organ approximating to that in the Muscidæ in the external, and to that of the Tipulidæ in the internal organs (Pl. 23. fig. 7).

Culicidæ and Tipulidæ.—I have failed in trying to dissect out this part in the Culicidæ as well as in the Tipulid Gynoplistia bella, but a comparison of these parts with those of Tipula oleracea and Pachyrrhina maculata, Meig., easily supplies the lacunæ. In these insects a long tube or flagellum proceeds, bending in a circle in the process, from the ejaculatory sac, of which it forms a part and continuation, to an organ which is evidently the theca, passing longitudinally through a passage in it, and working quite freely in the passage; it is capable of extrusion and retraction. It is contained in a membranous envelope, noticed by Dufour, which has been thought to be the containing membrane of the spermatozoa, but, as I shall show later, this does not agree with my explanation of the working of the apparatus (Pl. 23. fig. 15; Pl. 24. figs. 23, 24, 29).

*Rhyphida*.—In *Rhyphus fenestralis* this part in the interior presents the appearance of a long tangled thread, and it is similar in *R. punctatus*.

Stratiomyiidæ.—In Beris vallata (Forster) it is a hyaline tube, less stiliform in shape; springing from the same base, it has on either side two knife-like blades with serrated edges at the extremities (Pl. 24. figs. 32, 33).

Tabanidæ.—In Tabanus bromius two slender stiles seem capable of extrusion through the theca; they are enveloped in a delicate membrane, much covered with fine blunt setæ (Pl. 29. fig. 109).

Asilidæ.-In the Asilidæ an arrangement is found which is somewhat similar to that

of *Beris*, but the stile, obvious in that genus, is quite absorbed by the chitinous theca (Pl. 24. fig. 38).

*Empida*.—Nearly the same form is found in the Empide, though here the tube is again quite stillform. *Empis stercorea*, Linn., is the simplest combination that I am acquainted with; the part is readily seen on the pinned insect as a long stile. On a prepared specimen the junction with the theca is seen even with the lower powers of the microscope (Pl. 25. fig. 39). The part is practically the same in *Hilara cilipes*, Meig., but with more elaborate surroundings (Pl. 25. fig. 41). In the ovipositor of the female is a curious notched process which may possibly act as a guide to the delicate flagellum (Pl. 25. fig. 42).

Dolichopodidæ.—In spite of the greater development of the holding organs, the structure of the penis in the Dolichopodidæ shows a close relationship to the Stratiomyiidæ, the Asilidæ, and the Empidæ. The hyaline stiliform tube has developed processes, presumably of use in coitus, servations as in *Dolichopus griseipennis*, Stannius, and a leaf-shaped excrescence in *D. nobilitatus* (Linn.) (Pl. 25. figs. 43, 44, 49, 50).

Syrphidæ.—In the Syrphidæ the part is often a flexible membrane, as in Catabomba pyrastri, Linn. (Pl. 25. fig. 53). In Eristalis tenax (Linn.) and Syritta pipiens (Linn.) the ejaculatory duct opens into a horny box situated at or near the extremity of the theca (Pl. 26. figs. 56, 57, 64). In Sphærophoria scripta (Linn.) it consists of a membrane studded with the usual triangular plates; this is capable of inflation, and when in that condition takes a tricuspid shape.

Muscidæ.—In Sarcophaga carnaria (Linn.) and the majority of the Muscidæ, calyptrate and acalyptrate, it is a hyaline flexible membrane. In *Glossina tachinoides*, Westw., this part has membranous wings, studded with minute plates as in *S. scripta*, and capable of inflation or erection, as I have demonstrated by alternately raising and lowering the cover-glass.

Acalyptratæ.—In the Ortalidæ, Trypetidæ, and Lonchæidæ it is a long membranous tube, normally rolled on itself as a watch-spring is coiled, and when extruded not unlike an ovipositor in appearance (Pl. 28. fig. 96).

Ephydridæ.—A very peculiar shape is found in Notiphila nigricornis, Stenhammar, where a membrane, studded with aculeations of various size, rises from a chitinous theca (Pl. 28. fig. 98). The part in Parydra coarctata, Fall., is much like that in Bibio hortulanus. This small fly has several peculiarities about the structure of the mouth-parts that suggest that it is of very archaic type (Pl. 29. figs. 110, 111).

Homology with ovipositor.—This part appears to be homologous with the membranous structure of the ovipositor. This hypothesis is strengthened by the fact that in the Ortalidæ the penis has no chitinous parts except at the extremity.

## (e) THE THECA OF PENIS-SHEATH.

Structure.—This is the chitinous case that protects the ejaculatory duct; it is always highly chitinized, often with an anterior suture. It may be quite simple or consist of a number of plates. When appendages are present it invariably supports them, whether articulated or not. No socketed hairs or bristles have been noticed, unless they represent an aborted organ, as in *Oliviera lateralis*; but it often develops hooks, or processes like the paraphalli, without any articulation or break in the structure.

Bibionidæ.—In Bibio hortulanus and B. marci it is a ribbon-like process supporting the appendages and surrounding the curious plate which forms the penis, and which itself is a part of the theca (Pl. 23. fig. 4). In Scatopse notata it supports the membrane of the penis (Pl. 23. fig. 7).

Culicidæ.—In Culex pipiens, Linn., and an undetermined species, it is a membrane supported by lateral chitinous processes, an arrangement similar to that found in certain Tipulidæ (Pl. 23. figs. 13, 15; Pl. 24. fig. 29).

*Tipulidæ*.—In *Tipula oleracea* it is a very clearly differentiated part, supporting a pair of appendages and fused at the base with the double apodeme. The penis works freely through it, and there is also a central rod, which I regard as a part of the theca, which forms a third apodeme. These organs have muscular attachments which practically anchor the theca, as that part is not extruded, the long flagellum being pushed through it (Pl. 24. fig. 23).

In *Pachyrrhina maculosa*, Meig., are two chitinous pieces that represent the atrophying apodemes and support the theca, which is well developed and carries the appendages, but has not the central process of *Tipula oleracea* (Pl. 24. fig. 29). In *Gynoplistia bella*, Westw., an Australian insect, as well as in an undetermined British Tipulid, this part is very extraordinary, developing numerous hooks and supported by lateral columns as in the Culicidæ (Pl. 23. fig. 15).

In *Ptychoptera scutellaris*, Meig., the levers appear absent, but the theca is much developed. I have not succeeded in finding the orifice of the ejaculatory duct, but I have had but little material for examination (Pl. 24. fig. 20).

Stratiomyiidæ.—In Beris vallata it is attached to the last segment of the abdomen; it does not enclose, and is not soldered to, the penis, but appears to act as a grooved channel to guide it (Pl. 24. fig. 33).

Tabanidæ.—In Tabanus bromius the theca is quite similar to that of Pachyrrhina maculosa, but is articulated to the double apodemes, which are well-developed (Pl. 29. fig. 109). In Pangonia longirostris the part has much the same form.

Asilidæ.—In the Asilidæ is strongly chitinized, and broadening out at its bases contains the ejaculatory sac (Pl. 24. fig. 38).

*Empidæ*.—In *Empis stercorea* the theca has developed paired barbs, which are probably homologous with the paraphallus and the hypophallus (Pl. 25. fig. 39). In *Hilara cilipes* a number of barbed serrations cover a very pronounced organ; the penis is held in a neat appliance, through which it is extruded or retracted (Pl. 25. fig. 41).

Dolichopodidæ.—In Dolichopus plumipes, Scop., and other species of this genus, the whole segment is fused with the theca, though a suture can be detected (Pl. 25. fig. 43). In D. festivus, Haliday, paired barbs are found; in D. griseipennis only a single pair appears (Pl. 25. figs. 44, 50).

Syrphidæ.—In Catabomba pyrastri an arrangement is found not unlike that in Bibio hortulanus; the theca surrounds the penis with an enclosing wall, which supports the appendages (Pl. 25. fig. 53). In Eristalis tenax and Syritta pipens this part is

much enlarged and has developed levers at the base, by means of which it can be rotated (Pl. 25. figs. 56, 57, 58).

*Muscidæ*.—In many of the Muscidæ the theca not only forms a guard to the tube, but is also a platform which is fused with and supports the part called by Lowne the bulb \* (the lower part of the chitinous process which sustains the ejaculatory orifice), the appendages (the spine, palpi, and hooks), as well as the paraphallus and hypophallus (Pl. 26. figs. 62, 68). In *Glossina* the theca forms a wall round the double apodeme (Pl. 27. figs. 78, 84).

Lonchæidæ.—A very beautiful adaptation of this part is found in Toxoneura muliebris, Harris. This insect has a long ciliated penis with considerably more chitinous structure than Ulidia nigripennis, Meig. This penis at its base passes through a plate which bears the usual appendages, and is obviously the theca (Pl. 30. fig. 122). The same structure can be made out in Lonchæa nigrimana, Meig. In Palloptera ustulata, Fall., a remarkable chitinous process is found at the extremity of the ciliated ribbon which forms the male organ; a series of folds enclose the tube; from this rises a small column carrying the ejaculatory duct; attached to the folds is a single relatively large plate formed into a hook; this appears to be the upper part of the theca, much separated from its base, which is, as in T. muliebris, a chitinous ring bearing some appendages.

*Ephydridæ*.—In *Parydra coarctata* two rings of chitin support the part carrying the hyaline membrane of the duct; the larger ring bears two appendages (Pl. 29. fig. 111).

Homology with ovipositor.—The homology of this part with any distinct part of the ovipositor is not obvious, but possibly it may be represented in *Musca domestica* by the rods on the first two segments, counting, as before, the segment bearing the egg-guides as the first.

### (f) The Paraphalli.

Structure.—There are two lateral rods springing from the back part of the theca and coming forward. They are always strongly chitinized, and characterized in the genus *Musca* by minute transverse serrations on the extremities.

Nomenclature.- They were first pointed out, and are named, by Lowne.

*Empidæ and Dolichopodidæ*.—They are only markedly present in the Muscidæ; and we seem but to get a hint of their existence in the Empidæ and Dolichopodidæ, where the barbs on the theca already alluded to are probably homologous (Pl. 25. figs. 39 & 44).

Syrphidæ.—In Syritta pipiens the theca is hollowed out at the point, and in this half segment of a circle are one or two curious processes which may, or may not, represent these parts (Pl. 26. fig. 56).

In *Eristalis tenax* the theca is continued up to two serrated blades, which appear to be the paraphalli (Pl. 26. fig. 58).

Muscidæ.—In Sarcophaga these parts are represented by two plates springing laterally from the theca above the bulb, quite unlike the appearance of the parts in

\* 'Blow-fly,' p. 738.

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Musca (Pl. 26. fig. 60). They are well developed and characteristic in *Pollenia rudis*, Fabr., and some species of *Lucilia* (Pl. 26. fig. 62).

They were described from *Calliphora erythrocephala*, Meig., where the servations on the extremities are very marked (Pl. 26. figs. 68, 71). In *Glossina* the paraphalli, together with part of the theca, form a framework which supports an elaborate sensory apparatus and protects the orifice of the ejaculatory duct. The servated structures at the ends of these parts are still to be found at the extremities of the parts in *Glossina palpalis*, Des. (Pl. 26. figs. 63, 69).

They are present in *Anthomyia radicum* (Linn.), with curious processes at the extremities (Pl. 27. fig. 85).

Sepsidæ.—In the Sepsidæ there is an aculeated membrane which springs out of the lower part of the theca, which may be homologous with these parts (Pl. 28. fig. 99; Pl. 29. fig. 101).

Use.—The use of these various modifications will obviously vary with the type. In *Calliphora* and *Pollenia* the shape and the broadened serrated ends, to prevent the extremities slipping, suggest some application where their elasticity would come into play. As to homology with the ovipositor, they may be treated as outgrowths of the theca.

# (g) The Hypophallus.

Structure and Nomenclature.—Lowne has so-named the excressences of the theca which project from the front of that part, the long paraphalli starting from the back. It is a paired organ, open in front, but this is only to be seen by a very careful and difficult preparation of the part. It is strongly chitinized, but sometimes shading to a quite hyaline appearance, and usually has a wrinkled surface with more or less minute barbs.

*Empidæ and Dolichopodidæ.*—What I have said with regard to the presence of homologies of the paraphalli in the Empidæ and Dolichopodidæ will also apply to this part.

Muscidæ.—In the Muscidæ it is generally present; it is evident in Sarcophaga carnaria as the upper of the two anterior processes, cup-shaped in Pollenia rudis. Seen from the front of the organ in Calliphora, it has the appearance of lateral plates (Pl. 26. figs. 62, 68). In Anthomyia radicum it is well-marked, also in most of the Cordyluridæ (Pl. 27. fig. 85; Pl. 28. fig. 88).

Sepsidæ.—It is to be seen in Sepsis cynipsea (Pl. 28. fig. 99), but it is not so obvious in the Nemopoda that is figured (Pl. 29. fig. 101).

# (h) Spinus titillatorius.

Structure.—This part is a single unpaired organ, which lends it distinction, that otherwise it might not merit, as it is often absent, even in those families where it may be found in many species. It is situated immediately behind the penis. It is occasionally articulated, at other times it springs from the base of the theca without any suture. It is highly chitinized, but has a tendency to become membranous at the extremity.

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Nomenclature.—Lowne calls it "the spine"; I observed it in Scatophaga lutaria, Fabr., as an articulated organ, and thought it might be homologous with the "titillator" in *Periplaneta orientalis*, the hook which Lowne suggests is used in the transference of spermatophores \* from the male to the female organisms.

*Dolichopodidæ*.—I cannot find any trace of this part in the families of Diptera till I come to the Dolichopodidæ; there it is large and well developed, and in company with the other appendages to the theca (Pl. 25. fig. 45).

My identification of this part as the unpaired lancet under the hypopygium of *Dolichopus* is confirmed by the observations of Mr. Robert E. Snodgrass in his paper on the genitalia of that family  $\dagger$ .

A number of species show the spinus in its usual position as shown in Pl. 25. fig. 43, though the part varies much in shape. But when the appendages are absent from this situation, as in *Psilopa sipho*, the penis is surrounded by the theca, which supports two leaf-like lateral processes, and between them a single median stile which I recognize as the spinus.

Muscidæ.—It is absent in Sarcophaga carnaria and Oliviera lateralis (Pl. 26. fig. 60; Pl. 29. fig. 112), but it is generally present in the Muscidæ (Pl. 26. fig. 68; Pl. 27. fig. 85).

Lonchæidæ.—One of the most curious migrations of this part is in the Lonchæidæ. In the Dolichopodidæ we have found it near the base and at the extremity of the penis, and also in *Toxoneura muliebris*, Harr., it appears to be at the base of the long ciliated ribbon which forms that organ (Pl. 30. fig. 122), while in *Palloptera ustulata*, Fall., it appears as a relatively large hook, symmetrical in shape and articulated to the rather complicated chitinous part which forms the extremity of the penis, which in this species also consists of a long ciliated ribbon.

Use.—In use it fits into a fold of the ovipositor, as can be seen in Berlesi's remarkable section of *Musca domestica* "in copula" ‡.

*Homology.*—It is obvious that its homology in the ovipositor must be looked for after the determination of the homology of the theca.

#### (i) FORCIPES INTERIORES.

Structure.—These are two small blade-shaped hooks on both sides of the theca, generally articulated; they are more or less highly chitinized, with very short sharp spines springing from sockets; the surface is usually smooth.

*Nomenclature.*—Lowne calls them "posterior gonapophysis," but this is obviously indefinite, and I prefer my name of "forceps interior," as not only more definite, but descriptive of the part.

Mycetophilidæ.—In Sciara thomæ they are probably the paired blades springing from the root of the adminiculum (Pl. 23. fig. 1).

Bibionida.-In Bibio hortulanus they are difficult to differentiate, but I think are

<sup>• &#</sup>x27;Blow-fly,' p. 664.

<sup>† &</sup>quot;Hypopygium of the Dolichopodidæ," Sept. 28, 1904. Proc. Cal. Acad. Science, ser. 3, vol. iii. Zool. no. 11.

<sup>‡</sup> Riv. Patol. Vegetale, ix. (1902).

represented by the free, pointed, posterior processes (Pl. 23. fig. 4). They are quite evident in *Scatopse notata*, which has every part complete with the exception of the "spinus tittilatorius" (Pl. 23. fig. 7).

Culicidæ and Tipulidæ.—In the Culicidæ and the Tipulidæ they are represented, but it is difficult to say which are forcipes and which are palpi (Pl. 23. figs. 13, 15; Pl. 24. fig. 23).

Stratiomyiidæ.—In Beris vallata they appear to be the paired blades springing from the root of the penis (Pl. 24. figs. 32, 33).

Dolichopodida.—In the Dolichopodidae they can be differentiated from the palpi by their structure (Pl. 25. fig. 46).

Syrphidæ.—In Catabomba pyrastri they take the form of the curious band which encircles the penis (Pl. 25. fig. 53). In Syritta pipiens they are also much modified and changed into the two strongly chitinized pectinated organs that are on the head of the theca (Pl. 26. figs. 56, 57). In Eristalis tenax these organs are represented by two curious hooks placed laterally on each side of a chitinous receptacle, which is the orifice of the ejaculatory duct (Pl. 26. figs. 58, 59).

*Muscidæ*.—In the Muscidæ they are generally present, but not in so well-marked a type as in *Calliphora*, as may be seen by comparing that with *Sarcophaga* (Pl. 26. figs. 60, 68).

In *Glossina palpalis* and *G. tachinoides* they are fused with the "palpi genitalium" (Pl. 27. fig. 86).

Ortalidæ and Lonchæidæ.—They seem absent in Ulidia nigripennis, but are represented in Lonchæa nigrimana, Meig., which has a similar form of penis.

Ephydridæ.—They are represented in Parydra coarctata and Notiphila nigricornis (Pl. 28. fig. 98; Pl. 29. fig. 111).

Homology with ovipositor.—There are in the ovipositor of Musca domestica eight single rods and one double rod, fused at the base—besides this, seven or eight transverse setose plates; and the homology of this part must be sought amongst this rather confusing array \*.

#### (k) PALPI GENITALIUM.

*Structure.*—These are two small, palpiform organs, like the forcipes interiores situated on both sides of the theca but placed anteriorly to them. Sensory hairs and setæ are usually present.

Nomenclature.-Lowne calls the part the "anterior gonapophysis" +, but I prefer the

\* Note.—In the Culicidæ I have encountered a special difficulty in homologizing this part, as there are four interior hooks; these are placed symmetrically in front of the membrane supported by the lateral processes (Pl. 23. fig. 13). These lateral supports are probably the palpi genitalium, and, if that is so, there must be a double pair of forcipes interiores. Those figured as 10 and 12 represent a single pair.

In *Dolichopus festivus* there are apparently two pairs of palpi next each other; they can be differentiated by a curious venation on the head of one pair (Pl. 25. figs. 47 & 48). This is a similar difficulty to the previous one, and one which is not easy of explanation. There are many instances of failure of parts, but these two families are the only ones which show a redundance. Mr. Snodgrass, in his paper already alluded to, shows some complicated genital palpi; *D. erenatus* has several processes at its extremity, and this may be owing to a fusion of the double organ.

+ 'Blow-fly,' p. 740.

above name for the same reasons as in the case of the forcipes interiores. They are only anterior so far as regards the penis itself—as regards the insect, they are often, as in *Dolichopus* in posterior positions.

Bibionidæ.—In Bibio hortulanus I think these organs are represented by the bands supporting the penis (Pl. 23. fig. 4). In Scatopse notata their extremities are columnar, springing from a broader base; the column is capped by a bunch of sensory hairs, and there is a seta lower down (Pl. 23. fig. 6).

*Tipulidæ*.—It is impossible with the facts at my command to say definitely that the lateral arms of the theca in *Tipula oleracea* are not these organs, but at all events their function seems supplied by the bunches of setæ on the dorsal sides of the abdomen (Pl. 24. fig. 24). They seem absent in *Ptychoptera scutellaris*.

**Dolichopodidæ.**—I cannot identify these organs among the related families till we reach the Dolichopodidæ. In the genera *Dolichopus* and *Pæcilobothrus*, in the remarkable group of weapons situated between the forcipes superiores and the forcipes inferiores, are generally a pair of smooth large-headed organs with sensory setæ (Pl. 25. fig. 47); also a pair with a leaf-like venation, whose presence is not easy to account for (Pl. 25. fig. 48).

Syrphidæ.—In Catabomba pyrastri they are two hairy plates articulated to the theca (Pl. 25. fig. 53). In Syritta pipiens they seem atrophying, being represented by two weak lateral bands, which, however, carry a sense-organ (Pl. 26. figs. 56, 57). In Eristalis tenax they seem quite atrophied, two minute tubercles carrying scattered setæ only remaining.

Muscidæ.—In the Muscidæ they are at their greatest and most characteristic stage, but are occasionally absent, as in Olivieria lateralis, where small tubercles and bristles mark their site (Pl. 29. fig. 112). In Sarcophaga carnaria they are developed, but more of a hook shape, and though they are studded with hair-sockets, the hairs appear to be absent, but the inner side of the part appears to be soft and membranous (Pl. 26. fig. 60). In Pollenia rudis, Fabr., they are very characteristic both in shape and pubescence (Pl. 26. fig. 62). They are approximately of the same type in Calliphora erythrocephala, in Lucilia cæsar, Linn., and in Anthomyia radicum. In Glossina they are not articulated, and are fused with the forcipes interiores in G. palpalis and G. tachinoides (Pl. 27. fig. 86); in the former species they carry most remarkable hairs \*. In G. pallidipes, Austen, they are two broad plates with very long fine hair arranged symmetrically on the anterior side of the central organ (Pl. 27. fig. 78).

In the Cordyluridæ the parts often carry long setæ as in *Scatophaga litorea*, Fall. In *Norellia spinimana*, Fall., they seem to have exchanged places and functions as well as shape with the forcipes (Pl. 28. fig. 89). In *Fucellia fucorum*, Fall., they are absent, their places, exactly as in *Olivieria*, being marked by single bristles.

Lonchæidæ.—They can be traced in *L. nigrimana* and *Toxoneura muliebris* at the base of the penis, probably in an atrophying state (Pl. 30. fig. 122).

Sepside.-In Sepsis and Nemopoda they seem absent, though I have an imperfect

<sup>\* &</sup>quot;Genitalia of the Tsetse-fly, Glossina palpalis," Journ. Quek. Micr. Club, Nov. 1905, p. 236.

preparation of S. cynipsea, Linn., which appears to show them, but unfortunately the bases cannot be seen. They are certainly absent in many species, and the laminæ superiores have developed bunches of hair, and in at least one case (Pl. 29. fig. 103) tubercles which appear to be sensory, to compensate.

*Ephydridæ*.—Though the forcipes interiores are present in *Parydra coarctata*, there are no signs or remains of the palpi (Pl. 29. fig. 111).

Use.—These organs fulfil an important office, as when they are absent we find compensating sense-organs. In *Tipula oleracea* lateral bunches of hair, in *Pandora* scutellaris processes on either side of the theca, six bunches of fine black hair, and in Nemopoda elaborated laminæ superiores.

# (m) THE APODEMES OF THE PENIS, THE DOUBLE APODEME, OR THE GREAT APODEMES.

Structure.—These are the organs (or organ) that rotate the penis, often considerably elongating it in the process. They are found in three conditions: (1) as symmetrical paired organs, as in *Bibio hortulanus*, *Gynoplistia bella*, or *Tabanus bromius*; (2) as partially fused together, as in *Glossina* or *Sepsis*; (3) or fused or "united in the median line" as Lowne puts it, speaking of the part in *Calliphora*\*.

The part has a markedly laminated structure; when it is fused, a highly chitinized process runs longitudinally through the middle; it is fitted for the attachment of muscles.

Nomenclature.—Lowne calls these parts the "great apodemes": it is necessary to have an adjective to distinguish them from the apodeme of the ejaculatory sac, which is often very large and prominent; as I have found this part separate in several families I have suggested the name of the "double apodeme" to distinguish it from the other apodeme, which is always single.

*Mycetophilidæ*.—There are indications of the presence of such an organ in my preparations, but not sufficiently definite to quote.

Bibionidæ.—In Bibio the theca is attached to two strongly chitinized levers, not shown in the figure. In Scatopse notata the apodeme is fused. These extraordinary anomalies are quite in keeping with what I found while working on the homologies of the mouth-parts. Bibio had a type of trophi approximating to that in the Muscidæ, differing in this from nearly all the Nematocera, and in the Empidæ the genus Hybos differed in arrangement from the other genera in the family  $\dagger$ .

Culicidæ.—I have a preparation of *Dinocerites cancer*, Theobald, which shows two powerful apodemes placed laterally, and articulating on to the two processes which support the membrane of the penis, also one of *Culex* (?) which has the apodemes of exactly the same type as *Gynoplistia*.

*Tipulidæ*.—In *Tipula oleracea*, as I understand the apparatus, the long flagellum is pushed forward through the aperture in the theca by the rotation of the ejaculatory sac,

\* 'Blow-fly,' p. 743.

<sup>† &</sup>quot;The Mouth-parts of the Nemocera," Journ. Roy. Micr. Soc. 1904.

actuated by the apodeme of that part, and the organs under discussion, "fallen from their high estate," are reduced to act as the lateral levers of the theca, to which they are fused (Pl. 24. fig. 23). In *Gynoplistia bella* they are, on the contrary, of great importance and development, attached by muscles to the complicated mechanism of the theca, apparently to separately rotate the two central hooked processes (Pl. 23. fig. 15). In *Pachyrrhina maculosa* they are represented by two rather weak chitinous plates, laterally supporting the theca.

Stratiomyiidæ, Asilidæ, Empidæ, and Dolichopodidæ.—In Beris vallata, the Asilidæ, the Empidæ, and the Dolichopodidæ these levers seem absent, or are fused to the theca, the single ejaculatory apodeme doing all the work. In the undetermined Asilid, already alluded to and figured, the anterior portion of the theca sends out processes for the attachment of muscles, and possibly represents the fused apodemes (Pl. 24. fig. 38).

Syrphidæ.—This part is very difficult to make out in the Syrphidæ. It appears to be present in Sphæriophoria scripta, but seems in that case to be doing the work of the ejaculatory apodeme, which I cannot find. There is a suture down the organ and large lateral processes to support the theca. I cannot find it in Catabomba pyrastri, but am not sure of its absence, as in this family, as I shall show, the part migrates in a surprising manner. In Syritta pipiens, in the upper part of the theca, is an arched opening; this, seen from the front, has some curious and minute structure on its floor, the orifice of the ejaculatory duct. Examining the organ from the side, I am able to make out that this floor is the upper part of a chitinous box; and welded to this box, and working in the centre of the theca, is the great apodeme, quite single and extending downwards to the top of the ejaculatory apodeme, which is very large and evident. From this central position it may rotate the whole organ, but does not seem sufficiently powerful for that purpose (Pl. 26. figs. 56, 57).

In *Eristalis tenax* there is no domed aperture, but the orifice of the duct is also placed in a chitinous chest or box; to the front of this box is hinged the apodeme, which rotates it and the two hooks (forcipes interiores) which are attached to it. The whole organ (the theca) is rotated by its edges, which are rounded and thickened, and project at the base, forming levers (Pl. 26. fig. 58).

Muscidæ.—In the Muscidæ the organ is generally at the base of the theca and is fused for its whole length: it takes this characteristic form in Sarcophaga carnaria (Pl. 26. fig. 60), in Olivieria lateralis (Pl. 29. fig. 112), in Pollenia rudis (Pl. 26. fig. 62), in Calliphora erythrocephala (Pl. 26. fig. 68), in Anthomyia radicum (Pl. 27. fig. 85), in Norellia spinimana (Pl. 28. fig. 89) and Scatophaga litorea (Pl. 28. fig. 88), besides the great majority of the other species.

In Glossina there is another remarkable metamorphosis. It has become forked at its upper part as in G. palpalis (Pl. 27. fig. 72) and G. tachinoides (Pl. 27. fig. 75), or has spread out into a plate with an aperture to contain the ejaculatory sac, as in G. morsitans (Pl. 27. fig. 74) and G. pallidipes (Pl. 27. fig. 73). It works through the theca, which has become a wall surrounding it; and in G. palpalis, G. tachinoides, and G. pallidipes the upper ends are articulated on to the paraphalli, which, in their turn, are articulated on to the theca.

Lonchæidæ.—In Toxoneura muliebris it can be traced in a similar forked form at the base of the penis (Pl. 30. fig. 122), and in a fused form in L. nigrimana.

Sepsidæ.—In the Sepsidæ the part is very clearly seen to be a paired organ, though it becomes fused at its lower end (Pl. 28. fig. 99; Pl. 29. fig. 101).

Use.—These organs in all their conditions are attached to powerful muscles, which rotate the penis from its position of rest as in the Blow-fly, or extrude it as in *Tabanus* or *Bibio*.

Homology with ovipositor.—In the base of the ovipositor of Musca domestica are two rods which fuse at their lower end for no apparent reason; it has occurred to me that they represent these apodemes. Firstly, because they are at the base of all the other rods save one, as the apodemes are normally at the base of the theca; and secondly, because they are paired organs, agreeing in this respect with the apodemes in two important particulars (Pl. 29. fig. 107).

#### (n) DUCTUS EJACULATORIUS.

Structure.—This part is usually a delicate hyaline membrane. In Syritta pipiens it differs, having the appearance of a striated muscular tube with double walls, which spread out to form the ejaculatory sac, this peculiar structure ending here.

*Homology with ovipositor.*—It is obviously homologous with the vagina of the female insect.

## (o) "SACCULUS EJACULATORIUS."

Structure.—This most important organ of the genitalia undergoes bewildering changes of shape and situation; it is usually a hyaline pouch with the apodeme adhering to it, proceeding downwards from the penis; or it may be a chitinous sac, as in the Tipulidæ, or a part of the theca, as in the Asilidæ and Dolichopodidæ.

It will be convenient to describe the apodeme with the sac, so before proceeding to more details I shall give the structure of the

#### (p) EJACULATORY APODEME.

Structure.—This is a minute rod in many species, not unlike the microscopic lever that is found attached to each spiracle, but is more often spread out at the base into a spatulate or fan shape, to afford a larger space for the attachment of muscles. This part, when so modified, has the curious laminated structure noted in the double apodeme.

In what may be termed the head, that is to say the part in contact with membrane, or which is used to close the sac, a number of lighter circles, not unlike bristle-sockets, may be seen in some species. They are characteristic, but they require high powers and skilful manipulation to reveal. I have seen them in *Asilus crabroniformis*, Linn., the Asilid figured, and in the very distantly related *Glossina palpalis* and *G. pallidipes*.

Nomenclature.--Lowne noticed the part in Calliphora, calling it a sclerite\*; but this

\* 'Blow-fly,' p. 665.

not being definite enough in view of its importance in other families, I propose to call it the "ejaculatory apodeme."

*Bibionidæ.*—My preparations of *Sciara* and *Bibio* are not successful in showing these organs, but in the minute *Scatopse notata* I have been able to make them out quite clearly. The sac is an elastic globe, and the elaborate transverse levers, actuated by the apodeme, compress it, and force the seminal fluid through the duct (Pl. 23. figs. 8, 9).

*Tipulidæ.*—In *Tipula oleracea* the sac, as I said before, is hard and horny, with two processes, fitted for the attachment of muscles, fused on to it. The duct opens widely but soon narrows, forming the hyaline flagellum. The base of the apodeme is blunt, fitting into an opening in the sac, and is capable of closing the opening of the duct. The apodeme has two arms, and it is obvious, on looking at the parts, that when the right-hand or dorsal arm is drawn in that direction by its muscular attachments, the sac is rotated, the duct is closed (owing to the changed position of the apodeme in its containing cavity), and the flagellum is withdrawn into the theca. On the other hand, when the left or ventral lever is pulled, and the sac rotated in the contrary direction, it not only opens the duct, but protrudes the flagellum (Pl. 24. figs. 24, 26).

In *Pachyrrhina maculosa* the same arrangement is found, but the apodeme is of the more usual form, with a fan or disc instead of opposing arms (Pl. 24. figs. 30, 31).

In *Gynoplistia bella* the apodeme is seen in the centre, between the apodemes of the penis, but my preparations do not clearly show the structure of the sac (Pl. 23. fig. 15).

In *Ptychoptera scutellaris* an even more curious organ is found. Three flat plates, with muscular attachments, are fixed on three sides of a hollow chitinized receptacle which is situated immediately below the curious penis (Pl. 23. figs. 17, 18; Pl. 24. fig. 20).

Stratiomylidæ.—In Beris vallata the penis takes a curve, and is then bent on itself, broadening out into a cavity which forms the sac. In this cavity the apodeme is articulated in such a manner that when it is drawn towards the thorax it opens the sac and extrudes the penis, and when towards the posterior, contrary motions take place, a variation on the device in T. oleracea (Pl. 24. fig. 33).

Tabanidæ.—A very complicated mechanism exists in *Tabanus bromius*, and I only offer the following as a hypothetical explanation of the action of the parts.

The apodeme is placed in the centre of the theca, and reaches well up into that part; at the broadest part of the theca an articulation with another piece is apparent. From this point two very fine rods curve outwards, and then approach each other till they overlap and form a fine point, capable of easily passing through the opening in the point of the theca. These rods are contained in a membrane, which is the sac. On the apodeme being drawn forwards it would push the rods through the orifice of the theca. On being still further drawn, or being drawn backward and forward, it would separate the points and, at the same time, compress the sac against the containing sides of the theca, thus opening the orifice and expelling the spermatic fluid (Pl. 29. fig. 109).

Asilidæ.—In the Asilidæ a similar mechanism to that of *Beris* is seen, but with the difference that the part is much thickened and chitinized (Pl. 24. fig. 38).

*Empidæ.*—In the Empidæ we have another variation on the mechanism in *Tipula*. The flagellum, after turning back on itself, widens out into a sac, into which an apodeme SECOND SERIES.—ZOOLOGY, VOL. IX. 52 is inserted and acts in the same way, the muscles pulling it one way opening the passage and protruding the flagellum, the other way, closing the sac and withdrawing the flagellum (Pl. 25. fig. 41).

Dolichopodidæ.—In Dolichopus griseipennis a beautiful mechanism is present; the base of the apodeme is pierced by a neat fitting for the vas deferens, which, when the apodeme is in its normal position, fits against a pad and closes the duct. When it is drawn back, as is seen in the drawings (Pl. 25. figs. 50, 51), an elastic membrane is stretched across the space between the theca and the apodeme, leaving the ejaculatory duct free to the orifice. The changes in mechanism from the type of the Tipulidæ are brought about by the fixture of the flagellum to the theca; consequently the apodeme only does its proper work of containing or releasing the spermatic fluid, and does not rotate or extrude the penis.

Syrphidæ.—In Catabomba pyrastri the sac is a flexible hyaline membrane with a minute apodeme (Pl. 25. fig. 53). In Syritta pipiens an unusually large apodeme is found at the base of an enlargement of the ejaculatory duct which represents the sac; the head of the apodeme has a transverse plate and a swelling which appears to be modified to fit this space, and closes or opens the duct by backward and forward muscular action (Pl. 26. figs. 56, 57). In Eristalis tenax the sac is represented by a hyaline tube with a small apodeme, as in Catabomba, but all contained in the theca and fairly close to the orifice. The chitinous box at the extremity of the theca is fitted with a ciliated valve, allowing for a free passage outwards (Pl. 26. fig. 64).

Muscidæ.—In the greater proportion of the flies the sac and apodeme are of the same type and situation as in *Catabomba pyrastri*. The action of this arrangement is by no means obvious; either the apodeme is pressed against some other part by the attached muscles, so as to close the sac, or is drawn backwards and forwards, acting as a pump and driving the fluid through the ejaculatory duct (Pl. 26. figs. 60, 62, 68).

In *Calliphora* the sac is at a much greater distance from the theca than in *Pollenia* or *Scatophaga*. This part is found in a curious situation in *Glossina*, where the apodeme rests in the fork of the double apodeme (Pl. 27. figs. 72, 73, 74, 75), practically at the orifice of the duct, and it is a knowledge of the mechanism in this genus that has suggested my explanation of the part in *Tabanus*.

Lonchæidæ.—In Toxoneura muliebris the sac and small apodeme are at the base of the long ciliated penis, below the forked apodeme (Pl. 30. fig. 122).

Trypetide.—In Acidia heraclei (Linn.) the sac is in a precisely similar position, but the base of the apodeme is spatulate.

Sepsidæ.—In the Sepsidæ the apodeme has a remarkably long stalk (Pl. 28. fig. 94); this is also the case in the nearly related Diopsidæ.

Use.—This apparatus is arranged to control the flow of the seminal fluid, being so situated and held by muscular attachments that when the penis is in its normal position the sac is closed; a different process seems to be the rule in those Muscidæ where the ovipositor is long, as in *Musca domestica*; in such flies the valve would probably not be opened till after the elaborate interlocking of the parts shown in Berlesi's section had taken place.

Homology with oripositor.—The sac at the base of the oviduct in the Blow-fly appears to homologize with this part. It is in the passage leading from the sac into the uterus that the ducts from the receptacula seminis discharge, impregnating the ova in their passage. But Lowne regards it as homologous with the uterovaginal tube \*, which is after all exceedingly close to the part I suggest. In *Musca domestica* there is a cavity at the end of the passage into which the ductus ejaculatorius discharges, which is possibly also homologous. This is well shown in Berlesi's section already alluded to, but any longitudinal section of the ovipositor in its normal position in the abdomen which shows the receptacula seminis, or spermathecæ, will probably show the part I mean.

# (r) THE VAS DEFERENS.

The vas deferens is the tube which leads from the paragonia and testes to the sacculus ejaculatorius.

Structure.—It is usually a subhyaline membrane with many longitudinal wrinkles. It is of various lengths, short or long in different families. In *Dolichopus* it has a very marked muscular structure, and broadens out at its junction with the secretory organs. Besides its length, it has little to distinguish it in the various families.

Homology.—It homologizes with the oviduct of the female.

# (s) The Paragonia or Vesiculæ seminales.

These are a pair of sacs which open into the vas deferens. Their function is obscure, but Lowne † rejects the idea that they contain spermatozoa, and considers that in the Blow-fly at least, "the secretion coagulates with great rapidity in the ejaculatory duct or in the vagina of the female insect, and is apparently concerned in the formation of spermatophores."

*Homology.*—They are easily homologized with the glands which Lowne calls parovaria in *Calliphora*, and have been confused with the "glue-glands"<sup>‡</sup>.

# (t) VASA EFFERENTIA.

These are ducts which lead from the testes to the vas deferens. They are so named by Lowne §, but are the "vasa deferentia" of other writers. These organs are always present, usually of a hyaline structure and of varying length. They homologize with the "tubæ" of Lowne, which lead from the ovaries to the oviduct.

## (u) THE TESTES.

These are paired sacs, which secrete the spermatozoa; are mostly separated, and of an orange, white, or brown colour. Dufour says, however, that in *Laphria fulva*, Egger, both testes are enveloped in one receptacle, "un véritable scrotum"  $\parallel$ .

Structure.-In Musca domestica they are of a deep brown, and have the appearance

*	' Blow-fly,' p. 675.	+	' Blow-fly,' p. 663.
++	Ibid. p. 673.	ş	<i>Ibid.</i> p. 662.
11	Recherches anatomiques, etc. p. 198.		

of being chitinous, but Lowne says that this colour is due to the "pigmented epithelium which forms the walls"\*. In *Scatophaga* they are a reddish brown; in the Tipulidæ, according to Dufour, white.

Homology.—They homologize with the ovaries of the female.

*Phylogeny.*—The foregoing examination of the male armature shows that the greatest variations are in the central organ and in the ejaculatory duct; also that the families exhibit their relationship to the Tipulid or the Muscid type by the character of this duct, whether it is of the nature of a stiff flagellum or of a flexible membane. The Bibionidæ seem anomalous; the rest of the families appear to show that the structures of this part are characters of the two great divisions of Orthorrapha and Cyclorrapha.

#### SEGMENTS OF ABDOMEN.

Before proceeding to describe the ovipositor, I propose making some remarks on the number of segments in the abdomen of both the sexes. This number is known to be variable, as the following table, taken at random from the mounted Diptera in my collection, will show; but I think the normal is probably eight. In consequence of this variability, when making comparisons between the sexes it will be advisable to count from the last segment, that bearing the values.

Family.	Number of segments.		Family.	Number of segments.	
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Mycetophilidæ	9-10	8	Empidæ	8-9	7-8
Bibionidæ	8-9	8–9	Dolichopodidæ	7-8	S
Culicidæ	8	6-7-8	Syrphidæ	5-6-7-8	8
Tipulidæ	7-8-9	8	Museidæ	5-6-7-8	6-7-8
Rhyphidæ	8	8	Heliomyiidæ	6-7	7-8
Stratiomyiidæ	8-9	8–9	Ortalidæ	5-6	7-8
Tabanidæ	8-9	9	Sepsidæ	5	6
Asilidæ	7		Ephydridæ	5-6	4-7
Bombylidæ		8	Borboridx	5-6	7

#### THE OVIPOSITOR.

The ovipositor in Diptera varies in length and structure. In what are usually considered (on the evidence of fossil remains) the older families, it consists of valves or egg-guides, and is not telescopic or capable of extension (Pl. 24. fig. 21). It approximates to this form in *Bibio*, *Culex*, *Chironomus*, *Tabanus*, and *Tipula*, and also in some

\* ' Blow-fly,' p. 660.

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of the Muscidæ, calyptrate and acalyptrate. In *Stratiomys, Empis, Dolichopus*, and *Syrphus* it is found to be longer and more capable of extension. In some of the Muscidæ it is at its greatest proportionate length in its membranous form. In the acalyptrate Ortalidæ, Trypetidæ, and Lonchæidæ it is equally long, but hard and horny and capable of depositing the eggs under the cuticle of leaves. In the minute Phitomyzidæ it is shorter, but still a horny, minutely-aculeated organ.

"Receptacula."—An examination of a prepared slide of a female shows from one to three, rarely four, chitinous sacs, mostly of an oval or pyriform shape, with more or less short ducts leading from one end; these are the receptacula seminis or spermathecæ. In *Musca domestica* they are situated at the end of the long fold of the ovipositor into which the ductus ejaculatorius of the male discharges; they absorb the spermatozoa, and again eject them when the ova in their passage down the oviduct compress the receptacula.

In the preparations they are found either in the abdomen or in the extruded ovipositor, and possibly, on a cursory examination, might be mistaken for eggs.

"Glue-glands."—Excretory glands will also be found in some ovipositors, sometimes called "glue-glands." The eggs adhere to each other or to their resting-places by means of the fluid from these glands, with which they are anointed in their passage through the ovipositor.

Types in the Muscidæ.-In the Muscidæ there are several types of this organ :--

(1) That in *Musca domestica* is long and telescopic, with three joints, and has on the anal segment two feeling-organs or valves, a semi-ovoid and two triangular plates (these latter probably representing the eighth segment of the abdomen) and two other segments supported by ten chitinous rods (a pair of these rods being fused at the base), and a number of transverse setose plates (Pl. 29. fig. 107).

(2) In *Lucilia* it is also long and telescopic, but has plates instead of rods, and on the dorsal plate of the third segment, the anal segment counting as "one," are two pairs of spiracles close to each other.

(3) In *Calliphora* it is much shorter, but has plates and paired spiracles on the same segment as in *Lucilia*.

(4) In *Polietes lardaria* (Fabr.) it is again long and telescopic as in  $\mathcal{M}$ . domestica, has the usual values on the anal segment, but neither rods nor plates, the segments being marked by small transverse bristly bands of chitin, and without spiracles on the third segment.

(5) In Hydrotæa dentipes, Fabr., it is long and telescopic, has plates which seem to be thickening into rods, and two pairs of spiracles on the third segment, as in Calliphora and Lucilia.

(6) The very short ovipositor that is found in *Scatophaga* and *Anthomyza* (Pl. 28. figs. 90, 100; Pl. 30. fig. 131).

(7) The horny, extrusive ovipositor that is found in those families already alluded to (the Ortalidæ, Trypetidæ, Lonchæidæ, and Phitomyzidæ) (Pl. 28. fig. 95).

The Spiracles.—In comparing the ovipositor in different families, and homologizing it with the male armature, the presence or absence of spiracles on the segments might be thought to be a guide to relationships, but so far I have not been able to draw any conclusion from my observations on this point, so I shall content myself with stating them.

Lowne points out that on the sixth somite of the abdomen of the female Blow-fly, or the third from the end, are two pairs of spiracles close to each other. I find a similar arrangement on *Calliphora* or *Protocalliphora grænlandica*, Zett., and *Lucilia sericata*, Meig., but no traces of spiracles on *Musca domestica* and the Anthomyid *Polietes lardaria*, though in *Hydrotæa dentipes* and *Ophyra leucostoma*, Wied., the double spiracles are again evident.

In *Hilara cilipes* the number of segments differs, but counting from the anal segment, in the same place, are a single pair of spiracles (Pl. 25. fig. 42).

Arrangement.—For convenience of discussion and description the ovipositor may be divided up into four parts :—

- (1) The egg-guides or sensory organs and the other plates at the extremity.
- (2) The ultimate or anal segment.
- (3) The penultimate segment and the glue-glands.
- (4) The spiracle-bearing segments and the Receptacula seminis.

# The Egg-Guides and the Appendages of the Ultimate Segment of the Ovipositor.

*Egg-guides or valves.*—All the ovipositors that I have examined have some appendages on this segment. In a complete state, five parts are present—two dorsal valves or blades, two ventral, and a single plate between; but it is seldom that the organ is found in this state.

Nomenclature.—Nothing definite has been settled on the point of nomenclature. Dziedzicki has, in the paper before referred to, named the parts in the ovipositor, but these do not, in my opinion, fit the organ so well as his male nomenclature; so I propose to call the parts the valvulæ superiores, the valvulæ inferiores, and the lamella anterior. The valvulæ superiores will correspond with the dorsal plates of Lowne\*, while the valvulæ inferiores are represented in the Blow-fly by the anal scales.

Bibionidæ.—In Bibio hortulanus there are two large hairy valvulæ superiores, a single plate (the lamella anterior), and two ventral subtriangular pieces (the valvulæ inferiores) (Pl. 23. fig. 2).

Culicidæ.—In this family these parts are not so prominent, and their bases are usually hidden by the last plate. In Culex pipiens the upper valves are fairly pronounced, but the lower are only represented by hairy palpiform processes, well up in the dorsal region of the cavity made by the last plate. Dinocerites has also in the female striking genitalia, horny upper valves and fairly large lower valves, placed in the same situation as in Culex.

*Tipulidæ*.—In *Tipula oleracea* all the parts are present, the upper and lower valves very hard and blade-like in form (Pl. 24. fig. 21).

Trichocera hiemalis, Degeer, and Ptychoptera albimana (Fabr.) have only one pair of large blade-like valves on the end of the abdomen, the dorsal and ventral sides meeting

\* 'Blow-fly,' pp. 745-46.

at their base—these are the valual superiores; the valual inferiores seem atrophied, but there are signs in the interior of P. albimana of the presence of the lamella anterior.

Stratiomyiidæ.—In Beris vallata the valvulæ superiores are two-jointed, which is very unusual, the valvulæ inferiores very minute, a similar arrangement existing in B. nigra, Meig. (Pl. 24. figs. 34, 35). In Stratiomys chamæleon all the parts are present but relatively small. The valvulæ superiores have a curious sense-organ on the apex.

Tabanidæ.—In Tabanus bovinus, Linn., all the valves are hairy, and, as in S. chamæleon, relatively small; the valvulæ inferiores appear to have fused, but the plate is notched on the median line (Pl. 30. fig. 126).

*Empidæ.*—In *Hilara cilipes* only a pair of hairy processes are present (Pl. 25. fig. 42). In *Empis chioptera*, Fall., these processes are adhering to a membrane, the segment or apparent segment consisting of a dorsal and a ventral plate. These may represent the other valves and plate.

Dolichopodidæ.—In Dolichopus a very remarkable development of this part is found; two horny valves (v. superiores) are laterally placed, and below them are two ciliated lunules (v. inferiores). The valvulæ superiores are articulated on to a plate, cleft in the middle; on this is a remarkable series of blunt spines, presumably of use in coitus (Pl. 25. fig. 52). They are a feature of the ovipositor in this family, and are often double and treble the length of those in *D. griseipennis*. These contrivances for holding the partner in coitus, common enough in the male, are quite rare in the other sex. In the Bombylid *Comptosia ocellata*, New., the valvulæ inferiores have a number of long blunt hooks, *Pegomyia bicolor* has pads of hair, and *Norellia spinimana* (to which I shall again refer) has rows of short blunt spines on the abdomen (Pl. 28. fig. 90).

Syrphidæ.—In the Syrphidæ the valves are hairy and rather insignificant, but the plate is difficult to differentiate.

Muscidæ.—In the calyptrate Muscidæ the dorsal valves are hairy; they are opposite to a plate which is probably a fusion of the ventral valves, and they are attached to a strip of chitin which has, and sometimes has not, a suture in the middle (Musca domestica and Calliphora erythrocephala) (Pl. 29. fig. 106).

When the ovipositor is of the Ortalid type, generally a pair of hard short valves are present, carrying a few sensory setæ, the remaining parts not being distinguishable (Pl. 28. fig. 95).

Cordyluridæ.—In Scatophaga stercoraria the valvulæ superiores are very hairy and each carries a long seta; the valvulæ inferiores are horny plates, genuine egg-guides, and the lamella is well-marked (Pl. 30. fig. 131).

In Norellia spinimana are only two setose valves and two plates (Pl. 28. fig. 90).

Geomyzidæ.—In Anthomyza pallida, Zett., the valvulæ are peculiar; they are chitinous plates, studded with blunt spines; opposite to them are two valves; the plate is difficult to differentiate in my preparations (Pl. 28. fig. 100). In an unnamed slide in my collection (an Anthomyid) the dorsal valves have two short, strong, socketed setæ on each, besides many hairs; the other parts are of the *Musca domestica* type, but with very fine rods.

1.2.1

# The Ultimate Segment of the Ovipositor.

In families where the ovipositor is not extruded this part does not call for remark.

Stratiomyiidæ.—In Beris and Stratomys chamæleon it is a chitinous plate with no suggestions of other structure, though the edges in B. valata are convoluted and thickened transversely.

Empidæ.—In the Empidæ it consists of a dorsal and ventral plate.

Dolichopodidæ.—In Dolichopus griseipennis there are indications of the formation of two chitinous rods. On the ventral side, at the extremity, is a sensory membrane, covered with minute triangular plates (Pl. 25. fig. 52). In Pacilobothrus nobilitatus four rods show quite plainly.

Syrphidæ.—In Syritta pipiens are two chitinous levers which appear to be the continuation of the valvulæ, and there is a darkening of the chitin suggestive of the formation of a rod.

In *Eristalis intricarius* there are three transverse ridges of chitin with setæ. In the middle is the opening of a gland which is probably a glue-gland.

Muscidæ.—In Musca domestica this part contains four chitinous rods which are shorter and stouter than the rods in the following sections; there are also several transverse setose ridges. The membrane between this and the penultimate segment has minute triangular sensory plates (Pl. 29. fig. 107).

In *Calliphora erythrocephala* there are no rods, the part consisting of a dorsal and ventral plate; there are apodemes from the valves.

In *Polietes lardaria* are two transverse setose ridges, dorsal and ventral; the rest of the part is transparent membrane.

In Ulidia nigripennis this segment consists of apparently three plates forming a rod-like piercing-organ.

In Norellia spinimana this segment is part of the abdomen, and appears to consist of a chitinous plate, and bears the remarkable process of short spines already alluded to (Pl. 28. fig. 90).

#### The Penultimate Segment.

Stratiomyiidæ.—In Beris vallata and B. nigra plates, which do not quite encircle the abdomen, are found in this place. In S. chamæleon what seems to be the opening of a gland and lateral processes are found on this segment.

*Empida*.—In the Empidæ two plates usually form this part. In *Hilara cilipes* is the curious notched process previously alluded to, and in the interior wall is the opening of a glue-gland (Pl. 25. fig. 42).

Dolichopodidæ.—In Dolichopus griseipennis this part appears to be quite membranous; there is also a glue-gland with a funnel-shaped opening in the interior wall (Pl. 25. fig. 52). In D. festivus three plates are present, as is also the case in Pæcilobothrus nobilitatus, where there are also suggestions of the formation of rods.

Syrphidæ --- In Syritta pipiens the part presents no noticeable structure.

Muscidæ.-In Musca domestica, at the posterior part of the segment, are four small,

transverse, setose plates, and three long narrow rods longitudinally support the membrane (Pl. 29. fig. 107).

In Calliphora erythrocephala there is a dorsal plate opposed by a shorter ventral plate. Polictes lardaria has three transverse setose plates.

Ulidia nigripennis has four half-formed chitinous rods on this segment (Pl. 28. fig. 95). Before discussing the next section, "the spiracle-bearing segment," I propose making a few remarks upon a part that is occasionally met with and whose presence accounts for traces of chitinous structure found without any apparent reason in the ovipositor.

## The Apodeme in the Ovipositor.

Simuliidæ.—In Simulium reptans (Linn.) \* there is an apodeme at the extremity of the abdomen; it is a thin chitinous process and forks at its posterior part, the forks partially enclosing an opening (which appears to be that of the vagina) and having at their extremities some connexion with the external valves. The function of this part is to rotate the opening, as I have preparations which show the shaft of the apodeme in both anterior and posterior relation to the opening.

Asilidæ.—In an undetermined Asilid from Queensland there is, in a similar position, a plate with the posterior extremity furcate; near this part the orifices of the ducts of the three receptacula seminis open. This apparatus appears to be homologous with the apodeme in *Simulium*, and explains the frequent appearance of chitinous rods in *Syritta* (Syrphidæ), *Stratiomys* (Stratiomyidæ), and other insects.

Homology.—In homologizing this part with the ovipositor of Musca domestica, its furcation suggests that it is represented by the partially fused rods in the third segment, but its position points to other structures in a more anterior position. It appears to me that these levers are a development in the direction of the telescopic ovipositor, it being of advantage to insects to extrude the ovipositor even in a small degree.

Chironomidæ.—Chitinous structures are also found close to the valves of Chironomus plumosus (Linn.) and C. riparius, Meig.

#### The Spiracle-bearing Segment.

Bibionidæ.—In Bibio hortulanus, Dilophus febrilis (Linn.), D. albipennis, Meig., and Scatopse notata the abdomen has, on the segment next the penultimate segment, single paired spiracles, as on this part in those families where the ovipositor is telescopic.

Stratiomyiidæ.—In Beris vallata the spiracles are on the membranes on the sides of a central, ventral, smaller plate. In B. nigra the plate is large, consequently the spiracles are farther apart.

Tabanidæ.—In this family, unlike the Bibionidæ, the spiracles appear to be on the penultimate segment; but I think, from the evidence of a small triangular piece in *Hæmatopota pluvialis* (Linn.) and *H. crassicornis*, Wahlb., that the last segment has fused with the next and represents two.

Empidæ.—In the Empidæ the spiracles are about the middle of the segment.

\* There is some uncertainty as to this insect, but it is of the same size and colour, and if it is not the genuine S. reptans, Linn., it is almost impossible without special study of this family to separate the two species.

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Dolichopodida.—In Dolichopus griseipennis and D. festivus the spiracles are in the anterior part of the segment.

Syrphidæ.—In Syritta this segment has no structure to notice except a single pair of spiracles at the anterior part.

Muscidæ.—In Musca domestica three transverse setose plates at the posterior part of the segment, anterior to them three fine long rods, two of which are fused together at their anterior ends. I cannot find any spiracles on this segment (Pl. 29. fig. 107).

In Calliphora erythrocephala there is a dorsal plate opposed by a longer ventral plate; the posterior corners of the dorsal plate bear two pairs of spiracles close to each other. This is a striking character, which I find also in *Protocalliphora grænlandica*, Zett., and Lucilia sericata, Meig., as well as in the Anthomyids, Hydrotæa dentipes (Fabr.), Ophyra leucostoma, Wied., and Anthomyia pluvialis, Linn.

*Polietes lardaria* has no spiracles on this segment, the only structures being three transverse setose plates.

In Ulidia nigripennis, on this part are three plates, and a pair of spiracles is laterally arranged (Pl. 28. fig. 95).

Aberrant forms.—I shall now describe two ovipositors which are very unlike the usual plan of the part.

In the Tachinid *Phorocera serriventris*, Rond., or *concinnata*, Meig., a remarkable form is found. The valvulæ superiores are fused and formed into a single highly chitinized hook, which is bent in under the abdomen and appears much like the penis in many flies. Another process is found on one side with setæ, and on the other side another asymmetric part. Close to the hook are paired spiracles. The insect was in the viviparous stage, the abdomen being full of fully-formed larvæ (Pl. **30**. figs. 118, 119).

Lauxania ænea, Fall., is also very divergent from the general type. The dorsal edge is furnished with the usual paired organs (valvulæ superiores); opposite these the ventral plate is drawn out into a single strong lanceolate process, having on either side two plates which may be the homologues of the valvulæ inferiores (Pl. 30. fig. 121).

#### The Receptacula seminis.

Number.—The number of these organs varies from one to four; but in the Muscidæ it is nearly always three. When the organ is single it is usually of large size.

Nomenclature.—They are sometimes known as spermathecæ, but Dufour calls them "glandes sébifiques." I am under the impression that "receptacula seminis" is Lowne's name for the parts.

Bibionidæ.—In Bibio hortulanus and Dilophus febrilis (Linn.) they are three in number and globular in shape. In Scatopse notata oval, relatively large, and single (Pl. 23. figs. 3, 11).

Chironomidæ.—In a few females of Chironomus that I have examined I cannot find any; but in the genus Ceratopogon three are found.

Culicidæ and Tipulidæ.—In the Culicidæ and Tipulidæ these organs are globular and three in number.

Strationyida.—In the Strationyidæ they are more oval in shape and have characteristic long chitinized tubes, which continue for a similar distance in a hyaline condition, and are three in number.

Tabanidæ.—In Tabanus bovinus, Hæmatopota pluvialis, and H. crassicornis the receptacula are peculiar, relatively small, quite pyriform in shape, attached to exceedingly long tubes whose circumference is only a little less than that of the receptacula. They end in muscular outgrowths, which have the appearance of columns, the capitals being formed of a transverse plate which the tube pierces; these outgrowths penetrate the walls of, and open into, the oviduct. They are three in number (Pl. 30. figs. 123, 128).

Asilidæ.—Three globular receptacula with long muscular ducts are found in the Asilidæ.

Bombylidæ.—A similar arrangement and number of receptacula to that of the Tabanidæ are found in Comptosia ocellata.

*Empide.*—I have only found one receptaculum in the females of the Empidæ that I have examined.

Dolichopodide.—In the Dolichopodidæ, as well as several other families, the receptacula are not chitinous and do not show in my preparations. But the rectal papillæ four glands which surround a portion of the anal passage and whose exact function is not clearly demonstrated—are very prominent. They are shown on the ultimate segment of the ovipositor of *Dolichopus griseipennis* (Pl. 25. fig. 52), but this gives no real idea of their true form; they are cone-shaped, the base is a chitinous hoop which has some very fine aculeations scattered on its surface. This hoop rests on a membrane with tracheæ in its structure, and supports a transparent or subtransparent cone which is studded with numerous curious laminæ, which have one of the edges pectinated, resembling a scale of Lepidoptera (Pl. 30. figs. 124, 125).

They are present in equal development in both sexes, and are very evident in several species of *Dolichopus*, as well as in *Pacilobothrus*.

This part is, strictly speaking, not in the subject-matter of this paper; but as the receptacula in this family are difficult to find, and appear to be of a different structure from that which is usually found associated with the part in Diptera, I think it as well to draw attention to them, especially as they appear in Pl. 25. fig. 52, and as they might easily be mistaken for receptacula, unless the observer was familiar with Lowne's \* description of those organs in *Calliphora*.

Syrphidæ.—In Syritta pipiens and Eristalis tenax the receptacula are three in number, are of a flattened oval shape, and carry long tubes.

Muscidæ.—In the Muscidæ three receptacula are usually found; but my preparations of Stomoxys calcitrans (Linn.), Ilæmatobia stimulans, Meig., Glossina morsitans, and G. palpalis only show two receptacula. In the Anthomyzidæ the receptacula are three in number, and often have marks on the cuticle quite distinctive of the species. Anthomyia radicum has short dark papillæ on the surface (Pl. 30. fig. 133). Homalomyia manicata, Meig., shows short spines on the inside cuticle. Hylemyia cinerosa, Zett. (?),

\* 'Blow-fly,' pp. 417-418.

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thick knobs with broad bases; *Pegomyia bicolor*, Wied., fine blunt spines inside (Pl. 30. fig. 134). In the Cordyluridæ it is also variable, quite long and vermiform in *Scatophaga stercoraria* (Pl. 29. fig. 115; Pl. 30. fig. 116). In *Helomyza similis* the receptacula are four in number. In *Ulidia nigripennis* they are three in number and of very curious form (Pl. 28. fig. 95). In *Scioptera vibrans* (Linn.) they are four in number, but double, the pairs being joined by the tubes, each pair having only one duct (Pl. 30. fig. 132). Several preparations of *Lonchæa* and *Toxoneura muliebris*, two; *Balioptera tripunctata*, Fall., and *B. combinata* (Linn.), two; *Sepsis cynipsea*, two.

*Ephydridæ*.—All the Ephydridæ I have examined have a single receptaculum, but this is of a peculiar design. In the small *Hydrellia griseola*, Fall., it is very large and shaped like a thimble; in *Parydra coarctata* somewhat of the same shape, but longer, and from the flat end proceeds a thick stalk (Pl. 29. fig. 114).

Borboride.-Borborus has two, and Limnosina three receptacula.

#### Remarks on those Families whose Genitalia have not been analyzed.

I shall now make a few remarks on the families that have been omitted in the foregoing review.

Pulicidæ.—The Pulicidæ are a doubtful group, as some morphologists place them in a separate order (the Aphaniptera or the Siphonaptera). Mr. Verrall, however, includes them in his list of British Diptera. In *Pulex irritans* the penis is double and consists of two chitinous stiles, to each of which a hyaline membrane adheres. These stiles coil on themselves, at the interior extremities appearing to connect with a large gland (the testes?). In an interior position is a strong apodeme; between it and the two stiles is a membranous tube, longitudinally wrinkled, which in the Muscidæ I should recognize as the sacculus ejaculatorius but for the fact that no apodeme appears to be present. The upper part, with which the great apodeme connects, is furnished with two hairy processes (the forcipes superiores) and some complicated chitinous ones which my preparation does not clearly define. Behind the forcipes superiores is the pygidium, the curious sense-organ found in both sexes of the Pulicidæ.

In the female the values are represented by several hairy processes below the pygidium, and one large receptaculum seminis of peculiar shape is clearly seen (Pl. 29. fig. 113). In *Ceratopsyllus jubatus*, Wag., the flea parasitic on the bat, one of my preparations shows organs at the end of the abdomen which may represent the appendages of the theca, but these insects are so minute that I cannot definitely say so. The other parts resemble those in *P. irritans*. The double stile, so far as my knowledge goes, is not in favour of the idea that the Pulicidæ are degraded Diptera.

Cecidomyiidæ.—In the Cecidomyiidæ one preparation shows an armature approximating to that of the Chironomidæ. In another the forcipes superiores and inferiores, as well as the forcipes interiores, are evident and the penis is membranous; but it is difficult or impossible to determine specimens till the group has been more systematized; a study of the genitalia of prepared insects will probably be the easiest means, as otherwise they keep so badly that, after a few years, only specimens mounted in balsam are of much use for comparison.

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Simuliidæ.—In Simulium ornatum, Meig., the forcipes superiores are small and hairy; the forcipes inferiores large, and each have a small spine placed symmetrically opposite each other near the ends. On the theca appear to be barbed appendages, but my preparation is not satisfactory, and I cannot trace the apodeme. In S. reptans (Linn.) (?) I can make out an arrangement of the theca with some affinity to that found in the Culicidæ; there is, however, a central apodeme which is forked at its junction with the theca. The females have the usual valves, a single receptaculum, and a peculiarity in the shape of a bifurcate apodeme to the aperture of the vagina. This appears to answer to the double apodeme or to the fused rods in the ovipositor of Musca domestica.

Chironomidæ.—The Chironomidæ are a large group, but, like the Cecidomyiidæ, of fragile structure. I can trace all the valves and appendages in my preparations, but not beyond that, the apodemes and ductus ejaculatorius eluding me. In the females I cannot see the receptacula, these also not being of robust structure, except in a single preparation of *Ceratopogon obscurus*, Winn., where I find three, and those three relatively very large. I hope at some future time to make a special study of these insects.

Orphnephilidæ.—The Orphnephilidæ have only two European species, neither of which is in my collection.

Psychodidæ.—The Psychodidæ are minute and difficult of preparation. The females of some species have egg-guides somewhat similar to those on *Ptychoptera albimana* and *Trichocera hiemalis*. A male has four relatively very large forcipes, and I think I can trace the apodeme.

Leptidæ and Therevidæ.—The Leptidæ and Therevidæ are small groups of the Tabanid type at which I have hitherto had very little opportunity of working.

Scenopinidæ and Cyrtidæ.—The Scenopinidæ and Cyrtidæ are even smaller, both families only numbering five species in the British list. Dufour has some remarks on Scenopinus fenestralis in his paper already quoted.

Lonchopteridæ.—The genitalia of the Lonchopteridæ, like the venation of the wing, approximate to those of the Muscidæ; but the receptacula must be of a different structure, as they do not show in the preparations cleared in potash, whereas they show admirably in those of the Muscidæ treated in this manner.

*Platypezidæ.*—I have not had an opportunity of examining any species of the small group of the Platypezidæ.

Pipunculidæ.—In the Pipunculidæ the males have generally a very prominent hypopygium, with an armature something between that of the Empidæ and the Syrphidæ. In *Chalurus spurius*, Fall., the flagellum is furcate a short distance from the point; the theca also is furcate, and the flagellum enters it at this point. The rest of the theca is much like that in the Empidæ, but at the interior end, though it widens out, it does not form a sac, nor is it articulated with the ejaculatory apodeme. Instead of this, a hyaline membrane proceeds from it with the usual small apodeme, as it is found in the Muscidæ (Pl. 30. fig. 117).

Conopidæ.—In the Conopidæ the male has often a bulbous hypopygium, but the forcipes are not of very definite shape, more valvular than hamate, but covered with

many short spines and blunt bristles; both apodemes are easily made out in *Sicus ferrugineus* (Linn.) and *Myopa buccata* (Linn.).

*Œstridæ.*—The male of *Gastrophilus equi*, Fabr., has large horny forcipes, like those of the Conopidæ, more valvular than hamate, but without spinous processes; the appendages are large, but I have only very poor preparations of both sexes, and cannot make out either of the apodemes. The female has hairy valves which enclose a curious chitinous chamber in the vagina, and I can only make out two receptacula; but obviously this insect requires more study from fresh preparations before anything more definite can be said.

*Phycodromidæ*.—The genitalia of the Phycodromidæ are distinctly Muscid in type, but have a long ribbon-like process at the extremity. A species of *Cælopa* has on the end of the penis five triangular membranous appendages; from the central triangle, which is flanked on either side by a pair of the others, the ribbon is attached; a long central apodeme is easily made out. The ovipositor is much longer than that found in the Cordyluridæ, but not so long as in *Musca domestica*, and has the usual three receptacula.

Heteroneuridæ.—I have no preparations of the small Heteroneura family in my collection.

Sciomyzidæ.—In the Sciomyzidæ the genitalia are of the Muscid type in most species. Sciomyza cinerella, Fall., has both levers very much developed, and the female appears to have only two receptacula, but these are remarkably horny, covered with short barbs and with strongly chitinized stalks. The ovipositor is short, with hairy valves and two apodemes at the base of the penultimate segment.

Psilidæ.—The males of Loxocera albiseta (Schrank) have small genitalia of a rather indefinite character, and possibly other species of this group may give better results.

Micropezidæ and Piophilidæ.—In the Micropezidæ, also, I have had insufficient material, and even less in the minute Piophilidæ.

Drosophilidæ.—The male of Drosophila funebris (Fabr.) has most elaborately hamate genitalia of a decided Muscid type; the female has a short ovipositor not capable of extrusion and only two receptacula (so far as a single specimen is to be relied on).

Chloropidæ.—The males in the Chloropidæ have apodemes of the Muscid type, and the females long membranous ovipositors, which consist of three segments, and have a characteristic longitudinal striation. The receptacula are not chitinous, as none appear in my preparations that have been cleared in caustic potash.

Milichiidæ, Agromyzidæ, Asteiidæ.—I have no preparations of these families in my collection.

*Phoridæ*.—In some males of the Phoridæ there are suggestions of a petiolated hypopygium like that in the Dolichopodidæ, but the genitalia are peculiar and not easy to classify. The females of some species have an ovipositor which is remarkably like that of the Chloropidæ, and which also does not show any receptacula.

IIippoboscida.—In the Hippoboscida the penis appears to consist of several stiles, as in the Strationyiida. In *Melophagus ovinus* (Linn.) the double levers are evident, suggesting a Tabanid descent; the female has, however, the two pairs of paired spiracles which we find in some Muscidae.

Braulidæ.—In the male of Braula cæca, Nitz., the minute parasite of Apis mellifica, small as it is, I can trace the appendages, and they appear of more Muscid type than the genitalia of Melophagus.

*Nycteribiidæ*.—The Nycteribiidæ are a difficult group to study, and I have only had access to some preparations in the British Museum, and have had no opportunity of making dissections, the only satisfactory way of studying genitalia.

The male of *Nycteribia Dufourii*, Westw., has a large pair of forceps, quite ventrally placed, articulated at their bases; their points are highly chitinized, and are not unlike those of *Glossina palpalis*. The penis is small and the apodemes cannot be differentiated. There are many spines in the region of the laminæ superiores, but no actual plate; laterally there are two bulbous processes very thickly spined.

The ovipositor cannot be said to exist in the Pupipara, but there are relatively large processes at the extremity of the abdomen of the female.

In Cyclopodia Hopei, parasitic on one of the flying-foxes, the male has a rather pointed abdomen; on the ventral side of this are articulated a neat pair of forceps which meet at their points and quite cover the cavity of the hypopygium. Between their bases two small chitinous knobs can be seen. There are no lobular spined processes as in N. Dufourii, but the segment opposite the forcipes has a short row of blunt spines on its edge, which represents the laminæ superiores. The female cannot be said to have valves, but has two large tubercles situated dorsally and ventrally on the extremity of the abdomen; the larger is on the ventral side and is tufted with bristly hairs, and that side of the abdomen has many long strong spines.

In another species of this genus, also parasitic on a "flying-fox," labelled Nycteribia Westwoodii, in the Cabinet of the Quekett Microscopical Club, the forceps are more like those of N. Dufourii; it has the row of blunt spines representing the laminæ superiores, but no lateral processes. This specimen, which has been cleared and mounted under pressure, shows in the interior a very large aculeated membrane, with long chitinous spines and a strong apodeme, which appears to be the penis, but no appendages can be made out.

# Similarity of Appearance of Genitalia and Mouth-parts in Diptera.

A person acquainted with the mouth-parts of Flies, particularly with the armature of *Simulium* and *Tabanus*, must be struck, when examining the genitalia of the Muscidæ, by a similarity of appearance and arrangement. In both he finds a central organ surrounded by aculeate and setose appendages, and in both the central organ pierced by a tube or duct. It occurred to me that these parts, so widely separated in situation, were intimately connected, and that they were both influenced by an *identical law* of growth and development.

By "*identical law*" I mean such a law as governs the growth of the number of joints on the limbs; a law not absolutely inelastic or immutable, as can be seen in the tarsi, where, though five joints are generally found, a lesser number is sometimes met with. It regulates the growth of the appendages of both extremities.

Quite different from this law is that which governs the secondary sexual characters

that develop on all parts of insects: under the first law, though admitting infinite variety of form, those forms are rigidly confined within the limits of a fixed scheme and can be homologized throughout the Insecta; under the second law, though admitting an even greater variety of form and contrivance (all, it is true, with a very obvious objective), the forms are not capable of homologization; we can recognize that an identical cause has broadened and shortened the tarsi of *Platychirus* and *Dytiscus*, but the extraordinary suckers on the tarsi of the Beetle can only be recognized as homologous in its family; they have no counterpart in the fundamental scheme of Insecta.

A similar law, governed by a different necessity, has developed the "ptilinum" in both sexes of the *Cyclorrhapha* in Diptera.

If we could adopt the old idea of design in Nature, we might think of the genitalia and mouth-parts as formed on the same plan, or as the working-out of the same idea. Failing that, we assume that they might be derived from organs which, placed at both extremities of the organism, shaped themselves by unknown but similar laws of growth. So we find the extremities furnished with hamate appendages such as maxillæ or forcipes interiores, and sensory appendages such as maxillary or genital palpi, and these appendages surrounding and attached to a central organ which itself has special senseorgans attached to it, "taste-hairs" on the labium, or the aculeate membrane on the penis.

I submit that if it were a matter of development along the "lines of least resistance," or of growth similar to the second law, we might expect frequent departures from the unity of plan that we can trace in these organs; that possibly appendages fulfilling the functions of mouth-parts would be found attached to the fore legs, if not in most, at least in some species, as in that position they could be used with equal, if not greater, convenience. This is contrary to all experience, but when we leave the true insects, and examine such a group as the Arachnida, we notice the absence of the unity of design both in the mouth-parts and the genitalia.

Genitalia in the Arachnida and Hydrachnidæ.—In the Spiders the males have the genitalia on two palpiform processes which spring from the roots of the fore legs, as in *Meta segmentata* and *Stemonyphantes lineatus*, and these vary from extreme simplicity to extreme complexity; while in the Water-Mites a spermatophore is picked out of the genital pouch by the claws of one pair of legs and transferred to the genital pouch of the female, both organs having a similar situation on the centre of the abdomen.

In Odonata.—It may be argued that even in the true insects there is a departure from the general type in the Odonata, where the copulatory apparatus is in a segment far removed from the extremity of the abdomen, though the forcipes and the genital pore remain in their usual position. I have made only one or two dissections in this group, and these are not complete, but my preparations show a theca, genital palpi, forcipes interiores, a penis, and a spine, which can be homologized (putting aside the segmentation) with the corresponding parts in Diptera; this is in *Æschna cyanea*, Müll.

In Orthoptera.—Some of the Orthoptera also present a difficulty, as in many species a spermatophore is transferred by a hook to the cloaca of the female; this is, according to Lowne\*, most probably the method by which the common Cockroach, Periplaneta orientalis, Linn., is fertilized.

Homologics of the Genitalia in Periplaneta orientalis and Diptera.—With the view of homologizing the genitalia of the two orders, I have made a number of dissections of this *P. orientalis*, and have come to the following conclusions. The greatest difficulty of the investigation was the unsymmetrical character of the parts.

1. The whole combination, which in all the other insects that I have examined is always in the longitudinal plane of the abdomen, in *Periplaneta* is placed in a transverse position. What Lowne calls the left gonapophyses (the spinus titillatorius) is usually the most anterior part of the genitalia.

2. Though there is no duct opening in a penis, there are parts which represent the theca, the hypophallus, and the paraphalli.

3. The part which I homologize with the hypophallus is highly chitinized, has a structure of short triangular servations similar to that on the same part in the Blow-fly a structure which is constantly recurring in the different families of Diptera (Pl. 25. fig. 41; Pl. 26. fig. 68; Pl. 29. fig. 101).

4. These are grouped round the "conglobate gland" of Professor Miall<sup>†</sup>, the paraphalli forming the "saddle-shaped piece."

5. Opposite and distinct from these organs, on the right side of the insect, is a mechanism of a number of pieces forming a receptacle and fitted with a plate which acts as a lid. Below this, and supporting the base, is an apodeme which, from its structure and situation, I homologize with the ejaculatory apodeme in Diptera, more particularly as it is found in the Tipulidæ.

6. There are also pieces which, though they are not symmetrical, represent the forcipes interiores, and a hairy process which shows the site of an atrophied palpus.

7. The important great apodemes are difficult to find and equally difficult to display in a preparation. On either side of the left-hand part of the genitalia (the penis and its appendages), and forming part of the membrane at the bases, are two insignificant islands of chitin quite surrounded by a sea of wrinkled, transparent membrane. They appear to be functionless, and are nearly suboval plates, tapering to a point. Their microscopic structure is consistent with my idea that they are the atrophied remains of the apodemes.

These complete the list of pieces in the left-hand part, with the exception of a small subtriangular piece at the base of the titillator, which appears to be some part of its articulation to the theca.

A species of *Brachytrupes* has genitalia very different from *Periplaneta*. They are symmetrical; there is a central stillform simple penis, which appears to have the opening of the ductus ejaculatorius at its extremity. This is surrounded by a theca, bearing forcipes interiores and palpi genitalium, fused to it. A pair of lateral apodemes are

\* 'Blow-fly,' p. 664:
† 'The Cockroach,' Miall and Denny, p. 174.
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articulated to the theca. At the base of the penis is a sac surrounded by muscles, which may be some form of ejaculatory apparatus.

I have also made a few dissections and preparations in the Coleoptera, Lepidoptera, and Hymenoptera, which show that the male genitalia, as might be expected, since mouth and all other parts agree, can be homologized on the scheme originally constructed from the organs in the Diptera.

Coleoptera.—Lucanus cervus, Linn., has a long flagellum similar to that in the Ortalidæ (Pl. 28. fig. 96). This starts from a bulb articulated to the penis, which is supported by two apodemes. The ejaculatory duct can be traced to the bulb of the flagellum, and has a structure similar to that on the part in Syritta pipiens. The whole organ is swathed in several chitinous envelopes, probably representing segments of the abdomen, and the theca, which immediately surrounds the penis, supports the forcipes interiores.

Acilius sulcatus (Linn.), an aquatic insect, has the "titillator" much developed and occupying its usual position. This part is also to be seen in a preparation of a land beetle which I cannot satisfactorily identify.

In *Geotrupes stercorarius* (Linn.) the theca is long and cylindrical; it bears at its extremity two articulated plates, the forcipes interiores; through these protrudes a sensory membrane, which envelops a chitinous structure; this structure is extruded by two slender apodemes.

*Necrophorus interruptus*, Steph., is of the same type, but the forcipes interiores are longer, and the apodemes cannot be recognized.

Lepidoptera.—In the Lepidoptera the genitalia are mostly simple, often consisting of only the forcipes superiores and a horny central penis; but in Arctia caja (Linn.), which has a wide distribution, I find the forcipes superiores seemingly fused into a single piece, the theca supporting a pair of forcipes interiores and surrounding the base of a cylindrical penis, with a membranous process running through it; the membrane having the triangular aculeations so common in Diptera and also to be found on the genitalia of the drone in Apis mellifica. In Neuronia popularis a pair of apodemes can be differentiated.

Hymenoptera.—A Saw-fly, Cimbex ariana, Kirby, has the hypopygium turned in under the abdomen exactly as in Glossina; the plate carries cerci and hairy organs, representing the forcipes superiores and inferiores. It will be remembered that G. palpalis has forcipes superiores and the remains of atrophied forcipes inferiores in an identical situation. The theca surrounds the penis and bears the forcipes interiores and the palpi genitalium; but the penis in the Tenthredinidæ consists of paired convoluted valves, each supported by an apodeme, and the mechanism of the ejaculatory apparatus (if one exists?) is not obvious. I have found a similar penis in several species of Nematus.

I think it probable that an examination of a number of families in Insecta will yield types closer to Diptera than those considered, but there appears nothing to guide the enquirer to a particular genus or family. I now recur to my main argument, the relationship between the mouth-parts and the genitalia.

#### BOTH THE SEXES IN DIPTERA.

# Further Remarks on the Relationship between Genitalia and Mouth-parts.

In support of the idea that similar laws govern the growth of the genitalia and the mouth-parts, I have, in a tentative fashion, prepared a table of relationships, which gives the parts of the male and female which have already been homologized in the previous discussion, as well as a list of portions of the mouth-armature which, from structure or function, appear to be the counterparts of the genitalia. In justification of this selection I have some evidence which, taken by itself, might be treated as mere coincidence, but gains weight from the other parts fitting into their places.

Fulcrum or Submentum.—In the mouth-parts of the Muscidæ, embedded in the base of the proboscis, is a chitinous plate which, from its median suture and lateral continuations, is obviously a fusion of two organs. It is used to extrude and control the labium, having attachments for many muscles. Lowne calls it the "fulcrum," and says \*: "Gerstfeldt † is, I believe, the only author who has anticipated me in the statement that the maxillæ enter into the composition of the fulcrum, but he merely observes, 'The anterior lancet (labrum) shows distinctly, by the presence of a median raphe, that it is formed of two halves, which must be the blades of the maxillæ (Kieferladen). They rest upon a piece extending backwards (the fulcrum) which appears to be the united stipites, from which two slender, nail-shaped parts diverge downwards and backwards.'"

I have called ‡ the part the "submentum," which has been thought to be the cardines and stipites of the second pair of maxillæ (usually called the labium), differing in this from Lowne, who considers it to be the first pair of maxillæ, because I have shown that, together with this part (the fulcrum), there exist in *Hydrellia griseola*, Fall., nearly complete first maxillæ, and in identical situations in other Diptera these are nearly always present, the stipites and cardines often carrying the maxillary palpi.

**Relation** of the Great Apodeme to the Submentum.—The double apodemes, from their situation below the theca, from their paired character, and from their function, I consider to homologize with this part, the submentum or fulcrum.

I have shown the double apodemes to be separate paired organs in some species, in others partially fused, the upper part being forked, and in other species totally fused. It is remarkable how analogous this part seems to be with the submentum.

# "The Labial and Maxillary Palpi in Diptera," Trans. Linn. Soc. London, ser. II. Zool. vol. ix. (1903).

<sup>\* &#</sup>x27;Blow-fly,' p. 138.

<sup>† &#</sup>x27;Ueber die Mundtheile der saugenden Insecten.' 8vo. Dorpat, 1853.

#### Analogies.

Great Apodeme.—(1) It is present in its paired form in several (judging from the geological record) of the oldest families (Tipulidæ and Tabanidæ).

(2) It is present in its fused condition in the Cyclorrapha, only to be found in the Oolite, whereas the Nematocera and the Brachycera date from the Lias, or, in simpler language, it is found in the fused condition in the younger families, but still retaining traces of its former state.

(3) It performs the functions of an apodeme, governing the movements of the central organ.

(4) It is situated at the base of the central organ.

Submentum (fig. 137).—(1) This, when part of the second maxillæ, consists of the stipites and cardines of paired organs, the posts or levers, and hinges of a more or less complicated mechanism.

(2) It is fused in insects like *Periplaneta*, or in the Cyclorrapha, but still retains traces of its paired state.

(3) It performs the functions of an apodeme, governing the movements of the central organ.

(4) It is situated at the base of the central organ.

A plate from the ovipositor of an undetermined Asilid from Queensland, that has already been alluded to, is remarkably like in general outline and some points of structure to the submentum (fulcrum) in Diptera. This I consider is homologous with the apodemes, and consequently represents the submentum.

Labrum and Forcipes superiores.—Evidence in favour of another part is also forthcoming—the identification of the labrum as the representative of the fused forcipes superiores. I have repeatedly mentioned the hairy nature of these last-named parts, which will now be seen to have a connexion with the matter under discussion. I will state my reasons at length for my selection.

Hypopharynx (1).—There is only one *unpaired chitinous* organ in the mouth-parts, the hypopharynx, situated immediately behind the central organ, the labium.

Spinus.—There is only one *unpaired chitinous* organ in the genitalia, the spinus titillatorius, situated immediately behind the central organ, the penis; therefore one represents the other.

Composition of Labrum (2).—Covering and next to the hypopharynx is the labrum, an obvious fusion of paired organs, with often a cleft at the extremity, and always a median suture and symmetrical rows of bristle-cavities (Pl. 30. figs. 129, 130); probably a fusion of the lacinize of the maxillæ, the true labrum being the mouth-edge. This exists as a separate part in the Ephydridæ; *Parydra coarctata*, Fall.\*, shows it particularly well.

\* See Journ. Roy. Micr. Soc., 1904, pl. 8. fig. 7, where, however, I mark the part as the Clypeus, following the usual practice.

Forcipes superiores.—Covering and next to the spinus titillatorius are the forcipes superiores, nearly always hairy and setose, and occasionally fused as in Oliviera lateralis (Pl. 30. fig. 120) or Rutilia splendida. Therefore the labrum, or fusion of the lacinize of the maxillæ, represents the forcipes superiores.

But it may be pointed out that both the labrum and maxillæ are present in the Empidæ and Syrphidæ, as well as in all the flies with complete mouth-parts; to which it may be answered that the parts of the maxillæ present are the galeæ, which are the parts aborted in the Muscidæ—the often setose character of the laciniæ quite supporting this view.

Fig. 137.

DIAGRAM OF MOUTH-PARTS IN DIPTERA.

pr. Paraglossa.

Labium,

m. Mandible.lg. Ligula.g. Galea.lp. Labial palpus.mp. Maxillary palpus.pg. Palpiger.pf. Palpifer.mn. Mentum.s. Stipes.sm. Submentum.c. Cardo.lr. Labrum.h. Hypopharynx.

I now venture to submit a table of relationships of the genitalia and the mouth-parts of Diptera, as, if what I have already advanced can be accepted, the other parts appear to fall into their places. A counterpart for the very important labial palpi appears to be wanting, but that may be explained in the same way as their absence in the large Empid and Syrphid groups is explained.

	MALE GENITALIA.	Ov	IPOSITOI	R.	MOUTH-PARTS.		
<i>(</i> l	Forcipes inferiores.	Ventral plates or egg-guides.		g-guides.	Mandibles.		
b	" superiores.	Dorsal ", "		<b>?</b> ) .	Labrum or fusion of laciniæ.		
C	Laminæ superiores.	Ventral plate of abdomen, 4th from end.		domen, 4th	Mentum.		
d	Orifice of ejaculatory duct.	Aperture of vagina.			Orifice of pharynx.		
e	Theca.	Rods and chitinous structures: lamina interior.		structures :	Labium.		
f	Paraphalli.	22	37	22	Ligulæ.		
g	Hypophalli.	23	,,	33	Paraglossæ.		
h		23	99	29	Hypopharynx.		
i	Forcipes interiores.	33	33	29	Maxillæ (galeæ).		
<i>k</i>	Palpi genitalium.	22	77	79	Maxillary palpi.		
m	Double apodemes.	Double rod, Musca domestica. Apodeme, Simulium.			Submentum; or fused stipites and cardines of 2nd pair of maxillæ.		
n	Ductus ejaculatorius.	Vagina.			Pharynx.		
0	Sacculus ejaculatorius.	Utero-vaginal tube.					
<i>p</i>	Ejaculatory apodeme.		?				
r	Vas deferens.	Oviduct.			Œsophagus.		
s	Paragonia.	Parovaria or receptacula seminis.		cula seminis.			
<i>t</i>	Vasa efferentia.	Tubæ.					
<i>u</i>	Testes.	Ovaries.					

Table of Relationship of Genitalia and Mouth-armature in Diptera.

I have often sought for the reason why the armature of the male mouth is less than that of the females in the blood-sucking Culicidæ and Tabanidæ.

Compensation of development of Trophi and Genitalia.—The idea of an identical law of growth affords some explanation, because if that law exists it would include compensation; that is to say, if the mouth-parts were much developed, the genitalia might be expected to be simpler or *vice versa*. Let us apply this test, and see how it works out.

Differences in mouth of males and females.—The armature of the female Tabanid mouth consists of mandibles, maxillæ (the stipites, cardines, and galeæ), the maxillary palpi (the labial are aborted), the hypopharynx and the part usually called the labrum (the fusion of the laciniæ of the maxillæ), and the labium bearing the usual tracheated paraglossæ (labella).

The males have no mandibles, and the maxillæ are rudimentary or atrophying, but have the other parts that the female possesses.

1. Now as regards the genitalia, the females have a very simple type of ovipositor,

and one not capable of extrusion; while the male, as I have shown in Tabanus bromius, has complex genitalia.

Nearly identical conditions are found in the Culicidæ.

Cases where the genitalia are complex in both sexes :---

2. The male has very complex, though not complete, genitalia in *Tipula oleracea*, and the female a striking ovipositor. The mouth-parts are comparatively simple, the mandibles being fused into the labium; the galeæ of the maxillæ and the labial palpi are absent; the labrum and hypopharynx are very imperfect; the tracheæ of the paraglossæ are not well-developed, and the whole organ seems to have undergone great changes. In the Muscidæ the genitalia are quite as complex, and we find nearly the same armature on the mouth, except that the palpi are labial and not maxillary. Cases where the mouth-parts are nearly aborted :—

3. In *Gastropilus equi* the mouth-parts consist only of an aperture and two hairy processes. The compensation in this case seems to be in size, as the ovipositor is a very prominent part of the insect, and the genitalia of the male are large and chitinous.

Cases where the genitalia incline towards simplicity :----

4. Parydra coarctata has comparatively simple genitalia, the spinus and palpi genitalium being absent. The mouth-parts are proportionately very large; a distinct clypeus (which I have submitted is the true labrum) is present, and the structure of the tracheæ is abnormal.

Case where the genitalia is simple in mechanism but well-developed as to size :---

5. In *Empis stercorea*, whose genitalia I have already commented on, the mouth-parts are large, the labium, maxillæ, hypopharynx, and labrum well-developed and strong, the only weak parts being the maxillary palpi.

So-called teeth on Paraglossæ:-

1. In all cases where the ovipositor is of the Musca domestica type, the teeth on the labella are thin and transparent, or absent.2. In all cases where the ovipositor has hardened, as in the Ortalidæ and Lonchæidæ,

the teeth are quite absent.

3. In most cases where the teeth are strongly developed, as in the Cordyluridæ, the ovipositor is short as in Scalophaga stercoraria (Linn.) (Pl. 30. fig. 131); the exceptions are in the *Cænosia* group of the Anthomyzidæ, where very chitinized teeth are found, together with a long, membranous ovipositor. The males are of the Muscid type, which is complicated as a whole, but tends towards simplicity of the individual organs.

Summary as to the failure of parts in the male mouth.—From these cases it may be assumed that when the male mouth-armature is failing or variable, it is brought about by reason of a relationship between mouth and genitalia, the over-development of one part causing, by compensation, the failure or simplification of the other. That being so, the nature of the food in the blood-sucking species has no connexion with the failure of the mouth of the male, though it may possibly have acted indirectly on the genitalia by reason of its stimulating character.

The fact that in Stomoxys, Ilæmatobia, or Glossina both sexes are bloed-sucking and identical in mouth-armature, supports this view, as the mouth-armature is, though

highly modified, also much simplified. The labrum or upper lancet is only equalled in simplicity by that part in the Culicidæ, while the hypopharynx is in an atrophying condition in *Glossina*. In *Stomoxys* the male genitalia are relatively small, though in *Glossina* they are highly developed and modified, yet both are simplifications of the Muscid type, owing to the abortion and fusing of the appendages of the theca, the spinus, genital palpi, and interior hooks. There is no extrusile ovipositor in *Glossina*, but in *Stomoxys* there are indications that at some period it resembled that of *Musca domestica*; the joints appear to be there, but in a fused condition. I spent a considerable time unsuccessfully endeavouring to extend the organ. There is also simplification in the number of receptacula, which is always two in this group.

Analogy in the Mammalia.—In addition to what I have advanced in favour of the theory of the intimate connexion between the growth of the genitalia and of the mouth-parts, it may be pointed out that there are analogies in the Mammalia, where the effects of excision of the genitalia on the throat and voice, as well as beard, of the male are common knowledge.

Summary of the main argument.—I have now shown: (1) That the male genitalia and the mouth-armature are on the same general plan, of a central perforated organ surrounded by aculeate and sensory or possibly sensory appendages. (2) That they coincide in many details of structure and arrangement. (3) That the male and female genitalia are homologous. (4) That the male armature, the ovipositor, and the mouthparts have a central mechanism (double apodemes, apodeme of ovipositor, fulcrum or submentum), which guides or governs the whole, or traces or remains of such a part. (5) That the application of an hypothesis founded on the above data accounts for the hitherto unexplained failure of the male mouth-parts in the Culicidæ and the Tabanidæ. (6) That an intimate connexion is known to exist between the male genitalia and the throat, voice, and the hairy appendages of the mouth in the Mammalia.

Ancestral form of the Arthropoda.—Further, I am informed by Mr. H. M. Bernard, F.L.S., &c., that the idea that genitalia and mouth-parts are homologous is not new; the hypothesis has been advanced that, in a primitive ancestral form of the Arthropoda, these mechanisms were formed by adaptations of the legs of the end segments.

My opinions are arrived at by a close study of the mouth and genitalia of the principal families in Diptera, and almost wholly by methods of comparative anatomy. My arrival at what is practically the same conclusion, by an enquiry comparatively very narrow in its scope, being confined to a single Order, is evidence in favour of this hypothesis.

Weighing these facts, I submit that there is much evidence in favour of my main thesis, which may be formulated thus :---

Formula.—The external appendages of both extremities in Insecta are derived from two organs of the character of maxillæ, and all the variations of the parts are adaptations of these organs.

# METHODS OF WORK.

For the convenience of those who wish to examine genitalia or to test my statements, and are unacquainted with the usual procedure, I shall now explain my methods of work on these very minute parts. I will presume that the enquirer has the usual outfit of the worker in microscopy. Fresh or newly-killed insects are undoubtedly the best subjects; but specimens preserved in alcohol are nearly as good, and old pinned dry ones are often extremely useful. The genitalia, protected in a cavity, are as a rule intact, though the insect may have lost every other appendage. If a species is to be thoroughly studied, at least three specimens of each sex ought to be procured. I assume that they are newly-killed insects. (1) Immerse one of each sex in 15 per cent. solution of caustic potash; 10 per cent. solution will do but takes longer. This is to clear the insects, and the length of the process will depend on the density of the chitinous structure; a day may be enough, or it may take over a fortnight. In this process all the muscles and nerves are dissolved and destroyed, leaving the membranes, the exoskeleton, and all the chitinous structures. (2) After this is accomplished the preparations must be thoroughly washed in water; and (3) then placed in glacial acetic acid for 24 hours to get rid of the potash crystals and any fat that may have escaped the action of the chemical. (4) They must again be washed in water. (5) After this they are in a flaccid state, and can be readily arranged on a 3-inch slip in any desired position. The wings will be found to flatten better if the specimen is floated on to the slip. In the case of the male a lateral arrangement is best, as it more clearly shows the genitalia in their natural positions; but where possible it is well to have a preparation showing the ventral surface as well. A pair of strong clips, such as are used to hold papers, is useful in the next process. (6) After the insect has been arranged on the slide, another slip is placed above it; it is squeezed flat by applying a clip at one end, and the process is completed when the second clip is applied at the other end. There is now an opportunity for roughly examining the preparation with low powers to see that the organs are properly displayed, and that (for instance) a claw does not cover the hypopygium, or the trophi of the head are not hidden. If unsatisfactory, undo the clips, separate the slides (care is required in this), drop some water on the insect, and rearrange it. If, however, the initial effort is successful, tie the slips tightly together with fine twine, remove the clips, and (7) immerse in methylated spirit for at least 24 hours. In cases where the preparations have been over cleared, a stain is useful. Aniline blue is best in my experience; fuchsin is also good, but care must be taken not to overstain. A drop can be placed on the insect before the upper slide is applied. In the spirit the preparations will be dehydrated, and on the result of this process the success of the preparation as a microscopic object depends. After that they will be ready for transference to spirit of turpentine, which should be of the best quality procurable. (8) To do this, the slips must be withdrawn from the spirit with a pair of forceps, the string untied, the slips slowly and carefully separated, and the preparations taken from the slide on a sectionlifter. (9) After being at least 24 hours in turpentine they are ready for mounting in Canada balsam, though many microscopists recommend a further clearance in clove-oil.

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(10) A preparation is then lifted out with a section-lifter and placed in the centre of a slip, and examined on a microscope to see that no hairs, cotton-wool, or dust disfigure it, and that it presents the ventral side (if it is not a lateral preparation). (11) The moiety of the turpentine is then removed by means of blotting-paper, taking care that not too much is taken, as otherwise air will enter into the cavities. (12) Canada balsam dissolved in xylol is then applied, and the whole sealed with a cover-glass, which may be pressed down by the weak clip sold for this purpose. These preparations will be dry enough for use in about two days, and must be carefully studied, so that a good idea of the form and of the relative situation of the parts is arrived at, before proceeding to the separation and dissections which must be undertaken later. The microscopist will require a good high power. I recommend a 7th of Mr. Pillischer, of New Bond Street, as the best I know of for the purpose, as it is comparatively inexpensive, works at a greater distance than any similar magnification that I am acquainted with (which is its peculiar advantage over lenses of higher angular aperture), and gives good definition. With this must be used a powerful substage condenser to enable the light to pierce through the more chitinous parts.

To study accurately, drawings must be made, and where it is necessary to compare shape and size, those drawings ought to be made on squared paper corresponding to squares in the eyepiece of the microscope.

This is the comparatively easy part of the work; in what follows the student must not be discouraged by repeated failure, as he has to acquire the steadiness of nerve and nicety of movement necessary for dissecting under the microscope.

(1) The end of the abdomen must be removed and placed in a drop of water on a livebox or compressorium (the cover being removed), and the organs "teased" apart with the finest needles procurable. The forcipes superiores and inferiores must be separated from their articulated bases, and the penis and its appendages brought out free from its adhering duct and muscles. Place the cover-glass on, and the separated parts can be roughly examined with low and higher powers, and drawn, if desired. The muscles will often be found very hampering and obscuring; a drop of potash solution will facilitate their removal. If this is used, before proceeding further, drop water on the dissections and endeavour to remove the potash as thoroughly as possible; a little acetic acid will help, but this also must be washed away.

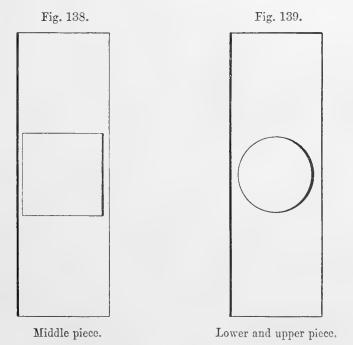
(2) Take a  $\frac{7}{8}$  cover-glass (thickest size), place a small drop of spirit on it, and place on it the parts, by means of a needle or a bristle. This is very difficult, and the coverglass must be examined with a lens to judge of success. Care must be taken to avoid the loss of parts by dropping off the needle, &c. Place some more spirit on the glass and place it on a piece of white paper, and both on the hot-plate, which must then be gradually heated. (3) As the spirit evaporates it must be replaced by dropping fresh; a glass rod drawn to a point answers best. This must be continued till all the water has been driven out of the dissections; it will sometimes be seen as a milky fluid on the edge of the glass, and can be removed with blotting-paper.

(4) Turpentine must now be dropped on the (by now) hot slide, and allowed partially to evaporate, always dropping fresh before the specimens are dry. Now put out the lamp and let the preparations gradually cool, never letting them get dry, or air will spoil them. (5) When cool, remove the superfluous turpentine with blotting-paper; and as quickly as possibly (6) place Canada balsam and a smaller and thinner cover-glass on the dissections.

(7) This  $\frac{7}{8}$ -glass, when dry, can be mounted between three slips of cardboard, the upper and lower punched with a circular hole (fig. 139), and the middle cut to the shape of the larger cover-glass (fig. 138). They can then be gummed together and placed in a press.

(8) For permanently sealing both these preparations I recommend spirit-varnish.

This last preparation mounted thus can be examined on both sides with high powers, which is necessary for a proper understanding of the mechanism and of the real shape of the parts.



In many cases it will now be necessary to take a fresh insect, dissect out the penis, and then undertake the still more difficult task of separating that into component parts, proceeding to mount it exactly as in the foregoing case.

The dissections can be done with an inch objective on a strong microscope with a flat stage; a telescopic tube is a convenience, as it permits of a quick amplification of magnitude.

The insects which have been preserved in spirit only need to be thoroughly soaked in water before dissection, but they will be found more brittle, and consequently more difficult to handle, though, on the other hand, muscles will detach more readily.

Dry specimens.—In the case of dried specimens, they may be placed in hot water for half an hour before dissection, or soaked for a few hours in cold.

*Air-bubbles.*—Air-bubbles can be driven to the side of the cover-glass by means of heated needles (not red-hot, or they will crack the cover-glass), or a nail is better, as it retains the heat longer.

Chilled balsam.—Sometimes, in spite of care, the specimen has not been sufficiently dehydrated, and the balsam is "chilled" and the whole slide a failure, as nothing can be clearly seen. The remedy requires careful nicety :—(1) Place a piece of white paper on the hot-plate; on the paper place the preparation. The paper prevents the glass becoming too hot, and also shows the situation of the dissections, which often cannot be seen without the white background. The balsam will soon melt, and the air will run in; (2) then lift off the upper glass with a fine pointed forceps, and place it balsam-side uppermost on the paper.

(N.B.—Do not use the forceps again till it has been dipped in spirit and the points wiped. The neglect of this precaution has caused many disasters, and the flow of many tears of the Recording Angel necessary for the obliteration of words \*.)

(3) Drop turpentine on the preparation; this will drive all the balsam to the sides, leaving the dissections in the middle, where the preparation can have a thorough washing in evaporating turpentine repeatedly dropped on it. (4) Then put out the lamp and proceed as before, dropping balsam, and sealing with the old or a fresh cover-glass.

Sections.—If abundance of material is available, sections of the hypopygium can be cut.

Mounting without pressure.-There yet remains another method, but it cannot be applied to insects larger than the house-fly, Musca domestica. This is the mounting of the whole insect without pressure; the initiatory processes are identical till it arrives at the pressing stage. (5) Instead of being placed on a slip, it is placed in a small saucer on its back and a little water poured in. The wings, legs, and proboscis are arranged in their desired position. (6) The water is drawn off and replaced with spirit; when the specimen is quite stiff it may be lifted out with a section-lifter and placed in a closed receptacle also filled with spirit, where it should remain for 48 hours or as much longer as is convenient, to set thoroughly and dehydrate. (7) It is desirable that this receptacle should have a flat bottom, as otherwise the arrangement of the insect will be altered and possibly spoilt. (8) It is then lifted out very carefully, with the section-lifter as before, and transferred to turpentine, but this must not be done till the operator is quite satisfied that it is very thoroughly dehydrated. Failures in this part of the process are more likely in this type of mounting than in the pressure type. (9) After 48 hours in the turpentine the insect can be lifted out and placed on a slide. (10) Cover it with plenty of balsam and place round it (11) three or four glass beads of a suitable size (I prefer transparent ones, zinc rings are equally good); these must have been prepared (12) by being washed in alcohol and afterwards in turpentine. Transfer them straight from the turpentine to the balsam, and their preparation will ensure that no air hangs to them and that they sink readily into the thick medium. (13) Place a cover-glass on the insect, which will not be injured by the pressure as the cover-glass will rest on the beads. (14) Put a weight (a small bullet answers well) on the cover-glass and then run in balsam under it till it is quite full; this will shrink in a day owing to the evaporization of the xylol; (15) and fresh must then be run in till it is quite set and firm, when it may be ringed in the usual manner.

\* Tristram Shandy: "And the Recording Angel, as he wrote it down, blotted it out with a tear."-STERNE.

This preparation is best suited for examination with a binocular microscope and lowpower objectives, and the position of the interior organs can be well seen in a successful slide. It remains to say that when only the chitinous and membranous structures are wanted, dissection is greatly facilitated by 24 hours' immersion in the potash solution.

# EXPLANATION OF THE PLATES.

The following letters are used in the female genitalia :---

- a. Valvula inferior, or ventral egg-guide.
- b. Valvula superior, or dorsal egg-guide.
- d. Aperture of the vagina.
- m. The apodeme or the double rod.
- n. Vagina.
- o. Utero-vaginal tube.
- r. Oviduct.
- s. Parovarium.

The following letters are used in the male genitalia :----

- a. Forceps inferior.
- b. Forceps superior.
- c. Laminæ superiores.
- d. Orifice of ejaculatory duct.
- e. Theca.
- f. Paraphallus.
- g. Hypophallus.
- h. Spinus titillatorius.
- i. Forceps interior.

- t. Tuba. u. Ovarium.
- w. Lamella anterior.
- x. Receptaculum.
- y. Egg (ovum).
- z. Glue-gland.
- x''. Rectal papilla (*Dolichopus* only).
- k. Palpus genitalium.
- m. Double apodemes.
- n. Ductus ejaculatorius.
- o. Sacculus ejaculatorius.
- p. Ejaculatory apodeme.
- r. Vas deferens.
- s. Paragonium.
- t. Vas efferens.
- u. Testis.

## **PLATE 23.**

- Fig. 1. Genitalia of Sciara thomæ (Linn.), &.
  - 2. Genitalia of Bibio hortulanus, Linn.,  ${\tt Q}$  .
  - 3. Receptaculum seminis of B. hortulanus, Linn., 2.
  - 4. Penis and appendages of B. hortulanus dissected out of abdomen.
  - 5. Forceps inferior of B. hortulanus  $\mathcal{J}$ .
  - 6. Palpus genitalium of *Scatopse notata* (Linn.), removed from its place on fig. 7, where it is hidden by the forceps interior.
  - 7. The genitalia of S. notata, drawn diagrammatically to show the arrangement of the parts; scen from the ventral aspect.
  - 8. Ejaculatory apodeme of S. notata, enlarged.
  - 9. Diagram of the sacculus ejaculatorius and its apodeme and duct (S. notata).
  - 10. One of the interior hooks in Culex (?).
  - 11. Extremity of abdomen of S. notata, showing the single receptaculum.
  - 12. Second interior hook in Culex (?). This and that figured as 10 are opposed by a similar pair of hooks on the front of the central organ.
  - 13. Central organ in Culex (?).
  - 14. Forcipes superiores of Anopheles cinereus.

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# MR. WALTER WESCHÉ ON THE GENITALIA OF

- Fig. 15. Central organ of *Gynoplistia bella*, Westw., showing the three apodemes and the changes in the theca.
  - 16. Forceps superior of Culex (?). This part in C. pipiens only differs by the articulated bristle at the extremity of the hook being of a different shape.
  - 17. Ventral view of hypopygium of *Ptychoptera scutellaris*, showing the situation of the ejaculatory apodeme ; the penis has been removed, and is shown in fig. 20.
  - 18. Ejaculatory apodeme of P. scutellaris.
  - 19. Forceps superior of Gynoplistia bella.

### PLATE 24.

Fig. 20. Central organ (penis) in P. scutellaris.

- 21. Ovipositor of Tipula oleracea, Linn., lateral view.
- 22. Forceps superior of T. oleracea.
- 23. Theca and flagellum of T. oleracea.
- 24. Diagram of the last segments of the male abdomen of *T. oleracea*, to show the arrangement of the ejaculatory apparatus. The forcipes superiores and inferiores have been removed.
- 25. Forceps inferior of T. oleracea.
- 26. Ejaculatory sac and apodeme of T. oleracea.
- 27. One of the processes which constitute the sense-organ on the plate of the forceps inferior of T. oleracea, seen from above.
- 28. The same part in section.
- 29. Theca and flagellum of Pachyrrhina maculosa, Meig.
- 30. Ejaculatory sac and apodeme of P. maculosa.
- 31. The same apodeme enlarged.
- 32. Extremity of the ductus ejaculatorius and forcipes interiores of Beris vallata (Forst.).
- 33. The last segments of the abdomen of the male of *B. vallata*, drawn diagrammatically to show the arrangement of the parts.
- 34. End of abdomen of B. vallata  $\mathcal{Q}$ .
- 35. End of abdomen of B. nigra, Meig., 9.
- 36. Forceps inferior of an undetermined Asilid from Mt. Gambier, S. Australia.
- 37. Forceps superior of same insect.
- 38. Ejaculatory duct of same insect, showing the arrangement of the ejaculatory sac and apodeme in the base of the theca.

#### **PLATE 25.**

Fig. 39. Penis of Empis stercorea, Linn.

- 40. Forceps superior of E. stercorea.
- 41. Penis of Hilara cilipes, Meig.
- 42. Ovipositor of H. cilipes.
- 43. Hypopygium of Dolichopus plumipes (Scop.).
- 44. Orifice of the ejaculatory duct and the end of the theca of D. festivus, Hal.
- 45. Spinus titillatorius of D. festivus, Hal.
- 46. Forceps interior of D. festivus.
- 47. Palpus genitalium of D. festivus.
- 48. Palpus genitalium ? of D. festivus (doubled part).
- 49. End of penis of Pæcilobothrus nobilitatus (Linn.).
- 50. Penis, ejaculatory apodeme, and vas deferens of Dolichopus griseipennis, Stann.
- 51. Part of same, enlarged and drawn diagrammatically to show the working of the ejaculatory apparatus.

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Fig. 52. Ovipositor of Dolichopus griseipennis, Stann.

- 53. Penis and appendages of Catabomba pyrastri (Linn.).
- 54. Forceps inferior of Syritta pipiens (Linn.).
- 55. Forceps superior of S. pipiens.

# **PLATE 26.**

Fig. 56. Penis of Syritta pipiens, drawn diagrammatically to show the apodeme and ductus ejaculatorius in the interior; seen from the front.

- 57. Side-yiew of the same part, and drawn in a similar manner to fig. 56.
- 58. Penis of Eristalis tenax (Linn.).
- 59. Forceps interior of E. tenax.
- 60. Penis of Sarcophaga carnaria (Linn.).
- 61. Forceps inferior of S. carnaria.
- 62. Penis of Pollenia rudis, Fabr.
- 63. Extremities of the paraphalli in Glossina palpalis, Des.
- 64. Diagram of the opening of the ejaculatory duct, and showing the sac and apodeme, of *Eristalis* tenax.
- 65. Forceps inferior of Anthomyia radicum (Linn.).
- 66. Laminæ superiores from an undetermined Anthomyid from Maryborough, Queensland,
- 67. Ejaculatory apodeme of Glossina palpalis.
- 68. Penis and appendages of Calliphora ergthrocephala, Meig.
- 69. Diagram of the arrangement of apodemes, theca, and paraphalli of Glossina palpalis.
- 70. Forceps superior of Anthomyia radicum.
- 71. Extremity of paraphallus of *C. erythrocephala*, to show the serrated edges characteristic of the structure.

# PLATE 27.

- Fig. 72. Double apodeme and ejaculatory apodeme of Glossina palpalis.
  - 73. The same of G. pallidipes, Aust.
  - 74. The same of G. morsitans, Westw.
  - 75. The same of G. tachinoides, Westw.
  - 76. Forceps inferior of G. palpalis.
  - 77. Forceps inferior of G. tachinoides.
  - 78. Penis of G. pallidipes.
  - 79. Forceps inferior of G. morsitans.
  - 80. Forceps inferior of G. pallidipes.
  - 81. Forceps inferior of Scatophaga litorea, Fall.
  - 82. Extremity of penis of G. morsitans.
  - 83. Forceps superior of S. litorea.
  - 84. Penis and appendages of G. tachinoides.
  - 85. Penis and appendages of Anthomyia radicum.
  - 86. Fused palpi and forceps of G. tachinoides.
  - 87. Laminæ superiores of S. litorea.

#### PLATE 28.

Fig. 88. Penis and appendages of S. litorea.

- 89. Penis and appendages of Norellia spinimana, Fall.
- 90. Ovipositor of N. spinimana.
- 91. Forcipes inferiores and superiores of N. spinimana.
- 92. Forcipes inferiores of Sepsis cynipsea (Linn.).
- 93. Forceps interior (?) of S. cynipsea.

Fig. 94. Ejaculatory apodeme of Sepsis cynipsea.

- 95. Ovipositor of Ulidia nigripennis, Loew.
- 96. Penis of U. nigripennis.
- 97. Laminæ superiores of Norellia spinimana.
- 98. Penis of Notiphila nigricornis, Stenh.
- 99. Penis and apodeme of Sepsis cynipsea.
- 100. Ovipositor of Anthomyia pallida, Zett.

### **PLATE 29.**

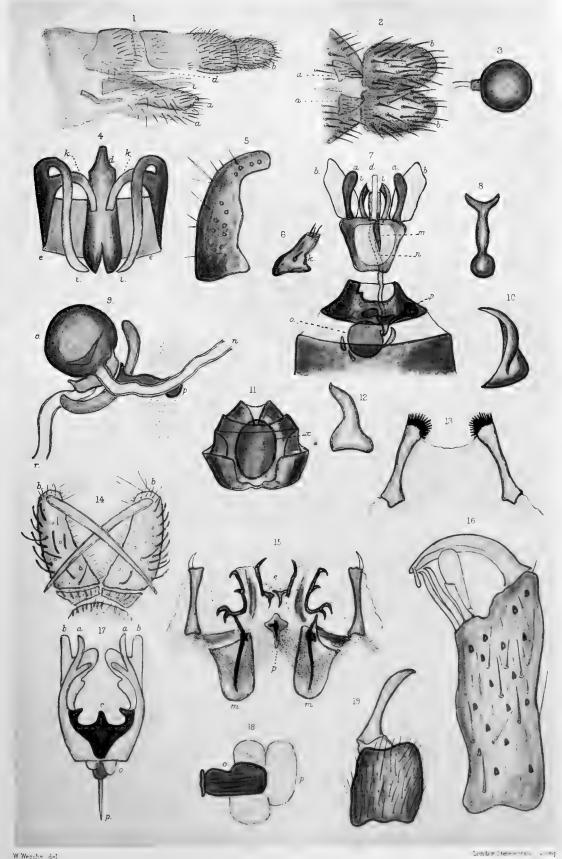
- Fig. 101. Penis and appendages from an undetermined species of Nemopoda from Jersey.
  - 102. Forceps inferior of same insect.
  - 103. Laminæ superiores of same insect.
  - 104. Diagram of genitalia of the male, showing arrangement of parts as usually found in Diptera, seen from ventral aspect.
  - 105. Ejaculatory apodeme of an undetermined species of Nemopoda from Jersey.
  - 106. The plates at the extremity of the ovipositor in Musca domestica, Linn.
  - 107. Ovipositor of M. domestica.
  - 108. Diagram of the genitalia of the male, seen in profile.
  - 109. Genitalia of Tabanus bromius, Linn.
  - 110. Penis of Parydra coarctata, Fall.
  - 111. The same seen from the front.
  - 112. Penis and appendages of Oliviera lateralis (Fabr.).
  - 113. Receptaculum of Pulex irritans, Linn.
  - 114. Receptaculum of Parydra coarctata, Fall.
  - 115. Receptaculum of Scatophaga lutaria (Fabr.).

#### PLATE 30.

- Fig. 116. Receptacula of Scatophaga stercoraria (Linn.).
  - 117. Penis of Chalurus spurius, Fall.
  - 118. Ventral side of abdomen of Phorocera serriventris, Rob.-Des.
  - 119. The hook of the ovipositor, as seen laterally, of the same insect.
  - 120. Fused forcipes superiores of Oliviera lateralis.
  - 121. Ovipositor of Lauxania ænea, Fall.
  - 122. The base of the penis in Toxoneura muliebris, Harr.
  - 123. Receptaculum of Tabanus bovinus, Linn.
  - 124. Rectal papilla of Pæcilobothrus nobilitatus (Linn.).
  - 125. A scale enlarged from the same part.
  - 126. Ovipositor of Tabanus bovinus.
  - 127. Extremity of penis of T. muliebris.
  - 128. Extremity of duct of receptaculum of T. bovinus.
  - 129. Labrum of Parydra coarctata.
  - 130. Labrum of Empis tessellata, Fabr.
  - 131. Ovipositor of Scatophaga stercoraria.
  - 132. Receptacula of Scioptera vibrans (Linn.).
  - 133. Receptaculum of Anthomyia radicum (Linn.).
  - 134. Receptaculum of Pegomyia bicolor, Walk.
  - 135. Receptaculum of Homalomyia manicata, Meig.
  - 136. Receptaculum of Schænomyza cinerella, Fall.

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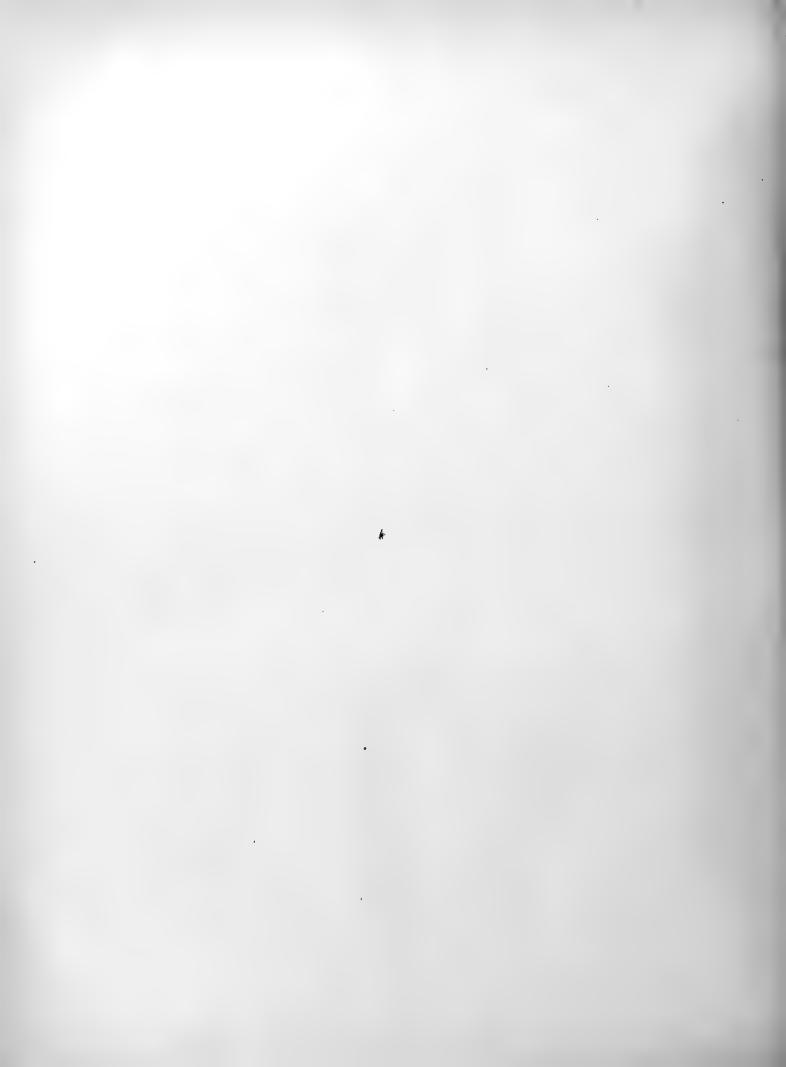
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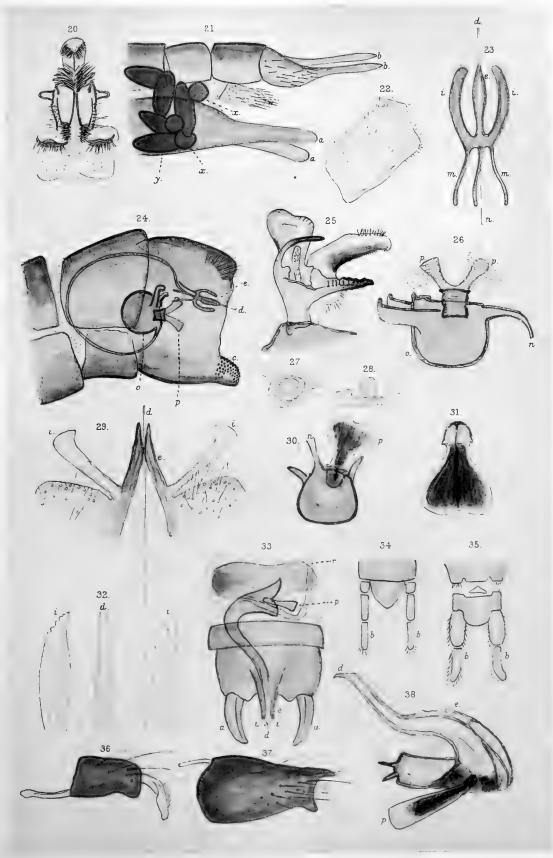


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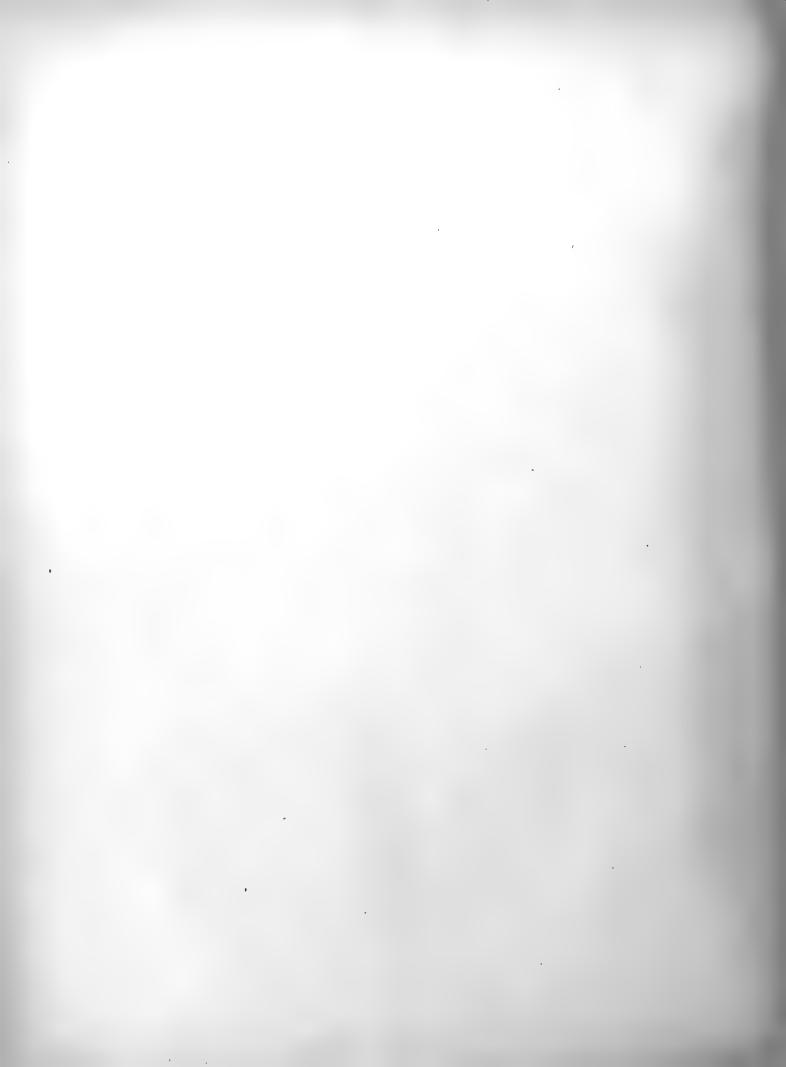


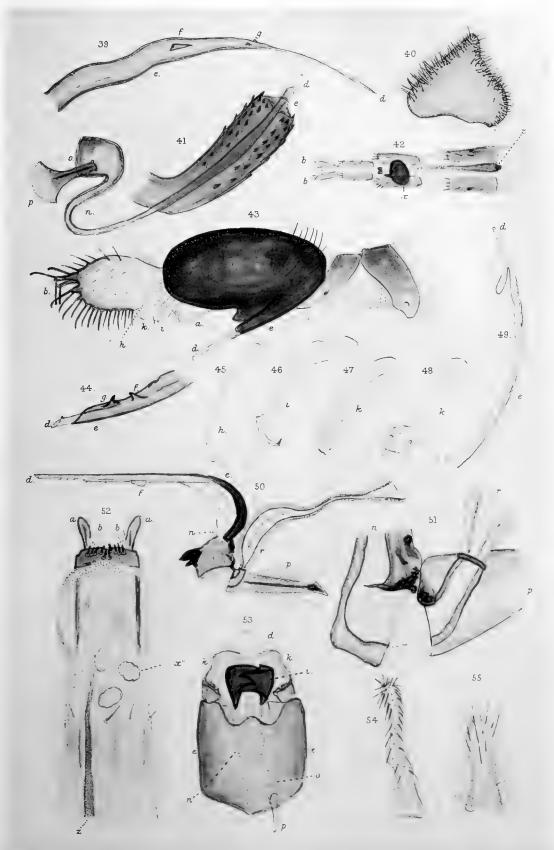


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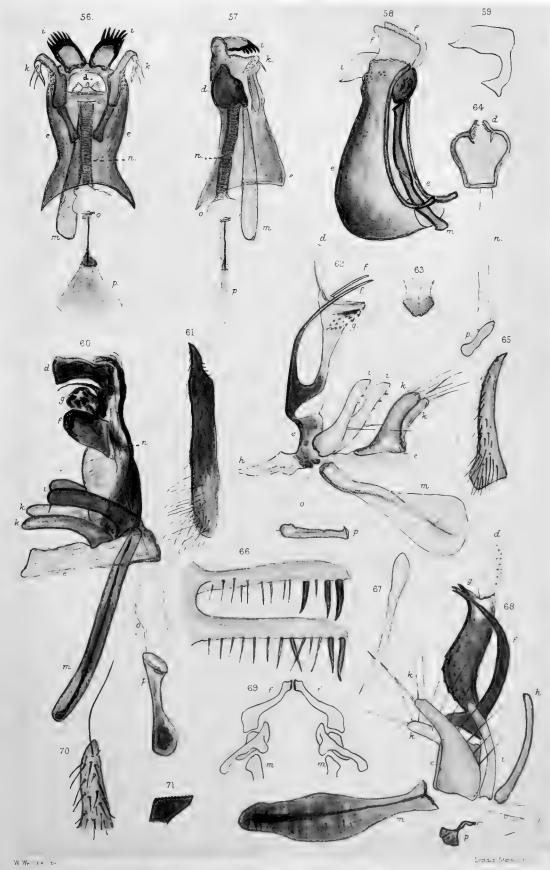
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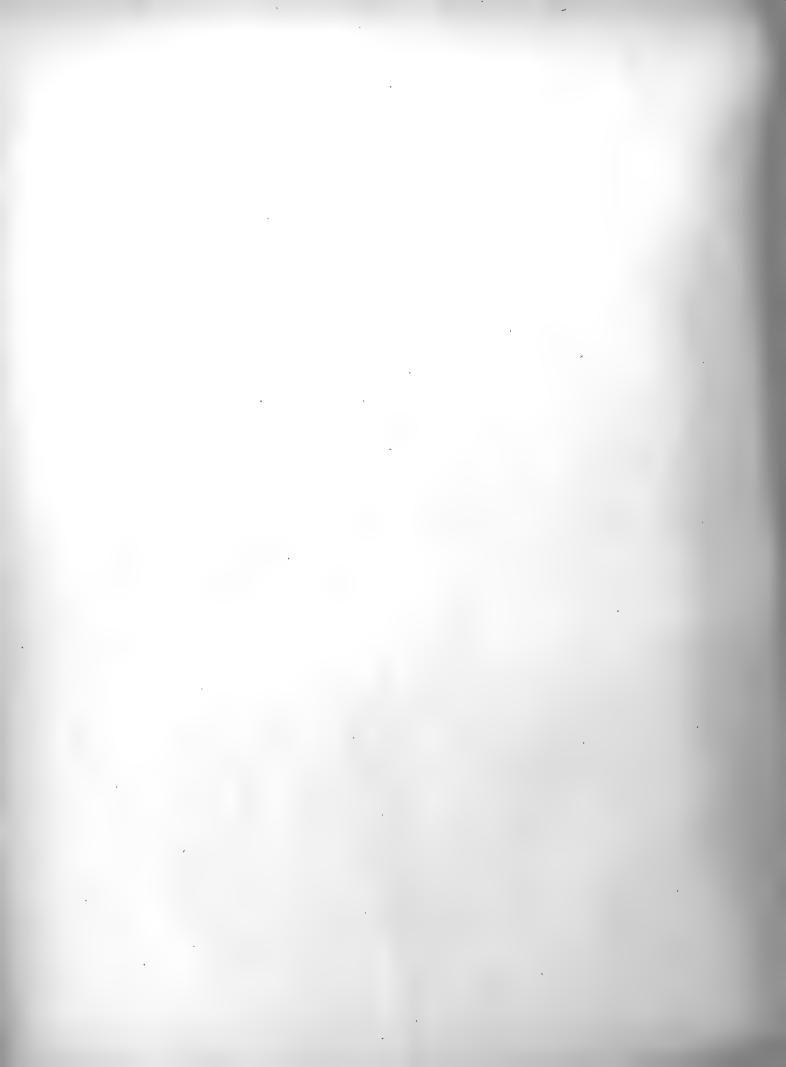
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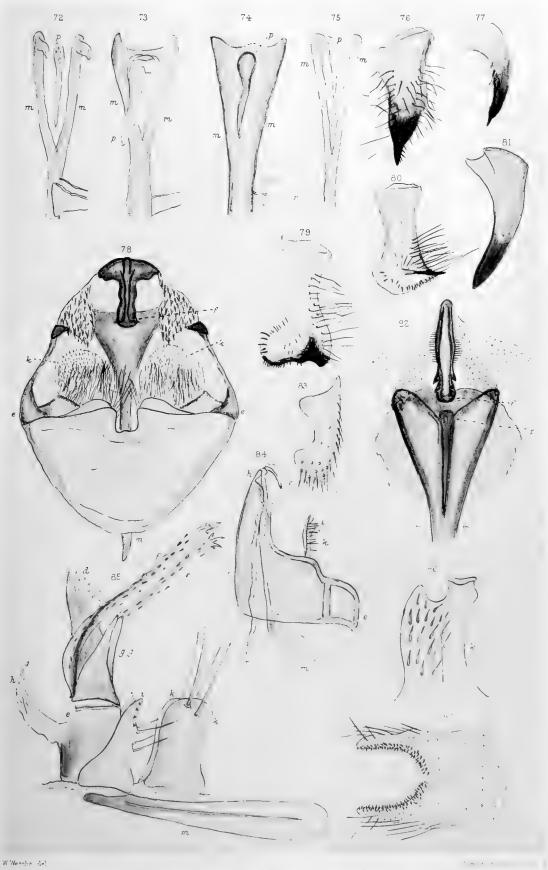
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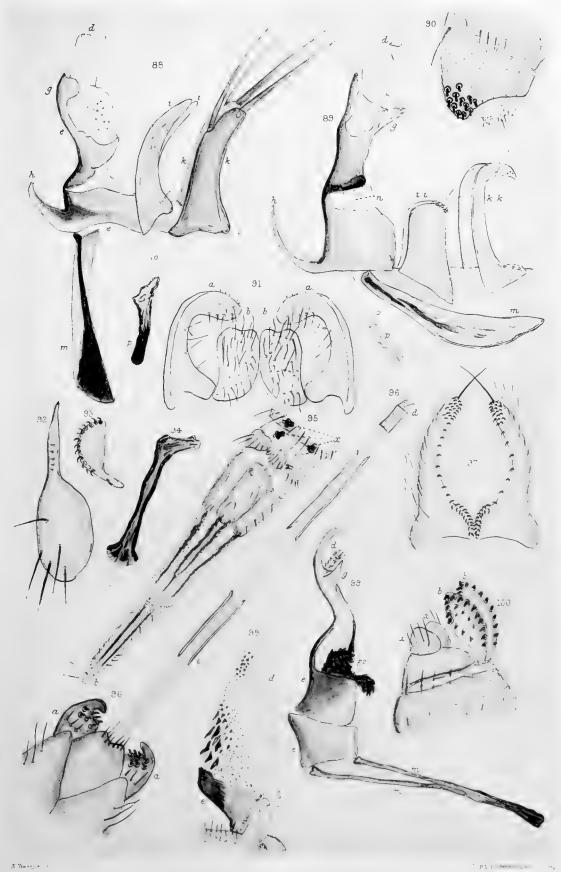




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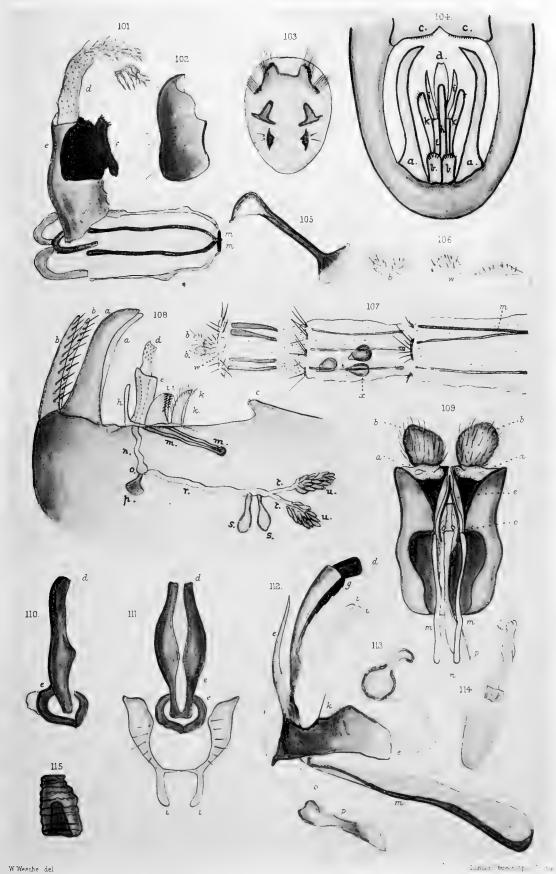
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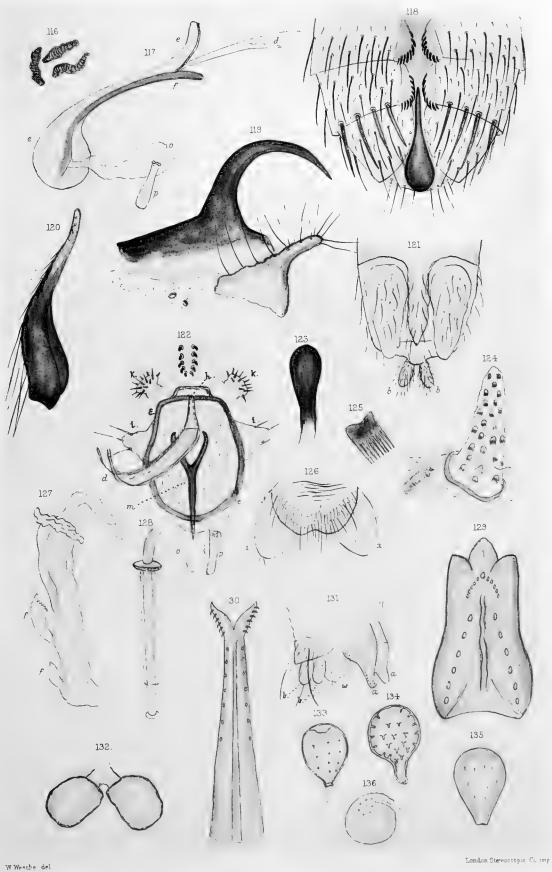
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[ 387 ]

 XI. On a Collection of Crustacea, Decapoda and Stomatopoda, chiefly from the Inland Sea of Japan; with Descriptions of New Species. By Dr. J. G. DE MAN, of Ierseke (Holland). (Communicated by the Rev. T. R. R. STEBBING, M.A., F.R.S., F.L.S.)

(Plates **31–33.**)

#### Read 1st November, 1906.

THE present collection, which was entrusted to me by Prof. F. Jeffrey Bell, of the British Museum, London, consists, firstly, of 30 species of Decapod and 2 of Stomatopod Crustacea, collected in the Inland Sea of Japan, mostly in deep water; secondly, of 7 Decapod species from four other different localities. The last named are interesting not only on account of two novelties, a new *Parathelphusa* and a new *Palæmon*, discovered respectively in the Chinese province of Yunnan and at Darjeeling, but also by the Mediterranean *Sicyonia sculpta* having been captured off Bahia; the most western limit of geographical distribution of this species was, indeed, hitherto the Cape Verde Islands, so far as I am aware. For *Potamon spinescens*, Calm., a new subgenus, *Parapotamon*, is created.

The Crustacea from the Inland Sea of Japan proved also to be of much interest. Five species are new to science, viz., a remarkable small Lambrus, for which a new subgenus, Oncodolambrus, is created, two new species of Crangon, and two of the genus Spirontocaris. Most of the other species are also remarkable. Thus a small species of Pinnotheridæ, viz., the rare Asthenognathus inæquipes, Stimps., was captured, a form described in 1858 and not found again since that year. I wish also to draw attention to the rare Arcania globata, Stimps., Galathea acanthomera, Stimps., and Leander longipes, Ortm. The discovery of the male of Spirontocaris rectirostris (Stimps.) is interesting; it shows considerable sexual differences from the hitherto only known female. Spirontocaris pandaloides (Stimps.), of which several specimens were caught, is also one of the numerous rare forms described, almost half a century ago, by that eminent American naturalist, which have not occurred in literature since that time.

Preliminary diagnoses of six new species have already been published in the 'Annals and Magazine of Natural History,' ser. 7, vol. xvii. 1906, pp. 400-406, and of the new *Parathelphusa* in the 'Zoologischer Anzeiger' of March 20, 1906.

# List of Species.

A.---INLAND SEA OF JAPAN.

Lambrus (Oncodolambrus) prædator, de Man.	Spirontocaris propugnatrix, de Man.
Lupa (Hellenus) hastatoides (Fabr.), de Haan.	S. alcimede, de Man.
Platygrapsus depressus (de Haan).	S. pandaloides, Stimpson.
Asthenognathus inæquipes, Stimpson.	Latreutes planirostris (de Haan).
Trigonoplax unguiformis (de Haan).	L. acicularis, Ortmann.
Leucosia rhomboidalis, de Haan.	L. laminirostris, Ortmann.
Myra fugax (Fabr.).	Hippolysmata vittata, Stimpson.
Arcania heptacantha (de Haan).	Alpheus brevirostris (Olivier).
A. globata, Stimpson.	A. japonicus, Miers.
Galathea acanthomera, Stimpson.	Penæus (Metapenæus) lamellatus, de Haan.
Crangon consobrinus, de Man.	P. (Metapenæus) akayebi, Rathbun.
C. cassiope, de Man.	P. (M.) acclivis, Rathbun.
Sclerocrangon angusticauda (de Haan).	P. (Parapeneopsis) tenellus, Sp. Bate.
Leander longipes, Ortmann.	P. (Trachypenæus) curvirostris, Stimpson.
L. paucidens, de Haan.	Chloridella affinis (Berthold).
Spirontocaris rectirostris (Stimpson).	C. fasciatu (de Haan).

B.—LAKE AT YUNNAN-FU, CHINA. eens, Calman. | Potamon (

Potamon (Parapotamon) spinescens, Calman.

Potamon (Parathelphusa) endymion, n. sp.

C.—DARJEELING, BENGAL.

Palæmon (Parapalæmon?) hendersoni, de Man.

D.—THURSDAY ISLAND, TORRES STRAITS. Penæus (Penæus) latisulcatus, Kishinouye, var.?

#### E.-Coast off Bahia.

Penæus (Penæus) brasiliensis, Latr. Sicyonia sculpta, H. M.-Edw., var.? Sicyonia carinata (Olivier).

A.—INLAND SEA OF JAPAN.

#### LAMBRUS, Leach.

#### ONCODOLAMBRUS, de Man.

Oncodolambrus, de Man, in Ann. & Mag. Nat. Hist. ser. 7, vol. xvii. 1906, p. 400.

Carapace broadly triangular, much broader than long. Rostrum acute, projecting and strongly deflexed. No postocular constriction. Branchial regions extraordinarily swollen, globulate, rounded, much higher and broader than the narrow cardiac region and devoid of tubercles and spines. Pterygostomian regions traversed by a ridge that runs parallel with the antero-lateral border. Chelipeds of moderate length, their margins dentate, their surfaces smooth. Ambulatory legs short.

Related to *Platylambrus*, Stimps., but distinguished by the considerably inflated and swollen branchial regions that are not tuberculate. The subgenus *Parthenopoides*, Miers, differs by the postero-lateral margins of the carapace running nearly in a straight line with the posterior margin.

# LAMBRUS (ONCODOLAMBRUS) PRÆDATOR \*, de Man. (Pl. 31. figs. 1-3.)

Lambrus (Oncodolambrus) prædator, de Man, in Ann. & Mag. Nat. Hist. ser. 7, vol. xvii. 1906, p. 400.

One male from Japan, the locality not defined.

Probably a species of small size. Measured in the middle line the carapace appears to be 7 mm. long, the front included, and the greatest breadth at the angles between the antero- and postero-lateral borders measures 10 mm.: the broadly triangular carapace is thus nearly once and a half as broad as long. The triangular, subacute front is prominent, but strongly, obliquely, deflexed. The lateral margins are parallel, though slightly concave, between the eyes and then curve inward; they are smooth and entire, but, on each side, the subfrontal process is visible as a small tooth or prominence, when the front is looked at from above, the subfrontal process being situated almost as far distant from the tip of the rostrum as from a transverse line that runs along the posterior border of the orbits. The breadth (1.8 mm.) of the front at its base is almost one-fifth of the greatest breadth of the carapace. The smooth upper surface of the front is concave between the eyes; the groove, here rather broad and deep, becomes gradually more shallow anteriorly; the groove gradually narrows backward on the upper surface of the somewhat elevated gastric region until its posterior end, when one observes a low rounded tubercle in the middle line.

The gastric region is slightly inclined from behind forwards. A little in front of the round tubercle the gastric region carries, on either side of the middle line, another obtuse tubercle that is much smaller and much less prominent. The cardiac region carries, in the middle line, two obtuse tubercles one behind the other, which are as large as the tubercle at the posterior end of the gastric region; the anterior cardiac tubercle is once and a half as far distant from the gastric tubercle as are the two cardiac from one another. Behind these prominences, which are, however, not so high as the swollen, branchial regions, one observes, on the posterior slope of the cardiac region, two other smaller tubercles, the anterior of which is probably double. The slightly convex and granulated posterior margin of the carapace carries five tubercles, namely, in the middle three smaller ones, of which the median one is a little larger than the two others and are contiguous to one another, and a larger tubercle on each side more laterally. The tubercles of the gastric and cardiac regions as also those of the posterior border of the carapace appear granulated under a very strong lens. The intestinal region carries, ion each side, in the angle between the cardiac and branchial regions, two very low prominences, separated by a shallow groove, the anterior being somewhat larger than the other.

The distance between the external orbital angles, which are not at all prominent, measures almost one-third of the greatest breadth of the carapace. The hepatic area situated between the orbits and the swollen, branchial regions are deeply concave; they are smooth, like the gastric and branchial regions, but finely punctate, the purctuation being more crowded on the gastric region. The considerably swollen and inflated

<sup>\*</sup> Prædator, robber: because, when looked at from in front, the crab seems to be burdened on each side with its prey.

branchial regions are nearly globular and very large, being twice as broad as the gastric region. There is no postocular constriction of the carapace. The antero-lateral margins which run at first outward, then curve backward and upward, terminating on the outer surface of the branchial globes in a triangular, compressed tooth which is directed outward; at the level of the subacute tips of these teeth the carapace shows its greatest breadth. The cristiform, antero-lateral margins are thus curved S-like; the described largest tooth is followed anteriorly by three or four others, that gradually become smaller, which, like the former, are granulated or denticulate on their margins. The anterior part of the antero-lateral border, defining the hepatic region laterally, is entire, not granulate. From the largest tooth the likewise cristiform and finely denticulate postero-lateral margin runs at first backward and upward, then it turns suddenly downward and inward at a right angle until near the base of the branchial regions; at this angle the postero-lateral margin carries another, rather obtuse tooth, which is smaller than that at the posterior end of the antero-lateral border and which is directed backward and outward. At the base of the branchial regions, finally, the postero-lateral margins curve for a short distance forward, not uniting therefore with the posterior border of the carapace; just at this curve they carry a rounded, obtuse tooth or prominence. From the angle where the postero-lateral margin turns suddenly downward a finely granulated ridge runs upon the upper surface of the branchial region forward and inward; just outside of this ridge the upper surface is a little concave, but more outward and forward it is regularly convex and also on the inner side of that ridge. For the rest the branchial regions are smooth, very finely punctate, the puncta being not crowded, except just near the granulated ridge above.

The orbital margins are smooth. The posterior wall of the orbits is marked with a narrow, linear fissure, the lower wall has a large triangular notch, and the obtuse, internal angle is little prominent. From the inner infraorbital tooth a ridge extends backward that makes a right angle with the acute tooth at the antero-lateral angle of the buccal frame. From the last-mentioned tooth a prominent granulated ridge runs obliquely backward on the pterygostomian regions, parallel with the antero-lateral border of the carapace; between the latter and the granulated ridge the subhepatic region is, just below the orbits, deeply concave. At the level of the middle of the buccal frame the pterygo-stomian ridge has a triangular notch.

The external maxillipeds are granular; on the inner half of the merus-joints the granules are larger. The sternum is granulated. The abdominal somites carry each a compressed, transverse tooth in the middle and another smaller one at the lateral angles; the teeth are granulated and there are granules between them; the second somite is visible when the carapace is looked at from above.

The chelipeds are subequal, the right a little longer than the left. The right cheliped, 16 mm. long, is *little more than twice as long as the carapace*, it is thus of moderate length. The arm, 7 mm. long, is quadrilateral and projects only one-third of its length beyond the carapace; its surfaces are smooth. The anterior surface makes a right angle with the lower; the edge between both is beset with small, subacute teeth. Both the anterior and the posterior borders carry small, compressed, triangular teeth, which are unequal; the upper border is also somewhat denticulate. The posterior margin of the carpus, which is smooth above and below, is sharp; it carries one tooth just beyond the middle and one at the distal end. The anterior border of the upper surface is granulate. The three sides of the trigonal palm are also smooth; the anterior edge is crenulate, the upper denticulate; the teeth are small, little prominent, but one, just beyond the middle, is somewhat larger than the rest. The sharp, cristiform, posterior margin carries four triangular teeth, one at each extremity and two in the middle; teeth and margin are, moreover, finely denticulate : that of the left cheliped carries six or seven teeth. The sharply-pointed fingers are much turned inward, the dactylus being at a right angle with the upper surface of the palm. The upper border of the dactylus is granulated, the first granule or tubercle near the articulation is much larger than the following, which become gradually smaller; the cutting-edge of the dactylus of the larger cheliped carries five low, obtuse teeth, of which the fifth, near the tip, is a little larger than the preceding. The immobile finger carries two much larger, obtuse teeth in the middle, the second of which is larger than the preceding one. The fingers of the left leg are less denticulate.

The ambulatory legs are also of moderate length, those of the first pair extend with only half their dactylopodite beyond the distal end of the arm of the chelipeds; their joints are laterally compressed. The upper margin of the merus is sharp, lamellar, and, in the legs of the last pair, faintly denticulate; the lower edge of the outer surface is, in the last pair of legs, beset with prominent, rather acute and unequal granules; on the meri of the two preceding pairs they are smaller, and on the legs of the first pair it is not the lower edge of the outer, but that of the inner surface which is granular. The upper margin of the two following joints is also lamellar and sharp, and the lower margin of the propodites is finely granulated. The terminal joints, slightly longer than the propodites, are tomentose, except at their tips. The coxæ of the fifth pair carry two acute teeth posteriorly, the outer larger than the inner.

The upper surface of the carapace is cream-coloured, the sides of the median regions are marked with wine-red spots; the chelipeds are red, and the fingers dark brown on their distal half, the tips being paler.

Lambrus (Parthenopoides) pteromerus, Ortm., from Japan, of which the type was examined by me, is a quite different, much larger species.

### LUPA, Leach.

# LUPA (HELLENUS) HASTATOIDES (Fabr.), de Haan.

Portunus (Amphitrite) hastatodes, de Haan, Fauna Japon., Crust. 1835, p. 39, Taf. 1. fig. 3. Neptunus (Amphitrite) hastatoides, de Man, in Spengel, Zool. Jahrb., Syst. viii. 1894–95, p. 557. Neptunus (Hellenus) hastatoides, Alcock, in Journ. Asiat. Soc. Bengal, vol. lxviii. pt. 11. 1899, p. 38.

One male from the Inland Sea of Japan, deep sea.

The two median teeth of the front are *distinctly less prominent* than the others, just as in de Haan's type specimen, mentioned by me (l. c.); in Indian specimens the two median teeth are usually as prominent as or even more prominent than the others, as was stated by me, and later also by Alcock, by whom a large number of individuals were examined.

The cephalothorax is 13.5 mm. long, measured in the middle line, the abdomen excluded; the external orbital angles are 10.75 mm. distant, and the tips of the large lateral spines 30.5 mm. The lateral angles of the posterior margin are spiniform. Penultimate joint of the abdomen 3 mm. long, its posterior margin straight, 2 mm. broad.

In both chelipeds the anterior border of the arm carries 4 spines; the right cheliped is a little larger than the left, the arms project nearly their whole length beyond the carapace.

The tip of the dactylus of the last pair of legs shows no trace at all of a dark fleck.

# PLATYGRAPSUS, Stimpson.

# PLATYGRAPSUS DEPRESSUS (de Haan).

Grapsus (Platynotus) depressus, de Haan, Fauna Japonica, Crust. 1835, p. 63, tab. 8. fig. 2. Platygrapsus depressus, Ortmann, in Spengel, Zool. Jahrb., Syst. vii. 1894, p. 716.

One male of medium size from the Inland Sea of Japan, caught in deep water.

This specimen, which has been compared with an adult typical male from the Leyden Museum, is 14.25 mm. broad and 12 mm. long; breadth of the anterior border of the front 6.6 mm. The right cheliped is much larger than the left, in both the inner angle of the carpus is subacute; the fingers of the right cheliped, which is just as long as the carapace, viz. 12 mm., are gaping and meet only at the tips; the arcuate and tapering dactylus carries a denticulate prominence in the middle, and between it and the tip six or seven small rounded teeth; the inner border of the lower finger carries also seven or eight small, somewhat unequal teeth. The smooth outer surface of the chela is finely punctate. The fingers of the other chela, which is 9.5 mm. long, are just as long as the palm, straight and shut almost close together; the cutting-edge of the immobile finger shows a dozen somewhat unequal conical teeth; as many teeth occur on the dactylus, but here they are very small, those near the tip being a little larger than the rest.

The legs are of a beautiful scarlet colour; the upper surface of the carapace is greenish, but the front and the antero-lateral margins are also red.

## ASTHENOGNATHUS, Stimpson.

# ASTHENOGNATHUS INÆQUIPES, Stimpson. (Pl. 31. figs. 4-6.)

Asthenognathus inaquipes, Stimpson, in Proc. Acad. Nat. Sciences Philadelphia, 1858, p. 107.

One egg-laden female from the Inland Sea of Japan, caught in deep water.

So far as I am aware, this species has not been found again since its first discovery almost half a century ago. It is a little smaller than Stimpson's type, also a female, the carapace of which was 6.8 mm. long and 9.5 mm. broad. The carapace of our specimen from the Inland Sea is 4.8 mm. long, measured in the middle line; the well-defined and granular antero rateral borders are slightly arched, diverging backward, and they meet with the somewhat shorter postero-lateral nearly at the level of the median part of the cervical groove, *i. e.* a little behind the middle of the carapace. The upper surface shows here its greatest breadth of 6.5 mm.; the proportion between this breadth and the length fully agrees with that of the dimensions indicated by Stimpson. The likewise granulated postero-lateral borders are also slightly arched, converging backward, but, different from *Tritodynamia* (confer Nobili, in 'Annales Mus. Nat. Hungarici,' iii. 1905, tab. 10. figs. 1 & 2), their concave side is turned inward, in *Tritodynamia*, however, outward. The postero-lateral borders almost reach to the posterior margin of the carapace. From the point where the antero- and postero-lateral borders meet, a granulated line proceeds backward on the side wall of the carapace, terminating above the antepenultimate legs; it is here that the carapace has its greatest width of 7.2 mm.

The upper surface, which is one-third broader than long, is slightly convex longitudinally; the median transverse groove, which is situated a little behind the middle and occupies about one-third of the breadth of the carapace, is broad and shallow; but the gastric region, which regularly curves into the strongly deflexed front, is barely demarcated from the hepatic regions. Whereas the larger anterior half of the cardiac region is slightly convex longitudinally, a shorter posterior part is somewhat depressed. Just in front of the posterior margin of the carapace, parallel with it, a *straight* ridge runs between the bases of the last pair of legs; at its lateral extremities this ridge curves forward and, running above the last pair of legs, appears here granular. The carapace is also slightly arched from side to side. Its upper surface is finely punctate, for the rest smooth; examined under the microscope it appears very finely granulate ("subtilissime granulata," Stimpson).

The distance, 3.7 mm., between the external orbital angles, which are not at all prominent, measures almost three-fifths of the greatest breadth of the upper surface and threefourths the length. The upper orbital margins regularly curve into the lateral margins of the front, which converge forward, so that the much deflexed front appears somewhat broader at its base than at its anterior border; the anterior border is 1.28 mm. broad, *about as broad as the orbits* and *one-fifth* of the breadth of the upper surface; at its base, however, the breadth of the front is almost one-third the greatest width of the carapace. When the latter is looked at from above the anterior margin of the front appears very slightly arcuate, but when the front itself is looked at from above the anterior margin appears broadly triangular, because it projects a little forward in the middle; the lateral margins of the front make distinct, somewhat obtuse angles with the anterior border. The frontal and supraorbital margins are smooth; frontal median furrow short and quite shallow.

Interantennular septum very narrow, if complete; antennular fossæ barely broader than long, well developed, like the antennulæ, which fold transversely (Pl. 31. fig. 4). The basal joint of the outer antennæ, situated between the basal antennulary joint and the small obtuse tooth at the inner lower angle of the orbits, is about as long as broad; the second joint, which is just as long, but only half as broad, reaches to the level of the front, and the much smaller third joint extends beyond it; the flagellum is 1.65 mm. long, longer than the breadth of the anterior border of the front, and reaching beyond the orbits. The orbits are well developed but incomplete below; the movable eyepeduncles are of a stout shape, being a little more than half as thick as long; the redbrown corneæ are distinctly facetted. The eye-peduncles are a little pubescent, and these minute hairs are, like those of the carapace, a little setose or ramified. Infraorbital ridge smooth, prominent, running a little below the orbits.

Epistome extremely short. The buccal cavern broadens backward, as the slightly arcuate lateral margins distinctly diverge; posteriorly it is 2.5 mm. broad, *little more than one-third* the greatest width of the carapace, and the buccal cavern appears once and a half as broad as it is long. The greater median part of the anterior border of the buccal frame is straight, whereas the smaller lateral parts are slightly convex. Palate quite smooth, without any trace of a median or lateral ridges.

The external maxillipeds are widely distant; the greatest width of the gap, at the boundary between merus and ischium, is more than once and a half as large as the breadth of each footjaw at that place; these maxillipeds are rather feeble (hence the name of Asthenognathus), for they do not quite reach to the anterior border of the buccal frame, leaving a small gap between them and this border. The ischium is 0.72 mm. long, quadrangular, its slightly concave anterior border is 0.38 mm. broad; it becomes somewhat broader backwards, so that it is 0.6 mm. broad in the middle; the ischium appears thus a little longer than broad in the middle. The slightly arcuate inner border is granulate, and one observes on its outer surface a shallow groove that runs nearer to the inner than to the outer border, with which it is parallel. The merus-joint is also quadrangular, but smaller than the ischium, for it is only 0.62 mm. long between the antero-external angle and the posterior border; this joint, 0.54 mm. broad in the middle, is but little longer than broad; the outer margin runs at first parallel with the somewhat arched inner (Pl. 31. fig. 4), but then it runs inward towards the ischium, so that it shows an obtuse angle in the middle. The anterior border of the merus is barely broader than the posterior, viz. 0.4 mm., makes right angles both with the inner and outer margins, and the antero-internal angle is rounded; a longitudinal groove runs, on the outer surface. near and parallel with the inner border along the whole length of the merus-joint. The palp is of moderate size and articulates near the antero-external angle of the merus; it consists of three joints that articulate at their distal ends. The carpus, 0.55 mm. long, measured along its outer border, is a little shorter than the merus and nearly twice as long as the following joint; the terminal joint is 0.38 mm. long, almost three times as long as thick at base, conical or rather sugarloaf-shaped; it is furnished with long setæ, and the inner borders of ischium and merus are also setose. The exognath, which is not concealed, reaches almost to the distal third or fourth of the outer border of the merus; near the middle of the ischium it is 0.23 mm. broad, about one-third of the breadth of this joint, but it distinctly narrows anteriorly. The gap between the outer footjaws is a little broader between the antero-internal angles of the merus-joints than at the base of the ischium-joints. The anterior border of the sternum is coarsely granulate.

The abdomen is 7-jointed and 5.6 mm. broad, a little less than the upper surface of the carapace; the penultimate joint of the abdomen, which is finely punctate and public public punctate in the middle line, whereas the antepenultimate

joint is 0.84 mm. long. The terminal joint is triangular, 0.8 mm. long and 1.4 mm. broad, almost twice as broad as long and barely shorter than the preceding; its posterior margin is arcuate, convex, the tip rounded.

The chelipeds (Pl. 31. fig. 5) are equal, rather feeble and small; they are 6 mm. long, almost as long as the upper surface of the carapace is broad. The arm is triangular, 2 mm. long, unarmed; its upper border is strongly curved and carries about in the middle a tuft of long setæ that are half as long as the merus. Stimpson describes the merus as "superne prominentia mediana setigera instructus," but I see no prominence at all. Carpus rounded internally. The chela, which is somewhat compressed and the fingers of which are slightly curved inward, is 3 mm. long, once and a half as long as the merus. The fingers, which are distinctly longer than the upper border of the palm, barely exceed the length of the lower border; the palm is 1.1 mm. high, so that the chelæ are nearly three times as long as broad. The fingers regularly taper to the pointed acute tips; they are of equal size, equally broad at their base, and they leave a small interspace between them that gradually narrows towards the tips; the cutting-edges are rather sharp, that of the immobile finger carries 6 or 7 very low obtuse teeth, nearly of equal size and extending along the two proximal thirds; the dactylus carries near the base two truncate, somewhat larger teeth, the first of which is little larger than the other, and beyond them the cutting-edge runs somewhat uneven, the distal third excepted. The upper border of the palm is a little hairy and seems to be slightly granular, but it cannot be described as sharp, as was done by Stimpson; his words "superne acuta" are apparently applicable to the dactylus. The outer surface of the palm and of the fingers is smooth, but a ridge proceeds along the lower border from the carpal articulation to the tip of the index, and the palmar portion of this ridge is granulated.

As regards their shape and their relative length, the ambulatory legs much agree with those of Tritodynamia japonica, Ortm. Those of the antepenultimate or third pair (fig. 6) are the longest of all, measuring 11.5 mm., i. e. once and a half the greatest width of the carapace; the legs of the fourth pair are 11 mm. long, barely shorter than the preceding; then follow those of the second pair, that are much shorter, measuring 8.5 mm.; whereas the legs of the fifth pair, 6 mm. long, are the shortest and smallest of all, reaching but little beyond the merus of the penultimate pair. The meri of the third legs are moderately enlarged, as they are almost three times as long as broad; the two following joints are nearly equally long, and the dactyli are barely shorter than the propodites. The straight dactyli are depressed and taper, about from the middle, to the pointed extremity; their outer surface is longitudinally grooved in the middle, the lateral margins are ridged, and one observes on either side of the ridges a fringe of stiff outstanding setæ. The lower margin of the outer surface of the merus is coarsely granulated, the arcuate upper border more finely and the borders of the two following joints are also partly granular. The legs of the penultimate pair much resemble those of the third, but the carpo- and propodites are a little broader in proportion to their length; the dactyli are as long as the propodi, but those of the second pair are a little longer than the propodi, measured in the middle. The dactyli of the small legs of the fifth pair, which are also a little longer than the propodites, are slightly recurved, and they 57 SECOND SERIES .- ZOOLOGY, VOL. IX.

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are furnished on their lower surface with a row of setæ, of which the first are little shorter than these joints, whereas the following regularly decrease in length towards the tips; the outer surface of the meri of these legs is distinctly granulated near the upper and lower borders. The upper surface of the ambulatory legs is covered, the dactyli excepted, with the same dark brown tomentum that one observes also on the side-walls of the carapace and near the lateral margins of the upper surface; the lateral margins of these legs are furnished with somewhat longer setæ.

Eggs numerous, globular, small.

The upper surface of the carapace has a very pale ochraceous colour.

On the legs of the fifth pair several pedunculated Infusoriæ were attached.

The genus *Tritodynamia*, Ortm., is apparently most closely related; its chief difference is probably presented by the external maxillipeds, the merus-joint of which is longer than broad and not shorter than the ischium, and furthermore by the insertion of the terminal joint on the inner border of the penultimate. The latter character was observed by Nobili in a new species referred by him to *Tritodynamia*; but it is still unknown whether this character occurs also in the typical species, *Trit. japonica*, because the outer footjaws of Ortmann's single specimen were much damaged. Probably, therefore, the genus *Tritodynamia* ought to be referred to the subfamily *Asthenognathinæ* (confer Alcock, in Journ. Asiat. Soc. Bengal, vol. lxix. part II. 1900, p. 294).

Geographical Distribution.—East coast of Nippon,  $38^{\circ}$  N. lat., on a sandy bottom (Stimpson).

## TRIGONOPLAX, H. M.-Edw.

# TRIGONOPLAX UNGUIFORMIS (de Haan).

Ocypode (Elamene) unguiformis, de Haan, Fauna Japonica, Crust. 1839, p. 75, tab. 29. fig. 1, ♂ ♀, and tab. H.

Elamena (Trigonoplax) unguiformis, Alcock, in Journ. Asiat. Soc. Bengal, vol. lxix. pt. 11. 1900, p. 387.

One male, collected in deep water, Inland Sea of Japan.

H. Milne-Edwards, in Annales Sciences Nat.  $3^{\circ}$  série, Zool. t. xx. 1853, p. 224, describes this species as having the carapace "arrondie en arrière et très-déprimée." These words are not quite exact, but liable to be misunderstood. The carapace, measured from the rather obtuse tip of the triangular front to the middle of the concave posterior margin of the carapace appears to be 7.4 mm. long; the greatest breadth above the insertion of the third pair of legs measures 9.4 mm. The undivided, smooth, and glabrous upper surface cannot be said to be "très-déprimée"; in a lateral view of the carapace the middle part of the upper surface corresponding to the cardiac area appears, indeed, to slope slightly downwards towards the front and more rapidly towards the posterior and the slightly carinate antero-lateral margins. The postero-lateral margins and the concave posterior border are distinctly lamellar.

The legs of the second and third pairs are five times as long as the length of the carapace without the front; the upper border of the meri terminates in a small tooth.

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#### FROM THE INLAND SEA OF JAPAN.

The legs are yellowish, the carapace orange-coloured.

Geographical Distribution.—Japan (de Haan); Bay of Tokyo, Kadsiyama, Kagoshima, Japan (Ortmann); Gulf of Martaban (Henderson); Andamans (Alcock).

# LEUCOSIA, Fabr.

# LEUCOSIA RHOMBOIDALIS, de Haan. (Pl. 31. fig. 7.)

Leucosia rhomboidalis, de Haan, Fauna Japonica, Crust. 1841, p. 134, pl. 33. fig. 5; Alcock, in Journ. Asiat. Soc. Bengal, vol. lxv. pt. 11. 1896, p. 234.

One adult male from the Inland Sea of Japan, caught in deep water.

The carapace is 16 mm. long and 13.75 mm. broad; its upper surface is lead- or slatecoloured, without the dark red spots described by Alcock. The abdomen (Pl. 31. fig. 7) does not exactly agree with the figure in the 'Fauna Japonica'; the penultimate segment narrows more distinctly distally and its lateral margins are very slightly arched, not at all concave; the antepenultimate joint is distinctly constricted not far from its posterior margin, as in *Leuc. maculata*, Stimps., which is regarded by Alcock as identical with this species. The edge of the pterygostomian region that forms the anterior boundary of the thoracic sinus is quite straight.

# MYRA, Leach.

# MYRA FUGAX (Fabr.).

Myra fugax (Fabr.), Alcock, in Journ. Asiat. Soc. Bengal, vol. lxv. pt. 11. 1896, p. 202.

One young male from the Inland Sea of Japan, deep water.

The carapace of this specimen, which agrees with the form described by Miers in 1879 under the name of  $Myra\ dubia$ , and apparently also with that described by Hilgendorf as  $Myra\ coalita$ , is 13.5 mm. long exclusive of the median spine, and 15 mm. when it is included; the carapace is 12.4 mm. broad. The upper surface, which is strongly convex transversely, agrees in its general shape with the figure of  $Myra\ carinata$  in Bell's Monograph, but the acute median spine is much shorter, being only once and a half as long as the lateral ones. The median granulated ridge is quite distinct, as also the raised cluster of granules on the well-defined intestinal region; punctiform granules are scattered on the upper surface, except quite anteriorly. The front and the adjacent parts of the flattened subhepatic regions are pubescent. Immediately behind the notch three or four beads of the lateral border are dentiform, and one observes another just above the last pair of legs. The chelipeds are 25 or 26 mm. long, not quite twice as long as the cephalothorax.

There is still a very young male specimen, without definite locality, that no doubt belongs also to this species; it is, in my opinion, that form which has been described by Dr. Alcock as a distinct species, *Myra pentacantha* (Alcock, *l. c.* p. 204). Measured in the middle line, the carapace appears to be 6.4 mm. long the median spine included, and 5.5 mm. without it; it is 5.1 mm. broad. The carapace is less strongly convex; not only is the intestinal region distinctly defined, but the branchio-cardiac grooves are also

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discernible. The median acute spine on the intestinal region is twice as long as the lateral ones. The carapace is marbled with red on either side of the median ridge, on each side of the front, and on the hepatic regions.

## ARCANIA, Leach.

# ARCANIA HEPTACANTHA (de Haan). (Pl. 31. figs. 8-10.)

Iphis heptacantha, de Haan, in Herklots, 'Symbolæ carcinologicæ: Études sur la Classe des Crustacés,' . Leyde, 1861, p. 27.

Two males and two sterile females of somewhat larger size, from the Inland Sea of Japan, deep water.

Through the kindness of the Direction of the Leyden Museum I was enabled to compare these specimens with the single type of *Iphis heptacantha*, de Haan, a description of which seems not to have appeared. This type specimen, the locality of which is unknown, is an adult female of larger size than the Japanese specimens; legs and footjaws are unfortunately wanting. The Japanese specimens no doubt belong to this species.

The cephalothorax of de Haan's type specimen is a little broader in proportion to its length; but this may be explained by its larger size (compare the measurements). Alcock's description of Arc. septemspinosa (Fabr.), Leach (in Journ. Asiat. Soc. Bengal, vol. lxv. pt. 11. no. 2, 1896, p. 265), is applicable to de Haan's type of Arc. heptacantha except as regards the length of the spines and perhaps also the following. The cardiac and intestinal regions are also separated on each side by a moderately deep groove from the branchial regions, which, according to Alcock's description, does not seem to be the case in Arc. septemspinosa. In Arc. heptacantha the surface of the carapace is finely granular; on the gastric, cardiac, and intestinal regions the granules are a little larger than on the branchial; from each of the two spines with which the latter are armed a somewhat irregular row of granules runs forward and inward on their surface; these granules have the same size as those of the gastric region, but between these rows the granulation is finer than on the median regions. The concavity just behind the crease or pucker that separates the hepatic from the branchial regions and the upper surface of the front are smooth. The lateral spines, that are somewhat directed backward and slightly curved upward, measure in de Haan's type specimen 6 mm., i. e. almost one-third the breadth of the carapace without the spines; the median spine on the transversely and longitudinally convex intestinal region, which is a little directed upward, is the shortest of the seven spines, measuring 1.75 mm., not quite one-third the length of the lateral spines. The four other spines, which have nearly the same size, are 2.4 mm. long, so that they appear a little larger than the spine on the intestinal region, measuring a little more than *one-third the lateral spines*. Exclusive of the spines, the cephalo-thorax, which is strongly convex transversely and as much longitudinally, appears in the Leyden type a little broader than long, in the largest of the Japanese specimens (a sterile female) nearly as long as broad. In the latter specimen the lateral spines are 3.25 mm. long, about one-fifth the width of the carapace without the spines, so that they are

comparatively shorter than in de Haan's adult female; the median spine on the intestinal region is just as long as the two spines on the posterior border, viz. 1.3 mm., measuring a little more than one-third the lateral spines, but the posterior two on the branchial region are, in this specimen, the shortest of all, measuring 0.9 mm. The posterior branchial spines are a little farther, viz. 7.3 mm., distant from the tips of the lateral spines than from that (5.75 mm.) of the median spine. The front and the depression between it and the gastric region are tomentose; the spines are also granular. In the Leyden type the front is a little less prominent and its lateral margins run somewhat more obliquely than in this female; but in the other specimens the obliquity is nearly the same. The chelipeds are equal, 37 mm. long, more than twice the length of the carapace (posterior spine included); they agree with the quoted description of Arc. septemspinosa and with the fig. 4, pl. 25, in Cuvier's 'Atlas du Règne Animal.' The slender fingers are one-fourth longer than the tapering hand, but carpus and palm appear also finely granulated under a lens. The meropodites of the ambulatory legs are finely granular, but the following joints seem to be smooth.

In the other female the five posterior spines are of equal length, but the two males agree with the larger female. In these specimens the whole upper surface of the carapace is slightly public public ent.

The abdomen of the male (Pl. 31. fig. 9) consists of five pieces; the penultimate segment is once and a half as long as broad and once and a half as long as the terminal piece.

#### Measurements in millimetres.

	1.	2.	3.	4	5.
	<b>♀</b> .	Ŷ.	<b>£</b> .	ð.	ð.
Breadth of the carapace, the lateral spines included	33	21	18.4	16.5	13.75
Length of the carapace, the posterior spine included	21.75	16.75	15	13	11.22
Breadth of the carapace, exclusive of the lateral spines	21.5	15.5	13.4	11.5	10
Length of the carapace, exclusive of the posterior spine .	20.5	15.75	14.2	12	10.5

No. 1. Leyden type of Iphis heptacantha, de Haan; Nos. 2-5. Inland Sea of Japan.

Whether this species differs from Arc. septemspinosa (Fabr.), Leach, by other characters than the *shorter* spines, is difficult to say, because I was unable to compare it with specimens of the latter. I will, however, observe that at the end of his quoted description of Arc. septemspinosa, Dr. Alcock adds :—" Of ninety-two specimens in the Indian Museum the lateral spines are found to vary a good deal in length: they are usually, in adults, about as long as the arm, and sometimes a good deal longer; but in the young they are usually much shorter than the arm."

Perhaps Arc. heptacantha is related to Arc. septemspinosa (Fabr.), var. gracilis, IIend., from the Gulf of Martaban, but it is difficult to decide, because his description is too short (Henderson, in Trans. Linn. Soc., ser. 2, Zool. vol. v. 1893, p. 403).

Arc. quinquespinosa, W.-Mason (Ill. Zool. 'Investigator,' Crust. pl. 24. fig. 6), is certainly a different species.

ARCANIA GLOBATA, Stimpson. (Pl. 31. figs. 11-13.)

Arcania globata, Stimpson, in Proc. Acad. Nat. Sciences Philadelphia, 1858, p. 160. Arcania globata, Miers, in Proc. Zool. Soc. 1879, p. 44. Arcania globata, Ortmann, in Zool. Jahrb., Syst. vi. 1892, p. 577.

One young male, collected at a depth of 8 fathems in the Inland Sea of Japan; bottom sandy. It is said to be here very rare.

Measured in the middle line, this specimen appears to be 8 mm. long, whereas the carapace is 7.25 mm. broad without the spines, and 9 mm. when they are included. Without the front the cephalothorax appears semiglobular, for the outline is circular and it is strongly convex transversely and also much longitudinally. The front, which is characteristic, is prominent, extending a little beyond the eye-peduncles. Its upper surface, which is a little convex longitudinally, is slightly furrowed in the median line, makes a very obtuse angle with the upper surface of the carapace, and appears to be situated at a much lower level than the latter, in a lateral view or when the carapace is looked at from in front. The breadth of the front is nearly one-fourth that of the carapace (the spines included) and it is a little broader than long; the slightly arcuate, lateral margins terminate each in a small subacute tooth, and the anterior border of the front between these two teeth is nearly straight, very slightly concave. The upper surface is rather thickly beset with slender, subacute spines; these spines, which are smooth and almost of equal length, appear to be very slightly curved forward in a lateral view of the carapace. A few similar spines, though much smaller, stand at the base of the front. The spines on the upper surface of the carapace are about 80 to 90 in number. Under a strong magnifying-glass the upper surface appears to be covered between the spines with small pointed spinules, especially anteriorly. A much stouter though barely longer spine stands on the middle of the well-defined intestinal region; this spine is granular and also slightly curved forward. Round the margin of the carapace are ten conical larger and acute spines that are all granulated and more or less curved upward; they are as stout as the already described stouter spine on the intestinal region. Of the five spines on each side, the third or middle one is placed just in the middle of the lateral margin and somewhat curved forward; the fourth spine has the same size as the third, and it is as far distant from the third as from the spine on the intestinal region. A fifth spine, a little shorter than the third and the fourth, is placed on the outer angle of the narrow posterior border of the carapace; this spine, which is directed backward and slightly outward, is also as far distant from the fourth spine as the fourth from the third. The second spine, which is a little smaller than the third, stands somewhat nearer to the latter than to the first; the distance between the first spine and the second is just two-thirds of that between the third and the fourth. The first to fourth spines and also the spine on the intestinal region are all placed at some, nearly equal, distance from the lower border of the carapace, *i. e.* from the base of the legs, but the fifth spine stands just near the base of the last leg. One observes, moreover, two smaller spinules on the posterior margin between the two spines of the fifth pair.

Eye-peduncles a little shorter than the front; the cornea, which is shining and dark

brown, carries anteriorly a small conical tooth or tubercle. Both the outer and the inner angle of the lower margin of the orbits are produced into an acute slender spine that reaches not as far forward as the eye-peduncles; the outer wall of the orbits carries on its free border a small spine, which is preceded on its outer surface by a somewhat larger one. The outer wall is separated on each side by a furrow from the front and from the pointed spine at the outer orbital angle; the latter spine carries a small acute tooth on its outer margin (Pl. 31. figs. 10 & 11).

The lateral margins of the buccal frame are considerably thickened anteriorly at the level of the merus-joint of the outer footjaws and terminate in a forwardly-directed spine that reaches as far forward as the spine at the internal angle of the orbits. The outer footjaws are granulated, like the lower surface of the carapace. The merus-joint, measured along the inner border, appears to be 1 mm. long, the ischium-joint 1.6 mm.; the former is thus more than half as long as the latter.

The 5-jointed, strongly granulated abdomen resembles that of Arc. 11-spinosa, de Haan; the same rather coarse granulation exists on the sternum. The chelipeds, 13 mm. long, are little more than once and a half as long as the carapace. The merus-joint, which is a little stouter than that of Arc. 11-spinosa, de Haan, is covered above with rounded, circular granules, mostly large, though with some smaller observable among them on the distal half; on the anterior border they are of a more conical shape and the posterior border carries four strong, nearly equidistant, and subequal, subacute spines, which are not described by the quoted authors, unless by Stimpson with the words "granulis plerumque subspiniformibus." Similar circular bead-like granules as on the upper surface also occur on the lower. Carpus and hand are closely beset with granules, which are, however, much smaller than those of the arm; the slender fingers, which shut close together and are almost once and a half as long as the upper border of the palm, are deeply furrowed longitudinally; they show a fine granulation under a strong magnifyingglass, they are a little hairy distally, and their prehensile edges are beset with numerous small teeth, a few of which are distinctly larger on the distal half of the fingers.

The ambulatory legs, smooth to the naked eye, are indeed covered with a close minute granulation, visible only by means of a strong magnifying-glass; the anterior border of the meropodites is *spinulose*, being beset with 5–9 small, spiniform, acute teeth, and the slender, slightly arcuate terminal joints are about as long as the propodites.

This pretty little crab has the front and a median band on the upper surface of the carapace white, the median band being half as broad as the front; adjacent to the band the upper surface is orange, but this colour gradually becomes paler laterally. The spines are also of a pale orange-colour, but those that stand on the band are white. The lower surface is uncoloured, but the sternum is marked anteriorly, on each side of the abdominal groove, with a triangular orange-coloured fleck, between that groove and the base of the chelipeds. The latter are pale reddish above; the proximal extremity of the merus is white, like the tips of the fingers. The ambulatory legs are uncoloured, but carpus and merus are partly reddish.

Arcania 11-spinosa is at once distinguished by the different shape of the front, by the carpus and chelæ being apparently smooth, and, no doubt, by other characters as well.

Geographical Distribution.—Chinese Sea, lat. 23°, depth 16-25 fathoms, bottom sandy or muddy (*Stimpson*); Corea Channel, lat. 34° 8′ N., long. 126° 24′ E., at a depth of 24 fathoms (*Miers*); Maizuru, Japan (*Ortmann*).

#### GALATHEA, Fabr.

## GALATHEA ACANTHOMERA, Stimpson. (Pl. 31, figs. 14, 15.)

Galathea acanthomera, Stimpson, in Proc. Acad. Nat. Sci. Philadelphia, 1860, p. 252.

Galathea orientalis, Ortmann, in Spengel, Zool. Jahrb., Syst. vi. 1892, p. 252, tab. 11. fig. 10 (nec Stimpson).

One male from the Inland Sea of Japan.

Through the kindness of Prof. Döderlein, of Strassburg, some specimens of Ortmann's *Galathea orientalis* from Kadsiyama, Japan, are lying before me, and though they show a few slight differences, especially as regards the rostral teeth, they belong no doubt to the same species as our specimen from the Inland Sea. As will appear from the following description, this species ought to be referred to *Gal. acanthomera*, Stimpson, and not to *Gal. orientalis* of the same author.

The carapace of our male is 7.2 mm. long and 5 mm. broad. The rostrum measured from the tip to a transverse line uniting the bases of the first, *i. e.* the posterior teeth, appears to be 2.7 mm. long and 1.5 mm. broad at its base; in a male from Kadsiyama of the same size the rostrum is 2.55 mm. long, but just as broad as the other. The length of the rostrum and its relative breadth are thus somewhat variable. The lateral teeth of the rostrum are all acuminate and pointed. The first or basal tooth is, in the male from Kadsiyama, directed straight forward and measures just one-third of the second, which is slightly turned inward, its outer margin being a little curved; the third tooth, one-third longer than the second and therefore the longest of all, and also the fourth, which is just as long as the second, are directed straight forward; the terminal spine, finally, measures two-fifths the whole length of the rostrum, is once and a half as long as the fourth lateral tooth, and its lateral margins carry a few, six or seven, microscopical teeth and some setæ. In another specimen the third and the fourth lateral teeth are nearly of equal length and the fourth is slightly turned outward. In an adult female from Kadsiyama the second tooth is also directed straight forward and its outer margin straight, not curved inward.

In the male from the Inland Sea the first tooth measures a little more than one-third the length of the second and is turned slightly outward; the second tooth projects straight forward and its outer margin is straight; the third is once and a half as long as the second, which is almost as long as the fourth, the third and the fourth being both directed straight forward. Length and shape of the rostral teeth are thus somewhat variable. Immediately posterior to a transverse line uniting the base of the incisions between the first and second lateral teeth, one observes, in the middle, *two spines* near together; these spines are, in the male from the Inland Sea, a little shorter than the basal teeth of the rostrum, they are twice as far distant from one another as they are long and a little farther distant from the basal teeth than from each other. The upper surface of the rostrum is somewhat hairy in the middle, short set being arranged in curved, parallel rows on each side and near the middle line; a longer set is inserted at the base of the fourth lateral tooth, in the middle, another nearly in the middle of the rostrum on either side of the median line.

The lateral borders of the carapace are armed with nine teeth, or rather spines. The first spine is, in the male from the Inland Sea, a little larger than the first lateral tooth of the rostrum and directed obliquely outward; it stands at the outer angle of the orbits. The second spine, a little less turned outward, is placed somewhat nearer to the first than to the cervical groove; one observes, between the second and this groove, the two following spines, viz. the third, somewhat smaller than the second, placed on the upper surface quite near the cervical groove and a little remote from the lateral margin, and the fourth, which is as large as the second, just below the lateral margin. Behind the cervical groove the lateral margin carries five other spines, which are equidistant and of equal size, as long as the second, except the last which is somewhat shorter. From each of the two spines, on the boundary between rostrum and gastric region, a ciliated ridge runs laterally towards the base of the second spine of the lateral margin of the carapace; posterior to the two spines one observes seven ciliated ridges, all reaching the lateral margins, except the second, which terminates at the cervical groove. Between the third and the fourth runs a short transverse ridge immediately in front of the cervical groove ; between the fourth and the fifth a ridge proceeds, parallel with them, from the lateral border until at some distance from the middle line; between the fifth and sixth two similar shorter ridges run from the lateral border inward, of which the posterior, which terminates at the ninth spine of the lateral margin, is almost twice as long as the other. Between the sixth ridge and the seventh a similar stria proceeds from the lateral border; this stria is a little shorter than the posterior of the two between the fifth ridge and the sixth. A ciliated stria runs from the fifth lateral spine inward along the cervical groove, another shorter one from the sixth lateral spine. All these ridges are ciliated; the cilia are long, viz. 0.3-0.35 mm. The upper surface of the carapace, of the rostrum, and of the abdomen is thickly and coarsely punctate; the anterior borders of the segments of the abdomen are ciliate and carry, moreover, a few rather long setæ, which occur also in very small number on the lateral parts of the upper surface of the carapace.

The antepenultimate joint of the antennal peduncle is bispinose, carrying a strong spine above and a similar one on the lower border; the penultimate joint is armed above with a single, somewhat smaller spine.

The external maxillipeds (Pl. 31. fig. 14), partly described already by Dr. Ortmann, show the following characters :--Measured along its outer margin, the ischium appears a little longer than the merus; in the male from the Inland Sea the ischium is 1.5 mm. long, the merus, however, 1.2 mm. The outer margin of the ischium terminates distally in a sharp tooth, which is slightly turned inward; the inner margin ends in a conical, stouter though shorter tooth. The two acuminate teeth on the inner margin of the merus are larger than those of the outer border; the anterior spine on the outer border is somewhat curved inward and stands at the distal end, the other nearly in the middle of the border. The outer margin of the carpus is armed, in the male from the Inland Sea, with three sharp

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spines, preceded by a very small, acute tooth; these spines are a little smaller than those of the outer border of the merus, and decrease a little in length from the posterior to the anterior. In the male from Kadsiyama the outer border of the carpus carries two spines, which conform to Ortmann's description, and they are also preceded by a very small acute tooth. The slender peduncle of the exopodite reaches a little beyond the merus.

In the male from the Inland Sea the chelipeds are a little unequal, one being 20 mm. long, the other 18 mm.: they agree with Ortmann's fig. 10. The dactylus of the larger chela carries a moderately strong, subacute tooth at one-third of its length from the articulation, and between this tooth and the tip are seen 25 small obtuse or subacute teeth; the immobile finger has only small teeth, no stronger ones, as also the fingers of the smaller leg.

The three following legs are also characteristic. The meropodites of the second pair (Pl. 31. fig. 15) are five times as long as broad, and their upper margin is armed, along its whole length, with 11-12 strong sharp teeth nearly of the same size; the lower margin is also a little denticulate. and terminates, at the distal end, in a sharp spine which slightly projects beyond the rounded extremity of this joint. The outer margin of the carpus is armed with 5-6 sharp spines, nearly of the same size as those of the merus; the spine at the far end is a little larger than the preceding. The propodites, one-fourth shorter than the meropodites and about six times as long as broad, carry, on the proximal half of their upper border, three or four spines, which are a little smaller than those of the merus, and their lower margin is beset with six movable spines, which have nearly the same size as those of the upper margin. The terminal joints, little more than half as long as the propodites, end in a curved claw, while their lower border carries six movable spines, which gradually increase in length from the first to the sixth. The upper border of the meropodites is furnished with setæ, which are partly plumose or ciliate; at the base of each spine, on the posterior surface, is a long hair and one or two shorter hairs near it. The posterior surface of the meropodites shows transverse rows of short setæ and near the lower margin longer hairs. The following joints are also setose. The legs of the third and fourth pairs agree with those described, but the spines on the upper border of the meri are, in the legs of the fourth pair, comparatively smaller.

The male from the Inland Sea is of a pale yellowish red, the rostrum is whitish, like the lateral teeth of the carapace; the ciliated ridges on the carapace and the segments of the abdomen are marked with small red spots. The mero- and propodites of the second to fourth legs are adorned each with two wine-red rings.

Gal. orientalis, Stimps., from Hong Kong is, no doubt, a different species. The carapace is described as "brevissime pubescens," whereas in Gal. acanthomera the cilia are long. The lateral margins of the carapace carry six teeth, in Gal. acanthomera nine; the first lateral tooth of the rostrum of Gal. orientalis is minute, the chelipeds "crassiusculi," the chela depressed, the dactylus bidentate, all characters not observed in Gal. acanthomera. The upper border of the meropodites is described as "confertim spinulata, spinulis minutis æqualibus," that of Gal. acanthomera, however, as "spinulis robustis ad 11 armato."

Geographical Distribution.—Bonin Islands (Stimpson); Japan, Kadsiyama, Sagami Bay, Maizuru, Tanagava, Kagoshima (Ortmann).

#### CRANGON, Fabr.

## CRANGON CONSOBRINUS, de Man. (Pl. 31, figs. 16–19.)

Crangon consobrinus, de Man, in Ann. & Mag. Nat. Hist. ser. 7, vol. xvii. 1906, p. 401. Crangon affinis, Ortmann, in Spengel, Zool. Jahrb., Syst. v. 1890, p. 531.

One adult egg-laden female from the Inland Sea of Japan, caught in deep water.

This species is closely allied to *Crangon alaskensis*, Lockington, from Mutiny Bay, Alaska \*, but as it is perhaps different, I think it well to publish a somewhat detailed description.

Measured in the middle line, this specimen appears to be 48 mm. long, from tip of rostrum to the end of the telson; the carapace, inclusive of the rostrum, measures  $11\frac{2}{3}$  mm., i. e. *one-fourth* of the whole length, without the rostrum it is 10 mm. long.

The rostrum is distinctly shorter than the eye-peduncles when they are directed straight forward, and reaches only to the corneæ; it is rather narrow, spatulate, the sides nearly parallel for a portion of their length, though the rostrum is very slightly narrowed behind the middle; the edges are somewhat upturned and the sides curve anteriorly to the rather acute tip. The carapace is pubescent on each side, but glabrous posteriorly and in the middle of the dorsal surface, but the short hairs are here perhaps partially worn off. The single median gastric spine, which is of usual size and slightly directed upward, is situated at one-fourth the length of the carapace from the tip of the rostrum, the distance between both tips being 3 mm. On each side is the hepatic spine, which has the same size as the gastric, and the three spines are situated in a transverse line. In its general shape the abdomen resembles that of Crangon vulgaris: it is three times as long as the carapace (rostrum included). The first, the second, and the third segments are rounded above; the third, however, shows a slight depression on each side of the median line just behind the middle. The fourth segment presents a trace of carination along a very short space on the posterior half; the faint and obtuse carina does not, however, reach either to the middle of the segment or to its posterior margin. The fifth segment is distinctly carinate; the rather obtuse carina arises about at one-sixth the length of this segment from its anterior extremi'y and terminates quite near the posterior margin. The sixth segment, which is 7 mm. long, resembles that of Crangon vulgaris, but its upper border has a shallow median groove; as in Crangon vulgaris, the sixth segment is sulcate beneath, the furrow is rather shallow, and, as in that species, there is a sharp tooth at the posterior end between the bases of the uropods. The telson is 10 mm. long, almost once and a half as long as the sixth segment and just as long as the carapace (rostrum excluded); the slender and gradually tapering telson, which is *faintly* grooved above, terminates in a sharp tooth, on each side of which three movable spinules are inserted; the second is the longest of all, twice as long as the others, and extends, like the third, a little beyond the extremity of the telson. The inner caudal swimmerets are just as long as the telson, the outer are very little shorter.

The eye-peduncles (Pl. 31. fig. 16) resemble those of *Crangon vulgaris*. The antennular peduncles reach just beyond the middle of the distance between the orbital margin of the

\* Rathbun, 'Decapod Crustaceans of the North-west Coast of North America,' 1904, p. 114.

carapace and the tip of the antennal scales; the process on the outer side of the base is rather narrow and does not quite reach to the distal end of the first joint, hardly exceeding the eye-peduncles when they are turned straight forward. The gradually tapering, inner flagellum, which surpasses somewhat the antennal scales, is a little longer than the peduncle, measured from the orbital margin of the carapace; the outer flagellum reaches to the end of the blade.

The external antennæ are just as long as the body. The scale (Pl. 31. fig. 18), measured along its straight outer margin, appears to be *four-fifths* the length of the carapace, exclusive of the rostrum; it resembles that of *Crangon alaskensis*, but it is only *three times as long as broad*; the end of the blade is rounded, not produced at the anterointernal angle, and much broader than the spine at this level; the spine extends almost as much beyond the blade as the end of the latter is broad. The antennal peduncle extends as far forward as the penultimate joint of the external maxillipeds, which just reach to the end of the blade.

The first pair of feet (fig. 19) are somewhat shorter than the antennal scales, reaching a little beyond the antennal peduncles. The chelæ, which are 5.6 mm. long and 1.5 mm. broad at the base of the spinous pollex, are a *little slenderer* than those of *Cr. alaskensis*, for they are *almost four times as long as broad*; the obliquity of the terminal margin is in both species the same.

The legs of the fifth pair reach as far forward as those of the first.

There is a slender spine on the sternum between the third pair of legs.

The single typical specimen of Ortmann's *Crangon affinis* from Maizuru, Japan, which is lying before me (Ortmann, *l. c.*), seems to belong to this species; the rostrum is, however, a little longer and the process on the outer side of the base of the antennular peduncle reaches almost to the end of the first joint. Ortmann's specimen carries a Bopyrid on the left side of the carapace.

Crangon affinis, de Haan, is certainly different. In this species, indeed, the external maxillipeds are longer than the antennal scales, and the latter are just as long as the carapace, the rostrum excluded. Nothing is said about the carination of the fifth abdominal segment. Unfortunately de Haan's types do not now exist in the Leyden Museum.

*Crangon propinquus*, Stimpson, differs by the third and the fourth segments being carinate, not the fifth. According to Miss Rathbun \*, the rostrum of this species should exceed the eyes.

CRANGON CASSIOPE, de Man. (Pl. 32. figs. 20-25.)

Crangon cassiope, de Man, in Ann. & Mag. Nat. Hist. ser. 7, vol. xvii. 1906, p. 402.

Two egg-laden females from the Inland Sea of Japan, captured in deep water, common on mud.

In its outer appearance *Crangon cassiope* much resembles the typical species of this genus, viz. *Crangon vulgaris*, but it is at once distinguished by the sixth segment of the abdomen, which is *convex*, not sulcate, beneath. This species appears therefore also

\* Rathbun, in Proc. U.S. Nat. Mus. xxvi. 1902, p. 42.

related to *Crangon alba*, Holmes, and *Crangon holmesi*, Rathb., from the North-west coast of North America. From the former it differs, however, at first sight by the blade of the antennal scale which agrees with that of *Crangon vulgaris*; from the latter also by the antennal scale, which measures only two-thirds the length of the carapace, exclusive of the rostrum, while the blade appears, moreover, broader at the extremity than that of Crangon holmesi.

The two specimens are nearly of the same size: they are 46.5 mm. and 44 mm. long from tip of rostrum to the end of the telson. In the larger specimen the carapace is 12.5 mm. long, rostrum included, and 11 mm. without it; in the other it is 11.75 mm. long, rostrum included, and 10.5 mm. without it, so that the carapace, rostrum included, is a little longer than one-third the abdomen.

Viewed from above this species closely resembles Crangon vulgaris, but the numerous small, dark spots with which carapace and abdomen of the common shrimp are mottled are almost wanting in Crangon cassiope. Small violet spots are, however, seen on the peduncle and inner flagellum of the inner antennæ, on the antennal scales, on the hepatic region of the carapace between the pterygostomian and hepatic spines, near the posterior margin of the carapace, on the telson and on the uropods.

Even on close inspection the carapace, on the terson and on the dropods. Even on close inspection the carapace shows no differences from that of *Crangon vulgaris*. The narrow, triangular rostrum is as short in proportion to the eye-peduncles as in that species, the gastric and the two hepatic spines agree also in both. The abdomen, viewed from above, also closely agrees with that of *Crangon vulgaris*; all the seven segments are rounded above, but *neither the sixth nor the seventh shows any* abdomen, viewed from above, also closely agrees with that of Orangon vulgaris; all the seven segments are rounded above, but neither the sixth nor the seventh shows any tendency to become flattened or grooved, as is sometimes the case in Crangon vulgaris. In the common shrimp the ventral surface of the sixth segment is marked by a moderately deep groove, which usually begins near the anterior margin and more or less gradually widens posteriorly; on the posterior end is a sharp spine, which is directed back-ward. In Crangon cassiope, however, the ventral surface appears in the middle of the segment rounded and convex, but the posterior fourth is slightly concave, and there is also a short, transverse, though quite shallow pit or depression at one-third of the segment from its anterior margin; instead of a sharp spine one sees in Crangon cassiope, at the posterior end, a subacute conical tubercle. On each side of the middle line the ventral surface is punctate; one observes numerous large puncta and between them many others that are quite minute. The two pairs of antenne closely resemble those of Crangon vulgaris. The antennal scales (Pl. 32, fig. 20) measure along their outer margin two-thirds the length of the carapace without the rostrum, and they are two and half times as long as broad; the end of the blade (fig. 21) is slightly rounded. makes a distinct angle with the inner margin, and is four times as broad as the adjacent part of the spine, which reaches considerably beyond it. The antennal scales closely As regards the inner antennae, I wish only to observe that the stylocerite is a little shorter than the first joint of the peduncle, and that these antennae otherwise fully agree with those of the common European shrimp. The external maxillipeds, which reach to the end of the antennal scales, do not fully

agree with those of a female of *Crangon vulgaris* from this country. Thus the joints of the endopodite are *broader* in proportion to their length. The terminal joint appears in an egg-bearing female of *Crangon vulgaris* of the same size six times, but in the female of *Crangon cassiope* five times as long as broad; the penultimate segment of *Crangon vulgaris* is a little more than four times, that of *Crangon cassiope* a little more than three times as long as broad; the antepenultimate joint, finally, is, in the common shrimp, about four times, but in *Crangon cassiope* three times as long as broad.

The first pair of feet (Pl. 32 fig. 23), which reach nearly to the end of the antennal scales, are *stouter* than those of *vulgaris*; the length of the chelæ is only *two and one-third* times the width measured from the inner base of the immovable spine, in *Crangon vulgaris*, however, *three times*. The obliquity of the anterior margin is in both species the same.

The second legs are also a little less slender than those of the common shrimp. The legs of the fourth pair reach with their dactyli beyond the tip of the antennal peduncles, those of the fifth (fig. 24) are but little shorter; these legs differ especially from those of *Crangon vulgaris* by comparatively *shorter* dactyli (fig. 25) and somewhat *slenderer* propodites. For example, the propodites of the fifth pair in an egg-laden female of *Crangon vulgaris* of the same size as the specimens of *Crangon cassiope* are seven times, but in *cassiope* eight times as long as broad; the dactyli are in *Crangon cassiope* half as long as the propodites, but in *Crangon vulgaris* they measure three-fourths the length of these joints, appearing thus comparatively once and a half as long as in our new species.

The globular eggs are small, diameter 0.45 mm.

## SCLEROCRANGON, G. O. Sars.

## SCLEROCRANGON ANGUSTICAUDA (de Haan).

Crangon angusticauda, de Haan, Fauna Japonica, Crust. 1849, p. 183, tab. 45. fig. 15; Stimpson, in Proc. Acad. Nat. Sci. Philadelphia, 1860, p. 25.

Sclerocrangon angusticauda, Ortmann, in Spengel, Zool. Jahrb., Syst. v. 1890, p. 533, and in Proc. Acad. Nat. Sci. Philad. 1895, p. 179.

One egg-laden female from the Inland Sea of Japan.

Length 32 mm. from tip of rostrum to the end of the telson; the carapace, 8.75 mm. long, the rostrum included, measures little more than one-fourth the whole length. Viewed from above, the rostrum, which is as long as broad at its base, appears a little shorter than the eyes; its slightly upturned lateral margins, which in a lateral view of the rostrum appear a little arcuate, curving at first upward and then very slightly downward, converge forward, so that the rostrum appears triangular, with rather obtuse tip. De Haan, however, describes the rostrum as "apice acutum."

The obtuse, flattened, median carinæ of the third to fifth abdominal somites are bounded on each side by a hairy, longitudinal furrow, into which issues the transverse furrow described by de Haan. The sixth segment carries above two obtuse carinæ, which converge backward and are even united for a short distance posteriorly; between the two carinæ it appears faintly furrowed, and the two carinæ are also bounded externally by a hairy groove.

The external maxillipeds reach with half their terminal joint beyond the antennal scales. Geographical Distribution.—Japan (de Haan); Simoda and Hakodadi (Stimpson); Kadsiyama (Ortmann).

LEANDER (Desm.), Stimpson.

LEANDER PAUCIDENS (de Haan).

Palæmon paucidens, de Haan, Fauna Japon., Crust. 1849, p. 170, tab. 45. fig. 11.
Leander paucidens, Stimpson, in Proc. Acad. Nat. Sci. Philadelphia, 1860, p. 40.
Palæmon paucidens, Rathbun, in Proc. U.S. National Museum, xxvi. 1902, p. 51.
Leander paucidens, Doflein, Ostasiatische Dekapoden, 1902, p. 640.

Ten specimens, among which are two adult, egg-laden females, from Hakone Lake, Japan, caught in July 1896, 2400 feet above sea.

The two egg-bearing females are respectively 54 and 55 mm. long, the other specimens are all smaller but one. The eggs are not very numerous, *large*, 1.8-2 mm. long and 1.4-1.5 mm. broad.

In five specimens the tip of the rostrum is injured, in the rest it is bifid at extremity; in one the rostrum is broken, two carry five teeth on the upper margin besides the apical tooth, the rest only four; usually the second tooth stands immediately before the frontal border of the carapace, rarely just above it. In two specimens the lower border is armed with three teeth, in six with two, and in one specimen there is only one tooth. In some specimens the rostrum is just as long as the scales, in others it overreaches them a little; in the larger specimens it is slightly upturned at extremity, in the rest it is straight.

In the larger, ova-bearing female, which is 55 mm. long, the external maxillipeds reach a little beyond the antennal peduncle; the legs of the first pair extend to the end of the scales and those of the second reach with their chelæ beyond them, the carpus extending to the end of the scales. The carpus of the second pair is once and a half as long as the chela.

Geographical Distribution.—Japan (de Haan): near the town of Simoda, in fresh water of a river, not far from the sea (Stimpson): Aomori, Rikuoku; Matsushima, Rikuzen; Misaki, Sagami; Lake Biwa, Matsubara, Omi (abundant); Kawatana; Kurume; Nagasaki, Hizen (Rathbun): Korea, Fusan; Gensan, brackish streams flowing into the sea (Rathbun): Nemuro, Yesso (Doflein): Iterup, Kurilen, August (Doflein).

## LEANDER LONGIPES, Ortmann. (Pl. 32. figs. 26-30.)

Leander longipes, Ortmann, in Spengel, Zool. Jahrb., Syst. v. 1890, p. 519, Taf. 37. fig. 13.

Palamon ortmanni, Rathbun, in Proc. U.S. National Museum, xxvi. 1902, p. 53 footnote.

Leander longirostris, de Man, in Notes from the Leyden Museum, iii. 1881, p. 141 (nec Palemon longirostris, H. M.-Edw., Hist. Nat. Crust. ii. p. 394=styliferus, H. M.-Edw., ibidem, Errata, vol. iii. p. 638, 1840).

One adult egg-laden female from the Inland Sea of Japan. Rare.

As usual, Dr. Ortmann has not indicated the length that this species attains: the present female is 58 mm. long from tip of rostrum to the end of the telson. The carapace is just half as long, viz. 29 mm., the rostrum included, and 11 mm. without it. The slender, elongate rostrum, which reaches with somewhat less than half its length beyond the antennal scales, is strongly recurved and about once and a half as long as the carapace. Different from Leander pacificus, Stimps., L. serratus, Penn., L. treillianus, Risso, and other species, the rostrum is hardly broadened at the level of the first tooth of the lower margin, so that it appears stiliform and not emarginate at base. As in Ortmann's typical male specimen from the Sagami Bay, the third tooth is placed immediately before the anterior margin of the carapace, the first two teeth standing upon it; the third tooth is followed by four other teeth, the first six are equidistant, but the seventh, which is placed just on the middle of the upturned part of the rostrum, is a little farther from the sixth than the sixth from the fifth. The seventh tooth is a little smaller than the preceding. As in Ortmann's specimen, there are three apical teeth, which are smaller than the preceding; the first apical tooth, i. e. the eighth of the whole series, is as far distant from the second as the third apical tooth from the tip. The first apical tooth is a little farther from the seventh tooth than the seventh from the sixth. The first tooth stands immediately before the middle of the carapace, and the fifth is situated above the distal end of the basal joint of the antennular peduncle. As in the typical male, the lower margin carries eight nearly equidistant teeth, of the same size as those of the upper border; the first is situated just below the fifth, the eighth just below the eighth of the upper margin, i. e. the first of the three apical teeth.

As was rightly observed by me in 1881 (*l. c.*), the branchiostegal spine, which is a little remote from the margin of the carapace, is distinctly *smaller* than the antennal. The abdominal segments are rounded. The telson (Pl. 32. fig. 26), once and a half as long as the sixth segment, gradually tapers backward and ends in a sharp tooth; of the lateral spinules the outer, 0.34 mm. long, are a little shorter than the median tooth, but the elongate slender inner spinules are *four times as long* and reach far beyond the latter (fig. 27). There are two pairs of spinules on the upper surface as usual.

The short flagellum, as long as the antennular peduncle, is united *for one-fourth* its length with the outer; 10 or 11 joints are grown together.

The external maxillipeds reach with their terminal joint beyond the antennal peduncle.

The legs of the first pair are as long as the scales; the carpus is almost twice as long as the chela, and the fingers are a little longer than the palm.

The legs of the second pair are unequal, the much longer right leg (fig. 28) reaches as far forward as the rostrum, the other only to the end of the antennal scales. The carpus of the right leg, 5.7 mm. long, is almost as long as the merus (6 mm.); the carpus, 0.5 mm. thick at the proximal end, is 0.92 mm. broad at the distal extremity, here thus twice as thick. The chela, 8.35 mm. long, is almost *once and a half* as long as the carpus, and also longer than the merus. The palm, a little shorter than the fingers, is distinctly *broader* than the distal end of the carpus, and its upper surface is about

three times as long as broad, the palm being 4.1 mm. long and 1.3 mm. broad in the middle. The slender fingers, which shut *close* together, are 4.25 mm. long; the dactylus carries two, small, equal, obtuse teeth near one another (Pl. 32. figs. 29, 30), the anterior of which is situated at one-fifth the length of the finger from the articulation; just opposite the middle between both teeth the immobile finger carries one single, somewhat smaller, subacute tooth; the finger-tips are strongly curved inward.

The three following legs are very *slender*: those of the third pair reach with their dactyli beyond the scales, those of the fifth even with one-third of their propodites. The propodites of the fifth pair, *e. g.*, are 8.4 mm. long and 0.32 mm. broad in the middle, *twenty-five times as long as broad*; they thicken somewhat at the distal end and are beset with a few spines on their distal half. The slender, tapering dactyli of the fifth pair measure *little more than one-fourth* of the propodites, viz. 2.36 mm.

The very numerous eggs are small, 0.6-0.7 mm. long and 0.45-0.5 mm. broad.

Two specimens, collected near Amoy, China, were (l. c.) wrongly referred by me in 1881 to Leander longirostris (Milne-Edwards, Hist. Nat. Crust. ii. p. 394): as is proved by the examination of one of them, now lying before me through the kindness of the Direction of the Leyden Museum, they belong in fact to L. longipes, Ortm. In 1881 the words of Milne-Edwards's description, "surmonté à sa base d'une crête sexdentée," were misunderstood or overlooked by me. As has been shown by Miss Rathbun, l. c. pp. 50 & 51, the species described by Milne-Edwards, l. c. p. 394, under the name of longirostris should henceforth bear that of styliferus, M.-Edw.

In my opinion, however, Miss Rathbun was wrong when creating for *L. longipes*, Ortm., the name *ortmanni*, because this species belongs to the genus *Leander*; de Haan's *longipes*, however, to the genus *Palæmon*. In that case the species mentioned by the learned carcinologist of Washington under the name of *Pal. japonicus* (Ortm.) should also be changed, because a "*Bithynis*" *japonica* has been described by de Haan.

Geographical Distribution.-Japan, Sagami Bay (Ortmann).

## SPIRONTOCARIS, Sp. Bate.

SPIRONTOCARIS RECTIROSTRIS (Stimpson). (Pl. 32. figs. 31-34.)

Hippolyte rectirostris, Stimpson, in Proc. Acad. Nat. Sciences Philadelphia, 1860, p. 33.

Spirontocaris rectirostris, de Man, in Ann. & Mag. Nat. Hist. ser. 7, vol. xvii. 1906, p. 403.

One male and one egg-laden female from the Inland Sea of Japan.

The female, which agrees pretty well with Stimpson's diagnosis, was captured in deep water; as the above were the only specimens caught, it is probably a rare species. Alive, the female was of a Prussian blue, the eggs were orange. The female is 35.5 mm. long from tip of rostrum to end of telson and has a stout shape; the carapace, rostrum included, measures nearly a third the whole length. The rostrum, which arises with an obtuse crest at one-third the length of the carapace from its posterior border, reaches to the end of the antennular peduncle; the free portion, which measures a little more than half the length of the carapace, projects straight forward. The upper margin carries six teeth, three of which are on the carapace, and the first of these stands just before its

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middle; the first four are equidistant, the fifth is almost once and a half as long as the fourth, and the sixth is as long as the fifth; the tip of the sixth tooth is three times as far from that of the fifth as from the extremity of the rostrum. The rostrum is a little dilated distally, just below the sixth tooth, and carries here *two* teeth, which are smaller than the first teeth of the upper border; the first is situated just below the middle of the sixth tooth, the second just below its tip, and the tip of the second is a little farther from the extremity of the rostrum than from the tip of the first tooth. According to Stimpson, the lower margin should be armed with *four* teeth. Posterior to the first tooth the lower margin appears slightly concave. Antennal spine short; pterygostomian spinule very small, but distinct.

Abdomen rounded above, geniculate at the third segment, which is slightly produced posteriorly into an obtuse lobe; on either side of the middle the tergum of the third segment carries a faintly impressed, longitudinal line, which runs from the posterior border to a little beyond the middle. The pleura of the fourth segment, which is a little longer than the fifth, ends in a small sharp spinule; the sixth segment, once and a half as long as the fifth and almost twice as long as broad in the middle, terminates, as also the fifth, in a sharp tooth at the postero-lateral angles. The tapering telson, which is one-third longer than the sixth segment, is armed on its flattened, upper surface with four pairs of spinules and terminates in a small, sharp tooth ; of the two spines on each side the inner are twice as long as the outer, which slightly reach beyond the median tooth. The basal joint of the uropods, which are a little longer than the telson, terminates in a sharp tooth at its postero-external angle.

The eye-peduncles, which carry a distinct ocellus close to the corneæ, reach with the latter beyond the lateral margin of the carapace.

The internal antennæ are little longer than the carapace and extend with half the inner flagellum beyond the antennal scales. Their peduncle is as long as the rostrum and reaches the middle of the antennal scales; the first joint is somewhat longer than the eye-peduncles when they are directed forward, and carries one or two spinules at the distal border of its upper surface; the large and broad stylocerite is acuminate and reaches beyond the middle of the second joint; the second joint, not quite half as long as the first and as broad as long, is armed, at the antero-external angle, with a strong spine, which is directed forward and outward; the terminal joint, finally, is half as long as the second and has a sharp tooth or spine at the distal end of its upper border. The upper flagellum is considerably thickened along three-fourths its length and the filiform terminal part extends beyond the scales. The basal joint of the antennal peduncle carries a slender spine on the distal border of its lower surface; the straight outer margin of the scale (Pl. 32. fig. 32), which measures one-seventh the whole length of the body, and is two and a half times as long as broad, terminates in a sharp spine, which reaches a little beyond the rounded or truncate extremity of the laminar portion. The antennal peduncle is as long as that of the inner antennæ, and the flagellum is somewhat shorter than the body.

The external maxillipeds, which are devoid of an exopodite, project with one-third their terminal joint beyond the antennal scales.

The legs of the first pair, which barely reach to the end of the scales, can hardly be described as "graciles," as they were by Stimpson. The merus,  $3\cdot 1$  mm. long, is nearly three times as long as broad and carries on its lower border proximally six or seven small, movable spinules and some plain setæ; the latter are also observed on the lower border of the ischium. The carpus, half as long as the chela, is somewhat excavated distally. The chela is little longer than the merus, and the fingers, which shut close together, measure one-third its whole length. Unfortunately, the right leg of the second pair is wanting, the left reaches to the end of the scales. The carpus, which was not described by Stimpson, is 3 mm. long, and seems to be composed of *six* joints; the first is a little longer than one-third the carpus, and the fifth is the shortest. The chela measures little more than one-third the carpus, and the fingers are half as long as the palm.

The legs of the third pair reach to the end of the scales, the following are a little shorter. The meropodites of the third and fourth pairs (the fifth pair are wanting) carry on their outer surface four or five movable spines, whereas their lower margin, like that of the ischium, is furnished with tufts of setæ.

The three posterior legs are marked with blue rings.

The oblong eggs are very numerous and small, 0.6-0.65 mm. long, 0.4-0.45 mm. broad.

If the other specimen be really the male of Spiront. rectirostris, the sexual differences are considerable: Stimpson apparently observed only the female, though he does not mention it. This specimen is 34.5 mm. long from tip of rostrum to the end of the telson, presenting the same size as the female, but the abdomen is less deep and appears therefore *slenderer*. The carapace is 12.5 mm. long, a little longer in proportion to the whole length than in the female. The rostrum, which just reaches beyond the distal end of the antennular peduncles for about 0.75 mm., projecting straight forward, arises more anteriorly than in the female, viz., at one-third the length of the carapace from its frontal border; the upper margin is armed with six teeth, which are of equal size and equidistant, and only two of them are placed upon the carapace. The upper margin appears between the most anterior tooth and the extremity of the rostrum somewhat convex, different from the female. As in the latter, the rostrum is dilated and just below the foremost tooth and the lower edge carries here also two teeth, which are much smaller than those of the upper margin; the second of these is as far distant from the tip of the rostrum as from the first. The antennal spine and the pterygostomian spinule agree with those of the female.

The third segment of the abdomen resembles that of the female, but the two impressed lines on the tergum are wanting. The fifth segment appears a little shorter in proportion to the fourth than in the female, the fourth being once and a half as long as the fifth; the sixth segment appears therefore twice as long as the fifth, but it is only once and a half as long as broad. The postero-lateral angles of the fourth, fifth, and sixth segments terminate in a sharp spinule. The telson, almost once and a half as long as the sixth segment, agrees with that of the female, but the four pairs of spinules reach farther backward, so that the most posterior pair is farther from the penultimate than from the posterior border, whereas in the female the contrary is the case.

The internal antennæ agree with those of the female, and the distal border of the first joint of the peduncle carries a sharp spine near the outer angle, which has the same size as the spine with which the second joint is armed, and the thickened portion of the outer flagellum reaches to the end of the antennal scales. The antennal scales (Pl. 31. fig. 34) are *more elongate* than those of the female; they are 6 mm. long, nearly one-sixth the whole length and a little more than three times as long as broad; the flagellum is as long as the body.

The most prominent difference from the female is exhibited by the external maxillipeds, which are *much longer*. These appendages, 25.5 mm. long, are *twice* as long as the carapace, rostrum included, and *their last two joints* extend beyond the antennal scales; the terminal joint, *just as long as the other joints together*, viz. 12.75 mm., is *much slenderer* than in the female and terminates in one single, brown-coloured, sharp point.

The legs of the first pair resemble those of the female, but they are *much larger*, half their chelæ extending beyond the antennal scales. The lower margin of the merus carries proximally eight small spines, similar to those of the female.

The legs of the second pair extend one-third of their carpus beyond the antennal scales. The merus is not articulate, the carpus is 7-articulate; the third joint is nearly as long as the first and the second taken together, and longer than the others; the sixth is the shortest, the fourth little longer than the fifth; the first, the second, the fifth, and the seventh are nearly the same length. The chela is a little shorter than the last three joints taken together, and the fingers are somewhat shorter than the palm.

The other legs agree with those of the female: the third extend a little beyond the scales; the merus of the third pair carries only three movable spinules on the distal half of its outer surface, that of the fourth only two, that of the fifth only one, near the carpal articulation.

The difference in colour is quite remarkable, for, when caught, the male is scarlet. Geographical Distribution.—Hakodadi, in deep water (Stimpson).

# SPIRONTOCARIS PROPUGNATRIX, de Man. (Pl. 32. figs. 35-41.)

Spirontocaris propugnatrix, de Man, in Ann. & Mag. Nat. Hist. ser. 7, vol. xvii. 1906, p. 404.

One specimen from the Inland Sea of Japan, caught at a depth of 6 fathoms; bottom sand, weeds, here and there stones. It was captured together with the specimens of *Spirontocaris pandaloides*, Stimpson.

Apparently a new species, distinguished by the *elongate* rostrum and its characteristic toothing. Measured from the tip of the rostrum to the end of the telson, this specimen, which has a *slender* shape, appears to be  $33^{\cdot}2$  mm. long; the carapace, rostrum included, is  $15^{\cdot}2$  mm. long, little shorter than the abdomen; without the rostrum, the carapace measures one-seventh the whole length. The rostrum, which is a *little more than twice* (namely  $2\frac{1}{6}$  times) as long as the remainder of the carapace, arises *at one-third* the

length of the carapace from its anterior border; it is *stiliform*, *very little dilated* at the level of the first tooth of the lower margin (Pl. 32. fig. 37), and tapers gradually to the acuminate tip. The upper margin, which is somewhat arched above the eyes, whereas the anterior half is *gently ascending*, is armed with 7 rather low teeth, *two* of which are on the carapace; these teeth, which reach to the middle of the free portion, grow gradually somewhat longer, so that the two anterior, which are of equal length, are longer than the preceding. The lower margin is armed with 10 teeth, of which the first is small and situated below the fifth of the upper margin; these ten teeth increase also in length from the first to the last, and reach to the tip of the rostrum (fig. 36). Two-fifths of the rostrum extend beyond the antennal scales.

Antennal spine small; supraorbital and pterygostomian spines wanting.

The abdomen is moderately geniculated, the upper border of the deflexed part making an angle of 45° with the remainder. The third segment is slightly produced into an obtuse lobe posteriorly. The fourth and fifth segments are of *subequal* length; the postero-lateral angle of the fourth is *obtuse*, but that of the fifth terminates in a sharp tooth. The sixth segment (fig. 39), almost twice as long as the fifth, is *twice as long as broad*, and its postero-lateral angle is sharp. The slender telson, almost *one-fourth longer* than the preceding segment, tapers gradually, so that the posterior margin measures but one-fourth its breadth proximally; the posterior margin (fig. 40) ends in the middle in a sharp tooth, and of the two spinules on either side the outer are twice as long as the inner. The upper surface carries four pairs of spinules; the anterior pair are as far from the base of the telson as the posterior pair from the posterior border. The uropods are barely longer than the telson.

There is a distinct ocellus near the cornea, and the rather slender eye-peduncles project their whole terminal joint beyond the carapace when they are directed transversely outward.

The peduncles of the internal antennæ, measuring little more than one-fourth the length of the rostrum, reach not quite to the middle of the antennal scales; the acuminate stylocerite reaches to the distal end of the first joint. The second and third joints are together half as long as the first; the second, which is once and a half as long as thick and twice as long as the third, is armed at its antero-external angle with a strong spine; the thickened outer flagellum reaches to the distal third of the scales, whereas the thin inner flagellum reaches slightly beyond them.

As in other species, there is a spine on the distal border of the lower surface of the basal joint of the outer antennæ. The scales are narrow, elongate, their outer margins straight; the membranous portion (fig. 41), which extends considerably beyond the strong spine, is obliquely truncate. The antennal peduncle reaches as far forward as that of the inner antennæ, the flagellum measures two-thirds the length of the body.

The external maxillipeds are very short, barely reaching to the end of the antennal peduncles; they seem to be devoid of an exopodite and an epipodite.

The legs of the first pair, still shorter, project with their fingers, which are half as long as the palm, beyond the basal joint of the antennal peduncle. The legs of the second pair extend with their chelæ beyond the antennal peduncle. The carpus, once and a half as long as the merus, is 7-articulate; the joints measure 0.32 mm., 0.22 mm., 0.54 mm., 0.36 mm., 0.3 mm., 0.22 mm., and 0.46 mm.; the second and sixth the shortest, the

0.36 mm., 0.3 mm., 0.22 mm., and 0.46 mm.; the second and sixth the shortest, the third the longest. The chela, 0.88 mm. long, is almost as long as the last three carpal joints together, and the fingers measure two-fifths the whole length of the chela. The following legs are slender. Those of the third pair project nearly with half the propodites beyond the antennal peduncles; the meropodites, eleven times as long as broad, carry on their outer surface a longitudinal row of 8 stout, movable spines, of which the last is inserted near the carpal articulation; the lower margin of the propodites is furnished with 9 movable spinules, which are smaller and thinner than those of the merus; the dactylus carries 6 spines on its lower margin, the last is stouter than the terminal claw, so that the dactylus appears to terminate in two claws. The following legs are gradually shorter; the meropodites of the fourth carry 7, those of the fifth 3 spines the fifth 3 spines.

The nearest allies of Spiront. propugnatrix are Spiront. stylus (Stimpson), Spiront. gracilis (Stimpson), and Spiront. amabilis, Lenz (confer Rathbun, 'Decapod Crustaceans of the North-west Coast of North America,' 1904).

# SPIRONTOCARIS ALCIMEDE, de Man. (Pl. 32. figs. 42-46.)

Spirontocaris alcimede, de Man, in Ann. & Mag. Nat. Hist. ser. 7, vol. xvii. 1906, p. 404.

Twelve specimens from the Inland Sea of Japan.

Closely related to Spiront. gracilis (Stimpson), and Spiront. flexa, Rathbun, from the North-west coast of North America, but apparently different. The largest specimen is 34 mm. long from the tip of the rostrum to the end of the

The largest specimen is 34 mm. long from the tip of the rostrum to the end of the telson; the abdomen, which is strongly geniculated at a right angle at the third segment, is almost once and a half as long as the carapace (rostrum included). The slender rostrum, the free part of which is once and a half as long as the remainder of the carapace, arises with an obtuse crest at one-third of the length of the cephalothorax from its anterior border; it projects at first horizontally forward, but is gently ascending from the anterior tooth of the upper margin and the acuminate extremity just reaches beyond the antennal scales. The upper margin, which is slightly arched above the eyes, is armed with 5, rarely 4, pointed teeth, of which *two always* stand on the carapace; these teeth grow usually a little longer from the first to the anterior, so that they cannot be said to be equidistant. The anterior tooth is situated in the middle of the free part or immediately behind it, so that the terminal half of the upper margin or somewhat more appears devoid of teeth; rarely the foremost tooth is situated in front of the middle, in which case the terminal part, devoid of teeth, appears somewhat shorter than the remainder. In front of the foremost tooth the upper limb is somewhat shorter than the remainder. The none of the foreness total the apper limb is very narrow and cannot be followed to the tip. The lower limb (Pl. 32. fig. 43) is *shallow*, convex, as in *Spiront. unalaskensis*, Rathbun, and *Spiront. tridens*, Rathbun, the width of the rostrum at the base of the lower margin being only  $\frac{1}{8} - \frac{1}{7}$  of its whole length. The lower limb, which gradually diminishes anteriorly, is armed with 6, 7, or 8, rarely 9, teeth, which are smaller than those of the upper border, grow usually longer distally and reach

to the tip. The toothing-formulæ of these specimens are the following :— $\frac{4}{7}$  two specimens;  $\frac{5}{6}$  four specimens;  $\frac{5}{7}$  two specimens;  $\frac{5}{8}$  three specimens;  $\frac{5}{9}$  one specimen.

According to the woodcuts in Miss Rathbun's excellent work, the lower limb of the rostrum appears in *Spiront. gracilis*, Stimpson, and *Spiront. flexa*, Rathbun, *narrow* along its whole length, *hardly broader* at its base than distally.

There is no supraorbital spine, the outer angle of the orbital margin terminates in a rounded tooth or lobe, and the antennal spine is of moderate length. In most specimens the antero-lateral angle of the carapace is rounded; in two specimens only (Pl. 32. fig. 42) a minute pterygostomian spinule occurs on one side of the body, whereas on the other side the carapace is rounded. The third segment of the strongly geniculated abdomen is produced posteriorly to a somewhat compressed hump or hunch, which is bent at a right, though rounded angle. The lateral sides of the third segment are somewhat punctate, near the posterior border, like the others, but also below the upper margin. The fourth segment, distinctly longer than the fifth, is rounded at the postero-lateral angle, but the fifth ends in a sharp tooth; the sixth segment, which is twice as long or almost twice as long as the fifth, is twice or barely twice as long as broad; its postero-lateral angle terminates in a sharp tooth. The telson, which is but little longer than the sixth segment and somewhat shorter than the uropods, terminates in a sharp tooth, and of the two spinules on either side of it the outer is half as long as the inner. The upper surface (fig. 44) carries 4, more rarely 5, pairs of spinules; in seven specimens there are 4 pairs, in two 5, in two 4 spinules are observed on one side, 5 on the other, and in the last individual the telson has 3 spinules on one side and 4 on the other.

The eye-peduncles, which carry a distinct ocellus close to the cornea, measure a little more than one-fourth the length of the carapace (rostrum excluded). The antennular peduncle (fig. 45) attains to one-third of the antennal scale; the acuminate stylocerite reaches to the distal end of the first joint, but never beyond it; the second joint, much shorter than the first, has a spine at its antero-external angle, and the third, half as long as the second, carries also a spine at the distal end of its upper border; the thickened portion of the outer flagellum reaches, in all the specimens, somewhat beyond the middle of the antennal scale. Antennal scale a little longer than the carapace (rostrum excluded), *slender*, six times as long as broad, hardly narrowing distally; the outer margin is a little concave, and the distal spine is not nearly so advanced as the membranous portion; there is a slender spine at the distal end of the basal joint at the lower side; the peduncle reaches to the middle of the second joint of the antennular peduncle, and the flagellum is little longer than the body.

The external maxillipeds, though produced a little beyond the antennal peduncle, attain only to one-third of the antennal scale; they are devoid of an exopodite, the upper margin of the antepenultimate joint terminates in a small acute tooth, and the terminal joint carries 7 or 8 brown-coloured teeth at the distal end.

The legs of the first pair extend their fingers beyond the basal joint of the outer antennæ, those of the second reach to the middle of the antennal scales. The joints of the carpus present in a specimen 32 mm. long the following dimensions, from the first to the last:—0.42 mm., 0.29 mm., 0.73 mm., 0.42 mm., 0.3 mm., 0.26 mm., and <math>0.52 mm.; the chela is 0.9 mm. long, and the palm is nearly once and a half as long as the fingers. The sixth joint of the carpus, just half as long as the last, is the *shortest*, the third, which is as long as the first and the second together, the *longest*, as in *Spiront. propugnatrix*, and the chela is almost as long as the last three joints taken together.

The third pair reach to the middle of the antennal scale, the following are a little shorter. The meropodites of the third legs, which are ten times as long as broad, carry a row of six spines on their outer surface, of which the last is inserted near the distal end of the lower margin; the lower margin of the propodites is armed with 14 or 15 pairs of spinules, those of the distal half increasing somewhat in length. The dactyli, which measure one-third the length of the propodites, terminate in two claws, of which the posterior is stouter than the other, and, between the former and the articulation, the posterior margin is armed with six movable spines, which slightly increase in length distally. The following legs are a little shorter; the meri of the fourth pair are armed with four, those of the fifth with three spines.

External maxillipeds and thoracic legs seem to be devoid of epipods.

Spiront. amabilis, Lenz, of Bare Island (Spengel's Zool. Jahrb., Syst. xiv. 1901, p. 432, pl. 32. figs. 2 a & 3), a typical specimen of which was kindly sent me by the Direction of the "Städtisches Museum" at Bremen, differs as follows :-- As in Spiront. alcimede, the outer angle of the orbital margin ends in a rounded tooth or lobe; in the figure in Lenz's paper it appears erroneously as sharp, and in both species there is, just below this angle, a sharp antennal spine, at the level of the upper border of the basal joint of the outer antennæ. Spiront. amabilis carries, however, below this spine, another also sharp tooth, apparently the pterygostomian spine, but this is altogether wanting in Spiront. alcimede. The third segment of the abdomen of Spiront. amabilis is less strongly curved, the posterior deflexed part is much shorter in proportion to the anterior than in our new species, and not compressed; the sixth has a slenderer shape, being almost three times as long (5 mm.) as broad anteriorly (1.9 mm.), and, according to the figure, the telson should carry six pairs of spinules (in the type specimen the telson is wanting). The carpus of the second legs is 7-jointed, in the figure it appears erroneously 6-jointed; it agrees with that of Spiront. alcimede, but the chela is as long as the last four joints taken together. There are, however, still more differences in the toothing of the rostrum, &c. (Concerning this locality, see Note A on page 454.)

# SPIRONTOCARIS PANDALOIDES (Stimpson). (Pl. 32. figs. 47, 48.)

Hippolyte pandaloides, Stimpson, in Proc. Acad. Nat. Sciences Philadelphia, 1860, p. 34.

Seven specimens from the Inland Sea of Japan, captured at a depth of six fathoms, bottom sand and weeds, here and there stones. These prawns are, when alive, brilliant emerald-green, and conform to Stimpson's "color viridis."

The *slender fusiform* body is moderately geniculated at the third segment of the abdomen, the upper border of the posterior deflexed part making an angle of nearly 45°

with the anterior. Six specimens are of subequal size, their length from the tip of the rostrum to the end of the telson varying between 50 and 56 mm.; the seventh is younger. 38.5 mm. long: the first six specimens are thus a little longer than was indicated by Stimpson, viz. 44 mm. The slender, stiliform rostrum is horizontal and straight, or the distal half is slightly turned upward; the free portion of the rostrum is once and a half as long as the upper border of the carapace, rarely a little shorter, and one-fourth or onefifth of it extends beyond the antennal scales. The upper margin, which arises with an obtuse carina a little before the middle of the carapace, carries in four adult specimens, in which the rostrum is normally developed, 7, 8, or 9 teeth. These teeth, which are rather small and two of which are always (also in the other specimens) situated on the carapace, reach either almost to the middle of the free part or a little beyond it, so that in one specimen the terminal part, which is devoid of teeth, appears a little longer than the rest, whereas in the others the terminal third or a little more appears unarmed. Two or more distal teeth are longer than the preceding; in one specimen they gradually increase in length, but in the others this is not the case, and the longer distal teeth are of equal or unequal length. This species is apparently variable as regards the number and the shape of these teeth. The lower margin is armed, in these four specimens, with 8, 10, or 12 teeth, that reach to the tip; they are partly larger than the teeth of the upper border, and grow also, more or less regularly, longer towards the tip. The basal part of the lower margin, posterior to the first tooth, is nearly straight. In these four specimens the toothing-formulæ are therefore:  $\frac{2}{10}, \frac{2}{10}, \frac{2}{8}, \frac{2}{8}$ , and  $\frac{9}{12}$ ; in two others, in which the rostrum is apparently not well developed, reaching not or barely beyond the antennal scales, the formulæ are:  $\frac{2}{9}$  and  $\frac{3}{9}$ ; in the young specimen, finally, it is  $\frac{2}{9}$ . Stimpson mentions  $\frac{10^{2}12}{10}$  as the toothing-formula, but in not one of our specimens do ten or twelve teeth occur on the upper border. Neither the upper nor the lower margin of the rostrum is ciliated.

Carapace and abdomen are smooth, though finely punctate. Antennal tooth slender, reaching to the middle of the basal joint of the outer antennæ; antero-lateral angle rounded, devoid of a pterygostomian spinule. Abdomen rounded, the third segment are moderately produced backward in an obtuse lobe. The pleuræ of the third segment are rounded posteriorly, those of the fourth are obtuse, but the fifth are produced, at the postero-lateral angle, in a sharp spine. Measured along its upper border, the sixth segment appears almost twice as long as the fifth, resembling that of *Spirontocaris stylus* (Stimps.) (cf. Rathbun, 'Decapod Crustaceans of the North-west Coast of North America,' 1904, p. 84). The sixth segment, the lower surface of which is rounded, and the postero-lateral angles of which terminate in a sharp tooth, is just twice as long as broad in the middle. The telson, which is a little longer than the sixth segment and a little more than four times as long as broad at its base, tapers rather strongly; its rounded upper surface, armed, according to Stimpson, with 6 pairs of spinules, carries in the six adult specimens 5 pairs, though in one of them there are 6 spinules on the left and 5 on the right side; the telson of the young individual has but 4 pairs. The telson

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terminates in a sharp tooth and carries two spinules on either side, of which the inner are twice as long as the outer.

The eye-peduncles, which present a distinct ocellus near the cornea, project almost entirely beyond the antero-lateral angle of the carapace, when directed transversely outward, and reach to the distal fifth of the first joint of the antennular peduncle.

The inner antennæ barely reach with their thin filiform, inner flagellum beyond the end of the antennal scales. The first joint of the peduncle, which is not quite half as long as the antennal scales, is three times as long as the second; the pointed stylocerite, the outer margin of which is straight, extends barely beyond the distal end of the first joint. The second joint, the outer border of which terminates distally in a small sharp tooth or spine, appears once and a half as long as broad when viewed from above, and twice as long as the third joint, which has also a small sharp tooth at the distal end. The shorter outer flagellum is considerably thickened along two-thirds of its length and beset with olfactory setæ.

The basal joint of the peduncle of the outer antennæ carries a small spine at the distal border of its lower surface. The blade of the scale, which is five times as long as broad, and the outer margin of which is straight, exceeds the small spine considerably by its rounded antero-internal angle. The peduncle reaches nearly to the distal end of the second joint of that of the inner antennæ, and the flagellum is about as long as the abdomen.

The mandibles are typical, and consist of a strong molar-process, an incisor-process, and a palp. The molar-process carries at the distal end a subacute conical tooth and another that is more obtuse; the distal end is yellow-coloured and thickly covered with short setulæ or bristles. The incisor-process, almost as long as the molar-process, but much narrower, tooth-like, narrows somewhat towards the distal extremity, which is divided into four acute teeth, the outer one of which is a little larger than the three others, which are of equal size; both processes are not connected and make a right angle with one another. The palp that originates at the base of the incisor-process is two-jointed; the terminal joint, as long as the other, is 0.45 mm. long, spathulate; its margins are fringed with pubescent setæ, a few of which occur also on the basal joint.

The external maxillipeds are short, reaching only to the distal end of the antennal peduncle, and are devoid of an exopodite; the antepenultimate joint is deeply hollowed out along the proximal half of its lower surface, and the penultimate is half as long as the terminal joint, which is armed with six sharp teeth at the distal end.

The legs of the first pair are very short, reaching only to the distal end of the basal joint of the antennal peduncle. The carpus, which slightly thickens distally, is a little shorter than the merus and than the chela; the fingers are about half as long as the palm; the dactylus terminates in two dark-brown claws, the fixed finger in one. The second legs (Pl. 32. fig. 48) barely reach beyond the antennal peduncle. The seven joints of the carpus, which is 4.24 mm. long, not yet twice as long as the merus, are, from the proximal to the distal end, respectively 0.65 mm., 0.38 mm., 1.02 mm., 0.7 mm., 0.5 mm., 0.34 mm., and 0.65 mm. long; the chela is 1.22 mm. long, the fingers 0.52 mm. These numbers show that the first and the seventh joints are equally long, that the

second and sixth are subequal, that the third is the longest and the sixth the shortest. The chela is almost twice as long as the last joint of the carpus, and the fingers are a little shorter than the palm.

The legs of the third pair reach to the end of the antennal peduncle, those of the fifth little beyond the anterior border of the carapace. The merus of the third legs is armed on its outer surface near the lower margin with 7 spines, that of the fourth with 6, that of the last pair with 3.

Geographical Distribution.---Hakodadi, Japan (Stimpson).

## LATREUTES, Stimpson.

## LATREUTES PLANIROSTRIS (de Haan).

Cyclorhynchus planirostris, de Haan, Fauna Japonica, Crust. 1849, p. 175, tab. 45. fig. 7. Rhynchocyclus planirostris, Miers, in Proc. Zool. Soc. 1879, p. 55. Latreutes planirostris, Ortmann, in Spengel, Zool. Jahrb., Syst. v. 1890, p. 505, Taf. 37. figs. 4 d-l, 4 n. Platybema planirostre, Rathbun, in Proc. U.S. Nat. Mus. vol. xxvi. 1902, p. 46.

One egg-bearing female from the Inland Sea of Japan; rare.

This specimen fully agrees with the ova-bearing females described by Miss Rathbun (l. c.). It is 28 mm. long from the tip of the rostrum to the end of the telson. The sixth abdominal segment is not quite twice as long as the fifth, and the telson is about once and a half as long as the latter. The carpus of the legs of the first pair is not carinate above. The legs of the second pair extend with their chela beyond the distal end of the antennal peduncles; the first joint is slightly longer than the third and both together are almost as long as the second; the chela, which is a little less broad than the distal extremity of the carpus, is little shorter than the second joint, and the fingers are distinctly shorter than the palm.

Geographical Distribution.—Japan (de Haan); Hakodate and North Coast of Nippon, 10-20 fathoms (Stimpson); Cape Sima, Nippon, 18 fathoms (Miers); Bay of Tokyo and Kagoshima, Japan (Ortmann); Hakodate, Hokkaido (Rathbun).

#### LATREUTES ACICULARIS, Ortmann.

Latreutes acicularis, Ortmann, in Spengel, Zool. Jahrb., Syst. v. 1890, p. 506, Taf. 37. figs. 6, 6 d-k, 6 n. Latreutes acicularis, Doflein, Ostasiatische Dekapoden, 1902, p. 638.

One ova-bearing female from the Inland Sea of Japan; deep water.

This specimen is 31 mm. long from the acute tip of the rostrum to the end of the telson, the carapace (rostrum included) being just half as long. The rostrum, which is one-third longer than the carapace, is unarmed above, except a minute spinule on the carapace, just behind the frontal border; it exceeds the antennal scales by one-third of its length. That part of the rostrum which is situated above the lateral carinæ is low and barely diminishes in height towards the tip; its upper margin is straight. The lower part of the rostrum is proximally about three times as high as the upper and gradually narrows towards the tip; it is armed near the latter with three sharp teeth.

Antennal tooth small. Along the distal end of the lower border of the carapace seven slender spines are observed, which diminish a little in length backward, and the foremost

of them is placed at the pterygostomian angle. The tapering telson terminates in a long slender tooth, which makes distinct angles with the posterior margin, and this margin is little broader than the tooth is long; of the two movable spines on either side the inner is three times as long as the outer and extends much beyond the median tooth. The rounded, upper surface of the telson carries two pairs of small spinules, the anterior pair somewhat nearer to the proximal than to the distal extremity.

External maxillipeds short, barely reaching beyond the insertion of the antennal peduncles. Fingers of the first pair of legs shorter than the palm, the latter a little thicker than the carpus. The first joint of the carpus of the second legs is about once and a half as long as the third, and both are a little longer than the second, which is twice as long as the third; the chela is just as long as the first and the third carpal joints taken together, the fingers being a little longer than the palm. The three other legs are slender and a little setose. The meropodites are armed with a sharp tooth near the distal end of their lower margin; the propodites carry six or seven movable spinules along the lower edge, which gradually grow longer and stronger towards the distal end; the slender dactyli, measuring a little more than one-third of the propodites, terminate in two strong claws, which are preceded on their lower margin by six movable spinules that diminish in length towards the articulation. So the meropodites of the fifth pair are 1.4 mm. long and six times as long as broad; the carpopodites are a little more than half as long as the meropodites, the propodites as long as the meropodites, but nine times as long as broad in the middle; the dactyli, finally, are 0.56 mm. long, measuring a little more than one-third of the propodites.

The ova are numerous, small, 0.5 mm. long, and once and a half as long as broad.

Geographical Distribution.—Japan, Kadsiyama (Ortmann); Hakodate, Yokohama (Doflein).

## LATREUTES LAMINIROSTRIS, Ortmann.

Latreutes laminirostris, Ortmann, in Spengel, Zool. Jahrb., Syst. v. 1890, p. 506.

One egg-laden female from the Inland Sea of Japan; deep water.

As usual, Dr. Ortmann has not mentioned, in the work referred to, the length attained by this remarkable species : the present female is 53 mm. long from the tip of the rostrum to the end of the telson. The rostrum (14 mm.) is one-fourth longer than the carapace (11 mm.). The tapering central axis of the rostrum runs at first straight forward, then slightly upward, whereas the pointed tip is again curved downward. That part of the rostrum which is situated above the central axis, and which is much lower than the inferior part, is slightly arched and carries six small acute equal teeth, four equidistant on the middle and two midway between them and the tip. Ortmann's typical specimen, also a female, was armed with nine teeth above. The lower edge carries seven much smaller teeth nearly of the same length, of which the first is situated midway between the distal end of the antennular peduncle and the first tooth of the upper edge; the inferior edge regularly curves, posteriorly, upward toward the central axis. The small spine on the carapace, which is a little larger than the upper teeth of the rostrum, is placed once and a half as far from the posterior border of the carapace as from the first tooth of the upper edge. The short eye-peduncles do not quite reach the extremity of the first joint of the antennular peduncle; there is a sharp, forwardly directed spine on the upper side of this extremity. Six sharp teeth or spinules occur at the pterygostomian angle of the carapace, and there is a small antennal spine just below the orbits.

The sixth segment of the abdomen is almost twice as long as the fifth, but a little shorter than the tapering telson, which is 7 mm. long; the postero-lateral angles are acute. The telson, which is rounded above, carries two pairs of minute spinules, which were overlooked by Ortmann; the anterior pair a little nearer to the proximal than to the distal extremity, the posterior a little nearer to the latter than to the anterior pair. The tip of the telson is not truncate ("abgestutzt"), as is said in the original description, but it ends in a sharp tooth, on either side of which are inserted, as usual, two movable spines, of which the outer is just as long as the median tooth, the inner twice as long. The lateral swimmerets are a little shorter than the telson.

The short external maxillipeds reach as far forward as the eye-peduncles. The second joint of the carpus of the second legs is twice as long as the first, the third appears a little shorter than the first; the chela is nearly as long as the second joint, the fingers slightly shorter than the palm.

Eggs very numerous, small.

This specimen is of a pale greenish colour, the gastric region more yellowish brown. *Geographical Distribution.*—Japan, 'Tanagava (*Ortmann*).

## HIPPOLYSMATA, Stimpson.

HIPPOLYSMATA VITTATA, Stimpson. (Pl. 33. figs. 49, 50.)

Hippolysmata vittata, Stimpson, in Proc. Acad. Nat. Sciences Philadelphia, 1860, p. 26.

Hippolysmata vittata, var. subtilis, Thallwitz, Decapoden-Studien, 1891, p. 22.

Nauticaris unirecedens, Spence Bate, Report on the 'Challenger' Macrura, 1888, p. 608, pl. 110. fig. 1. Nec Hippolysmata vittata, var., de Man, in Archiv f. Naturg. 53 Jahrg. 1888, p. 494.

Two egg-bearing females and one young specimen from the Inland Sea of Japan.

Dr. W. T. Calman, of the British Museum, was so kind as to examine for me the single typical specimen ( $\mathfrak{P}$ ) of *Nauticaris unirecedens*, Sp. Bate, from Hong Kong, and concluded that this species ought to be considered *identical* with *Hippolysmata vittata*, Stimps., from the same locality; this was also my supposition. "The type specimen of *Nauticaris unirecedens*," so wrote Dr. Calman to me, "is a little larger than is stated by Spence Bate. I think it would measure about 29 mm. in length, but I cannot attempt to straighten it for fear of damage. The postero-lateral angle of the fifth abdominal segment is distinctly more produced and more acute than in the original figure. The sixth segment is longer than the fifth (about 26: 20). The flagella of the antennules are wanting, and I cannot even find any fragments of them in the bottle. There are no arthrobranchiæ on the percopods, but there are epipods on all except the last pair. I have compared the specimen with Stimpson's description of *Hippolysmata vittata*, and I think it very likely, as you suggest, that it is the same species. At all events, I cannot find any character which distinctly contradicts this supposition."

The two egg-bearing females are respectively 33 mm. and 32 mm. long from the tip of the rostrum to the end of the telson, the carapace of the former being 12 mm. long, of the other 11.5 mm.; the young specimen is 22.5 mm. long, the carapace 8 mm. The carapace, rostrum included, measures little more than one-third of the whole length. The rostrum of the two larger specimens reaches to the distal end of the second joint of the antennular peduncle, that of the youngest individual little beyond the middle of that In the largest specimen the toothing-formula of the rostrum, which closely joint. resembles fig. 1 of plate 110 of the 'Challenger' Report, is  $\frac{7}{4}$ ; the first tooth, twice as far distant from the second as the second from the third, is little larger than the second, but the difference is not so great as on that figure. The distance of the first tooth from the frontal border is a little more than one-third the length of the carapace (rostrum excluded); two teeth are on the cephalothorax, the third is placed above the frontal margin. The foremost tooth is as far distant from the penultimate as from the pointed tip, which is situated on a somewhat lower level than the upper border of the carapace. The four teeth of the lower margin occur on its distal half and are considerably smaller than the upper ones; the first is situated just below the middle of the penultimate tooth of the upper border, the foremost tooth midway between the tip and the foremost one of the upper margin. In the other ova-bearing specimen the toothing-formula is  $\frac{8}{4}$ , just as in the 'Challenger' specimen of Nauticaris unirecedens, and three teeth are on the carapace, the fourth immediately before the frontal border; the foremost tooth is once and a half as far distant from the tip as from the penultimate tooth. Of the four small teeth of the lower margin, the first is situated just below the base of the foremost tooth of the upper margin, the two anterior in front of it. Except the first, the teeth of the upper border are equidistant, like those of the lower margin.

The rostrum of the youngest specimen shows the formula  $\frac{6}{4}$ ; two teeth are on the carapace, the third above the frontal border; the foremost tooth of the upper margin is a little farther from the tip than from the penultimate; of the four very small teeth of the lower margin, the first and the second are situated below the foremost tooth of the upper margin, the third and the fourth in front of it. In this youngest individual the tip of the rostrum is situated at the same level as the upper surface of the carapace. The slender antennal tooth reaches the cornea of the eyepeduncles; the pterygostomian spinule is small and sharp, though distinct in the three specimens.

The abdomen is rounded and smooth. The postero-lateral angle of the fifth segment terminates in a sharp point, much sharper than it appears in the quoted figure 1 of the 'Challenger' Report. The sixth segment is once and a half as long as the fifth; in Spence Bate's figure it appears shorter than the fifth, but, as is shown above, this figure is inaccurate. The postero-lateral angle of the sixth segment is acute, but not movable. The telson, which is not quite twice as long as the sixth segment, tapers posteriorly to the obtuse posterior border, which is in the middle acute and which, fringed, like the lateral margins, with ciliated setæ, carries on either side two movable spinules, of which the inner are much longer than the outer. The somewhat flattened upper surface carries two pairs of spinules. The uropods are little longer than the telson and carry no movable spine at base.

The stout eye-peduncles reach a little beyond the middle of the first joint of the antennular peduncle. The internal antennæ are, in the largest specimen, 38 mm. long, a little longer than the body; the peduncle agrees with Spence Bate's description and figure of Nautic. unirecedens; the sharp-pointed basal spine or stylocerite reaches barely beyond the eye-peduncles; the second joint is half as long as the first and twice as long as broad, the third half as long as the second. The two flagella, however, which are just as long as the body, do not agree with the figure in the 'Challenger' Report, nothing is said about them in the text, and, as is shown above, they are lost in the type specimen in the British Museum. I suppose, however, that they have been wrongly figured in the Report. These flagella are of equal length, filiform, but the outer one is slightly thickened at its base for a short distance (4.5 mm.), which is a little shorter than the peduncle, and this thickened part is beset with olfactory setæ.

The outer antennæ are as long as the inner; the basal joint of the peduncle, which reaches midway between the tip of the eye-peduncles and the distal end of the first joint of the antennular peduncle, carries a small spine at its outer angle; the flagella, 36 mm. long in the adult females, are a little longer than the body. The antennal scales barely narrow distally, and the small spine which terminates the slightly concave outer margin reaches barely beyond the truncate tip.

The pediform external maxillipeds project with half their terminal joint beyond the antennal scales; the exopodite reaches a little beyond the middle of the antepenultimate joint.

The legs of the first pair extend to the extremity of the antennal scales. The carpus is, in the adult, a little shorter than the chelæ, but slightly longer than the palm, that is once and a half as long as the fingers; the latter gape a little along their proximal half. The elongate, filiform legs of the second pair project with their small chela and the last joint of their carpus beyond the distal extremity of the basal thickened part of the outer antennular flagella. The carpus is composed of 22 joints; the penultimate joint is 0.3 mm. long, those in the middle are slightly longer, viz. 0.36 mm., and the last joint is twice as long as the penultimate. The chela, 1.22 mm. long, is twice as long as the last joint of the carpus, and the palm is a little longer than the fingers.

The three other legs apparently agree with those of the 'Challenger' specimen of *Nautic. unirecedens.* The meri carry on their outer surface a few movable spinules, those of the third pair, *e. g.*, five; the propodites carry similar spinules along their posterior margin in two rows, those of the third legs seven pairs; the dactyli, finally, measure, in the legs of the third pair, one-fourth of the propodites and are armed with six spines along their posterior margin, which gradually increase in length, the last being the terminal claw.

The eggs are very numerous, ovate, 0.6 mm. long and 0.4 mm. broad.

I am indebted to Prof. Heller, of Dresden, for having been enabled to examine the single type specimen of Thallwitz's variety *subtilis* from Cebu: it proved to differ from our specimens only by its smaller size.

One of the five specimens described (Archiv f. Naturg. liii. p. 494) by me in 1888 as a variety *amboinensis*, and which were collected by Dr. Brock at Amboina, is lying before me. It proves now to be a *different* species from *Hipp. vittata*, Stimps., and it may henceforth bear the name of *Hippolysmata amboinensis*. The whole animal has a *slenderer* appearance. The rostrum, the free part of which is almost as long as the carapace, has a *much slenderer* form than that of *Hipp. vittata*, and the first tooth of the upper margin is situated at one-fourth the length of the carapace from its frontal border. The sixth segment of the abdomen is more elongate, almost twice as long as the fifth, and barely shorter than the telson. The peduncles of the inner antennæ and the antennal scales are more elongate, slenderer, and the stylocerite is shorter than the ves, rudimentary. The legs are also *slenderer*. A more detailed description will be published hereafter.

The following remarks about the single type specimen of *Merhippolyte orientalis*, Sp. Bate, captured by the 'Challenger' Expedition at a depth of 800 fathoms off New Guinea, will, I think, be welcome. Dr. Calman wrote me about it as follows:—"With regard to *Merhippolyte orientalis*, I am sorry that I cannot give you many details. The type specimen is in such an extremely bad state that no one except Mr. Spence Bate would have thought for a moment of describing it as a new species! I attempted to make a sketch of the rostrum etc., but I thought it was not worth the trouble. The eyepeduncles are *shorter* than the first segment of the antennular peduncle, probably not more than two-thirds of its length, though on account of the membranous consistency of all the parts it is difficult to form an idea of the exact proportions. There is a wellmarked pterygostomial spinule on the carapace. The mandible has an incisor-process and a three-segmented palp. There are apparently arthrobranchiæ on the peræopods. All the peræopods are wanting. I doubt very much whether it would ever be possible to recognize the species again."

According to Calman's latest paper on the Hippolytidæ (Ann. Mag. Nat. Hist. ser. 7, vol. xvii. January 1906, p. 30), this species seems to be indeed a *Merhippolyte*.

Another species, which was described by me in 1892 and in 1902 under the name of *Merhippolyte orientalis* (in Max Weber's 'Decapoden des Indischen Archipels,' p. 407, and in Abhandl. Senckenb. naturforsch. Gesellschaft, Bd. xxv. p. 849), is certainly different from that deep-sea species of the 'Challenger' Expedition; it is also different from *Hippolysmata vittata* and *Hippolysmata amboinensis*, and may henceforth bear the name of *Hippolysmata kikenthali*, with some doubt as regards the genus, because the mandible was not examined by me.

Geographical Distribution of Hippolysmata vittata, Stimps.—Hongkong (Stimpson and Spence Bate); Cebu (Thallwitz); Pulau Bidan, Penang (Lanchester).

#### ALPHEUS, Fabr.

#### ALPHEUS BREVIROSTRIS (Olivier). (Pl. 33. figs. 51, 52.)

Palamon brevirostris, Olivier, in Encyclop. Méthod. t. viii. 1789, p. 664, pl. 319. fig. 4.
Alpheus brevirostris, Milne-Edwards, Hist. Nat. Crust. ii. 1837, p. 350.
Alpheus rapax, de Haan, Fauna Japonica, Crust. 1849, p. 177, tab. 45. fig. 2.
Alpheus rapax, de Man, in Max Weber's Zool. Ergebnisse, 1892, ii. p. 404.

Two egg-bearing females from the Inland Sea of Japan, deep water.

Before describing these two specimens, I wish to make some synonymical remarks about the species of the "*brevirostris*" section of this genus, to which section the two females doubtless belong.

In his great work ' Les Alpheidæ : Morphologie externe et interne etc.,' Ann. Sc. Nat., Zool. 8º sér. t. ix. 1899, p. 14, Prof. Coutière writes :--- "Il convient d'identifier A. malabaricus, de Haan, avec A. rapax, Fabricius (?), Spence Bate." In my opinion this identification is erroneous, and de Haan's A. malabaricus ought to be regarded as a proper species that henceforth may bear the name of brevicristatus, under which name this species has been figured by the author of the 'Fauna Japonica.' Before me are lying a typical specimen of A. malabaricus, de Haan, and another of A. rapax, de Haan, both from de Haan's typical collection in the Leyden Museum, both specimens in a dry state. Through the kindness of Prof. Döderlein, of Strassburg, I received also four specimens of an Alpheus from the Bay of Tokyo, described by Dr. Ortmann under the name of A. malabaricus (in Zool. Jahrb., Syst. v. 1890, p. 481), and two, also from that Bay, of Ortmann's A. rapax (l. c. p. 481). The examination of these specimens proved that Ortmann's A. malabaricus is really the same species as that which was described by de Haan under this name and figured under the name of A. brevicristatus; and furthermore that this species is no doubt different from Spence Bate's A. rapax (Report on the 'Challenger' Macrura, p. 552, pl. 99. fig. 1). The rostrum of A. malabaricus passes backward into a carina which is subacute and strongly compressed between the eyes, but which soon broadens behind the corner and becoming obtuse and rounded passes into the surface of the gastric region; its shape is therefore characteristic. The second joint of the antennular peduncle of Spence Bate's A. rapax is described as three times as long as the first, but in his fig. 1c it appears little more than twice as long; the peduncle resembles therefore that of de Haan's malabaricus. In de Haan's A. malabaricus the antennal scale barely extends beyond the antennular peduncle, whereas in the fig. 1 c of the 'Challenger' Report it reaches much beyond it. The telson of A. brevieristatus appears broader in proportion to its length, and the spinules of the posterior pair are situated closer together than those of the anterior, whereas this is not the case in fig. 1z.

Not only the chelipeds, but also the four other legs, present a slenderer shape than those of A. brevieristatus. In both chelipeds the upper border of the merus is obtuse and quite unarmed, but in Spence Bate's A. rapax the upper margin ends in a sharp tooth. In the latter species the upper margin of the larger chela carries no trace of the transverse

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furrow near the articulation of the dactylus characteristic of *Alpheus brevicristatus*, and the carinæ on the outer surface of the palm are neither described nor figured in the 'Challenger' Report. The dactylus of the smaller chela of *A. brevicristatus* has a slenderer form. These two species are therefore certainly different.

It is on the authority of Coutière, who has compared the type of A. brevirostris, Oliv., with the Leyden type of de Haan's A. rapax, that these two species are considered also now by me as identical, though I may observe that in de Haan's A. rapax the upper border of the larger chela presents no trace at all of the transverse groove near the articulation of the dactylus which is characteristic of A. brevirostris (vide Coutière, l. c. p. 230, fig. 281, and in Bull. Soc. Entom. France, 1898, p. 250, fig. 1), and that the antennal scale reaches barely or not beyond the antennular peduncle. In my opinion it would be preferable to consider A. rapax of Fabricius as identical with A. brevirostris, Oliv., for Fabricius's description is fully applicable to the latter. The two specimens, apparently both males, of A. rapax, received from the Museum of Strassburg, seem at first sight to belong to two different species. The larger specimen, which is 65 mm. long from the tip of the rostrum to the end of the telson, fully agrees with the Leyden type of A. rapax, de Haan, and ought thus to be referred to A. brevirostris, Oliv. The other specimen, however, 55 mm. long, belongs perhaps to that species which has been described and figured by Spence Bate under the name of A. rapax (l. c. p. 552, pl. 99. fig. 1). It fully agrees with it, except the antennal scale, which, though a little longer than the peduncles of the outer and inner antennæ, has a less slender shape, being proximally broader in proportion to its length, whereas the terminal spine barely reaches beyond the tip of the scale. As regards the shape of the antennal scale and the peduncles of both pairs of antennæ, this specimen agrees with that of A. brevirostris, except that in the latter the antennal peduncle extends a little beyond the tip of the scale. The rostral carina, acute and strongly compressed between the eyes, does not reach so far backward as in the other older specimen, but fades away soon behind the eyes. All the legs are a little slenderer than in the specimen of A. brevirostris. Both the larger and the smaller chela closely resemble those of Spence Bate's A. rapax. The larger chela is 29 mm. long and 8.75 mm. broad, the palm being 17.5 mm. long, the fingers 11.5 mm.; the smaller chela is 28 mm. long, the fingers three times as long as the palm, and the greatest breadth of the chela, about in the middle, is almost one-fourth of its length. The fact that the fingers are longer in proportion to the length of the palm than in the 'Challenger' species may be explained by the larger size of our specimen. Ortmann referred both specimens to A. rapax, de Haan = brevirostris, Oliv. (teste Coutière); perhaps he will eventually prove to be right, if the length of the fingers of the smaller chela of *A. brevirostris* is shown to be so very variable.

The two egg-laden females from the Inland Sea of Japan are of equal size, adult, 55 mm. long from the tip of the rostrum to the end of the telson. The rostrum reaches in one female almost to the distal end of the first joint of the antennular peduncle, in the other only to the middle of this joint; it passes into a carina, which between the eyes is sharp, strongly compressed; the upper edge, between the eyes slightly concave, runs obliquely upward and, reaching the upper surface of the carapace, becomes obtuse, even

a little flattened, and gradually fades away about on the middle of the cephalothorax. The surface of the latter is punctate, the puncta being larger posteriorly.

The surface of the latter is punctate, the puncta being larger posteriorly. The telson, 7.5 mm. long and 4 mm. broad at its base, resembles that of the 'Challenger' *rapax*, but the spinules of the posterior pair stand closer together. The lateral swimmerets extend a little beyond it. The second joint of the antennular peduncle is in one specimen twice, in the other almost twice, as long as the first and almost three times as long as the third; the flattened stylocerite ends in a sharp spinule which reaches to the extremity of the first joint of the peduncle. The antennal scale, slightly longer than the antennular peduncle, has the same form as in the adult male from Strassburg; it has a much stouter shape than that of Spence Bate's *rapax*-specimen, the scale being 7 mm. long and 2.75 mm. broad proximally; the terminal spine barely reaches beyond the tip of the scale and its outer margin is slightly concave. The antennal peduncles, reaching only to the middle of the third joint of the inner antennæ, are shorter than the scales, whereas in the adult male from the Strassburg Museum they reach a little beyond them. The external maxillipeds reach to the end of the antennal scales.

In the addit mate from the Strassburg Museum they reach a fittle beyond them. The external maxillipeds reach to the end of the antennal scales. In one specimen the larger cheliped is placed on the right side, in the other on the left. The larger cheliped resembles that of the 'Challenger' specimen of A. rapax (l. c. pl. 99. fig. 1 k). The upper border of the merus terminates in a sharp tooth, the rather sharp infero-internal edge is beset with very small teeth and ends in a much stronger pointed tooth. The chela is in one specimen 20 mm. long and 5.5 mm. broad, the fingers being 7.4 mm. long. The larger chela of the other female is 17 mm. long, 5.4 mm. broad, the fingers 7.25 mm. long. The outer and the inner surfaces of the larger chela are finely granulated, except the distal half of the fingers which is smooth; the outer surface of the fixed finger is slightly concave, that of the palm presents no trace of carinæ; the two carinæ on the upper border are distinct, the inner, fringed with long hairs and continued to the carpal articulation, more than the outer, which fades away nearly on the middle of the palm. The lower edge of the chela is also fringed with hairs internally, from the carpal articulation to the tip of the immobile finger, and the hairs along the upper border are continued to the tip of the dactylus.

carpal articulation to the tip of the immobile finger, and the hairs along the upper border are continued to the tip of the dactylus. The smaller cheliped (Pl. 33. figs. 51, 52) also much resembles that of the 'Challenger' *rapax*-specimen, but the immobile finger is distinctly broader at its base than the dactylus, whereas in fig. 1 of pl. 99 the dactylus appears broader than the immobile finger. The merus, as slender as on that figure, is armed with the same teeth as that of the larger cheliped. The chela is strongly compressed. In the larger female it is 17.25 mm. long, the palm 6.25 mm. long and 3.5 mm. broad; in the other specimen these numbers are 14.5 mm., 5.5 mm., and 3.7 mm. The fingers gape a little and are compressed, especially the immobile, which at its flattened base is *distinctly broader* than the dactylus, whereas both taper towards the pointed, crossing tips; their inner edges are hairy. The upper and lower borders of the chela of the dactylus are fringed with long hairs on their inner side.

The four following legs closely resemble those of the older specimen, 65 mm. long, of Ortmann's  $\mathcal{A}$ . rapax from the Bay of Tokyo, mentioned above. The second joint of the carpus of the second legs is 4 mm. long, a little longer than the first (3.5 mm.). The

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meri of the third pair are 10.25 mm. long and 1.9 mm. broad,  $5\frac{1}{2}$  times as long as broad; those of the fourth pair are 7.5 mm. long and 1.75 mm. broad; those of the fifth are 6.75 mm. long and 1 mm. broad.

The ova are very numerous and small, 0.6-0.62 mm. long and somewhat less broad.

The red upper surface of the body is marked with symmetrically arranged spots and striæ of a white colour, but the fourth segment of the abdomen is adorned on either side with *a dark red-brown spot*, which is quite characteristic. The red inner surface of the larger chela with a few large white flecks near the upper and lower borders; similar flecks occur also on the inner surface of the palm of the smaller chela, and its fingers are almost entirely white.

The ova-bearing female from the river near Pare-Pare, Celebes (de Man, in Weber, Zool. Ergebn. 1892, ii. p. 404), was also examined by me, and seemed to belong to the same species as the two females from the Inland Sea of Japan. Its size is a little smaller, the upper surface of the telson is a little more rounded, and, in consequence of its smaller size, the rostral crest is not continued so far backward; but otherwise there are no differences.

## ALPHEUS JAPONICUS, Miers. (Pl. 33. fig. 53.)

Alpheus japonicus, Miers, in Proc. Zool. Soc. 1879, p. 53.

Alpheus japonicus, Ortmann, in Spengel, Zool. Jahrb., Syst. v. 1890, p. 476, Taf. 36. fig. 14.

Alpheus longimanus, Spence Bate, Report on the 'Challenger' Macrura, 1888, p. 551, pl. 98. fig. 4.

Two males from the Inland Sea of Japan and one egg-bearing female without definite locality, but no doubt also from the Inland Sea. This Prawn is common in 8-15 fathoms.

The two male specimens are 45 mm. long; the female 40 mm. from the tip of the rostrum to the end of the telson.

The sharp-pointed rostrum is little shorter than the visible part of the first joint of the antennular peduncle and extends horizontally forward. The second joint of the antennular peduncle is about once and a half as long as the visible part of the first, and the third is shorter than the first; the flattened and broad stylocerite ends distally in a sharp spinule, which reaches almost to the distal end of the first joint of the antennular peduncle. The small spinule on the basal joint of the antennal peduncle is placed on the distal edge of its lower surface, and is therefore not visible from above. The antennal scale, the outer margin of which is slightly concave, is as long as the peduncle of the inner antennæ and a little shorter than that of the outer. The telson, the lateral margins of which are slightly prominent in the middle, carries two pairs of spinules.

The external maxillipeds are a little shorter than the antennal peduncles; according to Spence Bate, they should extend to a little beyond them.

In both male specimens the left cheliped is the larger. The infero-internal margin of the merus is fringed with hair and terminates in a sharp tooth; the infero-external margin is very finely denticulate, and its upper border ends also in a sharp tooth. The larger chela, which is a little more than three times as long as broad, agrees with the quoted descriptions and figures; the fingers are little more than half as long as the palm. The merus of the other cheliped agrees with the described one, but there is no tooth at the far end of the upper border and that of the infra-internal border is also rudimentary. The wrist is a little longer than that of the left cheliped.

This species now proves to belong to those of the "edwardsi"-section, in which the dactylus of the smaller cheliped presents the "Balæniceps"-form in the male, whereas that of the female is simple. Miers makes no mention of this character, but only two specimens were at his disposal, probably females. Spence Bate was able to examine both males and females ; but the difference was nevertheless overlooked by him, and his fig. 4 k'represents apparently the smaller cheliped of a female. In both males the smaller chela (Pl. 33. fig. 53) is a little longer than the larger, and in both the fingers are somewhat shorter than the palm. The straight upper margin of the palm, which distinctly narrows distally, terminates in an acute lobe a short distance behind the articulation of the fingers, but the lower margin has no constriction at all; the longitudinal depressions on the inner and on the outer side of the palm are distinct. Just as on the larger chela, a sharp spine occurs on either side of the articulation of the dactylus. The dactylus has the well-known "Balæniceps"-form : two crests, which are beset with stiff setæ and which arise from the middle of the finger, run, on its outer and inner side, forward and upward, and unite at a short distance behind the tip; looked at from above the dactylus appears here somewhat broadened, whereas it is narrowest in the middle. The fingers shut close together, and their hooked tips cross one another.

The larger cheliped of the female is wanting; the smaller agrees with the figure 4k' in the 'Challenger' Report. The upper border of the merus is unarmed, but there is a sharp tooth or spine at the distal end of the infero-internal margin. The fingers are distinctly somewhat longer than the palm, and the slender tapering dactylus is *simple*, without hairy carinæ. Both the upper and the lower border of the palm are *entire*, without a constriction or lobe behind the articulation of the fingers. The inner surface of the larger chela is finely granulated; the granules are wanting on the triangular depression, on the middle of the palm, and at the base of the immobile finger, except in the middle; the dactylus is smooth, except at its base. The granulation on the outer surface is less distinct.

The carpus of the second pair of legs is 5-articulate; the first joint is almost as long as the three following taken together, the fifth is once and a half as long as the two preceding, which are equal and the shortest of all. The fingers are a little longer than the palm. The other legs are slender, smooth, unarmed.

Eggs very numerous and small.

The upper surface of the body and of the peduncles of the internal antennæ, as also the inner surface of the chelipeds, are reddish.

Coutière ("Les Alpheidæ," in Ann. Sc. Nat., Zool. 8° sér. ix. 1899, p. 35) is inclined to regard this species also as a variety of *A. edwardsii*, but I am not of that opinion.

This Prawn is named the Clawcracker, because it makes a loud cracking noise with its claws which can be heard under water; if the noise is made while the animal is being handled it is instinctively dropped, owing to the slight shock received. The exertion is so great that the end of the big claw is frequently cast off.

#### Measurements in millimetres.

Length of the body from the tip of the rostrum to	3.	3.	<b></b> .
the end of the telson	46	46	40
Length of the carapace	15	15	13
Length of the larger chela	28.5	31	
Greatest breadth of the palm of the larger chela	8	9	
Length of the fingers	10	10	
Length of the smaller chela	34	35	16.2
Greatest breadth of the palm	3.75	4.25	2
Length of the fingers	16	15.5	9.5

Geographical Distribution.—Lat. 34° 6' N., long. 136° 15' E., at 11 fathoms; lat. 35° 7' N., long. 136° 55' E., at 3 fathoms (*Miers*); off Yokorka, Japan, in from 5 to 20 fathoms, and off Kobé, Japan, depth 8 to 50 fathoms (*Spence Bate*); Bay of Tokyo and Tanagava, Japan (*Ortmann*).

#### PENÆUS, Fabricius.

#### PENÆUS (METAPENÆUS) LAMELLATUS, de Haan.

Penœus lamellatus, de Haan, Fauna Japonica, Crust. 1849, p. 193, tab. 46. figs. 4 & 5.

Penæus lamellatus, Miers, in Proc. Zool. Soc. 1878, p. 308.

Penæus lamellatus, Kishinouye, in Journ. Fish. Bureau, Tokyo, vol. viii. no. 1, 1900, p. 25, pl. 6. fig. 1.

Parapenæus lamellatus, Rathbun, in Proc. U.S. Nat. Museum, xxvi. 1902, p. 38.

One adult female from the Inland Sea of Japan.

This beautiful specimen is 75 mm. long from tip of rostrum to the end of the telson. The upper margin of the rostrum, which, extending just beyond the eyes, reaches as far forward as the first joint of the antennular peduncle and as the setose scale or prosartema, carries nine teeth; of these the first is placed immediately before the middle of the carapace and the fifth above the frontal margin; the second is almost as far from the fifth as from the first. When this female is compared with a typical male from the Leyden Museum, lying before me, the lower margin of the rostrum appears to run, in the Leyden type, a little more oblique than in the female, and this is also the case with the teeth of the upper margin, especially with the first and the second, so that these teeth are in the male a little more erect. I cannot decide whether this is a sexual, a local, or an individual difference.

The upper margins of the first three teeth of the rostrum and of the carina on the third to sixth segments of the abdomen are marbled with blue and yellow, and the hairs with which the appendages of the body, excepting the eye-peduncles and the upper antennæ, are furnished are of a beautiful red colour.

The external maxillipeds, which reach to the tip of the antennal scales, are provided with an exopodite that reaches almost to the middle of the carpopodite. The perceopods are also all furnished with a well-developed exopodite; the exopodites of the fifth pair reach just beyond the ischium, whereas those of the first reach nearly to the distal end of the merus.

Geographical Distribution.—West coast of the island of Yezo, near Cape Sooga, lat. 45° N. (de Haan); Hizen, Nagasaki (Rathbun).

## PENÆUS (METAPENÆUS) AKAYEBI, Rathbun. (Pl. 33. fig. 54.)

Penæus velutinus, Spence Bate, 'Challenger' Macrura, 1888, p. 253 (part.), nec Pen. velutinus, Dana.

Penæus velutinus, Kishinouye, in Journ. Fish. Bureau, Tokyo, viii. no. 1, 1900, p. 26, pl. 6. fig. 2; pl. 7. figs. 11, 11 a, 11 b.

Parapenæus akayebi, Rathbun, in Proc. U.S. Nat. Museum, xxvi. 1902, p. 39.

? Metapenæus stridulans, W.-Mason, Alcock, in Ann. & Mag. Nat. Hist. ser. 7, xvi. 1905, p. 526.

One male and one female from the Inland Sea of Japan, caught in deep water.

According to the label, this species, which is very common, has curious pea-green eyes, the body covered with red mottled spots.

The male is 57 mm. long from tip of rostrum to the end of the telson; the carapace with the rostrum is 17.5 mm. long, without the rostrum 10 mm.; the sixth segment of the abdomen, measured on median line, appears to be 8.75 mm. long, 4.6 mm. broad anteriorly, 3.7 mm. broad posteriorly. The rostrum, which reaches to the end of the second joint of the antennular peduncle, is horizontal and 1+6-toothed; the gastric tooth is situated at the anterior fourth of the carapace, as in Kishinouye's figure; according to Miss Rathbun, it should be situated in adult individuals "a little in front of the anterior third"; the foremost tooth is a little farther from the tip than from the penultimate. The telson, which is little longer than the sixth segment, is armed with one immovable spiniform tooth, which is preceded by three movable spines.

The short flagella of the inner antennæ are little more than twice as long as the terminal joint of their peduncle; they are of equal length, but the upper is much stouter than the gradually tapering lower flagellum, and they reach entirely beyond the antennal scales.

The external maxillipeds extend almost to the tip of the rostrum; their exopodite reaches to the middle of the merus.

All the thoracic legs carry an exopodite.

The female is 60 mm. long; the carapace, rostrum included, 19.5 mm., without it 11 mm.; the sixth segment of the abdomen is, measured on median line, 9.5 mm. long, 5 mm. broad anteriorly, 4 mm. posteriorly; the telson, 9.75 mm. long, has its lateral margins armed as in the male. The very slightly ascending rostrum, which reaches to the end of the second joint of the antennular peduncle, is 1+7-toothed; the three or four anterior teeth decrease a little in size, and the anterior tooth is a little farther from the tip than from the penultimate, whereas the gastric tooth is situated at the anterior fourth as in the male.

The external maxillipeds and the thoracic legs agree with those of the male; those of the fifth pair carry also an exopodite.

Both in the male and in the female the carapace carries a pair of stridulating-organs, first mentioned by Dr. Alcock in his description of *Metapenœus stridulans* (Ann. & Mag.

Nat. Hist. ser. 7, xvi. 1905, p. 526). Each organ consists of a smooth, quite glabrous band, which, arising from the posterior end of the branchiostegite, curves forward, slightly narrowing distally; this band carries 18-20 smooth transverse ridges that run parallel with one another; they are broadest in the middle of the organ and gradually narrow towards both extremities.

Alcock suggests that *Penæus akayebi*, Rathb., may prove to be identical with *Metapenæus stridulans*, W.-Mason, from the east coast of Bengal. I hesitate, however, to identify them, because they belong to a section of this subgenus the species of which are very closely related and chiefly distinguishable by such slight differences as the shape of the sixth pleonic segment and the proportion of its length to that of the carapace. Though Alcock's description of *Metap. stridulans* agrees very well with these specimens, these characters are not spoken of. I suppose even that *Pen. akayebi* is a different species, for the stridulating-organ of *Metap. stridulans* is usually composed of 5, occasionally of as many as 12, transverse ridges, whereas 18–20 are observed in *Pen. akayebi*. Moreover, the closely related *Pen. (Metapenæus) acclivis*, Rathb., is also furnished with these remarkable organs, and the description of *Metap. stridulans* agrees very well with this species.

In *Metap. stridulans* the "second abdominal tergum is medially carinated in less than its posterior half," and this carina is sulcate; in *Pen. akayebi* this carina is hardly grooved, and runs *in the middle* of the tergum.

Geographical Distribution.—Inland Sea, Bay of Ise, Japan (Kishinouye): Wakanoura, Kii; Onomichi, Bingo; Kawatana; Hizen, Nagasaki; Mogi, near Nagasaki, Japan (Rathbun).

# PENÆUS (METAPENÆUS) ACCLIVIS, Rathbun. (Pl. 33. fig. 55.)

Parapenaus acclivis, Rathbun, in Proc. U.S. Nat. Museum, xxvi. 1902, p. 41, figs. 12-14.

One female from the Inland Sea of Japan, captured at a depth between 5 and 20 fathoms or more.

This specimen is 80 mm. long from tip of rostrum to the extremity of the telson. Measured on median line, the carapace appears to be 26.5 mm. long, the rostrum included, and 16 mm. without it; the sixth segment of the abdomen is 11.3 mm. long just *seven-tenths* as long as the carapace; the greatest width of this segment anteriorly is 7.25 mm., whereas it is 5.5 mm. broad posteriorly. The telson is 14.5 mm. long, just twice as long as the greatest width of the sixth segment anteriorly; the telson, which gradually tapers to the acuminate tip, is armed with one pair of immovable spines, which are preceded by three pairs of strong movable ones; the immovable spine on either side is barely longer than the anterior movable one, and the two following grow gradually longer, so that the third is three times as long as the anterior spine and slightly extends beyond the immovable. The outer swimmerets hardly reach beyond the extremity of the telson, the inner not at all.

When the peduncles of the inner antennæ are placed immediately below the rostrum, the latter appears to reach a little beyond the end of the second antennular segment,

but in the usual horizontal position of the peduncle it does not appear to extend to the extremity of the second joint. As regards its usual shape, the rostrum *exactly agrees* with Miss Rathbun's figure, but there are only *six* teeth on the free part; the gastric tooth is situated at the anterior fourth of the carapace. The six teeth of the free part are equidistant and of equal size except the anterior, which appears distinctly smaller than the preceding; this anterior tooth is once and a half as far from the penultimate as from the tip of the rostrum.

The stylocerite of the inner antennæ reaches to the end of the first joint, which carries a spine at the far end of its outer border; the short flagella, which extend beyond the antennal scales, are nearly twice as long as the terminal joint of the antennular peduncles; they are subequal in length, but the upper is a little shorter. The basal joint of the antennal peduncle has no spine at the outer angle or on the distal border of the lower surface; the outer margin of the scale is very slightly arcuate proximally, and the distal spine reaches as far forward as the laminar portion.

The last two joints of the external maxillipeds extend beyond the antennal peduncle, reaching almost to the tip of the rostrum; their exopodite reaches to the end of the merus-joint. The outer footjaws, as also the legs of the first and of the second pair, are unispinose at base, but the legs of the first pair carry, moreover, a spine at the distal end of the lower margin of their ischium. The legs of the third pair attain the tip of the antennal scales, those of the fifth extend with little more than their dactylopodites beyond the antennal peduncles, while the legs of the fourth pair are but little shorter. The terminal joints of the fifth legs are little more than half as long as their propodites.

The thelycum does not fully agree with the figure of the original paper; it is therefore figured afresh (Pl. 33. fig. 55).

The stridulating-organ of this species much resembles that of *Pen. (Metap.) akayebi*, Rathb., but there are only 13 or 14 ridges, which gradually narrow, like the organ itself, towards the anterior end.

Geographical Distribution.-Mogi, near Nagasaki (Rathbun).

# PENÆUS (PARAPENEOPSIS) TENELLUS, Sp. Bate.

Penæus tenellus, Spence Bate, Report on the 'Challenger' Macrura, 1888, p. 270.

Penæus tenellus, Kishinouye, in Journ. Fish. Burcau, Tokyo, viii. no. 1, 1900, p. 22, pl. 6. fig. 3, pl. 7. fig. 8 A & B.

Penæus crucifer, Ortmann, in Zool. Jahrb., Syst. v. 1890, p. 451, Taf. 36. fig. 5 a, b.

One female from the Inland Sea of Japan, captured at a depth between 5 and 20 fathoms or more.

This specimen is not yet full-grown, being 52 mm. long from the tip of the rostrum to the end of the telson, whereas, according to Kishinouye, the female attains a length of 75 mm. The body is described, both by Spence Bate and Kishinouye, as being smooth and naked; in the present female, however, the carapace is very finely scubrous, being covered rather closely with minute spinules which are only 0.03-0.05 mm. long; still smaller spinules occur also on the telson and perhaps here and there on the other segments of the abdomen.

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This species is characterized by all the rostral teeth standing upon the free part of the rostrum, there being none on the carapace. Of the eight teeth, the first, which is situated upon the anterior border of the carapace, appears a little smaller than the two following; these are also larger than the rest, which slightly decrease in size distally; the anterior tooth is about once and a half as far distant from the tip of the rostrum as from the penultimate.

A longitudinal fissure proceeds from the anterior border of the carapace, immediately above the antennal spine, backward, and extends along two-thirds of the length of the carapace; it was first described by Kishinouye. There is also a third transverse suture at the level of the third pair of legs. Stridulating-organs wanting.

The rather obtuse carina of the fourth segment of the abdomen arises at one-seventh of its length from the anterior extremity. The telson is not "about half the length of the lateral plates of the rhipidura," but measures about two-thirds their length, the basal joints included. The furrow on the upper surface reaches little beyond the middle of the telson.

The stylocerite of the inner antennæ reaches not quite so far forward as the antennal peduncle, which extends to the middle of the corneæ; the antennular peduncle is 9 mm. long, the flagella  $7\cdot2$  mm. The basal joint of the antennal peduncle carries a spine at the outer angle; the spine at the distal end of the very slightly arcuate outer margin of the scale reaches not quite to the rounded extremity of the laminar portion. The flagellum is almost twice as long as the body.

The external maxillipeds, which project with their terminal joint beyond the antennal peduncles, reach to the middle of the scales.

The legs of the third pair extend to the distal extremity of the antennal peduncles and are unarmed at base, and those of the fifth reach just beyond the rostrum, to the terminal third part of the scales. (See additional Note B on page 454.)

Geographical Distribution.—Bay of Kobe, Japan (Spence Bate); Inland Sea of Japan and along the lower half of this Empire (Kishinouye); Maizuru, Japan (Ortmann).

PENÆUS (TRACHYPENÆUS) CURVIROSTRIS, Stimpson. (Pl. 33. figs. 56-58.)

Penæus curvirostris, Stimpson, in Proc. Acad. Nat. Sciences Philadelphia, 1860, p. 44.

Penæus curvirostris, Ortmann, in Spengel, Zool. Jahrb., Syst. v. 1890, p. 451, Taf. 36. fig. 4 a, b.

Penæus curvirostris, Kishinouye, in Journ. Fish. Bureau, Tokyo, vol. viii. no. 1, 1900, p. 23, pl. 6. fig. 4. Parapenæus curvirostris, Rathbun, in Proc. U.S. Nat. Mus. xxvi. 1902, p. 38.

Trachypenæus curvirostris, Alcock, in Ann. & Mag. Nat. Hist. ser. 7, vol. xvi. 1905, p. 523.

Penæus anchoralis, Spence Bate, 'Challenger' Macrura, 1888, p. 258, pl. 35. fig. 1 (partim ?).

Two females from the Inland Sea of Japan, caught in deep water.

They are nearly equally long, one measuring 80 mm., the other 78 mm. from the tip of the rostrum to the end of the telson. In both specimens carapace and abdomen are tomentose and scabrous with short adjacent setæ and microscopical spinules; the setæ are 0.15-0.16 mm. long, the spinules 0.03-0.04 mm. The lower margin of the rostrum, which reaches to the distal end of the second joint of the antennular peduncle, is distinctly curved in its ascent upwards and fringed with long cilia. In the female, which is 80 mm. long, the upper margin is 1+7-toothed; the gastric or first tooth, which is

situated still a little farther from the second than the second from the fourth, is a little smaller than the second; the first and the second are placed upon the carapace, the third reaches for the greater part of its length beyond the anterior margin of the carapace; the second, third, and fourth teeth are a little larger than the following, which decrease in size, and the anterior tooth is a little farther from the pointed tip of the rostrum than from the penultimate. In the other specimen the formula is 1+8; the second tooth is very little farther from the fifth than from the first or gastric tooth, and the latter is also somewhat smaller than the second; the following teeth are, as in the other specimen, equidistant, the two or three foremost are a little smaller than the preceding, and the anterior tooth is twice as far from the penultimate as from the acuminate tip, which is directed horizontally forward; two teeth are on the carapace, the third is situated above the anterior border. The lateral carinæ of the rostrum do not reach beyond the anterior border of the carapace. The postrostral ridge is distinct, and extends until quite near the posterior margin of the carapace. The sulcus gastro-frontalis (Stimpson) is indistinct in both specimens, as are also the cardiaco-branchial grooves; the antennal and the gastro-hepatic sulci are well developed, and the antero-lateral part of the cervical groove, situated just below the hepatic spine and beginning, at some distance from the anterior border of the carapace, at the posterior end of the antennal carina, is rather deep but short, being hardly once and a half as long as its distance from the anterior border. The outer angle of the orbital margin is produced into a sharp though small tooth; antennal and hepatic spines well developed, the former a little the larger. Pterygostomian angle angular, though not produced into a tooth or spine. Stridulating-organs wanting.

Characteristic of this species (Pl. 33. fig. 57) is a fissure about in the middle of the lower margin of the first segment of the abdomen, distinctly visible in Spence Bate's fig. 1 of Penæus anchoralis, which is identical with Pen. curvirostris. In both specimens the second segment of the abdomen carries a short median carina as far from the anterior as from the posterior margin of this segment; the carina of the third segment reaches from the posterior margin to the anterior fourth part, the carinæ of the fourth and fifth terminate in a narrow cleft at the posterior extremity, but the carina of the third segment does not; the carina of the sixth segment, which is little longer than broad, is, in the specimen 78 mm. long, posteriorly more strongly curved backward than in the other. The telson, which is very little longer than the sixth segment, but one-third shorter than the outer swimmerets, terminates (fig. 58) in an acuminate pointed tip; it is deeply grooved in the middle of the upper surface, and the lateral margins carry four movable, very small spinules ; the foremost or first spinule is inserted at little more than one-third, the posterior or fourth at one-seventh the length of the telson from the posterior extremity, the second is inserted just midway between the first and the fourth, and the third immediately in front of the fourth; the fourth is twice as large as the third, and the two anterior are a little larger than the third. Stimpson describes the telson as similar to that of de Haan's Pen. monoceros, where it is armed with three minute spinules, and Kishinouye describes it likewise : Ortmann (Spengel, Zool. Jahrb., Syst. v. 1890, p. 447) was therefore apparently wrong when denying their existence altogether;

Spence Bate is also inaccurate, for ('Challenger' Macrura, 1888, p. 259) he says "that one small spinule is visible on close inspection," whereas (p. 261) he describes three spinules.

The antennular flagella are of equal length and only *one-third* shorter than their peduncle, *i.e.*, the distance between its distal extremity and the anterior border of the carapace; the spine at the far end of the outer margin of the first joint of the peduncle is slightly directed outward.

There is only a minute spinule on the distal border of the lower surface of the basal joint of the outer antennæ. The peduncle reaches as far forward as the stylocerite of the inner antennæ, *i. e.* to the middle of the corneæ, and the flagellum is a little more than twice as long as the body. The outer margin of the antennal scales, which reach as far forward as the antennular peduncles, appears very slightly arched; the spine at the distal end extends as far forward as the laminar portion, which in the specimen 78 mm. long narrows a little more distally than in the other, an individual difference of course.

The external maxillipeds, of which the terminal joint extends beyond the antennal peduncles, reaching almost to the middle of the scales, are described by Stimpson as "nudi" on their outer surface; in our two specimens they are, however, distinctly hairy; the exopodite reaches to the distal end of the merus-joint of the endopodite.

The legs of the first and of the second pair are unispinose at base, their second joint being armed with a spine; the third legs, which reach to the tip of the antennal scales, are *unarmed*. The slender legs of the fifth pair reach to the tip of the eyes or slightly beyond them; their dactyli are little more than half as long as the propodites.

Both specimens seem to have copulated. The thelycum (Pl. 33. fig. 56) agrees with Ortmann's and Kishinouye's figures, in the female 78 mm. long: the amorphous gumlike substance with which it is covered resembles Kishinouye's figure 10c; but in the other it has a remarkable shape, appearing as *a narrow, asymmetric, shield-like body*, somewhat pointed at the distal end and divided by a transverse suture in the middle; it is of a whitish colour, whereas the lateral margins are of a pale violet (fig. 56).

Carapace and abdomen marked with innumerable small dots or points of a dark, perhaps bluish, colour; they are quite well visible in Spence Bate's figure 1 of *Pen.* anchoralis.

Penæus anchoralis, Sp. Bate, was founded upon specimens from the Arafura Sea and from Yokohama; those from the latter locality are no doubt identical with Pen. curvirostris, Stimps., those from the Arafura Sea certainly belonged to Pen. granulosus, Hasw., but it is difficult to say whether Haswell's species, though most closely related to Pen. curvirostris, is indeed identical with it or not. The second segment of the abdomen of Pen. granulosus seems to be destitute of the small crest near the centre of the upper border which is characteristic of curvirostris; the apex of the telson is acute, but not developed into a spine as in the Japanese species, and finally the lateral margins should be armed in Pen. granulosus only with a single, weak spine. The last named difference explains perhaps the fact that Spence Bate describes at one place the existence of one, but at another page that of three spinules on the lateral margins of the telson.

Dr. Alcock's suggestion that Pen. affinis (de Haan) = Pen. barbatus, de Haan, should

also be identical with *Penæus curvirostris* is, no doubt, erroneous. The carapace of *Pen. barbatus* is rounded and devoid of a postrostral ridge; the anterior margin carries a spine below the basal joint of the outer antennæ, which does not occur in *Pen. curvirostris*; and in *Pen. barbatus* there is a faint ridge posterior to the hepatic spine, no trace of which exists in *Pen. curvirostris*.

The external maxillipeds of de Haan's species reach to the tip of the antennal scales and the third legs are also unispinose.

Pen. monoceros of de Haan = Pen. ensis, de Haan, appears, on the contrary, most closely related to Pen. curvirostris. The rostrum reaches, however, to the end of the antennal scales, and from the hepatic spine a ridge goes backward to the posterior margin of the carapace. The outer flagellum of the internal antennæ is not longer than the eyepeduncles. The third legs are also unispinose at base; and the second somite of the abdomen seems to be devoid of a rudimentary crest on the upper border.

Pen. monoceros, Fabr., is also a different species (vide de Man, in Max Weber's Zool. Ergebnisse, 1892, t. ii. p. 513, pl. 29. fig. 54).

Geographical Distribution.—Simoda (Stimpson): Yokohama ('Challenger'): Arafura Sea (Spence Bate): Kochi, Bays of Tokyo and Sagami (Ortmann): Hakodate, Hokkaido; Aomori, Rikuoku; Hizen, Nagasaki (Rathbun): Pacific Coast of Japan from the Bay of Awomori to Kagoshima (Kishinouye).

# Stomatopoda.

# CHLORIDELLA, Miers \*.

### CHLORIDELLA AFFINIS (Berthold).

Squilla affinis, Berthold, 'Reptilien aus Neu-Grenada und Crustaccen aus China,' Göttingen, 1846, p. 26, tab. 3. figs. 1, 2; Bigelow, in Proc. U.S. Nat. Museum, xvii. 1894, p. 538 (ubi synon.).
Chloridella affinis, Rathbun, in Proc. U.S. Nat. Museum, xxvi. 1902, p. 55.

One specimen from the Inland Sea of Japan.

In this specimen, which is 45 mm. long from the tip of the rostrum to the end of the telson, the oblique corneal axis of the eyes is 3.2 mm. long, *i. e.* 0.07 of the length of the body; according to Bigelow it is comparatively a little shorter in adult individuals, measuring here only 0.05 of the length of the body.

The antero-lateral spines of the carapace reach just beyond the suture between the latter and the rostrum, whereas in adult specimens they are shorter than it. The median carina of the carapace is bifurcated for  $\frac{11}{40}$  of its length. The rostrum carries on its anterior half a feeble median ridge. The telson carries between the marginal spines, on each side of the middle line, one lateral, nine intermediate, and four submedian denticles. The submedian spines of the telson are probably provided with movable tips, which in that case should be a juvenile character.

\* This species and the following are provisionally placed in the genus *Chloridella*, Miers, but it appears to me probable that it will prove necessary to create a new name for the genus including those species that were referred by Bigelow to Squilla, J. C. Fabr.

### CHLORIDELLA FASCIATA (de Haan).

Squilla fasciata, de Haan, Fauna Japonica, Crust. 1849, p. 224, tab. 51. fig. 4. Chloridella fasciata, Rathbun, in Proc. U.S. Nat. Museum, xxvi. 1902, p. 54 (ubi synon.).

Two specimens from the Inland Sea of Japan.

This species seems to be rare, for neither Miers in 1880 nor Bigelow in 1894, when describing this species, had specimens of it at their disposal, whereas only two were collected by the 'Challenger' Expedition, also in the Inland Sea of Japan.

The present specimens are respectively 51 mm. and 40 mm. long from the tip of the rostrum to the end of the telson, about as long as those that were described by Brooks; de Haan's single type specimen was 5 centim. long. The eyes are described by Brooks as "nearly cylindrical"; in our specimen, 40 mm. long, the peduncle and still more the corneal axis are distinctly somewhat compressed, and the latter, which is directed somewhat obliquely as in *Chlor. affinis*, Berthold, measures 0.045 of the length of the body.

The spiniform teeth at the antero-lateral angles of the carapace are directed a little outward and reach almost as far forward as the suture between carapace and rostrum.

The tooth on the middle of the outer margin of the inner spine of the basal prolongation of the uropods is obtuse, though not rounded, and the inner border is armed with twelve or thirteen sharp teeth, which slightly increase in length distally; the 'Challenger' specimens presented here only seven or eight teeth. The terminal paddle of the exopodite measures two-thirds the length of the first joint, the outer margin of which is furnished with eight movable spines, which increase in size and in length distally. According to Brooks, the paddle measured in the 'Challenger' specimens half the length of the proximal joint. The length of the telson, measured in the middle line, is threefourths its greatest width. The median crest, which ends posteriorly in a sharp tooth, carries a small notch at one-fourth of its length from the base. Between the marginal spines are observed on each side one lateral, eight intermediate, and four or five submedian denticles, which are all very sharp. There are, in the smaller specimen, on the left side five, on the right four submedian denticles. According to the label, this species presents a red colour above; in the larger specimen the carapace and abdominal terga are mottled with minute dark points.

Geographical Distribution.—Japan (de Haan); Inland Sea of Japan, depth 15 fathoms, bottom blue mud (Brooks).

## B.-LAKE AT YUNNAN-FU, CHINA.

# POTAMON, Savigny.

### PARAPOTAMON, nov. subgen.

A new subgenus *Parapotamon* is proposed for those Potamonidæ that present the general characters of *Parathelphusa*, but in which the fingers of both chelipeds are spoon-shaped, excavated at the tips. In the typical species of *Parathelphusa*, *Parath.* tridentata, H. M.-Edw., and *Parath. sinensis*, H. M.-Edw., the fingers are distally acute, pointed, and the other species of this subgenus seem to agree with them as regards this character. In the remarkable new species of River-Crab from Yunnan, however, that

was described last year by Dr. Calman as *Parath. spinescens*, both fingers of both chelipeds are spoon-shaped: though in old males the fingers of the larger cheliped become obtuse, gradually losing their spoon-like shape, as may be observed in some species of *Leptodius*. *Pot. spinescens* becomes therefore the type of the new subgenus *Parapotamon*.

### POTAMON (PARAPOTAMON) SPINESCENS, Calman.

# Parathelphusa spinescens, Calman, in Ann. & Mag. Nat. Hist. ser. 7, vol. xvi. 1905, p. 156.

Four males and one female without eggs from the Yunnan-Fu Lake, China.

In the youngest male and in the female of the same size the antero-lateral margins are armed on each side with five spiniform teeth; in the male, however, the last tooth on the left side is rudimentary and a smaller granule is situated just before it. In the male the right cheliped is somewhat larger than the left. The right chela, which is 24 mm. long, is almost just as long as the length of the cephalothorax in the middle line; the fingers are a little shorter than the palm and barely longer than the palm is high. Though the dactylus is nearly straight, there is, however, a small hiatus between both fingers; both fingers carry fine punctuations, which are partly arranged in longitudinal rows. In Calman's somewhat larger male the dactylus was "slightly arched and very obscurely furrowed." The outer surface of the palm is quite smooth, finely punctate. The fingers of the left chela are just as long as the palm. The anterior border, articulating with the chela of the upper surface of the carpus, carries a few small denticulations; otherwise the upper surface is smooth, punctate. In the female the right chela is very slightly larger than the left; the fingers are a little shorter than the palm and a little longer than the latter is high. Fingers and palm of the left cheliped are equally long. The fingers of both chelipeds are, in this male and in the female, spoon-shaped; the margins of the spoon-shaped tips of the fingers are white. The three other males are of much larger size; in the largest the cephalothorax is 54 mm. broad, the antero-lateral margin of the right side is armed with five teeth, that of the left with seven, the last being rudimentary; the first and second are grown together at the base, as are also the third and fourth. (See Note C on page 454.)

## Measurements in millimetres.

	1.	2.	3.					
	ð.	ି -	우.					
Greatest breadth of the cephalothorax at the level of the								
penultimate antero-lateral teeth	54	34.5	34					
Length of the cephalothorax in the middle line, without the								
abdomen	38	25	24					
Distance between the external orbital angles	32	21.5	21					
Breadth of the frontal border	14.5	10	10					
Length of the larger (right) chela	54	24	20					

Nos. 1 and 2 the largest and the youngest males, No. 3 the female.

Both specimens were collected, together with the types described by Dr. Calman, in the lake at Yunnan-Fu.

POTAMON (PARATHELPHUSA) ENDYMION, de Man. (Pl. 33. figs. 59-63.)

Potamon (Parathelphusa) endymion, de Man, in Zoologischer Anzeiger, xxx. 1906, p. 35.

Two egg-laden females from the lake at Yunnan-Fu, China, that were collected together with specimens of *Potamon* (*Parapotamon*) spinescens (Calman).

This species is related to *Pot. spinescens*, Calman, and *Pot. (Parapthelphusa) lanzi*, Doflein, but is of smaller size.

Carapace three-fourths as long as broad, just as in Pot. spinescens, when the lateral spines are included; the carapace presents its greatest width at about one-third of its length from the frontal margin. The upper surface, flattened on its posterior half, curves anteriorly towards the rather steeply deflexed front; it is also flattened transversely, but the anterior branchial regions are somewhat swollen, more than in Potamon spinescens, and they slope steeply down to the antero-lateral border, which is not the case in Calman's species. The two lateral furrows of the H-like figure on the middle of the carapace are shallow, though distinct, but the transverse median part is hardly On the outer side of each lateral furrow a transverse impression is discernible. observed, bounding the inner part of the anterior branchial region posteriorly. The posterior branchial regions are also somewhat inflated and separated by shallow impressions from the anterior. The branchio-cardiac impressions are shallow, like those between the intestinal and branchial areæ. The distance between the external orbital angles is little more than half the greatest width of the carapace (the spines included), the proportion being in the larger specimen as 5:9, but in the other female that distance is comparatively larger. As in Pot. (Parapotamon) spinescens, the postfrontal crest is only represented by the two barely prominent, epigastric lobes; the mesogastric furrow between them is, however, somewhat deeper, and, instead of being rugose, these lobes are distinctly granular, each being beset with ten or twelve rounded granules. An oblique, shallow, though interrupted furrow or impression defines the gastric region laterally; on each side of it is another impression, of which the outer one, on the branchial region, is larger than the other. The gastric and epibranchial regions slope anteriorly down, so that the upper surface is somewhat concave behind the orbits. The gastric region is granular anteriorly, the granules being similar to those of the epigastric lobes; the swollen, anterior branchial lobes are also granular anteriorly and near the antero-lateral border, but the granules near the latter are somewhat larger. In the younger female they are less distinct. The rest of the upper surface is smooth, very finely punctate.

The front (Pl. 33. fig. 60) resembles that of *Potamon spinescens*, but its upper surface is distinctly granular; the granules are, however, smaller than those of the epigastric lobes; in the larger specimen the anterior border is *half as broad* as the distance between the external orbital angles. The finely granulated frontal margin is notched in the middle line, nearly as in *Potamon spinescens*, and the external angles are rounded; it makes right angles with the lateral margins, so that the latter run at first parallel and then curve outward. The upper orbital margin is also granular in the middle and externally, but in the younger specimen it is still smooth, like the frontal border. The external orbital

angles are not sharp and reach almost as far forward as the front. The antero-lateral margin is not shorter than the postero-lateral. The slightly convex outer edge of the flattened, extraorbital tooth is beset with three or four subacute granules, but its upper surface is smooth. The granules of the extraorbital tooth are followed, in the larger female, by six or seven spiniform, sharp teeth, of which the last is much smaller than the rest, which are subequal and nearly of the same size; in the other specimen there are eight spines on the left and seven on the right side, those of the left being a little more unequal. These teeth or spines are smooth and glabrous. The lateral spines of Pot. (Parapotamon) spinescens are more acuminate and there are only five or six on each side. The rounded postero-lateral margins are smooth, converge less strongly backward than those of Pot. spinescens, and run almost parallel. The posterior margin of the carapace is just half as broad as the latter is long and appears thus comparatively broader than in Pot. spinescens; it is also much more concave than in that species.

The orbits are, in the larger specimen, a little more than half as broad as the frontal border; as they have exactly the same measurements in both females, they appear in the younger specimen comparatively larger. They are differently formed than in *Pot. spinescens.* The orbits are more regularly oval, their outer margin being more regularly curved (Pl. 33. fig. 60); the lower margin is more distinctly crenulate than the upper, and, as in *Pot. (Parapotamon) spinescens,* the inner angle is not produced at all, but there is an internal suborbital lobe, inserted between the inner angle and the basal joint of the outer antennæ. In *Pot. spinescens* this lobe is semi-elliptical, obtuse, its outer surface is concave, and it reaches beyond the middle of the orbital hiatus; in *Pot. endymion* the lobe is subacute and considerably smaller, its length being only one-third of the width of the orbital hiatus. The basal joint of the outer antennæ has also a different form in the two species; in *Pot. spinescens* it is just as long as broad, it does not reach the front, and its outer surface is slightly convex; in this new species, however, the basal joint is longer than broad, its outer surface is quite flat, and it narrows distinctly towards the front, which it attains (fig. 61).

The subhepatic and subbranchial regions are smooth, but the pterygostomian area is somewhat granular on its outer half.

The epistome, which is smooth, is a *little longer* in proportion to its breadth than in *Pot. spinescens.* In that species the granulated posterior margin is not prominent in the middle, but the granulated ridge, which extends from the middle backward into the buccal cavity, is very prominent. In *Pot. endymion* we observe just the contrary, the granulated posterior margin of the epistome forms a prominent tooth in the middle line, but the ridge into the buccal cavity is hardly distinguishable.

The external maxillipeds (fig. 62) are characteristic. The longitudinal groove on the ischium, which in *Pot. spinescens* is well-marked, is wanting, or, at the utmost, a faint trace of it is discernible; this joint is punctate, the puncta are a little larger and more crowded near the inner border. The merus-joint, which in *Pot. spinescens* is once and a half as broad as long, appears in *Pot. endymion hardly broader than long*; in the larger female it is 2 mm. long, but only 2.4 mm. broad; it is quadrangular, the straight inner border and the equally long antero-internal being much shorter than the

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oblique outer border, which is nearly straight, though curving a little at each extremity; anteriorly the merus-joint is obtuse. On this joint the puncta are larger near the inner border. The finely punctate exognath reaches barely as far forward as the inner border of the ischium, but in *Pot. spinescens* it extends almost to the middle of the merus.

The finely, though rather densely, punctate terminal joint of the oval abdomen is regularly rounded, its posterior border is just twice as broad as this joint is long; the penultimate joint is almost exactly as long as the terminal, the preceding grow gradually shorter; the punctuations are very fine and rare.

In both females the right cheliped is somewhat larger than the left. The upper margin of the merus carries a subterminal spine, which is preceded by a smaller one, and several sharp granules; the lower margin carries also four or five, subacute, spiniform teeth and there are a few granules on the anterior border. The lower surface of the merus is unarmed, presenting no tooth or spine near the carpal articulation. Just as in Pot. (Parapotamon) spinescens and Pot. (Parathelphusa) lanzi, Dofl., the carpus is armed internally with two unequal, pointed spines, of which the upper is the larger; its upper surface is somewhat granulated, the granules being larger on the inner side. The length of the larger chela is two-thirds of the greatest width of the carapace; the palm is a little longer than the fingers and a little longer than its height at the articulation of the latter. The rounded upper border of the palm and its outer surface are beset with subacute granules, which are rather small and not very numerous; the lower margin is smooth, as also the inner surface. Characteristic is the immobile finger (Pl. 33. fig. 63) of the larger cheliped. This finger is somewhat curved at its base, the prehensile edge is here emarginate, whereas the lower border bulges somewhat out; between the emargination and the subacute tip of the finger it carries eight or nine small, obtuse, somewhat unequal teeth. As the dactylus is nearly straight, there is proximally a small interspace between the fingers; the dactylus carries on the proximal half of its upper border six or seven obtuse granules, and it presents longitudinal rows of puncta, one of which runs on the middle of the upper border. The dactylus is provided with eleven or twelve obtuse teeth, which diminish in size towards the tip. The immobile finger is punctate and marked with a longitudinal furrow on its outer surface.

The fingers of the smaller chela are barely shorter than the palm, the immobile finger is not emarginate at its base and scarcely bulges out; each finger carries about a dozen low, obtuse or subacute teeth, which diminish in size towards the tip; the tips of the fingers are pointed.

The ambulatory legs are smooth, somewhat punctate. The upper margin of the merus is slightly denticulate and ends in a sharp, though small, subterminal tooth; these teeth are, however, on the last pair and in the younger specimen less distinct. The upper border of the following two joints is also finely denticulate internally; the lower border terminates, both at the outer and at the inner side, in a small sharp tooth and one or two smaller teeth occur on the middle of that border. The spinulose dactylopodites are, on all the legs, *distinctly longer* than the propodites. The ambulatory legs of the younger individual are a little pubescent on the upper border of the joints.

The eggs are not numerous, globular, large, their diameter being 1.75-1.8 mm.

Pot. (Parathelphusa) endymion may easily be distinguished from Pot. (Parapotamon) spinescens, Calman, by the shape of the carapace, by the granulations on the anterior regions and on the chelipeds, by the more numerous teeth on the antero-lateral border, by the shape of the orbits and of the epistome, by the characters of the outer footjaws, by the remarkable shape of the immobile finger, by the extremities of the fingers, which are not spoon-shaped, &c.

Pot. (Parathelphusa) lanzi, Dofl. (Pl. 33. figs. 64, 65), of which several typical specimens, both males and females, were kindly sent me for examination by Dr. Doflein, of Munich, is also a quite different species. The cephalothorax of this larger species is longer in proportion to its breadth, it is somewhat more arched both longitudinally and from side to side, the interregional furrows are deeper, the lateral parts of the postfrontal crest much more distinct, the lateral margins of the front more oblique, the antero-lateral teeth, the orbits, the epistome, the outer footjaws, all are different from *Pot. endymion*; the chelipeds, the chelæ, and the tapering fingers are slenderer, their pointed tips more acuminate, the immobile finger presents the usual form; the characters of the ambulatory legs finally are also different.

# Measurements in millimetres of the two specimens of Pot. endymion.

						No. 1.	No. 2.
Greatest width of the carapace, the spines included						22.5	20
Length of the carapace, in the middle line, the abde	ome	en	exc	lud	led	17	15
Distance between the external orbital angles		٠				12.6	· 12·3
Breadth of the frontal margin						6	5.2
Breadth of the posterior margin						8.25	7.5
Breadth of the orbits		•				3.25	3.25
Height of the orbits						2.25	2.25
Length of the larger chela						14.3	12
,, ,, palm					٠	8.5	7
Height of the palm at the articulation of the fingers				•		6.75	5.3



Measurements in millimetres of four typical specimens of Potamon lanzi, Dofl., from the lower River Han, China, a few days from Hankow (Museum of Munich).

	്ം	ð.	Ŷ.	<b>♀</b> .
Greatest width of the carapace, spines included	35.5	26	31.2	30
Length of the carapace in the middle line, without the				
abdomen	29	22.3	29	24.5
Distance between the external orbital angles	2.4	19.5	23.75	20.3
Breadth of the frontal margin	10	8	10	8.2
", " posterior margin	11	9	13.5	11.3
Breadth of the orbits	6	5.2	6	5.2
Height of the orbits	4	3.2	3.6	3.5
Length of the antepenultimate joint of the abdomen	2.6	2.2		
,,, penultimate ,, ,, ,,	3.6	3	• • •	
			63*	

		ਹੈ.	ð.	Ŷ.	♀.
Breadth of	the anterior margin of the penultimate joint	6	4.6		
29 J	posterior ,, ,, ,,	7.75	6		
Length of	the terminal joint	5	3.6		
22 22	larger chela	27.5	18.6	22.5	18
<b>,,</b> ,,	palm	15.5	10	13	10
Height of	the palm at the articulation of the fingers	11.3	7	9.3	6.75

# Measurements of four typical specimens of P. lanzi (continued).

#### C.-DARJEELING, BENGAL.

PALEMON (PARAPALEMON?) HENDERSONI, de Man. (Pl. 33. figs. 66-68.)

Palamon (Parapalamon?) hendersoni, de Man, in Ann. & Mag. Nat. Hist. ser. 7, vol. xvii. 1906, p. 405.

Three specimens from Darjeeling, fresh water, at a height of 2500 feet, collected by Mr. J. A. Gammie.

Apparently a new species, which I have the pleasure of dedicating to Prof. J. R. Henderson, of Madras, author of "A Contribution to Indian Carcinology," and other useful papers. This species is somewhat related to *Pal. altifrons*, Hend., from Delhi and Lahore, to *Pal. scabriculus*, Heller, from Ceylon, and *Pal. (Macrobrachium) latimanus*, v. Martens.

The largest specimen is 61 mm. long from the tip of the rostrum to the end of the telson; the carapace, rostrum included, is 25 mm. long, almost half the length of the whole body. The carapace is *scabriculate* on its anterior half, being closely covered with minute spinules; the branchial regions are smooth, finely punctate, but on the upper surface of the carapace the scabriculate area reaches nearly to the posterior border. The rostrum, which is short, reaching only to the middle of the penultimate joint of the antennular peduncle, arises from the anterior third of the carapace, and its free part is directed obliquely downward, so that the acute tip is situated at a much lower level than the surface of the carapace. The upper border (Pl. 33. fig. 66) is armed, in the two larger specimens, with seven rather small and low teeth, in the third with six. The first tooth, situated at one-fifth of the length of the carapace from the frontal border, is, in the two larger specimens, twice as far from the second as are the following, which reach to the tip; in the third specimen, however, the six teeth are equidistant. The first three teeth are situated on the cephalothorax. The nearly straight lower border carries, in the largest specimen, one single tooth not far from the tip and placed immediately below the foremost tooth of the upper border; in the smallest specimen there is also one tooth on the lower border, but it is situated between the foremost tooth of the upper margin and the tip. In the third specimen, which is 52 mm. long, the lower border carries two teeth, situated just behind and before the foremost tooth of the upper border. The formulæ of the three specimens are therefore:  $\frac{3+4}{1}$ ,  $\frac{3+4}{2}$ , and  $\frac{3+3}{1}$ . The free part of the rostrum is narrow, and that part which is situated above the lateral crest appears in the middle of the free part but little higher than that below it.

The antennal spine is *small* and reaches barely beyond the frontal border. The hepatic spine is *extremely small* and, in the two larger individuals, it is even wanting on the right

side; it is placed rather far below the other, for their tips are twice as far from one another as the hepatic spine from the frontal border of the carapace.

The telson, once and a half as long as the sixth segment and almost three times as long as broad at its base, ends in an acute tooth; the inner of the two spines on either side exceeds, as usual, the tip of the telson. Of the two pairs of spinules on the upper surface, the anterior stand a little behind the middle; the four spinules are, in the larger specimen, arranged in a quadrant, but in the others the posterior pair are situated a little closer to

the anterior than the spinules of the anterior pair are distant from one another. The eye-peduncles are small and reach barely beyond the middle of the first joint of the peduncle of the inner antennæ. The two outer flagella are united for a short distance, which is barely as long as the last joint of the peduncle. The external maxillipeds reach as far forward as the peduncles of the inner antennæ.

The legs of the first pair extend, in the largest individual, with the distal fifth of their carpus beyond the tip of the antennal scales, but in the following somewhat smaller specimen by one-third of the carpus; those of the third specimen are lost. The carpus is as long as the merus and one-third longer than the chela, their proportion being as 4:3; the fingers are nearly as long as the palm.

Unfortunately only in the largest specimen one leg of the second pair is present, in the two others both are wanting. The remaining leg (Pl. 33. fig. 68) is the left and, as I conclude from the size of the coxæ, apparently the smaller. This leg is 48 mm. long, twice as long as the carapace, the rostrum included, but a little shorter than the whole body; one-fourth of the carpus extends beyond the antennal scales. The merus, 8.5 mm. long, when measured along its upper border, is cylindrical, but it is somewhat thickened distally; it is here 3.4 mm. thick, at the proximal end, however, 2 mm.; this joint reaches as far forward as the peduncles of the inner antennæ. The carpus, 6.5 mm. long, is distinctly shorter than the merus; it regularly thickens a little towards the distal end and, though generally cylindrical, appears very slightly compressed, as this joint is 3.6 mm. broad at the distal end of its upper surface, but 3.25 mm. at that of its lateral side. The chela is 22 mm. long, three times as long as the carpus, the palm is 10.25 mm. long, appearing very slightly shorter than the fingers. The upper surface of the palm is 3.7 mm. broad at the articulation of the fingers, 3.6 mm. in the middle, and still a little less broad at the proximal extremity, being therefore barely broader than the carpus; in a lateral view, however, palm and fingers appear to narrow regularly from the carpal articulation to the tips of the fingers, the palm being 3 mm. thick proximally and  $2\cdot3$  mm. at the articulation of the dactylus. The palm appears therefore also *slightly compressed* in the proportion of 3: 4. Viewed from above, the fingers do not appear to narrow towards their tips, which are strongly curved inward; they shut close together. The fingers are *somewhat tomentose*; the fixed finger carries a very small, conical tooth at the end of the cutting-edge, *i. e.*, at about one-third of its length from the articulation, and between this tooth and the articulation an elongate low prominence is observed which carries two or three small obtuse teeth. The cutting-edge of the dactylus terminates also in a small, conical tooth just behind the middle, and midway between this tooth and the articulation is a slightly larger, somewhat compressed, conical tooth. The ischium- and the merus-joints are closely beset with minute spinules, which are a little larger on the lower border; carpus and palm are also everywhere covered with similar minute spinules, but the larger spinules of the lower border of the merus are wanting. The fingers are devoid of spinules, except a few at their base.

The three following legs are *moderately slender*; those of the third pair reach to the distal end of the antennal scales, the fourth are a little shorter, and the fifth extend but little beyond the middle of the scales. The merus-joint of the third pair is somewhat spinulose and setose on its lower border; on the two following legs the spinules and setae become gradually less numerous; the rest of the surface is nearly smooth. The carpoand propodites are also nearly smooth, but the latter are spinulose on their lower border.

*Pal. altifrons*, Hend., differs by the more numerous teeth on the upper border of the rostrum, which has a different form, being vertically deep and having the apex placed in the same horizontal line as the surface of the carapace. The second legs are practically cylindrical, have a slenderer form, and the fingers are shorter than the palm.

*Pal. scabriculus*, Heller, is also distinguished by the more numerous teeth of the somewhat longer rostrum, six of which are placed on the carapace. The carpus of the second legs is not shorter than the merus, and the fingers are much longer than the palm.

*Pal. latimanus*, v. Mart., finally, of which a male 75 mm. long, from the Island of Halmahera, is lying before me, differs also by its vertically deeper and longer rostrum; the telson has a slenderer shape, and the characters of the second legs are different. The carpus, indeed, is much thinner at its base, its shape being thus quite different; the fingers are shorter than the palm, their cutting-edges shorter, their teeth much more numerous; the palm, finally, is distinctly broader than the carpus.

These three species show, however, no doubt, still other differences of less importance.

### D.-THURSDAY ISLAND, TORRES STRAITS.

# PENÆUS (PENÆUS) LATISULCATUS, Kishinouye, var.? (Pl. 33. fig. 69.)

Penæus latisulcatus, Kishinouye, in Journ. Fish Bureau, Tokyo, vol. viii. no. 1, 1900, p. 12, pl. 2. fig. 2, pl. 7. fig. 2 A.

One female, dredged in 5 fathoms, May 21st, at Thursday Island, Torres Straits.

This specimen agrees pretty well with Kishinouye's description of *Pen. latisulcatus* from Japan, except as regards the thelycum. This female is 87 mm. long from the tip of the rostrum to the end of the telson. The rostrum reaches to the middle of the third joint of the antennular peduncle and is armed above with ten teeth, below with one; the first tooth, which stands just before the middle of the carapace, is a little more than twice as far from the second as the second from the third, and the distance of the foremost tooth from the tip is but little shorter than that between the two first teeth. The distance (12.8 mm.) behind the posterior tooth is a little more than once and a half as long as that (7.75 mm.) from this tooth to the orbit. The first four teeth are on the upper surface of the carapace, and the fifth is situated just above the orbital

margin. The single tooth of the lower margin is situated immediately below the foremost tooth of the upper. The dorsal carina, which is distinctly grooved and which terminates abruptly at the distance of 1 mm. from the posterior margin, widens a little backward; the also quite distinct, lateral furrows are *much broader*, nearly twice than the median groove and reach as far backward as the latter.

The fifth and the sixth segments of the abdomen are carinate, the carina of the sixth terminating in an acute tooth; on the outer surface of these segments are observed, just below the middle, three short ridges which run parallel with one another, the lower margin of the sixth terminates in a small acute tooth. The telson, little longer than the sixth segment, is deeply grooved in the middle line, and the lateral margins carry on the posterior half three small movable spines; the middle spine is twice as far from the anterior as from the posterior, and the posterior is as far from the tip as from the anterior spine.

The external maxillipeds reach to the distal end of the first joint of the antennular peduncle. The legs of the first pair extend to the middle of the antepenultimate joint of the outer footjaws, those of the second pair to the distal end of the penultimate joint, those of the third pair finally reach by their fingers beyond the extremity of the external maxillipeds. The subequal legs of the fourth and fifth pairs reach to the distal end of the antennal peduncles. The basipodites of the legs of the first and second pairs are armed on their inner border with a slender spine, and the arched lower margin of the following joint terminates, in the first pair of legs, in a *very small* acute tooth (no spine).

The thelycum (Pl. 33. fig. 69) is composed of two lateral walls, the outer surface of which is flattened, triangular, and narrowing somewhat anteriorly; the inner margins of these plates are in contact along their posterior half, whereas they diverge along the anterior. The two lateral walls lean anteriorly on an arched transverse piece, situated between the coxæ of the fourth pair of legs posteriorly and bounding the cavity anteriorly; this transverse piece carries anteriorly a concave protuberance, barely as long as the transverse piece itself, and terminating anteriorly in a small subacute tooth.

The thelycum of the typical Japanese *Pen. latisulcatus* differs apparently by the lateral plates, which are in contact with each other nearly along their whole length, and the protuberance has also a different form. Perhaps this species may therefore eventually prove to be distinct, though I fully agree with the opinion of Lanchester (in Proc. Zool. Soc. 1901, vol. ii. p. 571), "that too little is known about the thelycum, and its possibly seasonal varieties within the same species, to justify the founding of a new variety on this character."

Probably one female from Thursday Island should be referred to *Pen. caniculatus*, Oliv., var. *australiensis*, Sp. Bate, but I hesitate to do so, as this variety is still insufficiently known.

#### E.-COAST OFF BAHIA.

#### PENÆUS (PENÆUS) BRASILIENSIS, Latr.

Penœus brasiliensis, Latreille, in Nouv. Dict. Hist. Nat. xxv. p. 256 (1817); Miers, in Proc. Zool. Soc. 1878, pp. 299, 306; von Martens, in Archiv f. Naturgeschichte, xxxviii. Jahrg. 1872, p. 140; Rathbun, in U.S. Fish Commission Bulletin for 1900, vol. ii, p. 100.

Five young specimens, dredged in a depth of  $2\frac{1}{2}$  fathoms off Bahia.

The largest specimen is 80 mm. long from the tip of the rostrum to the end of the telson, the smallest measures 65 mm. In all the basipodite of the first and second pairs of legs is armed with an acute spine, as also the ischium of the first pair; the third pair of legs is unarmed. In each specimen the lower margin of the rostrum is armed with *two* teeth; in three specimens the anterior of these teeth is placed just below the foremost tooth of the upper border, in the two others the posterior tooth is placed below it. In two specimens the upper border is armed with nine teeth, in one with ten, in two with eleven, and in all the first four teeth are placed upon the carapace.

According to Miss Rathbun, the carina on the fourth segment of the abdomen is very sharp in adult individuals which are 165 mm. long; in our younger specimens this carina is still only faintly developed. Otherwise these specimens agree with the descriptions in the references given above.

### SICYONIA, H. M.-Edw.

### SICYONIA SCULPTA, H. M.-Edw., var.?

Sicyonia sculpta, H. Milne-Edwards, Hist. Nat. Crust. ii. p. 409; Heller, Die Crustaceen des südlichen Europa, 1863, p. 291; Spence Bate, Report on the 'Challenger' Macrura, p. 294, pl. 43. fig. 1.

Two females without eggs and one male were dredged off Bahia at a depth of  $2\frac{1}{2}$  fathoms.

Sicyonia sculpta, which inhabits the Mediterranean and Adriatic Seas, has also been captured off St. Vincent, Cape Verde Islands, by the 'Challenger' Expedition, and the 'Challenger' specimen seemed, according to the author of that Report, to agree with the Mediterranean species. When I now, however, compare the three specimens captured off Bahia with a specimen ( $\mathfrak{P}$ ) from Messina belonging to the Strassburg Museum (vide Ortmann, in Spengel, Zool. Jahrb., Syst. v. 1890, p. 453), I observe indubitable differences.

The two females are 40 mm. and 34 mm. long from the tip of the rostrum to the end of the telson, the younger male measures 32 mm. The specimen from Messina is 37 mm. long. The principal differences are the following ;—The rostrum of the Mediterranean specimen projects almost horizontally forward, exactly as in the 'Challenger' female (Spence Bate, *l. c.* fig. 1), but the rostrum of the three American specimens is *more obliquely directed upward*, the straight lower margin, indeed, making an angle of about  $30^{\circ}$  with the upper border of the carapace. As regards the teeth on the latter and on the rostrum, the American specimens agree with that from Messina, but the third tooth, which stands at the base of the rostrum, is *much smaller* than the two preceding on the upper border of the carapace and than the corresponding tooth in the Mediterranean specimen. The straight upper border of the rostrum is armed with three teeth of equal size, of which the third or anterior, placed immediately behind the acute tip, is, in the larger female a little farther from the second than the second from the first, whereas in the two other specimens the second is a little farther from the first than from the third.

The straight lower margin of the rostrum ends in a sharp tooth, and, exactly as in the specimen from Messina, there are between this tooth and the tip, which is curved downward, nearer to the tip than to the tooth, two other pointed teeth which are also curved downward. According to Milne-Edwards the lower margin should carry only one tooth, according to Heller one or two, according to Spence Bate also one; Spence Bate is here, however, inaccurate, for he figures (l. c. fig. 1") two teeth below the tip. In the specimen from Messina, as well as in those that were captured off Bahia, there are six teeth between the tip of the rostrum and the posterior margin of the carapace and three teeth below the tip.

The abdomen agrees with that of the specimen from Messina, but the grooves, both the transverse and the oblique, are in the American specimens much less deep and shallower.

The third difference which I observe is presented by the first three pairs of legs, which in the specimens caught off Bahia are *a little slenderer*.

If the differences described are, indeed, constant, the American species should form a variety, for which the name *americana* is proposed.

# SICYONIA CARINATA (Olivier).

Sicyonia carinata (Olivier), Spence Bate, Report on the 'Challenger' Macrura, p. 294, pl. 43. figs. 2, 3.

Three young specimens, dredged off Bahia,  $2\frac{1}{2}$  fathoms.

The largest specimen is 38 mm. long from tip of rostrum to the end of the telson.

These specimens fully agree, especially as regards the toothing of the rostrum, with the above cited figures of the 'Challenger' Report, the upper border of the rostrum carrying two teeth behind the acute tip and one immediately below it.

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# EXPLANATION OF THE PLATES.

The specimens figured are from the Inland Sea of Japan, unless otherwise stated ...

#### PLATE 31.

Fig 1. Lambrus (Oncodolambrus) prædator, de Man. × 3.

2. ,, Cephalothorax viewed from in front,  $\times$  3.

- 3. . ,, Lower surface of the anterior part of the cephalothorax,  $\times$  10.
- 4. Asthenognathus inæquipes, Stimpson. Inferior view of the cervical region,  $\times$  17. (The oblique position of the figure is accidental.)

. . .

- 5. ,, Left cheliped of the female,  $\times$  17 (the chela is turned a little backward, so that the full height of the palm is not visible).
- 6. ,, Right leg of the antepenultimate pair,  $\times 8\frac{1}{2}$  (all the joints covered with a dark tomentum except the dactylus).

7. Leucosia rhomboidalis, de Haan. Abdomen of the male,  $\times$  3.

8. Arcania heptacantha (de Haan). Female,  $\times$  2.

9. ,, Abdomen of a young male,  $\times$  3.

10. ,, Cheliped of the female,  $\times$  2.

11. Arcania globata, Stimpson.  $\times$  3.

12. ,, Front and anterior part of the cephalothorax viewed from above,  $\times$  10.

13. ,, The same, lateral view,  $\times$  10.

14. Galathea acanthomera, Stimpson. External maxilliped of the right side of a male,  $\times 17$ .

15. , Leg of the second pair of the same,  $\times$  10.

16. Crangon consobrinus, de Man. Anterior part of carapace and eye-peduncles, × 8.

17. ,, Tip of rostrum,  $\times$  50.

18. ,, Antennal scale, without the set $\mathfrak{x}$ ,  $\times$  8.

19. , Chela,  $\times$  8.

#### PLATE 32.

Fig. 20. Crangon cassiope, de Man. Antennal scale without the setæ, × 5.

21. ,, Extremity of the scale, without the setæ,  $\times$  25.

- 22. ,, External maxilliped,  $\times$  5.
- 23. ,, Chela,  $\times$  10.
- 24. ,, Left leg of the fifth pair,  $\times$  5.
- 25. ,, Dactylus of the same leg,  $\times$  10.

26. Leander longipes, Ortmann. Telson of the egg-bearing female,  $\times$  5.

27. ,, Extremity of the telson,  $\times$  25.

28. ,, Right leg of the second pair,  $\times 4$ .

29. ,, Toothing of the same leg,  $\times$  25.

30. ,, Tceth, more magnified,  $\times$  50.

31. Spirontocaris rectirostris (Stimpson). Egg-bearing female,  $\times$  3.

32. ,, Antennal scale, without the setx,  $\times$  6.

33. ,, Supposed male,  $\times$  3.

34. ,, Antennal scale of the male,  $\times$  6, also without the setæ.

35. Spirontocaris propugnatrix, de Man.  $\times$  3.

- 36. ,, Extremity of the rostrum,  $\times$  6.
- 37. , Part of the rostrum, where the teeth of the lower margin begin,  $\times$  6.
- 38. ,, Anterior part of the carapace,  $\times$  10.

Fig. 39. Spirontocaris propugnatrix. Posterior half of abdomen,  $\times$  6.

- 40. ,, Extremity of telson,  $\times$  50.
- 41. ,, Extremity of left antennal scale,  $\times$  10, without the setæ.
- 42. Spirontocaris alcimede, de Man.  $\times$  3. One of the specimens in which a pterygostomian spinule occurs.
- 43. ,, Rostrum of another specimen, which is  $\frac{5}{9}$  toothed,  $\times$  6. (The rostrum of this figure should point upward.)
- 44. ,, Posterior half of the abdomen of the same individual,  $\times$  6.

45. ,, Eye-peduncles and both pairs of antennæ of the same specimen,  $\times$  6.

46. ,, Leg of the second pair of the same specimen,  $\times$  10.

- 47. Spirontocaris pandaloides, Stimpson. Cephalothorax, rostrum, and antennal scale of an adult specimen,  $\times 3$ .
- 48. ,, Leg of the second pair of another individual,  $\times$  10.

## **PLATE 33.**

Fig. 49. Hippolysmata vittata, Stimpson. Cephalothorax, antennulæ, and antennæ of an egg-bearing female,  $\times$  3.

50. ,, Terminal part of the abdomen of the same female,  $\times$  3.

- 51 & 52. Alpheus brevirostris (Olivier). Chelæ of the smaller cheliped in the two egg-bearing females, viewed from the outer side, × 3.
- 53. Alpheus japonicus, Miers. Chela and carpus of the smaller cheliped of one of the two males, viewed from the upper or inner side,  $\times 2$ .
- 54. Penæus (Metapenæus) akayebi, Rathbun. Stridulating-organ of the female, on the right side of the carapace, × 17.
- 55. Penæus (Metapenæus) acclivis, Rathbun. Thelycum, viewed from outer side, × 5.
- 56. Penæus (Trachypenæus) curvirostris, Stimpson. Thelycum, × 5.
- 57. ,, First segment of the abdomen, lateral view, presenting the fissure near the lower margin,  $\times$  3.
- 58. ,, Telson of the same female,  $\times$  5.
- 59. Potamon (Parathelphusa) endymion, de Man. Egg-bearing female from the lake at Yunnan-Fu, China, × 2.
- 60. ,, Anterior part of the cephalothorax,  $\times$  3.
- 61. ,, Lower side of the anterior part of the cephalothorax,  $\times$  3.
- 62. ,, External maxillipeds of the same female,  $\times$  3.
- 63. " Right (larger) chela of the same female,  $\times$  3.
- 64. Potamon (Parathelphusa) lanzi, Doflein, typical male specimen from the lower Han River, China (belonging to the Museum of Munich), external maxilliped, × 3.
- 65. ,, Larger (right) chela of the same male, outer side,  $\times 2$ .
- 66. Palæmon (Parapalæmon?) hendersoni, de Man, anterior part of the cephalothorax of the largest specimen from Darjeeling, in which an hepatic spine is wanting, × 3.
- 67. ,, Telson of the same specimen,  $\times$  3.
- 68. ,, Left leg of the second pair of the same specimen,  $\times$  3.
- 69. Penæus (Penæus) latisulcatus, Kishinouye, var.? Thelycum, viewed from the outer side,  $\times$  6.

# ADDITIONAL NOTES.

#### **A**.

(Page 418.) According to Lenz's paper in Spengel's Zool. Jahrb., Syst. xiv. 1901, p. 429, Bare Island should be situated between Vancouver Island and the continent; afterwards, however, Prof. Lenz informed me that this very small island is situated close to the east coast of the northern island of New Zcaland, between lat. 40° and Cape Kidnappers.

### В.

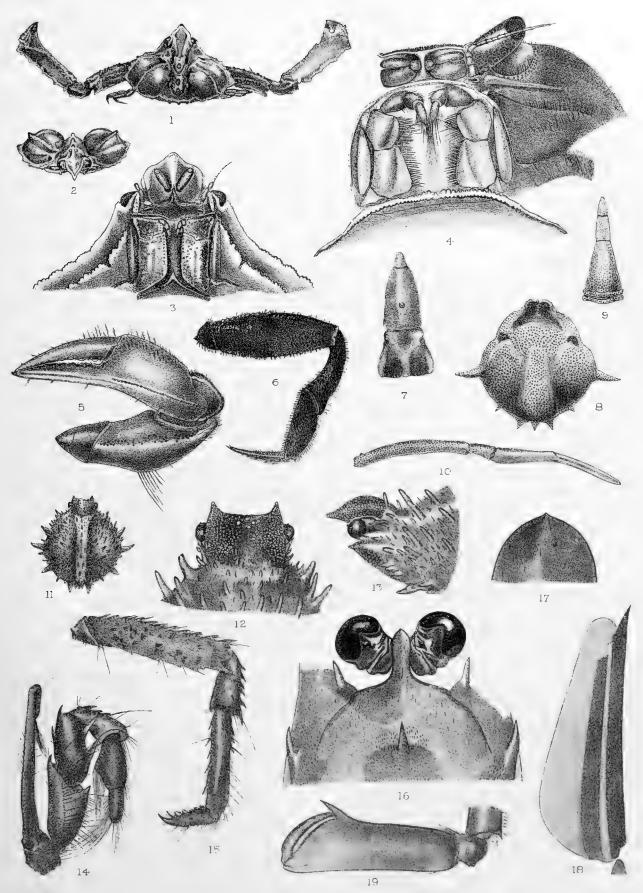
(Page 436.) PENÆUS TENELLUS. The thoracic legs seem to be devoid of epipodites, and the exopodite of the fifth pair is rudimentary or wanting. *Parapeneopsis acclivirostris*, Alcock, has a longer rostrum, recurved at the tip, the thelycum different, and the antennular flagella are shorter.

# C.

(Page 441.) POTAMON SPINESCENS. The fingers of the *smaller* cheliped are also, in these adult males, distinctly spoon-shaped, excavated at the tips, but those of the larger leg show a tendency to lose this spoon-like shape, the fingers appearing obtuse at their tips. Whereas the fingers of the smaller cheliped still shut nearly close together, those of the larger become gradually more gaping, and in the largest specimen the dactylus is strongly *arched* and there is a *large* interspace between both fingers; the excavation of the tips of the fingers has become quite indistinct, though it is still perceptible. The larger chela of this male is just as long as the cephalothorax is broad; the palm, measured horizon-tally, appears once and half as long as the fingers, and the height of the palm near the articulation of the dactylus is equal to the horizontal length of the fingers. Palm and fingers are quite smooth; the dactylus carries 12 or 13 obtuse teeth of different size, of which the first, near the base, is larger than the rest; the immobile finger is also armed with some obtuse, unequal teeth.

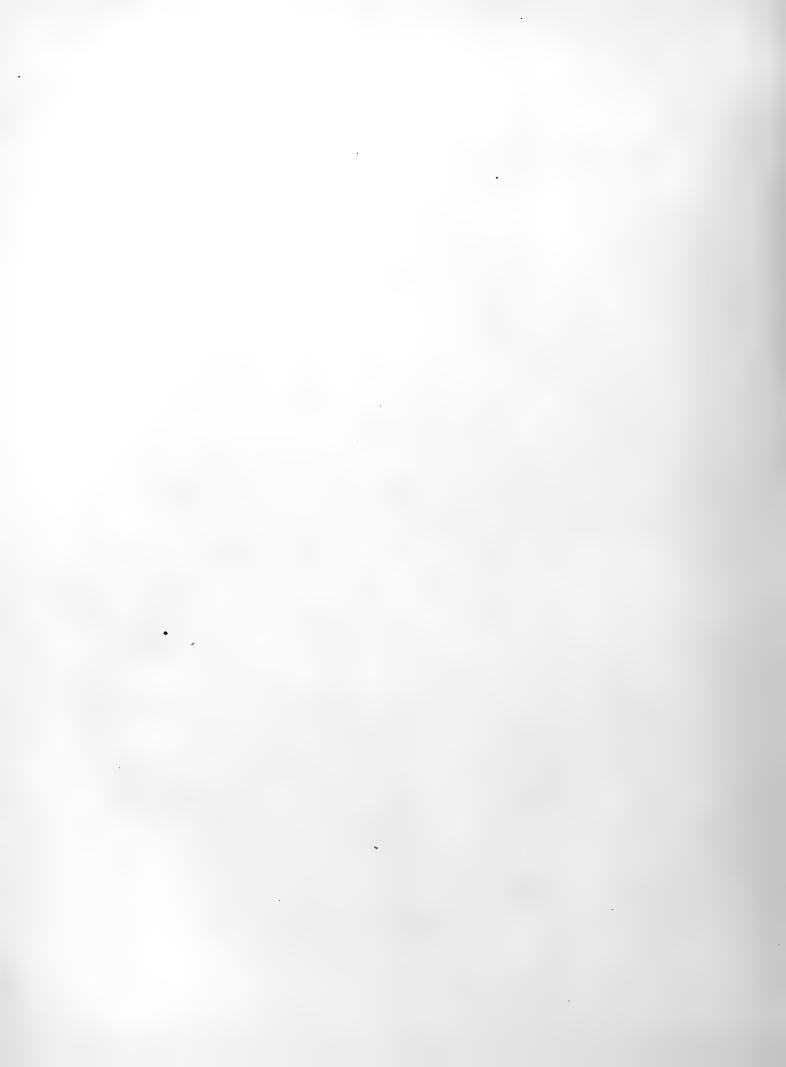
The chelipeds are yellow, but the upper surface of the carpus, the upper border of the palm and of the dactylus, as also the upper end of the arm, are of a beautiful red.

[12th February, 1907.]

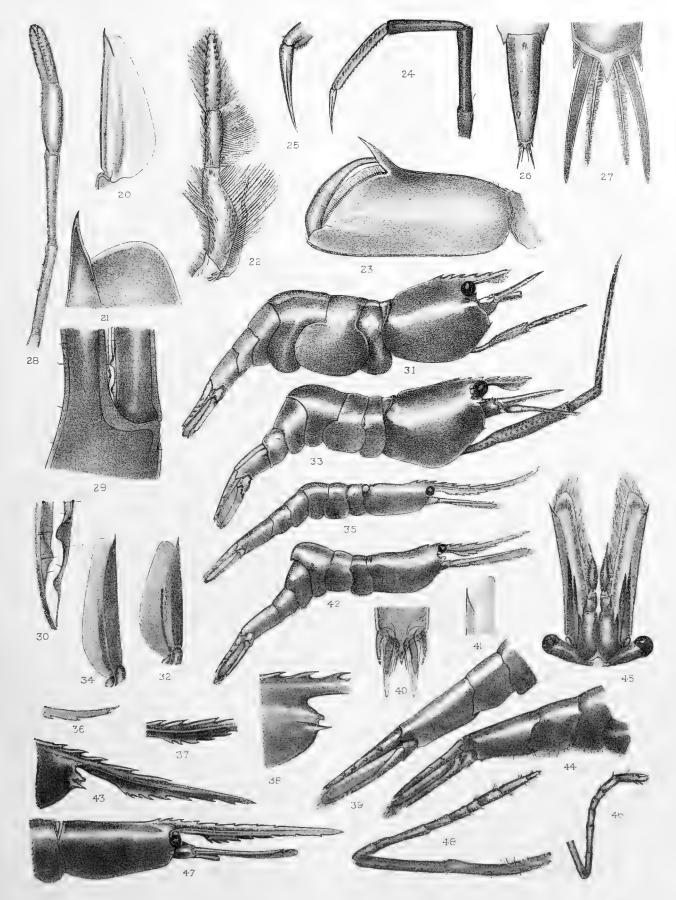


J.T. PENNIE PEIDLUTH ED'N?

CRUSTACEA FROM JAPAN.

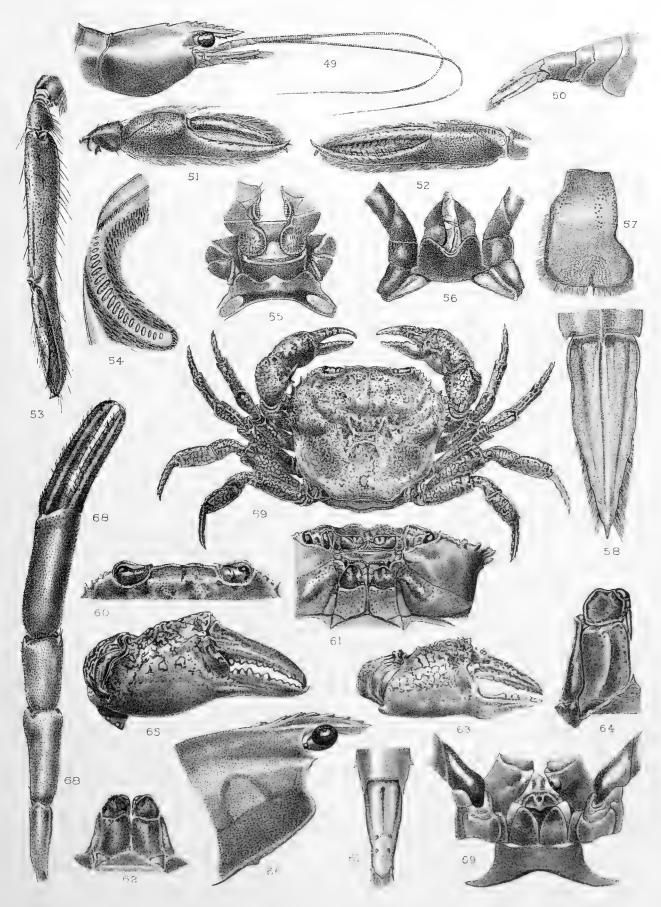


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J.T. REMNIE REID, LITH ED-MH

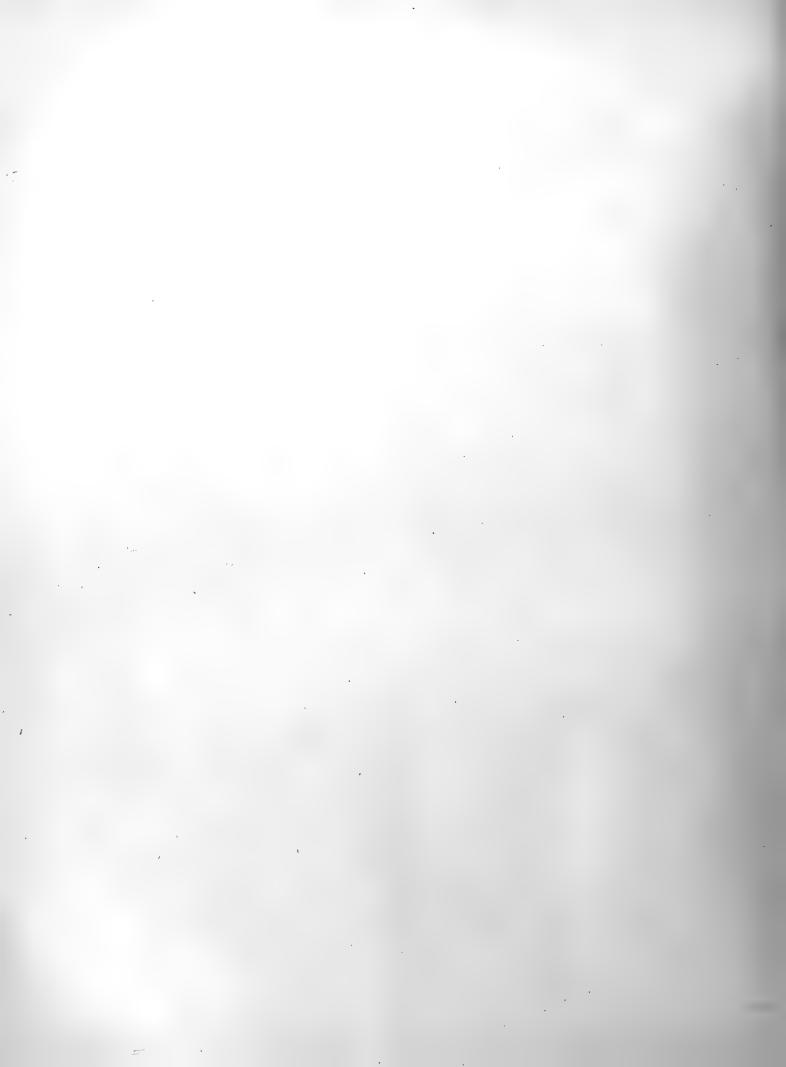




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JI. HENNIE REID, LITH. EDINR

CRUSTACEA FROM JAPAN AND OTHER COUNTRIES.



# [455]

XII. On Cercococcus eremobius, gen. et sp. nov., an Aberrant Form of Coccidæ. By HUGH Scott, B.A. (Cantab.). (Communicated by J. J. LISTER, M.A., F.R.S., F.L.S.)

# (Plate 34.)

Read 18th April, 1907.

THE species of Coccid which I have to describe in this paper was found on a desertplant growing on the hill known as Djebel-el-Melah, "the Mountain of Salt," in one of the southern spurs of the great central plateau of Algeria, where the mountains slope down to the Algerian Sahara, a few miles north of the oasis of Biskra. The hill consists of beds of rock-salt and gypsum overlaid by Cretaceous strata. At this place was growing a specimen of a Cistaceous plant, Helianthemum kahiricum, Delile, found throughout the Algerian Sahara, and having a general distribution from Syria to Algeria: for this determination I am indebted to Dr. Stapf, of the Herbarium of the Royal Gardens, Kew. The specimen is a dwarf woody shrub, reaching about four inches from the ground. It bears on its twigs conspicuous white masses of a substance somewhat like cotton-wool in appearance. The small oblong-lanceolate leaves of the plant are, as in so many desert-plants, covered with hairs, which are very minute in this These hairs give a greyish colour to the plant, but are not otherwise conspicuous, case. whereas the wool-like masses are decidedly so, contrasting strongly with the leaves and twigs, as will be seen in Pl. 34. fig. 1, which shows almost the whole plant. The infected plant was collected on Dec. 25, 1906, by Mr. J. J. Lister, who found that each of the wool-like masses contains a Coccid. Not having time to investigate the matter himself, Mr. Lister very kindly handed the material to me for examination.

I owe my best thanks to Mr. Robert Newstead for kindly examining specimens, and for pointing out the salient features and systematic position of the insect; also to Dr. David Sharp for much help and advice in dealing with it. With this assistance it has been possible to make out fairly satisfactorily its characters.

It is necessary to form a new genus of the subfamily *Dactylopiinæ*, closely allied to *Asterolecanium* \*, Signoret. The following is a diagnosis :--

# CERCOCOCCUS, gen. nov.

Fem. adult. Corpus prolongatum, caudâ distinctâ munitum. Lobi anales magni, setigeri. Antennæ minutæ. Insectum omnino carens pedibus.

Maris puparium nullo modo translucens, extrinsecus filis longis. Mas incognitus.

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<sup>\*</sup> Astero-Lecanium (Targ.), Sign. (1868), Ann. Soc. ent. France, 1869, p. 101; Asterolecanium, Targ. 1869 [sec. Fernald, Cat. Coce. p. 49], Sign. (1808), Ann. Soc. ent. France, 1870, p. 276.

CERCOCOCCUS EREMOBIUS, sp. nov.

Fem. adult. Corpus subrotundum; supra fortiter convexum, ad latera obsolete transversim sulcatum, tribus seriebus longitudinalibus tuberculorum perparum elevatorum, foveis numerosissimis fila albida emittentibus, insectum omnino tegentia; infra convexum. Cauda brevis, depressa.

Adult female. It will thus be seen that the most striking characters are the prolongation of the body to form a perfectly distinct tail terminated by large anal lobes, and the presence of very numerous pits scattered over the dorsal surface, from which emerge long curling threads, which together form the dense white covering that entirely conceals the insect and its ovisac. The ovisac, too, is itself a highly remarkable structure.

The body of the insect, considered apart from the tail, has a very rounded and convex appearance. Dorsally there is a steep posterior slope down to the tail, which is depressed and considerably below the general surface. Ventrally, the surface of the tail is continuous with that of the trunk. No traces of asymmetry, such as are exhibited by the adult females of some species of *Lecanium*, are visible. The colour of the specimens preserved in formalin and afterwards transferred to spirit is orange, lighter on the ventral surface. When freshly found they also appeared to be orange, though no close examination was then made. They vary considerably in size; a large specimen measures about  $3\frac{1}{3}$  mm. long by  $2\frac{3}{4}$  mm. broad, while a smaller one was only about  $2\frac{1}{3}$  mm. long. This is no doubt due to differences in the degree of maturity.

The transverse depressions at the sides of the body are somewhat vague. Posteriorly, where the surface of the trunk slopes down to the tail, there are others extending right across the body. The basal portion of the tail also shows a kind of segmentation, which in the distal part becomes, dorsally, very obscure. The tubercles (Pl. 34. fig. 4, a, a) of the median and lateral longitudinal rows are only very slightly elevated. They are serially arranged with respect to the transverse furrows, one tubercle standing between each two depressions. They will be mentioned again in connection with the excretory products of the insect. A description of the pits (Pl. 34. fig. 4) scattered so densely over the dorsal surface of the trunk is left till the peculiarities of the integument as a whole are dealt with.

The ventral surface (Pl. 34. fig. 2), with the exception of a few minute setæ only visible under a high power of the microscope, is smooth, lacking the pits so numerous on the dorsal. At either side it has two well-marked longitudinal furrows (Pl. 34. fig. 2a, b), into the inner of which open the spiracles. An inconspicuous transverse furrow leads from the inner to the outer longitudinal furrow, at the point where the posterior spiracle is placed. Just in front of the anterior spiracle, the inner furrow converges with and joins the outer. In front of this point of union the outer furrow curves round towards the middle line, so that it approaches, but does not meet, its fellow of the opposite side of the body.

In this anterior part of the furrow lies the antenna (Pl. 34. figs. 2c, 3), which consists of a single short chitinous piece, round in surface view, bearing a short thick spine and four or more setæ.

The surface of the trunk within the inner furrows is strongly convex, and at the centre of it is the rostrum, sunk in a depression. The loop of the rostral filaments is long. There is no trace of legs or feet, or of eyes.

The spiracles (Pl. 34. fig. 2, d), as previously mentioned, open, two on either side of the body, into the inner longitudinal furrows. Like the antenne, they are more strongly chitinised and darker in colour than the surrounding integument. Each consists of a shallow circular chamber, in the external floor of which is the orifice to the exterior, while an opening in the internal floor leads into a tracheal trunk. In connection with each spiracle is a curiously shaped structure, strongly chitinised, and very conspicuous in specimens that have been emptied of their soft parts by treatment with caustic potash. This structure is adjacent to the side of the stigmatic chamber remote from the lateral margin of the body, and extends forwards and slightly towards the middle line. In transverse sections it appears as a ridge projecting from the cuticle into the interior of the body, and muscles extending from the dorsal surface are attached to it at one point. On the side of the stigmatic chamber nearer the lateral margin of the body is a group of cutaneous glands, which will be spoken of later.

The ventral surface of the posterior part of the trunk and of the tail shows very distinct division into eight segments (Pl. 34. fig. 2). The anal orifice is surrounded by eight setæ (Pl. 34. fig. 9) rising from a slender chitinous ring, which has a beaded appearance. Just anterior to this anal ring rise a large and a small pair of setæ in close proximity to each other (Pl. 34. fig. 9), and the integument of the terminal segment in this region bears a number of very minute projections (Pl. 34. fig. 9, a). Between the anal lobes is a shorter median lobe (Pl. 34. fig. 9, b), dorsal to the anus. Each anal lobe (Pl. 34. fig. 9, c) is large; it bears a long seta at its extremity, and five smaller ones (the arrangement of which is shown in the figure) on its more proximal portions. Every seta rises from a chitinised base, having the form of a cup with a raised and thickened rim. The genital aperture is a somewhat transverse opening in the ventral middle line, in the region of the furrow between the sixth and seventh segments; the integument immediately surrounding it shows extremely fine strike radiating from it (Pl. 34. fig. 9, d).

Passing now to a consideration of the integument and the excretory products of the insect, the most striking feature of all is the very numerous threads secreted by cutaneous glands on the dorsal surface. These form a dense covering completely concealing not only the body of the female, but also the ovisac in which it lies, and produce the conspicuous wool-like masses on the infected plant. The covering of threads as a whole looks opaque and white : but when highly magnified each thread is seen to be perfectly transparent, colourless, and glass-like; cylindrical, curving, and sometimes with a certain amount of longitudinal striation in the interior of its substance (Pl. 34. fig. 7). The threads vary in thickness; the diameter of cross-section of a rather thick one measured was about  $12 \mu$ . These threads are insoluble in cold wax-dissolving reagents. But Dr. Hopkins, to whom I am much indebted for examining them, states that they are formed of a wax freely soluble in hot reagents. It dissolves in boiling absolute alcohol, and separates on cooling into glistening plates of homogeneous appearance.

These crystals, which melt at  $92^{\circ}$  C., seem to represent the entire substance, which is practically a pure chemical compound: a mere trace remains in the alcohol from which they separated. The wax is clearly a different kind to that called coccerine, described by C. Liebermann (Berichte der Deutschen chem. Gesell., Bd. xviii. p. 1975), which melted at  $106^{\circ}$ .

These threads are produced by unicellular glands placed in pairs beneath pits in the integument. Each pit (Pl. 34. figs. 4, 10 a, 11, 12, 17) is formed by an invagination of the cuticle, but its walls are thinner than the cuticle covering the surface between the pits (Pl. 34, fig. 17). The area of the cross-section of the pit is about the same throughout. On its floor there are two pore-plates lying close together, so that they appear somewhat like a figure of eight (Pl. 34. fig. 10). The term "pore-plate" is not meant to imply the presence of any perforations in the plate, for I have seen no trace of any such. It is used to indicate a specialised portion of the integument lying over a gland, and through which the secretion of that gland passes to the exterior \*. If there are no perforations in these plates, the very interesting physiological question arises as to the form in which the secretion is produced by the glandular cells, and the manner in which it traverses the chitinous membrane between it and the exterior. Berlese (l. c.) considers that in all insects the chitinous integument is uninterrupted by any perforations, so that dermal secretions of all kinds must pass through an extremely thin membrane. Each pore-plate has a broad rim, sloping slightly downwards and inwards, like the surface of a funnel, and more strongly chitinised than the surrounding cuticle; moreover, the rim is transversely striated, and under a high magnification a dark dot is often apparent in the centre of each of the striæ. The striæ do not appear in sections in any way as pores perforating the rim. The outline of each pore-plate is in the form of an oval flattened at one side, the flattened sides of the two ovals being adjacent, but not quite contiguous. The outer margin of the flattened side of the rim has at its central point a small concavity. The two concavities, being opposite to one another, leave a slightly widened space (Pl. 34. fig. 10, b), in which there rise, between the two poreplates, two minute papillæ (Pl. 34. figs. 11 a, 12, 17 b). These appear to be evaginations of the thin cuticle between the rims; they are in a line at right angles to the long diameter of the pair of pore-plates, and hence when the pair is seen-as it very frequently is-from the side, the two minute papillæ appear as a single one (Pl. 34. fig. 11, a). However, under a high power, and in some transverse sections, the two can be seen, quite distinct from each other. The space within the rim of each pore-plate is closed by a membrane having an indistinctly dotted or mottled appearance.

These pore-plates are almost invariably in pairs, as described above. In a single case there were seen three of them together, forming a roughly triangular figure. They vary considerably in size, larger and smaller pairs being interspersed over the dorsal surface of the trunk; but the two pore-plates of each individual pair are of equal size. They are exceedingly numerous over the whole dorsal surface of the trunk, where they seem to have no definite orientation, their long diameters lying in all directions. They are extremely conspicuous in preparations of specimens that have been treated with caustic

\* A. Berlese, 'Gli Insetti,' vol. i. p. 492 and footnote.

potash. On the tail they are very scantily distributed, and only the smaller ones are present. On the ventral surface of the insect they are almost absent; there are a few small pairs arranged more or less definitely on each of the segments of the posterior region, and a small pair on each anal lobe.

Under each pore-plate is a single large glandular cell (Pl. 34. fig. 17, a), about 48  $\mu$  across in a direction parallel to the surface of the body. The two cells under each pair of pore-plates lie touching one another, and their contiguous sides are flattened. In transverse sections each pair may thus appear to be a bicellular gland. But each cell has its own pore-plate and secretes its own thread, for two separate threads emerge from each of the pits in the integument (Pl. 34. fig. 14); therefore each pair of cells must be looked upon as consisting of two unicellular glands in close proximity to one another.

The substance of each of these glandular cells is divided into two portions. Immediately under the pore-plate is a small well-defined part, much clearer and less deeply staining than the rest. The remainder of the cell, which contains a large oval nucleus, is much less clear and stains fairly deeply; this part has, in sections stained with hæmatoxylin and orange G, the peculiarity, which it shares with the chitinous cuticle, of taking up the latter stain, whereas its nucleus and the adjacent hypodermal and subhypodermal tissues take up the hæmatoxylin. The arrangement of these pits and glands with respect to the said hypodermis is worth noting. Beneath the hypodermis is a loose layer of subhypodermal cells (Pl. 34. fig. 17, e). The hypodermal layer is interrupted by the invagination of the chitinous cuticle to form the walls of the pit, and beneath the floor of the pit is represented only by the two glandular cells. On the other hand, the subhypodermal layer, at the point where it abuts against the walls of the pit, is invaginated so that it forms a loose capsule ensheathing the pair of glandular cells (Pl. 34. fig. 17, f).

On the dorsal surface of the tail, beyond the area of the pairs of pore-plates described above, and in the region of the fourth segment, there are two groups of curious structures, one on either side of the middle line. They are pits in the integument, and when seen in side view are like hollow inverted cones with obtuse and rounded apices (Pl. 34. fig. 10, d). They vary in shape, size, and arrangement. They are usually, but not always, in pairs; their number varies in different individuals, and is not even always the same in the two groups borne by one individual; usually there are five or six pits in each group. They are more strongly chitinised than the surrounding cuticle. The upper part of their walls looks homogeneous, while the lower or apical portion has a cribriform or sieve-like appearance. However, there do not seem to be any perforations as in a true sieve-plate, but merely thinner and more lightly-staining areas lying in the meshes of a network of thicker substance. It has not been possible to determine whether there are any glands in connection with these remarkable structures, but their appearance suggests that they may be essentially the same as the pore-plates already described, though they differ from them in detail.

There is another widely-distributed kind of cutaneous gland, characterised by the possession of a long, narrow, chitinous duct opening on a level with the general surface of the cuticle (Pl. 34. fig. 15, a). The duct is a narrow tube perpendicular to the surface

of the body, and having a straight or almost straight course for some distance. The first part of this straight tube has delicate walls (Pl. 34. fig. 11. b), often shrivelled in prepared specimens. The remainder has slightly thicker walls (fig. 11, c). At the end of the straight tube there is a very curious sharp bend (Pl. 34. figs. 11 d, 16); just on the outer side of the bend the walls of the duct are very slightly invaginated. Beyond the bend the walls of the duct are thinner again, as in the first portion. Immediately beyond the bend the duct is very narrow; it then broadens, and terminates in a slightly swollen end, the cavity of which is increased by numerous minute rounded diverticula, giving to the end the appearance of a morula (Pl. 34, figs. 11 e, 15, 16). The portion of the duct from the region of the bend to its termination is buried in the interior of a large glandular cell, measuring about  $34 \mu$  across. The substance of this cell consists of a well-defined inner clear portion, which stains very faintly, and an outer granular portion, which stains fairly deeply. The granular part is usually very thin, except in one region remote from the point of entry of the duct and containing the nucleus (Pl. 34. fig. 16, a). The inner clear part sometimes shows refractive globules (Pl. 34. fig. 16), more frequently striæ radiating from the termination of the duct (Pl. 34. fig. 15, b). How far these appearances are artificial it is impossible to say, but it seems probable that the striæ really represent a fibrillar structure of the protoplasm, such as has been described and figured by Prof. A. Berlese \* as existing in the interior or excretory portion of many glandular cells in insects. There is a mass of protoplasm appearing to be of the same consistency as the granular portion of the gland, and containing several rather small nuclei, surrounding the duct at its point of entry into the gland-cell (Pl. 34. fig. 15, c). This mass, though in close contact with the gland-cell, is clearly marked off from it; but does not itself, in the sections examined, always show definite division into several small cells, though indications of such division are present. I have endeavoured without success to determine whether these small cells are accessory glandular cells pouring a secretion into the duct at its bend, as might be suspected from the curious conformation of the latter; but there is no evidence that such is the case. The small cells show no special glandular structure and no division whatever into two portions, as do the large unicellular glands. Traces of a loose capsule of subhypodermal tissue can sometimes be seen surrounding the glands and their ducts.

The glands of this kind are numerous over the whole dorsal surface in the spaces between the pits of the thread-producing glands, their ducts being shown in fig. 10, f (Pl. 34). They are also numerous over areas where the thread-producing glands are almost entirely absent, that is, on the dorsal surface of the tail and the ventral surface of the trunk. They are more sparingly distributed on the ventral surface of the tail. No excretory products have been seen in connection with their orifices, so that it is not possible to state what part they play in the life-history of the insect.

A third kind of cutaneous glands must be noticed. They are much more localised in their distribution than the preceding, and are confined to the ventral surface. Their pore-plates lie in seven transverse bands in the posterior region of the body, near the \* 'Gli Insetti,' vol. i. p. 408 & fig. 559. hind margins of the segments. The most anterior band is ill-defined, and its poreplates few. The next four bands are well-defined and continuous, consisting of two or three irregular rows of pore-plates. The next band (Pl. 34. fig. 9, e)—at the posterior margin of the sixth segment—resembles these, but is interrupted in the middle line by the genital aperture (Pl. 34. fig. 9, d). The band on the seventh segment merely consists of a small group of pore-plates on either side of the middle line; a few poreplates are also present on the terminal segment. On the more anterior part of the body these pore-plates are only present in small groups just external to each spiracle and antenna.

These pore-plates have a distinct form of their own. As usual, they are more strongly chitinised than the surrounding cuticle. They are not arranged in pairs. Each (Pl. 34. fig. 13, also fig. 9) is circular, with a broad rim, immediately within which is a circle of dots. The space within these stains more deeply than the rest, but has a rather indistinct central dot of more lightly-staining substance. The glands in connection with these plates lie immediately below the chitinous derma. They are somewhat elongated, narrower in the portion nearer the derma, and much smaller than any previously described; those in the posterior region of the body measure about 18  $\mu$  in a direction perpendicular to the body-surface. I cannot be quite certain whether those in the posterior region consist of one or more cells. In connection with each spiracular group of pore-plates there can be seen a number of closely-packed, elongated, somewhat pear-shaped cells, each with a distinct nucleus.

Judging from analogy with allied forms, which fill their stigmatic grooves with wax \*, the position of some of the glands of the third kind with respect to the spiracles might suggest that they may have this function. Moreover, on the inner surface of some of the ovisacs can be seen four patches of white amorphous substance, corresponding roughly with the positions where the spiracles would lie when the female was in the ovisac; but, though extremely probable, it is not certain that the amorphous substance is wax. In connection with this, it may be mentioned that Berlese †, in describing certain species of *Lecanium*, figures plates which are like the pore-plates described above, and which are found in the stigmatic grooves and belong to glands that secrete wax into these grooves.

Ovisac (Pl. 34. fig. 5).—The white mass of threads arising from the dorsal surface conceals not only the insect, but also the curious ovisac in which it lies. The ovisacs are fixed to the twigs, for in the material examined the insects are always attached to the woody stems, and not to the small leaves, of the plant. In the great majority of specimens the ovisac has the form of a widely-open cup or basket; opaque, brownishyellow, with smooth inner surface, and the outer surface rough and bearing a number of white threads similar to those arising from the dorsal surface of the insect. It is closely adapted to the shape of the creature's body, and there is a deep impression in the margin at one point, and sometimes a slight spout-like prolongation, in which the tail of the

\* A. Berlese, 'Le Cocciniglie Italiane,' pt. ii. pp. 132, 133 & 182, 183 [ex Riv. Pat. Veg. vol. iii. No. 1-8]; Newstead, 'Monograph of British Coccidæ,' vol. i. p. 15.

† 'Le Cocciniglie Italiane,' pt. ii. tav. 5. fig. 2 a.

#### MR. HUGH SCOTT ON AN

insect lies extended. Under the microscope there can be seen in the walls a structure consisting, not of interlacing threads, but of branches anastomosing in all directions (Pl. 34. fig. 6, a). They are colourless, transparent, and glassy in appearance, and very minute, their thickness being less than half that of the white threads covering the insect's body. The skeleton that they form is best seen in the margin of the cup; in the rest of the walls it is covered with opaque material (Pl. 34. fig. 6, b) of brownish and yellowish colour, with felted masses of threads, and with some of the larger white threads so characteristic of the insect. In the denser portions the substance of the ovisac has to some extent a radiate arrangement; irregular thicker parts run from the base towards the margin of the cup, and alternate with thinner and more translucent portions. The ovisac, like the white threads, will not dissolve in cold chloroform, xylol, or ether. The mode of its formation cannot be made out in the preserved material.

Such is the structure in the great majority of specimens. But in a very few of the dried specimens the ovisac has proved to be completely closed except for an opening on the somewhat spout-like prolongation corresponding to the tail of the insect. As mentioned above, in the open cups there is a depression in the wall to accommodate the tail, and in one case this depression was just arched over, so that it formed a round hole (Pl. 34, fig. 5, a). This is probably an intermediate stage between the open depression and the closed prolongation containing the tail. It appears as if, at a later stage in the life-history than that attained by most of these specimens, more secretory material is added to the open cup, so that the latter becomes a closed structure, completely shutting in the female, as is the case in the allied genus *Asterolecanium* \*. One of these closed structures was empty, the other contained a much shrivelled female. This latter one bore on its outer surface a number of the white threads, but they formed a mass much smaller than that of the threads covering the females seated in open cups.

In several of the specimens preserved in formalin, each of the tubercles of the dorsal longitudinal rows bears a small plate or flake of glass-like secretion, insoluble in cold waxdissolving reagents. Each of these flakes is attached at its central part to the surface of the tubercle, and has in its peripheral portions exact impressions of the pairs of poreplates of the circumjacent integument. Through some of these impressions rise the threads secreted from the pore-plates beneath. The whole appearance suggests that the secretion has been poured out from glands on the tubercle, has flowed in all directions from this central point, surrounding the bases of the threads emerging from the pits, and has hardened into the transparent flake, receiving in the process impressions of the pits and pore-plates of the integument. It is possible that, by further excretion, the separate flakes on the tubercles may grow in extent till they unite and form a single complete covering to the dorsal surface, continuous at the sides with the margins of the cup-like ovisac, thereby transforming the latter into a closed structure. But there is no proof that such is the case.

*Male Puparium* (Pl. 34. fig. 8).—The puparia are attached to the woody stems of the *Helianthemum*. Each is about  $1\frac{2}{3}$  mm. long, much smaller than the ovisac, elongate-

\* Newstead, ' Monograph of British Coccidæ,' vol. ii. p. 150.

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ovate, narrowed posteriorly, quite opaque, white or very pale greenish, thus differing in colour from the ovisac. The inner surface of the walls is smooth, the outer surface rough. Externally there are a number of white threads similar to those secreted by the female; they are more numerous near the anterior end. Their presence in this structure formed by the male is interesting. The microscopic composition of the puparium is much like that of the felted parts of the ovisac, but there is no disposition into more opaque and more translucent portions. The puparia are empty, each having a neat, transverse slit at the posterior end, where the male has emerged (Pl. 34. fig. 8, a).

The mycelium of an Ascomycete fungus is found ramifying in the walls of some of the puparia and ovisacs, and outside the bases of some of the latter. The dark masses of spores formed in the mycelium appear as sooty-looking specks. Within one of the closed ovisacs mentioned above were a number of dried and empty perithecia of the fungus. Mr. R. H. Biffen, who has kindly examined the fungus, states that, although he has found no ascospores, the form of the perithecia and spore-masses in the mycelium are strongly conclusive of its being a species of *Capnodium*. Newstead \* states that the honey-dew secreted by British Coccids is almost invariably attacked, shortly after deposition, by a fungus of the genus *Meliola*. This is allied to *Capnodium*. Berlese + also speaks of fungi habitually accompanying Coccids on plants. It is therefore probable that the fungus in question nourishes itself on certain excretory products of the Algerian Coccid.

It should be mentioned that a single dried-up female specimen was found entangled in the mass of threads belonging to another individual, and that it contained within its shrivelled integument a number of oblong-ovoid bodies, also in a desiccated condition. The specimen was one of those preserved in formalin, and must therefore have been dead and desiccated at the time when the infected plant was found. Its condition unfortunately makes it impossible to ascertain the nature of the ovoid bodies which it contains.

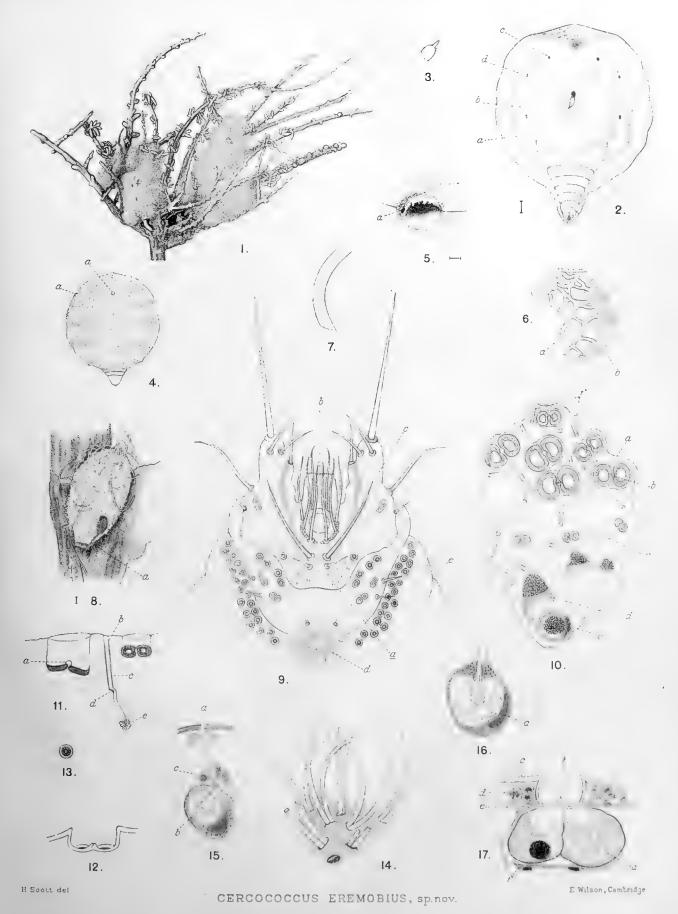
Cercococcus eremobius was found in the desert, on a plant which is essentially a desert-plant. The greatest peculiarity about the insect is the thick covering of white threads, corresponding to which is the large development of cutaneous glands. An analogy is suggested between this character and that of those numerous desert-plants which are clothed with hairs, which serve them in good stead by preventing excessive loss of moisture; and it is possible that the covering of threads may benefit the insect in the same manner that the hairs benefit the plants. It may be emphasised again that they can hardly serve any purpose of protective similarity to surroundings, since they form conspicuous white masses on the twigs. Since the locality where the creature was found is by no means inaccessible, it is to be hoped that before long fresh supplies of material will be obtained, including both sexes and all stages, so that the whole life-history of this interesting insect can be elucidated.

\* 'Monograph of British Coccidæ,' Ray Soc. vol. i. p. 19.

† A. Berlese, 'Le Cocciniglie Italiane,' pt. i. p. 43 [ex Riv. Pat. Veg. vol. ii. No. 1-8].

# EXPLANATION OF PLATE 34.

- Fig. 1. The specimen of *Helianthemum kahiricum* bearing *Cercococcus eremobius*. Nearly two-thirds natural size.
- Fig. 2. Ventral view of adult female. a, outer, b, inner longitudinal furrow of the right side; c, antenna; d, anterior spiracle.
- Fig. 3. Antenna in side view, showing the spine and two of the hairs.
- Fig. 4. Dorsal view of adult female. *a*, *a*, tubercles of the median and lateral longitudinal rows. The dots represent the numerous pits of the thread-producing glands.
- Fig. 5. Ovisac on a twig.  $\alpha$ , hole in which the tail of the insect lay.
- Fig. 6. Portion of the wall of the ovisac, highly magnified. *a*, anastomosing branches; *b*, opaque material.
- Fig. 7. Part of one of the threads secreted from the dorsal surface, showing the longitudinally striated appearance. To same scale as fig. 6.
- Fig. 8. Male puparium on a twig. a, slit at posterior end.
- Fig. 9. Ventral view of extremity of tail of adult female, showing the anal ring and orifice. a, minute papillæ on the integument; b, median lobe, dorsal to the anus; c, one of the anal lobes; d, genital aperture; e, transverse band of circular pore-plates on the sixth segment.
- Fig. 10. Portion of the dorsal integument of a specimen treated with caustic potash, highly magnified. In the upper part are some of the numerous pairs of pore-plates. a, outline of floor of one of the pits; b, space left between the two concavities in the margins of the rims; c, commencement of the tail-region, where the pore-plate pairs are almost completely absent. In the lower part of the figure are some of the pits with sieve-like walls; d, pit in side view; e, one in surface view; f, narrow ducts of glands of the second kind.
- Fig. 11. Two of the dorsal pits in side view, each with a pair of pore-plates at the bottom; a, papillæ between the pore-plates. In the middle, a duct of a gland of the second kind; b, thin-walled portion of straight tube; c, its thicker-walled portion; d, bend in the duct; e, terminal swelling.
- Fig. 12. One of the dorsal pits and pairs of porc-plates, from a transverse section torn in such a way as to show the pair of papillæ between the pore-plates.
- Fig. 13. A single circular pore-plate from one of the transverse ventral bands. To same scale as fig. 10.
- Fig. 14. Part of the dorsal surface of a dried specimen, showing some of the pits, each with two threads emerging from it; the greater part of the threads cut away.
- Fig. 15. One of the glands of the second kind. *a*, aperture of duct on outer surface of body; *b*, inner secretory portion of gland-cell showing radial striæ; *c*, accessory cells.
- Fig. 16. Part of one of the same glands, more highly magnified. a, nucleus of glandular cell.
- Fig. 17. Transverse section through one of the pairs of thread-producing cells. The section only passes through the nucleus of one gland. a, one of the cells; b, papilla between the two poreplates; c, cuticle of the general body-surface; d, hypodermis; e, subhypodermal layer, and f, the sheath which it forms round the glands.



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## XIII. Observations on Australasian Polyclads. By Professor W. A. HASWELL, M.A., D.Sc., F.R.S., F.L.S.

### (Plates 35-37.)

#### Read 6th June, 1907.

**T**HE Polyclads of Australasia have hitherto received very little attention. Stimpson's "Descriptions of some new Marine Invertebrates" (22), published in 1855, contains diagnoses of several members of the group obtained in Port Jackson. Schmarda in the first volume of his 'Neue wirbellose Thiere,' issued in 1859, published some observations on several species from New South Wales and New Zealand. In Saville Kent's 'Great Barrier Reef' three species are referred to as *Pseudoceros Kentii*, n. sp., von Graff, *Pseudoceros dimidiatus*, n. sp., von Graff, and *Prostheceræus flavomaculatus*, n. sp., von Graff, but I am not aware that any account of them has been published. Woodworth (26) described a few species from the same locality. Marianne Plehn (18) described a species from New Zealand and the Chatham Islands, and another from Tasmania. T. W. Kirk (10) described two New Zealand species, and T. F. Cheeseman (2) two more. Lastly, Laidlaw (11) described *Leptoplana australis* and *Stylochus vigilax* from specimens in the collection of the British Museum, and recognized a speciemen of *Cryptocelides Loveni*, Bergendal, labelled "Port Phillip, J. B. Wilson."

Of Stimpson's descriptions it is impossible to make any use, and the same holds good of Schmarda's. Though, presumably, the forms from Port Jackson described by these authors are the same as some of those dealt with in the following pages, it is quite impossible, without the opportunity of examining the original specimens, to attain to any certainty in this direction. Thus it is quite possible that Stimpson's *Dioncus badius* was the species here referred to as *Leptoplana australis*, Laidlaw, and at first I was disposed to name it *Leptoplana badia* in order to retain the old name; but on reconsideration I came to the conclusion that it would be better to avoid any identifications of such a merely conjectural kind, and to set Stimpson's and Schmarda's names aside altogether.

Lang's comment on Stimpson's paper may be quoted here :—" Die Diagnosen sind alle sehr kümmerlich. Bei dem gänzlichen Fehlen der Abbildungen werden deshalb die Arten wohl kaum wieder mit Sicherheit zu erkennen sein. Ihre generische Zugehörigkeit ist in den meisten Fällen nicht zu errathen " (17, p. 17). Of Schmarda's descriptions the same author observes :—" Leider sind die anatomischen Beobachtungen äusserst kümmerlich und die Angaben über Fehlen oder Vorhandensein und Stellung der Augen, Lage und Natur der Oeffnungen des Körpers, Form des Pharynx etc. wohl nicht ganz zuverlässig; so dass vielen der beschriebenen Arten ihre Stellung im System nicht mit Sicherheit angewiesen werden kann" (op. cit. p. 19).

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of the Australian Museum, Sydney, and Prof. W. B. Benham, of Dunedin, N.Z., by both of whom I was given the opportunity of examining specimens from the collections under their charge, to Mr. Chas. Hedley for specimens collected at Masthead Island and Cooktown, and to Mr. S. J. Johnston, B.A., B.Sc., Senior Demonstrator of Biology, Sydney University, for the specimens of *Diplosolenia*.

The most important morphological and physiological results embodied in the following are :—(1) the discovery of a new Planocerid (named *Tripylocelis*) with three reproductive apertures; (2) the discovery of a *Cryptocelis*-like form with a genito-intestinal canal; (3) the evidence of a peculiar mode of copulation by localized perforation in the new Australian genus *Echinoplana*.

The nomenclature of the parts of the female reproductive apparatus of the Polyclads is somewhat confused, and, without any intention of dogmatizing as to homologies, it is necessary that I should state here the terms used in the following descriptions, and the sense in which they are employed. The term ovaries needs no comment. The oviducts are the ducts by which the ova reach the uteri. The uteri are the two elongated chambers in which the fully-developed ova collect, and in which they undergo maturation and may become fertilized. The ducts by which the ova pass out from the uteri are the uterine ducts; very commonly the right and left uterine ducts unite to form a median uterine duct. The remainder of the apparatus consists of a median passage to the whole of which I apply the term vagina. The part of this into which the female aperture directly leads is the antrum femininum. This, or a part of it, may have its walls thickened to form a bursa copulatrix. The part following on this is the ootype ; this is the region into which the ducts of the shell-glands open. The ootype usually runs upwards and forwards, or directly upwards, and bends sharply back to pass into the dorsal limb of the vagina, the shell-gland ducts being frequently continued on this for some distance, and even on the terminal portions of the uterine ducts. Into the dorsal limb of the vagina open the uterine ducts, or median duct, as the case may be. Beyond this point the vagina may be prolonged backwards. Sometimes it terminates in a median sac, the receptaculum seminis; rarely there are two receptacula, right and left. In a few cases the vagina terminates behind by opening on the ventral surface of the body by a posterior female aperture.

## TRIPYLOCELIS TYPICA, n. g., n. sp. (Plate 35.)

In the living condition this Polyclad is about 1.5 to 2 cm. in length, and in breadth about 0.75 to 1 cm.—the breadth not being more than half the length. The brain, tentacles, and eyes are in the first fifth. The mouth is in front of the middle. The male aperture is in the last third. The space between the male and female apertures is about one-half of that between the latter and the posterior margin.

The tentacles are in the form of elongated cones; they are not retractile into depressions at their bases. The arrangement of the eyes (Pl. 35. fig. 2) is fairly constant. Each tentacular group comprises some twelve to twenty. Two or three small eyes are usually to be detected in the tentacles above the level of the others. Of the remainder there are rarely any situated directly over the brain; but they all, or nearly all, lie in

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front of or behind it, those in front being the more numerous (about 50), arranged in two parallel groups with a small space between them.

The colouring varies somewhat, but is never very pronounced. Some specimens are almost colourless, but for the light green ramifications of the intestinal caca; but in most there is a faint diffused brown tint due to the presence of minute dots of brown pigment, which are most numerous in the region behind the pharynx. The ventral surface is usually of a light brown colour except in the more central parts, where the pharynx and principal parts of the genital apparatus appear white. One of the most striking features in the aspect of the living animal is the conspicuousness of the intestine and its main branches owing to their presenting the appearance of narrow, dark greenish lines on the dorsal aspect of the animal.

The mouth leads into the pharynx by a funnel-like passage. The pharynx has about eight to ten pairs of lateral folds and the intestine gives off about the same number of main diverticula. Pharynx and intestine are almost conterminous.

The two vasa deferentia (Pl. 35. fig. 1) join at about the point of union of the anterior and middle thirds of the penis. The median duct thus formed runs forwards with an almost straight course for some distance; it is slightly dilated, and its wall is somewhat thickened, so that it may be regarded as forming a median vesicula seminalis. Further forwards it becomes narrower, and is thrown into a number of coils, in the ordinary, retracted condition of the penis. Eventually, when it reaches a point a little distance in front of the anterior end of the penis, it bends sharply round, and runs almost straight back through the axis of the granule-gland papilla, where the ducts of the granuleglands open into it (granule-gland reservoir).

The penis (figs. 1 & 3) is an elongated muscular cylinder, without spines or other special chitinous developments, straight in a well-extended specimen, but more or less bent in a specimen contracted in the direction of the long axis. In front it is quite circular in cross-section; further back it is more or less compressed. Its walls consist of outer longitudinal and inner circular layers of muscular fibres of approximately equal thickness, and of a layer of columnar epithelium bounding the lumen. Surrounding it is a thick mass of retiform parenchyma.

Projecting backwards into the lumen of the penis from its anterior end is the conical papilla (granule-gland papilla) perforated by the terminal part of the ejaculatory duct, having the ducts of the granule-glands opening into it. This papilla is formed of an involution of the muscular wall of the penis filled with the retiform tissue that surrounds it.

The chief (anterior) female aperture leads into an ootype (fig. 1) of long-oval form with greatly plicated walls. At its anterior end this bends back and passes into the dorsal limb of the vagina. The latter runs backwards near the dorsal surface of the body, and receives from below the unpaired duets formed by the union of the right and left uterine duets. Instead of terminating blindly or expanding into a receptaculum seminis, as in most other Polyclads, the vagina then bends downwards and opens on the ventral surface some little distance behind the main female aperture (Pl. 35. figs. 1, 5, & 6). This posterior continuation of the oviduet has a thick muscular wall; its epithelium is

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raised up into a number of longitudinal ridges. Behind the point where the median uterine duct leaves it below a process of epithelium projects into the lumen; this may, perhaps, act as a valve for preventing the passage of the eggs backwards to the posterior female aperture.

The uteri are wide tubes containing, in the sexually active animal, numbers of ripe eggs, together with quantities of spermatozoa. The eggs are all at the same stage. In each is the usual centrally-placed spindle with four chromosomes.

This appears to be the fourth Polyclad genus in which a second female aperture has been discovered. But in other respects the four forms have very little in common. Lang's genus *Trigonoporus* \*, of which two American species—*T. folium* and *T. dendriticus* †—have been described by Verrill, has no tentacles, has numerous scattered cephalic eyes, and has a separate prostate with independent duct. Of the affinities of *Bergendalia*, Laidlaw, little is known, but in that genus the second aperture leads into the antrum femininum. *Laidlawia*, Herzig, has the aperture in question on the dorsal instead of the ventral side, and there is a well-developed receptaculum seminis. In *Polyporus*, Plehn, there is a close correspondence in the relations of this aperture with what we find in *Tripylocelis*. The single specimen of *Polyporus* found was not sexually mature, so that little was ascertainable regarding the reproductive apparatus; but there are pores all round leading into the intestinal branches, and there are no eyes.

If we leave the occurrence of the third reproductive aperture out of account the closest relationships of *Tripylocelis* are with the Planoceridæ. The members of Lang's group B of the species which he referred to the genus *Planocera* are, apparently, the nearest relatives. But the relationship is by no means very close, the differences in the male reproductive apparatus being very considerable.

*Tripylocelis typica* is perhaps the commonest Polyclad that occurs between tidal limits in Port Jackson. It is chiefly to be found in tidal pools among the thalli of *Ulva* and can usually be obtained in considerable numbers by pulling the Algæ to pieces and shaking them out in a vessel of water.

It is an extremely active form, swims vigorously, and on the surface of a solid object is able to progress rapidly by advancing lateral lobes, which are able to adhere to the surface, and are pushed forward from right and left sides alternately—the result being a kind of "walking," as distinguished from "creeping" or "looping" locomotion.

The following is a definition of the genus Tripylocelis :---

Planoceridæ with fairly broad, oval, leaf-shaped body, with conical non-retractile tentacles. Brain-tentacles and eyes relatively further forward than in *Planocera*—in the first fifth or thereabouts. Two groups of tentacular eyes, and smaller eyes just in front of and behind the brain; no marginal eyes. Three genital apertures. Male aperture a considerable distance behind the pharyngeal sac. Principal female aperture not far behind the male: second female aperture on the ventral surface not far behind the first. Penis muscular, without sheath and without chitinous parts. A small median

\* 17, p. 502.

† As pointed out by Laidlaw (14), the generic position of these is doubtful.

vesicula. Prostate-gland reservoir situated in the course of the ejaculatory duct. No bursa copulatrix. Vagina continued backwards to open on the ventral surface by the second female aperture.

The discovery by Herzig (9) of a Polyclad (named by him Laidlawia) which has a second female aperture situated not on the ventral but on the dorsal side, may be regarded as of some importance, as it may help us towards a determination of the homologies of the parts. A correspondence with the Trematode "canal of Laurer" and with the Cestode "vagina" and receptaculum seminis obviously suggests itself. Bergendal has recently described a Triclad with a second female aperture, and I have shown that such an opening (dorsally situated) occurs in the Accala, so that an arrangement of this kind would seem to be very widespread in the Platodes. In all such cases the object of the arrangement is, most probably, to enable fresh supplies of spermatozoa to be taken in without any interference with the passage outwards of the fertilized ova. But it may be that in some cases the canal has lost its function, though still persisting, or may have become adapted to other uses.

# DIPLOSOLENIA JOHNSTONI, n. g., n. sp. (Plate 36. figs. 1 & 2.)

This is a very large Polyclad, one preserved specimen measuring 6 cm. in length and 3 cm. in breadth. The mouth is somewhat in front of the middle—in the third centimetre. The reproductive apertures are situated close together (or combined in one) at the junction of the fourth and fifth centimetres. The tentacles are rather long and of conical shape : they are placed a little behind the junction of the first and second centimetres. The eyes are in two very compact groups, each comprising about 30, at the bases of the tentacles, and two longitudinally extended less compact groups between them, each of these also comprising about 30. The dorsal surface is almost black, with a narrow light margin.

The pharynx has about twelve pairs of lateral folds.

In two of the specimens, which have the penis exserted and a considerable length of the stylet projecting, the male and female apertures are separated by a distinct interval. On the other hand, in the specimens with the penis retracted the parts of the body-wall in the neighbourhood of the apertures become involuted to form a kind of common antrum having but a single external opening.

The ventral part of the vagina is a long narrow passage the lumen of which has a triangular cross-section in the greater part of its extent. Its muscular investment is thin, and it has an epithelium of long narrow cells. In the posterior part of its extent, in the specimen sectioned, the lumen is filled entirely with the shell-gland secretion which completely saturates the epithelium. Further forwards numerous spermatozoa are also present; but in the anterior part of the passage these disappear and the lumen is filled with the shell-gland secretion.

The vagina becomes bent back sharply on itself, the dorsal limb running back to a point just over the base of the (exserted) stylet, where it bifurcates to form the ducts of the two lateral receptacula seminis which run almost transversely outwards (fig. 2). This dorsal part of the vagina is a narrow cylindrical tube, with an epithelium of

comparatively short and broad cells and a thick muscular wall. Not far behind its origin it receives on the ventral side a median duct formed by the union of the right and left uterine ducts. In the lumen of these there are many spermatozoa.

The two receptacula seminis (fig. 1) are of great size, and when distended with sperms become very conspicuous structures. In a mounted specimen 30 mm. in length one of them is 4 mm. long. In the distended condition the stretched wall is very thin and its structure is difficult of determination. But in the collapsed state the wall appears relatively thick, and is found to have essentially the same structure as that of the unpaired receptacle of *Leptoplana australis*. It has a thick muscular investment, and an epithelium of large cells, each of which has a prominent rounded process at its inner end, having the appearance of an exuding droplet of secretion.

Each lateral vas deferens is dilated to form an extensive elongated seminal vesicle, but this does not appear specially thickened—at least in the distended condition it is in in the specimen sectioned. From the two lateral vesiculæ a pair of narrow ducts run inwards and at the base of the penis unite to form the ejaculatory duct.

The penis is enclosed within an elongated sheath. The penis itself consists of a very thin-walled chitinous tube enclosed in a thick layer of circularly-arranged fibres. The tube or stylet is 5 or 6 mm. in length, tapering to a sharp point at its free end, slightly dilated and funnel-shaped proximally. The layer of circular fibres is continued, somewhat reduced in thickness, over the portion of the penis which is protruded in the specimen sectioned: its function must be to bring about peristaltic contractions of the thin-walled chitinous tube and so of enclosed ducts. Within the tube is a layer of longitudinal muscular fibres: internally the lumen is occupied by a core of parenchyma in which run ejaculatory and prostatic ducts, the former towards the centre, the latter towards the dorsal side.

The prostate is a median structure which extends forwards as far as a point a little in front of the point of union of the oviducts. Its duct, at first narrow, widens, then becomes narrower and sinuous, then expands into a channel devoid of epithelial lining, which acts as a reservoir. This runs back for some distance parallel with the ventral limb of the vagina and on its ventral side. This sinus or reservoir passes behind into a narrow cylindrical duct with well-defined walls, which runs to the base of the penis and traverses that organ throughout its length, running within the hollow stylet, parallel with and dorsal to the ejaculatory duct, but remaining separate from the latter.

The following are the chief features which distinguish this genus:—There is a pair of nuchal tentacles with groups of tentacular eyes: no marginal eyes. Reproductive apertures closely approximated. Vagina long and narrow throughout, without bursa copulatrix. A pair of large receptacula seminis. Duct of prostate separate from ejaculatory duct throughout its entire length. A pair of vesiculæ seminales in the form of large dilatations of the right and left vasa deferentia. An elongated penial stylet.

So far as I am aware, only two Polyclads are known to possess paired receptacula, viz. *Discocelis tigrina*, Lang ("horseshoe-shaped gland"), and *Leptoplana subviridis*, Plehn (Laidlaw). This character, together with the complete separation of prostatic

and ejaculatory ducts, would suffice to distinguish *Diplosolenia* from all other *Planoceridæ*.

*Idioplana*, Woodworth (26), resembles *Diplosolenia* in the exceptional feature of the complete separation of prostatic and ejaculatory ducts; but it has marginal eyes, has, apparently, no penial stylet, and has a median vesicula.

*Planocera* has the ejaculatory and prostatic ducts uniting to form a common duct; its penis is lined with chitinous spines, and the vagina gives rise to a bursa copulatrix: the receptaculum seminis is unpaired.

Stylochoplana, again, has the prostate intercalated in the course of the ejaculatory duct, has a median vesicula, a single receptaculum, and possesses a bursa copulatrix; while Stylochus has marginal eyes, the reproductive apertures situated close to the posterior end, has the prostate separate, but with its duct uniting with the ejaculatory duct, a single vesicula, and no receptaculum.

*Paraplanocera*, though it has paired vesiculæ, resembles *Planocera* in the character of the penis and in the unpaired receptaculum; it also has a muscular diverticulum of the vagina of the nature of a bursa copulatrix.

LEPTOPLANA AUSTRALIS, Laidlaw. (Plate 36. figs. 3-5.)

This is, so far as my data go, the most widely distributed, as well as one of the largest, of the Australasian Polyclads. It is one of the commonest of the Port Jackson species, and was obtained also at Jervis Bay, on the southern part of the New South Wales coast. It is by far the commonest species on the coast of Tasmania, and it extends also to New Zealand.

Leptoplana australis may be identical with Dioneus badius of Stimpson (23), or with D. oblengus of the same author, both of which were found in Port Jackson, and it may also be the same as Polycelis australis of Schmarda (20), which was found on the New South Wales coast. But the characters given by the authors named are not of a nature to justify even generic determination. Thus Stimpson's definition of the genus Dioneus runs:—" Corpus planum, dilatatum. Caput corpore continuum. Os subcentrale. Ocelli numerosi, in umbones duos claros subdistantes dispositi. Maricolæ." The description which he gives of D. badius is as follows:—" Body half as broad as long, of a reddish-brown colour above, with a flake-white dust intermixed. Anteriorly there are two prominent circular knobs, which contain, scattered over the entire surface, the very numerous and minute eyes. Below the body is of a pale sepia colour, except the white digestive organs, and the mouth is placed behind the centre. Length 1.5; breadth 0.75 inch." D. oblongus is stated to differ from D. badius mainly in having a clear space around the eyes on each knob.

Schmarda's *Polycelis australis* may be this species, but the characters given and the figure would not warrant an identification. The following is the description :---

"Der Körper ist platt, länglich, vorn abgerundet und rückwärts kaum weniger verschmächtigt. Die Farbe des Rückens ist dunkelbraun mit unterbrochener blasser Mittellinie. Die Bauchseite ist röthlichbraun. Länge 30 mm., Breite 13 mm. Die Augen stehen in zwei Gruppen am ende des ersten Sechstels, sie sind einander sehr genähert und besitzen einen weissen Hof der sich nach vorn und auswärts in einen kurzen Streifen fortsetzt welcher mit dem der anderen Seite divergirt. Die Mundöffnung ist zwar auch hier wie bei der vorigen Species central; die Geschlechtsöffnungen sind jedoch dem Centrum sehr viel näher gerückt und liegen im zweiten Drittel des Korpers. Das Parenchym ist dicker und stärker, als es bei andern *Polycelis* der Fall ist."

Schmarda found his specimens on the coast of the Illawarra district, New South Wales, and in Auckland Harbour, New Zealand.

Leptoplana australis reaches a large size; the largest specimens I have seen alive were 33 inches long. It is subject to great variation in colour. The larger specimens are very dark—some almost black, with a lighter line round the edge. Smaller specimens are much lighter—some with only a light general shade of brown, through which run the branching mottled bands of olive-green that represent the ramifications of the intestine.

Quite conspicuous features of the upper surface are the two clear colourless rounded knobs on which the "tentacular" groups of eyes are borne. These are situated at about the junction of the first fourth of the length of the body with the second. They are of oval or elliptical outline, with the long axis directed forwards and outwards. Each of them comprises about forty eyes. Smaller eyes are arranged in two groups separated by a definite mesial space; they are more numerous than the tentacular eyes, and are almost entirely in front of them.

The ventral surface is grey, the reproductive apparatus (or rather certain portions of it) forming a more or less pronounced white pattern on it. The mouth is always a little in front of the middle; the male reproductive aperture is about halfway between the mouth and the posterior border, and the female aperture a short distance behind the male.

The pharynx gives off about fifteen to seventeen pairs of diverticula, and the number of main intestinal branches is about the same.

The vesicula seminalis is at the junction of the lateral vasa deferentia and the ejaculatory duct. From this the ejaculatory duct runs forwards to the prostate reservoir. The latter is a thick-walled, long, oval body, the appearance of which in the entire specimen differs a good deal according to the way in which it lies. In an end view it presents a remarkable wheel-like appearance which is not recognizable in a lateral view. In sections this wheel-like effect is found to be due to the presence of a ring of longitudinal recesses which open into the lumen at the end nearest the base of the penis after traversing the wall of the organ throughout its length.

From the end of the prostate reservoir opposite that at which it enters the ejaculatory duct runs forwards to the base of the penis. The latter is of great length. It encloses a narrow, twice-curved, hollow, chitinous stylet, dilated into a funnel proximally, and distally tapering to a fine point. In the two largest specimens it is sharply bent near the apex.

The female aperture leads into the antrum femininum, which runs upwards and backwards as a wide passage to open into the ootype or shell-gland reservoir. The latter is remarkably developed, much wider than the antrum, with a minutely folded

inner surface : it is produced backwards some distance behind the female aperture. Its wall is very thick and muscular, as is that of the antrum, which may be regarded as assuming the character of a bursa copulatrix. In front it narrows somewhat; at its anterior end it bends sharply back as it passes into the narrow receptacular duct or vagina. The right and left uterine ducts run almost transversely inwards from the corresponding uteri, and unite to form a short unpaired duct which enters the vagina just over the male aperture. Behind this junction the backward prolongation of the vagina runs as a narrow tube on the left side of the ootype to open immediately behind the posterior extremity of the latter into a very large sac (receptaculum seminis). The anterior part of the duct is slightly constricted at regular intervals-the constrictions producing a beaded appearance. In some specimens this beaded appearance extends throughout its length. The receptaculum itself is a sac with folded walls lined by a large-celled columnar epithelium. Sometimes it appears collapsed and empty or nearly so: more frequently it contains a great mass of spermatozoa together with granules or droplets of a secretion evidently derived from the columnar cells. In some specimens sperms occur throughout the length of the duct.

The entire reproductive system of L. australis has a very close resemblance to that of L. fallax, Diesing, as described by Quatrefages (21). The chief differences appear to be that in the latter species the penial stylet is coiled on itself, the vagina is sinuous, and the accessory sac is unsymmetrically developed \*. L. alcinoi and L. vitrea, as figured and described by Lang (17), resemble L. australis in the peculiar internal structure of the prostate reservoir, but differ from it in other respects—notably in the relatively slight development of the receptaculum seminis.

There is a considerable difference between individuals of L. *australis*, when fixed, as regards the length of the posterior prolongation of the vagina (duct of the receptaculum seminis) and the size of the receptaculum itself. But it seems most probable that this is due to differences in the condition of the parts and the degree of contraction which they have undergone.

*L. australis* occurs at a comparatively high level between tide-marks, and is to be found by turning over stones.

In sections of one of the Port Jackson specimens I was interested to find in the pharynx unmistakable fragments of an Enteropneust. This was the more remarkable since no Enteropneust has ever been recorded as occurring in Port Jackson.

In the intestine of a Tasmanian specimen was the lingual ribbon of a Gastropod.

What may be a dwarf variety of this species is common in Lyttleton Harbour, N.Z. Preserved specimens are under 1 cm. in length. In the living condition it is transparent, with some brown pigment on the dorsal surface, and is of very delicate consistency, so that it is very difficult to obtain entire specimens. The eyes are much fewer in number than in mature specimens of the ordinary L. *australis*, but in this respect there is a correspondence with immature specimens of that form. In

<sup>\*</sup> In Quatrefages's figure the lateral uterine ducts are represented as opening separately, and, moreover, as opening, not into the vagina, but into the ootype, which is obviously an error.

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small specimens of the latter, however, the reproductive apparatus is undeveloped, whereas the small forms now under consideration are sexually mature. In the reproductive system the main differences may be reduced to differences in proportions: the penial stylet, granule reservoir, vesicula seminalis, antrum femininum, and receptaculum seminis have all the same general character as in L. australis. Perhaps the most important difference is in the great relative width of the dorsal limb of the vagina (or duct of the seminal receptacle).

From Lyttleton Harbour, from Waiheke, Auckland Harbour, and from Kaikoura, I have specimens of *Leptoplana* differing little from the Australian specimens which I have referred to *L. australis*. The tentacular groups of eves are denser owing to the larger size of the individual eyes, but in other respects there is a close correspondence. In one of the specimens (from Kaikoura) the penial stylet, instead of tapering to a fine point, ends in a truncated extremity provided with a circlet of hook-like processes; and in another (from Auckland Harbour) it is nearly straight and relatively short. But such differences are probably merely individual variations.

Of the identity of this common Australian species with Luidlaw's Leptoplana australis (11) I have no great doubt, though the description given is not very full. The arrangement of the eyes agrees fairly well; and the reference to the "long nearly straight stylet" of the penis, to the prostate divided into some six or seven longitudinal chambers, as well as the allusion to L. alcinoi as an allied species, all seem to point to this determination. The colour given, dark chocolate-brown, is unusual.

The British Museum specimens described by Laidlaw were collected in Port Phillip by Dr. R. Lendenfeld.

It is a somewhat remarkable fact that Plehn (18) records the occurrence in French Pass (northern New Zealand), and also in the Chatham Islands, of a species of *Leptoplana* which corresponds in many respects with *L. australis*, but which has only one genital aperture, like that author's *L. californica* (19), and is not regarded by her as distinct from the latter species. In the hope of finding something corresponding to this, I have looked over my Australian, Tasmanian, and New Zealand specimens set down as *L. australis*; but they all have the two separate apertures, and I have as yet seen nothing corresponding with Plehn's species.

## MICROCELIS SCHAUINSLANDI, Plehn (18).

A solitary specimen which I obtained at St. Helens, on the east coast of Tasmania, resembles Plehn's (18) species (also from Tasmania) in such points as are capable of being made out. It has the same general very characteristic arrangement of the eyes and posterior position of the pharynx, but the specimen was damaged and little can be made of the reproductive apparatus. It was observed to be, like *Cryptocelis*, an exceedingly sluggish form of unusually firm consistency. Its colour on the upper surface was brown, very distinctly mottled.

Resembling the above in the posterior position of the pharynx, the marginal eyes, the two separate but closely approximated reproductive apertures, and the presence of a median receptaculum seminis, is a New Zealand Polyclad which I have found under stones in Lyttleton Harbour. But in this the numerous minute eyes over the brainregion are (imperfectly) divided into two by a narrow space, and though they extend forwards nearly to the anterior margin, it is only as a relatively narrow band. Moreover, the marginal eyes only extend over less than a half of the margin. The female aperture leads vertically upwards to the ootype, which runs forwards a short distance and narrows as it bends backwards. Into the dorsal limb on the ventral aspect the uterine ducts open at a point nearly directly over the female aperture. Posteriorly the vagina is produced and terminates in a large and complicated receptaculum seminis. The male apparatus was not distinguishable in the entire mounted specimen, and sections are not available at present.

ECHINOPLANA CELERRIMA, n. g., n. sp. (Plate 36. figs. 6 & 7; Plate 37. figs. 1-3.)

This is a rather small Polyclad, averaging about 1.5 cm. in length and 6 mm. in breadth at the broadest part (towards the anterior end). The colour varies somewhat and is never very pronounced. Usually the dorsal surface has a reddish-brown tint. There are no tentacles. The eyes (Plate 37. fig. 1) are arranged in two somewhat elongated groups, one on either side of the brain, each including about thirty. The brain and the eyes are in the first fifth of the length of the body. The mouth is distinctly behind the middle. The male aperture is about halfway between that and the posterior end—at about the junction of the third fourth with the last. The female aperture is a considerable distance behind the male, nearer the posterior end than to the latter. In front of it is a peculiar, transversely corrugated area of the integument. In front of the male aperture in the living specimen the penis is usually plainly recognizable as a narrow elongated brown object.

The pharynx has twelve to fifteen pairs of lateral folds, and the number of pairs of intestinal cæca is about the same. The main intestine extends some distance in front of the anterior extremity of the pharynx.

The lateral vasa deferentia (Pl. 37. fig. 2) open into an elongated median vesicula seminalis, which terminates in front in a very fine duct (duct of vesicula). This traverses from before backwards a conical papilla projecting backwards into the lumen of the granule reservoir from its auterior extremity and opens into the latter.

The granule reservoir is of great length: it has the form of a tube with muscular walls, wider at its proximal or anterior end than at its distal or posterior, with three sharp bends in its course. In its posterior part it presents about half a dozen slight regular constrictions. Its muscular layers are of considerable thickness and its epithelium is thrown into a series of longitudinal folds.

The ejaculatory duct, narrow and coiled where it leaves the granule reservoir, widens posteriorly as it traverses the penis. The anterior narrow part has a very definite cylindrical epithelium surrounded by a condensed layer of the muscular fibres of the penis; many granule-gland ducts traverse the muscular layers and perforate the cells of the epithelium to open into the lumen. Posteriorly the duct soon loses its epithelium and becomes beset with the horny teeth described below.

The penis consists of an enormously thick mass of muscular fibres occupying the greater part of the vertical diameter of the body and about a tenth part of the transverse. In the living animal, and to a still more marked degree in preserved specimens, its position is indicated by a rounded elevation on the dorsal surface. There is no enclosing sheath or sac, the more peripheral muscular fibres passing into the muscular layers of the body-wall or into the layers of parenchyma-muscle that surround the various neighbouring organs (intestinal branches, vasa deferentia, uteri). The muscular fibres are some longitudinal in direction, some circular, some radial, but they are not arranged in any definite layers or zones. At the external aperture the muscular mass is quite continuous with the muscular layers of the body-wall. The entire lumen of the penis (distal part of ejaculatory duct) is lined with horny spines or teeth. These (Pl. 36. figs. 6 & 7) are largest in the neighbourhood of the external opening, gradually decreasing in size anteriorly. The larger spines are slightly curved, pointed, and have a shape comparable to that of the claw of a bird. In the smaller spines the base is relatively more expanded than in the larger and the distal part more abruptly curved. In the neighbourhood of the opening a process from the underlying tissue projects into the cavity of the spine: further forwards this is not recognizable.

The female aperture leads into a narrow passage surrounded by a thick mass of parenchyma with numerous muscular fibres. Through this mass run numerous shellgland ducts, and these perforate the epithelium of the passage in all parts except the part immediately adjacent to the aperture, so that an antrum as distinct from an ootype or shell-gland reservoir can hardly be said to exist. This part of the ootype gives off laterally a number of very short and small diverticula, which have a fairly regular arrangement. When it approaches near the dorsal surface of the body it expands in the interior of a rounded prominence which projects dorsally in this region a little in front of the female aperture. As it passes forwards it becomes narrower and gives off short irregular diverticula. When it reaches the muscular mass of the penis projecting behind the male aperture it passes to the left, and is continued forwards as a narrow diverticulum (Pl. 37. fig. 3) for some distance beyond the male reproductive aperture. Not far from its anterior extremity it receives on its dorsal side the common uterine duct. This unsymmetrical anterior prolongation of the vagina has not a specially developed muscular layer, so that it cannot be looked upon as a bursa copulatrix. On the other hand, the ducts of the shell-glands open into it in much greater abundance than into the central part of the ootype itself, and it is best looked upon as a prolongation of the latter. The reflected portion, or dorsal limb of the vagina, produced backwards in most Polyclads beyond the point at which it receives the uterine duct, and frequently leading to a receptaculum seminis, is here entirely absent.

Clear evidence of the mode of action of the copulatory parts of the reproductive apparatus is afforded by two of my series of sections. In one, a transverse series, there is traceable a long narrow object running obliquely, on one side only, through the thick mass of tissue referred to above as surrounding the vagina, the upper end lying near the lumen of the latter. Traced downwards this body is found to run to the ventral surface, where it terminates by perforating the epidermis of the corrugated area in front of the female aperture, projecting slightly on the exterior. In front, between this body and the lumen of the vagina, the tissue is unusually open and spongy, and in the interstices are numerous spermatozoa, entirely absent in other parts. Moreover, in the adjoining part of the lumen, and in that part alone, there are numerous spermatozoa. The long narrow body is found, when examined under a high power, to consist of a strand of globules of prostate secretion, or something indistinguishable from it in appearance, mixed with spermatozoa. Its entire length is roughly about 0.6 mm.

There can be little doubt that we have here to do with a wound inflicted by the formidably armed penis. The copulating individuals were applied together by their ventral surfaces, the corrugated areas acting like the suckers of the *Cotylea*, as organs of adhesion, when the penis of the one was driven in through the mass of tissue surrounding the lumen of the vagina, nearly penetrating as far as the latter. The spermatozoa and prostate secretion were then discharged and the penis withdrawn, a plug of prostate secretion closing up the wound and thus preventing the escape of the spermatozoa. The passage of the spermatozoa to the interior of the lumen is facilitated by the fact that in the middle region of the vagina there are very few shell-gland ducts passing inwards and perforating the epithelium.

In another specimen, cut into a series of longitudinal vertical sections, the same thing appears. Here there is a large mass of spermatozoa in the substance of the wall of the vagina, and this is connected with the ventral surface in front of the corrugated area by a narrow cleft filled with prostate secretion mixed with spermatozoa, the plug of this material projecting freely on the surface. But in this case the perforation has actually passed through the epithelium of the vagina, and in this position a portion of the mass of spermatozoa projects freely into the lumen.

Such a mode of copulation as this—by perforation of the body-wall in a definite locality —bas not been proved to occur in other Polyclads, and is certainly exceptional in that class. Perhaps it may be found to occur in the case of other forms with chitinous penial parts and a thick-walled bursa copulatrix. I have found a similar type of copulation to characterize *Prorhynchus* (7) and *Stratiodrilus* (8).

The ova in the uterus are all in the stage with a centrally placed spindle and, usually, a spermatozoon (rarely more than one) in various phases of transition in the cytoplasm.

*Echinoplana* is apparently more nearly allied to *Leptoplana* than to any described genus. But it differs in several very important points from the members of that genus. The entire structure of the male copulatory apparatus is widely different from what we find in *Leptoplana* or in any related form. The same holds good of the corresponding parts of the female reproductive apparatus. The complete absence of a reflected or dorsal limb of the vagina is a very special feature, and the massive vagina with its unsymmetrically placed anterior diverticulum is as characteristic, in its way, as the penis with its array of teeth.

*Paraplanocera*, Laidlaw (15), has a similar diverticulum of the vagina, or, more strictly, has a bursa which is in the form of a muscular diverticulum of the vagina; but it has no other points of resemblance to the form now under consideration, though the penis has small chitinous spines. *Paraplanocera* has tentacles, an independent prostate, paired vesiculæ, and a receptaculum seminis.

Echinoplana may be defined as a Leptoplanid without tentacles or marginal eyes. Two

clongated groups of tentacular eyes. Mouth behind the middle of the ventral surface. Separate male and female reproductive apertures. A median vesicula, between which and the penis is an elongated prostate reservoir. A very large penis without sheath, lined internally with numerous chitinous teeth. Ventral limb of vagina (antrum and ootype) with very thick walls. No dorsal limb present. Single unsymmetrical diverticulum projecting forwards from vagina. No receptaculum seminis.

Echinoplana celerrima is one of the commonest of the Polyclads of Port Jackson. It is characterized by great alertness and activity. In addition to the ordinary swimming and creeping movements, it progresses like *Tripylocelis*, but much more actively, by a kind of "walking." Lateral lobes of the extremely mobile body assume the function of lateral appendages. It is interesting to note that a precisely similar mode of locomotion was observed by Lang in *Planocera Graffii*, of which he writes—" Wenn *Planocera Graffii* abwechselnd rechts und links Partien des vorderen Körperrandes vorstreckt und dann den Körper nachzieht so sieht es beinahe aus wie wenn sie sich derselben als Füsse bediente" (17, p. 635).

## ENTEROGONIA PIGRANS, n. g., n. sp. (Plate 37. fig. 4.)

This Polyclad is of oval or elliptical outline, 1 cm. in length in the preserved condition and 5 or 6 mm. in breadth. It is a thickish form, of comparatively firm consistency, remarkable for its extremely sluggish movements. The general colour is greenish or dark grey on the dorsal side; when the living animal is examined with a simple lens, this becomes resolved into innumerable spots of dark olive, very minute towards the margin, larger towards the middle. The ventral surface is reddish grey, except where the pharynx and main testicular ducts show white. In two of the specimens there is a dark spot towards the posterior end—the appearance being produced by the intestinal branches here being of a peculiarly dark colour. This does not appear to be constant; but when it does occur it probably is in some way associated with the occurrence of the genito-intestinal passage referred to below.

The mouth is considerably behind the middle of the body, and, in the fixed specimen, the reproductive apertures are situated very close together, and are nearer to the posterior edge than to the mouth. There are numerous scattered minute eyes over the brain-region, and between the latter and the anterior margin, as well as marginal eyes running all round the periphery. The eyes over the brain-region are quite irregularly distributed, and not in any way bilaterally grouped, a feature which would in itself distinguish the present species from Lang's *Cestoplana alba* and *C. compacta* (17, p. 472).

The male aperture leads into a nearly vertical antrum, the epithelium of which is thickened and raised into ridges. Here are situated the unicellular glands corresponding to the prostate glands. Into the antrum projects the penis in the form of a short muscular papilla entirely devoid of chitinous parts. The ejaculatory duct, formed by the unicn of the lateral vasa deferentia, is a sinuous tube which presents no appearance of becoming thickened or dilated to form a *vesicula seminalis*.

The antrum femininum is a vertical chamber with a fairly thick muscular wall. The ootype curves forwards and upwards from the antrum and bends sharply downwards and

backwards to form the dorsal limb of the vagina. The ootype is characterized by the development of a peculiar spiral ridge of its epithelium. The dorsal limb of the vagina, after receiving on its ventral side the common duct formed by the union of the lateral uterine ducts, runs backwards as a narrowing tube, which opens behind into the median posterior branch of the intestine—a *genito-intestinal passage* being thus established.

The absence of distinct prostate glands, other than the glandular cells in the wall of the antrum, and other features connect this form with *Discocelis*. But in that genus there is a pair of lateral receptacula, and there is a common genital atrium. In Laidlaw's recently-created genus *Thalamoplana* (16) there are distinct male and female apertures; but there is a concentric receptaculum seminis, and the prostatic cells in the epithelium of the antrum are raised on muscular ridges. *Microcelis*, Plehn (18), is also allied, but has a large receptaculum. The occurrence of the genito-intestinal canal is of such importance that it seems desirable to distinguish the Australian form from the members of these allied genera.

The discovery of the genito-intestinal canal helps to connect more definitely the receptaculum seminis of Polyclads with parts that occur in other Platodes. The correspondence of the canal in question with the similarly-named canal in the *Heterocotylea* cannot well be doubted; while the homology between the latter and the Laurer's canal of the *Malacocotylea*, though it may be open to question, seems to have the balance of evidence in its favour \*. If we accept this conclusion, we must regard as representing Laurer's canal in the Polyclads not only the genito-intestinal canal of *Enterogonia*, but the receptaculum seminis of the *Acotylea* in general (unpaired in most, paired in *Discocelis tigrina*, *Leptoplana subviridis*, and *Diplosolenia*, with an opening on the dorsal surface in *Laidlavia*), and the posterior female passage of *Trigonoporus* and *Tripylocelis*.

## CESTOPLANA AUSTRALIS, n. sp. (Plate 37. fig. 5.)

I have only obtained a single specimen of a species of *Cestoplana*, which, superficially at least, is very like the European species *C. rubrocincta*, Grube. It is a long and narrow Polyclad, which, as Lang remarks, might readily be taken for a Nemertean; its length was 2 cm., its breadth 3 mm. The upper surface is of a light neutral tint in front, becoming reddish orange further back. Close to each lateral border runs a band of the most vivid vermilion, and a median band of the same runs along the whole length. In front the lateral bands bend inwards and unite with one another some little distance from the anterior extremity. Posteriorly the two lateral bands unite just in front of the slight notch or depression at the posterior end, but the median band terminates a short distance in front of this. The narrow space between the latera band and the lateral border is almost colourless. There are very many very minute eyes scattered over the anterior portion, with the exception of a zone round the margin.

The only external difference which I can detect between the Australian and European species is that in the former the three longitudinal bands completely fuse, whereas in

\* See Goto, 5, p. 154.

the latter they do not. The specimen was immature and the reproductive system undeveloped.

This somewhat aberrant Polyclad creeps, but never swims. As Lang remarks of the European form, the anterior portion begins to move while the posterior is still at rest.

Found between tide-limits in Port Jackson (Woollahra Point).

PSEUDOCEROS (?) CARDINALIS, n. sp. (Plate 37. fig. 6.)

The length of the preserved specimens is 1 cm., the breadth 8 mm. The colour of the upper surface in the living animal was bright scarlet.

The tentacles are very inconspicuous, being mere blunt lobes at the sides of the anterior median notch. The central group of eyes numbers about 150 altogether. It is obscurely divided into two behind by a very narrow space, but is undivided in front. The tentacular eyes are difficult to count, owing to their being very closely aggregated anteriorly; but there appear to be about 100 on each tentacle, distributed equally on the dorsal and ventral surfaces. The mouth is situated just below the brain. The male reproductive aperture is at the beginning of the second sixth of the entire length, and is only a short distance behind the mouth. The female aperture is about one-sixth of the length behind this. The sucker is situated about the middle of the length of the body; it has the form of a disk elevated above the general level of the ventral surface.

The wall of the bell-shaped pharynx is devoid of the foldings characteristic of other species of *Pseudoceros*.

The male apparatus is single. There is a conical penis, which contains a chitinous stylet; there is a pear-shaped granule reservoir, and a large long-oval vesicula seminalis thrice the length of the granule reservoir.

Two specimens were obtained together on an oar-weed brought up by the trawl in Iron Cove River, Port Jackson.

Of the two specimens obtained, one was mounted entire, the other was cut into sections. The latter was found to contain ripe ova in the uteri, but the testes were immature and contained no spermatozoa, and the vesicula seminalis contained only a granular mass. There were no spermatozoa in the uteri; but in the parenchyma, near the dorsal surface, directly over the ootype, was a large mass of mature spermatozoa which must have been received by perforation of the penis of another individual, and there was a similar mass somewhat further forwards \*.

The nature of the pharynx distinguishes this from the described species of *Pseudo*ceros, with which in other respects it is nearly allied. The generic position of this and also of the following species cannot be looked upon as definitely settled.

## PSEUDOCEROS (?) LIMBATUS, n. sp.

The length of the preserved specimen is 1.5 cm., the breadth 0.5 cm. I am indebted to Mr. Alan McCulloch for a coloured sketch of the living animal, in which the upper surface is light red with a well-defined marginal band of purple.

\* These contained spermatozoa of two distinct kinds.

The tentacles are comparatively large, subtriangular, and to judge from Mr. Mc-Culloch's sketch, must, in the living animal, have extended well beyond the notch in which they are situated. There are about 30-40 eyes in each tentacle and about 40 on each side above. The cerebral eyes are concentrated into a single dense clump. The mouth is situated just behind the brain. Both of the reproductive apertures are situated well in advance of the middle of the body, the male at about the junction of the second and third sevenths, the female close behind it.

The sucker is somewhat in front of the middle. It is not an elevated disk as in *Pseudoceros cardinalis*, but a shallow circular pit with a radial arrangement of its muscular fibres. The pharynx is small and situated anteriorly, but is strongly plicated.

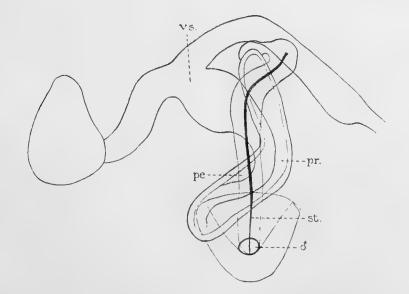
The penis, which is directed backwards, has a tubular chitinous stylet. There is a small, oval, prostate reservoir and a large prostate. The male apparatus is situated partly below, but mainly behind the pharynx. The female apparatus appears to be quite simple.

But for the character of the pharynx, this form might perhaps be included in the genus *Prostheceræus*; but a plicated pharynx does not appear to occur in any of the *Euryleptidæ*, and, in spite of certain points of divergence from the other species, I think it best to refer it, for the present, to the genus *Pseudoceros*.

The only specimen was obtained by Mr. Chas. Hedley, F.L.S., on a reef at Masthead Island, Capricorn Group, Queensland.

PROSTHECERÆUS ANOMALUS, n. sp.

The tentacles are of moderate size in the preserved specimen and in the form of flattened cones. The cerebral eyes are arranged in two closely approximated groups over the brain—about 30 in each group. There are about 100 tentacular eyes. The



mouth, which is very small, is situated immediately behind the brain. The male aperture is just behind the pharynx; the female aperture is a little distance behind the male. The sucker is situated at about the middle of the length.

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The pharynx is cylindrical, about a sixth of the entire length. The intestine is fairly wide, nearly half the length, with numerous pairs of cæca, the branches of which anastomose.

The penis (text-fig., pe.) contains a very slender elongated chitinous stylet (*st*.). The prostate (pr.) is relatively long and narrow.

The ootype is nearly vertical in position. Continuing it backwards is the wide vagina; the latter bifurcates behind into two thick tubes, which pass almost transversely outwards, each becoming divided into two. Each of these opens into a wide thinwalled sac, and there are thus four of these—the *receptacula seminis*. From the vagina, on its ventral side, is given off the median uterine duct, which soon bifurcates.

The female reproductive apparatus of this species thus appears to differ in a radical way from that of the species of the genus described or figured by Lang. The presence of the four receptacula connected by their ducts with the vagina is, in fact, so far as I am aware, a quite unique condition. In the other *Cotylea* in which they have been found to occur the "accessory glands" are connected with the oviducts (see Lang, pp. 297-300, pl. 23. figs. 1 & 3, pl. 24. fig. 1, &c.).

I have only one example of this interesting form—an old stained and mounted specimen obtained in Port Jackson.

PROSTHIOSTOMUM MACULATUM, n. sp. (Plate 37. fig. 7.)

The largest specimen is about 2 cm. in length and 7 mm. in breadth in the preserved condition. Both anterior and posterior ends are rounded. The general colour of the dorsal surface is light brown with a few large darker spots. The "cerebral" eyes are disposed in two elongated imperfectly separated groups completely united in front, each comprising about 50 in a mature specimen. There are about 100 marginal or submarginal eyes in front of these. The mouth is situated immediately behind the cerebral eyes at the junction of the first and second sevenths of the length. The sucker is a little behind the middle of the body; the reproductive apertures, a little in front of this, are nearly in the middle.

The sucker is a pit with a narrow opening. The integument lining it has its epidermis greatly thickened, and is thrown into a number of radiating folds around a longitudinal slit bordered with a number of minute papillæ.

The cylindrical pharynx is about 5 mm. in length (about a fourth of the total length) and 1.5 mm. in diameter. There are about 12 pairs of intestinal cæca.

The structure of the reproductive apparatus agrees closely with that of the corresponding parts in P. siphunculus, as described by Lang.

The antrum masculinum extends in a vertical direction for a short distance, passes slightly behind the male aperture, then runs forwards again, becoming strongly bent on itself. At its anterior end is the papilla, from which the apex of the penial stylet projects. The prostate reservoir is a small rounded dilatation of the ejaculatory duct. The median vesicula is of great relative size with very muscular walls. The lateral (accessory) vesiculæ seminales are smaller, spherical bodies with very thick walls and small lumina The female aperture leads into an antrum which takes the form of a bursa copulatrix with very thick walls. The ootype has a very contracted lumen with folded walls; it extends downwards to the neighbourhood of the ventral surface. The shell-glands are very highly developed, extending through more than one-half of the length of the body.

In a specimen which has been cut into longitudinal vertical sections there is beneath the integument of the dorsal surface, in the region immediately behind the sucker, a great mass of spermatozoa, and a similar mass on and around the sucker on the ventral surface. The sections are imperfect, and though a fissure enclosing spermatozoa is to be traced downwards from the dorsally situated mass, it is impossible to determine to what extent this has been formed by *post-mortem* treatment. In any case there is sufficient evidence of the occurrence here of an indirect form of copulation by perforation of the integument.

In view of this observation it is of interest to note that Lang expresses a suspicion that the structure of the parts in *Prosthiostomum* points to self-fertilization (17, p. 638).

From *Prosthiostomum siphunculus*, Delle Chiaje (sp.), and from *P. dohrnii*, Lang (17), this Australian species is distinguished by the number and arrangement of the eyes; and similar differences distinguish it from Laidlaw's (15) two species, *P. elegans* and *P. cooperi*, from the Maldives.

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## EXPLANATION OF THE PLATES.

#### Lettering.

d., anterior diverticulum of ootype. ej., ejaculatory duct. int., intestinal cæca. m., mouth. oot., ootype. p., penis. p.s., penis-sheath. p.st., penial stylet. pr., prostate reservoir or prostate ducts. r., receptaculum seminis. r.d., duct of receptaculum. sh.gld., shell-glands. ut., uterus. ut.d., uterine duct. va., dorsal limb of the vagina. v.d., vasa deferentia. v.s., vesicula seminalis.

#### PLATE 35.

Fig. 1. Trip	pylocelis typica.	General view of the organization. $\times$ 15.
2.	<b>33 33</b>	Brain, eyes, and outline of tentacles.
3.	,, ,,	Transverse section passing through the proximal part of the penis.
4.	(ر (ر	Transverse section at the point where the lateral uterine ducts unite.
5 & 6.	23 23	Two successive transverse sections passing through vagina and its ventral
		aperture ( 9 <sup>2</sup> ).
7.	22 23	Diagrammatic lateral view of the reproductive ducts.

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## **PLATE 36.**

Fig.	1.	Diplosolenia johnstoni.	General view of the reproductive ducts from the ventral aspect,
			Vasa deferentia and ejaculatory duct shaded ; ootype dotted.
	2.	,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,,	Transverse section passing through the point of union of the ducts of
			the receptacula seminis.
	3.	Leptoplana australis.	General view of the reproductive ducts from the ventral aspect.
	4.	<b>33</b> 33	Diagrammatic lateral view of the reproductive apparatus. Epithelia.
			dotted ; muscular layers shaded.
	5.	** **	Eyes. The two oval bodies are the anterior appendages of the brain.
	68	z 7. Echinoplana celerr	<i>ima.</i> Spines of the penis. $\times$ 500.

## PLATE 37.

Fig. 1. Echinoplana celerrima. Brain and eyes; from stained and mounted specimen.

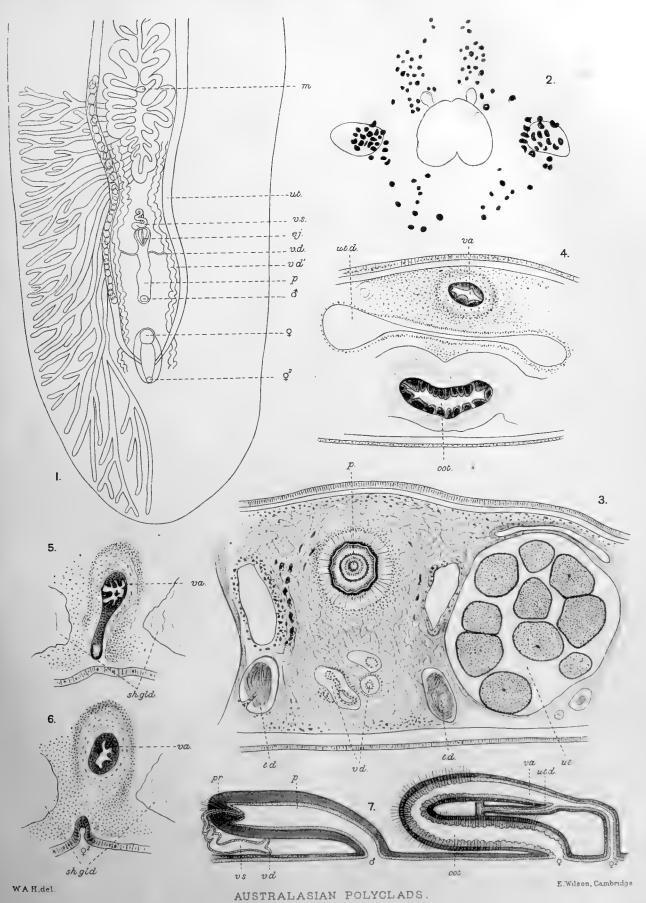
2. ,, ,, General view of the reproductive apparatus, from the ventral aspect.

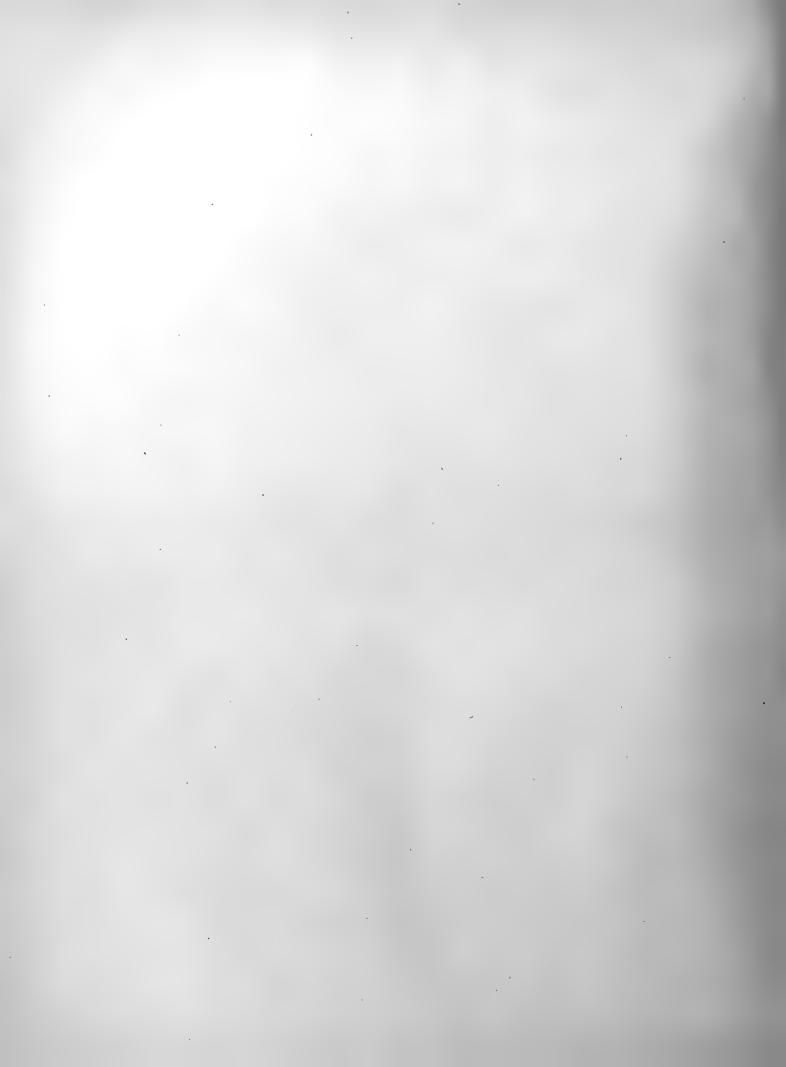
- 3. ", ", Transverse section passing through the point of union of the uterine duct with the diverticulum of the ootype.
- 4. Enterogonia pigrans. Diagrammatic lateral view of the reproductive apparatus, showing the genito-intestinal canal. Epithelial parts dotted; muscular layers shaded.
- 5. Cestoplana australis. Outline magnified, to show arrangement of vermilion bands.

6. Pseudoceros cardinalis. Ventral view of male reproductive ducts.

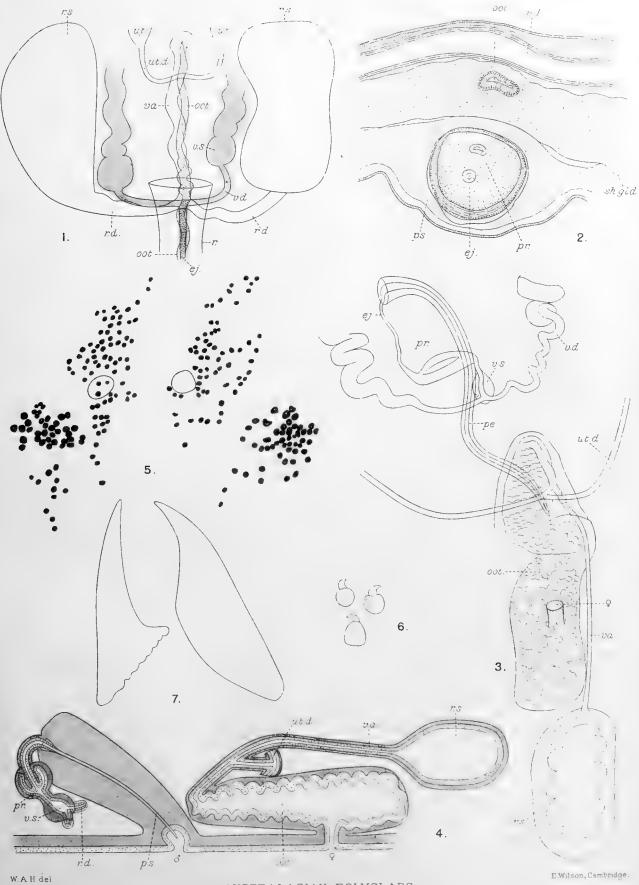
7. Prosthiostomum inaculatum. Cerebral eyes.

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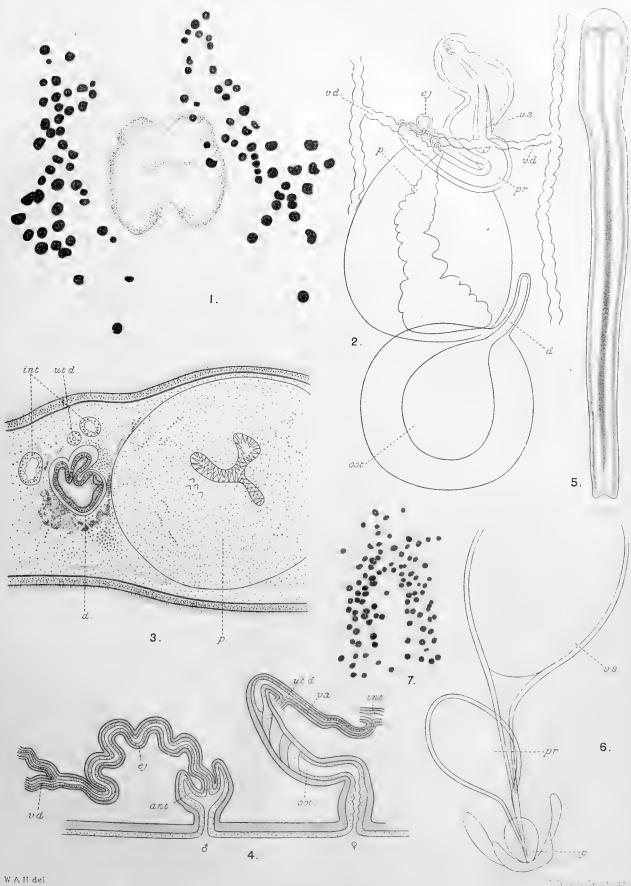


AUSTRALASIAN POLYCLADS.

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AUSTRALASIAN POLYCLADS



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# TRANSACTIONS

OF

# THE LINNEAN SOCIETY OF LONDON.

## A CONTRIBUTION TOWARDS OUR KNOWLEDGE OF THE MORPHOLOGY OF THE OWLS.—PART II. OSTEOLOGY.

BY W. P. PYCRAFT, A.L.S., F.Z.S.



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ON SOME POINTS IN THE VISCERAL ANATOMY OF THE CHARACINIDÆ, WITH AN ENQUIRY INTO THE RELATIONS OF THE DUCTUS PNEUMATICUS IN THE PHYSOSTOMI GENERALLY.

> BY WALTER S. ROWNTREE, B.Sc., F.L.S.



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# THE LINNEAN SOCIETY OF LONDON.

## ON THE EVOLUTION OF THE AUSTRALIAN MARSUPIALIA; WITH REMARKS ON THE RELATIONSHIPS OF THE MARSUPIALS IN GENERAL.

ΒY

### B. ARTHUR BENSLEY, B.A. (Tor.), PH.D. (Col.), University of Toronto, Canada.

(Communicated by Prof. G. B. Howes, D.Sc., LL.D., F.R.S., Scc. Linn. Soc.)



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II. Part	I. 1879	1 4	0 0	18 0			1896		0	0 18	0
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Part	III. 1882	1 8	0 1	1 0			1896		0	0 6	0
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Part	II. 1887		0 1	-1 0			1902		0		9
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Part	VI. 1891	0 12	0 0	9 0		Part III.	1903	1 4	0	0 18	0

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#### THE

# TRANSACTIONS

OF

# THE LINNEAN SOCIETY OF LONDON.

## THE LABIAL AND MAXILLARY PALPI IN DIPTERA.

 $\mathbf{B}\mathbf{Y}$ 

WALTER WESCHÉ, F.R.M.S.

(Communicated by GEORGE MASSEE, F.L.S.)



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I. Part	I. 1875	.140	0 18 (	V. Par	t VII. 1891	0 6 0	0.4 6
Part	II. 1875	. 0 6 0	0 4 6	Par	tVIII. 1892	0 8 0	0 6 0
Part	III. 1876	. 1 8 0	1 1 (	Par	t IX. 1892	0 12 0	0 9 0
Part	IV. 1877	. 0 16 0	0 12 (	) Par	t X. 1893	1 8 0	1 1 0
Part	V. 1877	. 0 18 0	0 13 6	B Par	t XI. 1894	0 2 6	0 2 0
Part	VI. 1877	. 1 2 0	0 16 6	VI. Par	t I. 1894	2 0 0	1 10 0
Part	VII. 1878			Par	t II. 1894	1 11 0	$1 \ 3 \ 3$
Part	VIII. 1879	. 1 0 0	0 15 (	)   Par	rt III. 1894	0 10 0	0 7 6
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## TRANSACTIONS

OF

# THE LINNEAN SOCIETY OF LONDON.

ON THE

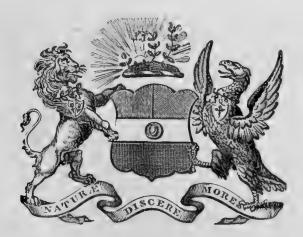
### ANATOMY AND DEVELOPMENT OF COMYS INFELIX, EMBLETON, A HYMENOPTEROUS PARASITE OF LECANIUM HEMISPHÆRICUM.

BY

ALICE L. EMBLETON, B.Sc.,

1851 EXHIBITION SCIENCE RESEARCH SCHOLAR, ASSOCIATE OF THE UNIVERSITY OF WALES (CARDIFF COLLEGE).

(Communicated by Dr. DAVID SHARP, F.R.S., F.L.S.)



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		£ s.	d. £	s. e	d.			£ s. d.	£ s. d.
I. Part	I. 1875		0 0	18	0	V. Part VI	III. 1892	0 8 0	. 0 6 0
Part	II. 1875		0 0	4	6	Part 1	IX. 1892		. 0 9 0
Part	III. 1876		0 1	1	0	. Part	X. 1893		. 1 1 0
Part	IV. 1877		0 0		0	Part	XI. 1894	0 2 6	. 0 2 0
Part	V. 1877		0 0		6	VI. Part	I. 1894	2 0 0	. 1 10 0
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V. Part	I. 1888	0 12	0 0	9	0		III. 1903		
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[VOL. IX. PART 6.

THE

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OF

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LITTORAL POLYCHÆTA FROM THE CAPE OF GOOD HOPE

BY

ARTHUR WILLEY, D.Sc., F.R.S., Colombo Museum, Ceylon.

(Communicated by Dr. W. G. RIDEWOOD, F.L.S.)

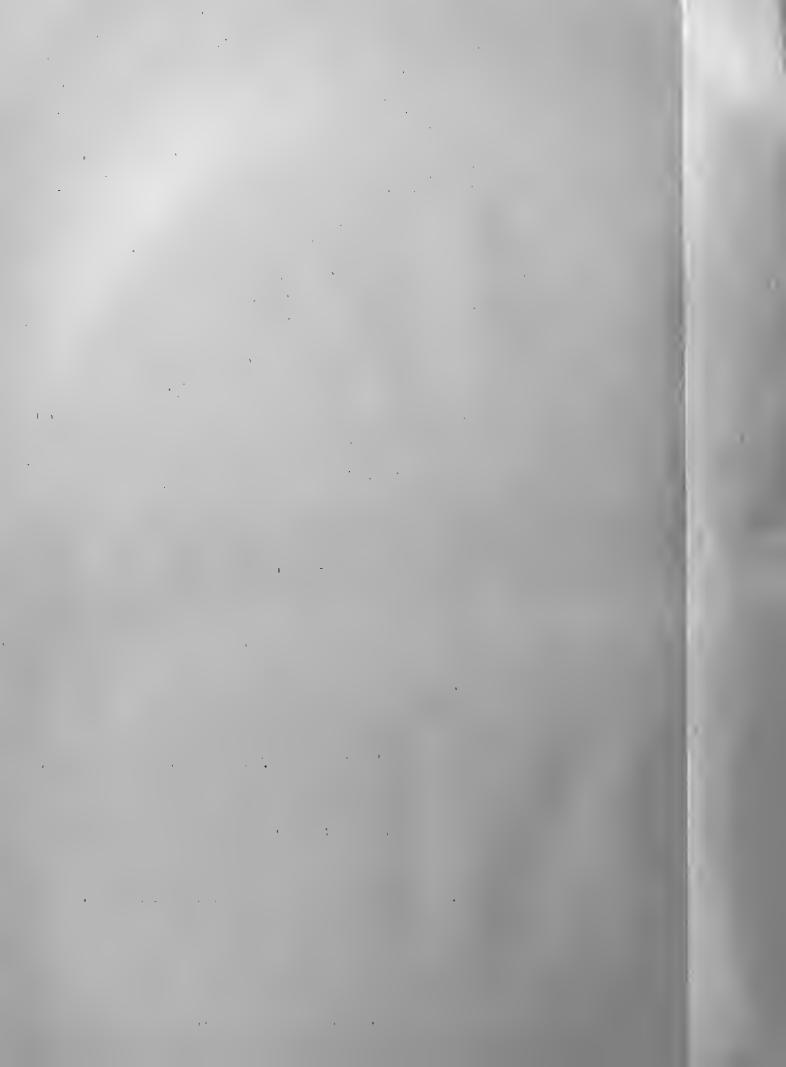


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OF

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## ON THE EVOLUTION OF TOPOGRAPHICAL RELATIONS AMONG THE DOCOGLOSSA!

ΒY

H. J. FLEURE, D.Sc., Fellow of the University of Wales. (Communicated by Professor W. A. HERDMAN, F.R.S., F.L.S.)



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T Dawi I		$d$ . $\pounds$ s.			£ s. d.	£ s. d.
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#### THE

## TRANSACTIONS

OF

# THE LINNEAN SOCIETY OF LONDON.

## ON SOME SPECIES OF THE GENUS PALÆMON, FABR., FROM TAHITI, SHANGHAI, NEW GUINEA, AND WEST AFRICA.

BY

DR. J. G. DE MAN, of Ierseke (Holland). (Communicated by Rev. T. R. R. STEBBING, M.A., F.R.S., Sec.L.S.)



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wrapper):-		. 7		1			
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I. Lart Part	I. 1875 II. 1875			V. Part	XI. 1894	026	0 2' 0
		*		VI. Part	I. 1894	2 0 0	1 10 0
Part	III. 1876			Part	II. 1894	1 11 0	$1 \ 3 \ 3$
Part	IV. 1877			Part	III. 1894	0 10 0	0 7 6
Part	V. 1877			Part	IV. 1896	1 4 0	0 18 0
Part	VI. 1877			Part	V. 1896	0 10 0	0 7 6
Part	VII. 1878			Part	VI. 1896	0 8 0	0 6 0
Part				Part 7	VII. 1896	0 12 0	0 9 0
II. Part				PartV	III. 1897	0 2 6	0 2 0
Part	II. 1881			VII. Part	I. 1896	0 10 . 0	0 7 6
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Part	XI. 1884		0 7 6	Part	X. 1900		0 4 6
Part	XII. 1885	0 6 0	0 4 6	Part	XI. 1900		0 2 0
Part	XIII. 1884	0 6 0	$0 \ 4 \ 6$				
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Part	XV. 1885	0 4 6	0 3 6	Part	II. 1900		0 7 6
Part	XVI. 1885	0 5 0	0 3 9		III. 1900		
Part	XVII. 1886	0 3 0	$0\ 2\ 3$	Part	IV. 1901		
Part 2	XVIII. 1888	0 2 6	$0 \ 2 \ 0$	Part	V. 1901		0 3 9
III. Part	I. 1884	1 14 0	1 5 6	Part	VI. 1901		
Part	II. 1884	1 12 0	$1 \ 4 \ 0$		VII. 1901		
Part	III. 1885	1 10 0	$1 \ 2 \ 6$		III. 1902		0 3 0
Part	IV. 1885	0 8 0	0 6 0		IX. 1902		0 3 9
Part	V. 1887	0 8 0	0 6 0	Part	X. 1903		0 15 0
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				Part	IV. 1904	0 6 0	0 4 6
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Part				Part	VI. 1904	0 6 0	0 4 6
	V. 1890			Part V	VII. 1904	0 6 0	0 4 6
Part	VI. 1891				III. 1904	0 10 0	0 7 6
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Part	IX. 1892			Part	II. 1904	0 8 0	0 6 0
Part	X. 1893	1 8 0	1 1 0	0			

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# TRANSACTIONS

OF

# THE LINNEAN SOCIETY OF LONDON.

## OBSERVATIONS ON SOME UNDESCRIBED OR LITTLE-KNOWN SPECIES OF HEMIPTERA-HOMOPTERA OF THE FAMILY MEMBRACIDÆ,

BY

G. BOWDLER BUCKTON, F.R.S., F.L.S.



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I. Part	I. 1875			VI. Part	I. 1894		$\begin{array}{cccccccccccccccccccccccccccccccccccc$
Part	II. 1875				II. 1894		
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Part	V. 1877		0 10	1	IV. 1896 V. 1896		
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#### THE

# TRANSACTIONS

OF

# THE LINNEAN SOCIETY OF LONDON.

## THE GENITALIA OF BOTH THE SEXES IN DIPTERA, AND THEIR RELATION TO THE ARMATURE OF THE MOUTH.

BY

WALTER WESCHE, F.R.M.S.

(Communicated by JOHN HOPKINSON, F.L.S.)



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July 1906.





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## TRANSACTIONS

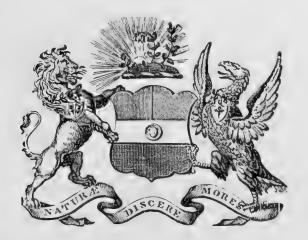
 $\mathbf{OF}$ 

# THE LINNEAN SOCIETY OF LONDON,

## ON A COLLECTION OF CRUSTACEA, DECAPODA AND STOMATOPODA, CHIEFLY FROM THE INLAND SEA OF JAPAN; WITH DESCRIPTIONS OF NEW SPECIES.

 $\mathbf{B}\mathbf{Y}$ 

DR. J. G. DE MAN, of Ierseke (Holland). (Communicated by Rev. T. R. R. STEBBING, M.A., F.R.S., F.L.S.)



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I. Pari	s IVIII. 1875-79	$\pounds s. d.$ 0.8100	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	VIII. Part I. 1900	£ s. d.	$\begin{array}{cccc} \pounds & s. & d. \\ 0 & 7 & 6 \end{array}$
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THE

# TRANSACTIONS

OF

# THE LINNEAN SOCIETY OF LONDON.

## ON CERCOCOCCUS EREMOBIUS, GEN. ET SP. N., AN ABERRANT FORM OF COCCIDÆ.

BY

HUGH SCOTT, B.A. (Cantab.). (Communicated by J. J. LISTER, M.A., F.R.S., F.L.S.)



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Volume.	When Published.	Price t Publ			ice to lows.	Volun	ie,	I	When Publishee	đ.		ice to Publi				Price. Fellow	
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2nd Ser. ZOOLOGY.]

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THE

## TRANSACTIONS

OF

# THE LINNEAN SOCIETY OF LONDON.

## OBSERVATIONS ON AUSTRALASIAN POLYCLADS,

BY

PROF. W. A. HASWELL, M.A., D.Sc., F.R.S., F.L.S.



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III. P				Part IV, 1901,, 0 14 0 0 10 6
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	art VI. 1888			Part VIII. 1902 0 4 0 0 3 0
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IV. P				Part X. 1903 1 0 0 0 15 0
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	art III. 1888		0 12 0	Part XII. 1903 0 10 0 0 7 6
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OF

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