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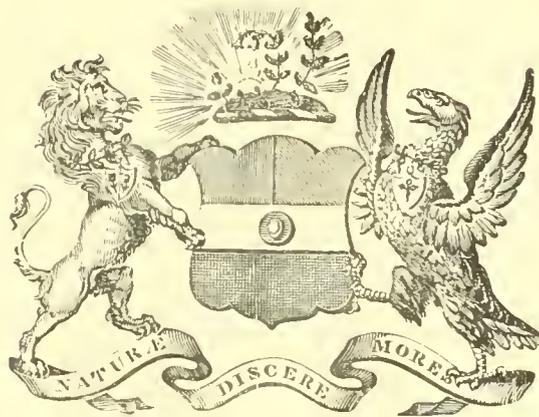






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ERRATA.

- Page 180, line 22 from top, for *Fierasfer dentalus* read *Fierasfer dentatus*.  
 Page 228, line 9 from bottom, for *Pterolysis* read *Pterylosis*.  
 Page 242, line 19 from bottom, for *Scops leucotis*, Temm., read *Scops leucotis*, Temm.  
 Page 285, line 3 from bottom, for *Chlamyophorus* read *Chlamylophorus*.  
 Page 516, line 17 from top, for *Prolagus aenigensis*, Kön., read *Prolagus aenigensis*, Kön.

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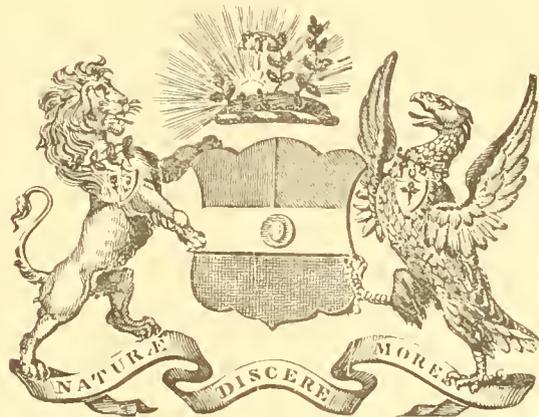
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REPORT ON A COLLECTION OF CEPHALOPODA  
FROM THE CALCUTTA MUSEUM.

BY

EDWIN S. GOODRICH, B.A., F.L.S.,

ASSISTANT TO THE LINACRE PROFESSOR OF COMPARATIVE ANATOMY, OXFORD.



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*December 1896.*



TRANSACTIONS  
OF  
THE LINNEAN SOCIETY.

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I. *Report on a Collection of Cephalopoda from the Calcutta Museum.* By EDWIN S. GOODRICH, B.A., F.L.S., Assistant to the Linacre Professor of Comp. Anatomy, Oxford.

(Plates 1-5.)

Read 19th December, 1895.

LAST year Professor E. Ray Lankester received for examination from the Calcutta Museum a large collection of Cephalopods, which he kindly handed over to me to be identified. The work was carried on at the Oxford Museum and at the British Museum, Cromwell Road, and I must express my thanks to Dr. A. Günther and Mr. E. A. Smith for placing the collections in the latter Institution at my disposal.

The present collection is composed almost entirely of specimens captured during the voyages of H.M.S. 'Investigator.' It contains 162 specimens, belonging to 28 genera.

Eleven new species are described, belonging to the genera *Iniotheuthis*, *Sepia*, *Loliolus*, *Sepioteuthis*, *Abralia*, *Cheirotheuthis*, *Histiopsis*, *Taonius*, and *Octopus*. No new genus has been founded; but four genera included are new to the Indian region. Of these the genus *Calliotheuthis* has been recorded from the Atlantic and Pacific regions; the genus *Histiopsis* from the Atlantic; and the genera *Loliolus* and *Iniotheuthis* from the Pacific and Japanese regions.

## DECAPODA MYOPSIDA.

## Family SEPIOLINI.

*INIOTEUTHIS MACULOSA*, n. sp. (Pl. 1. figs. 1, 2, & 3.)

One specimen from the Andamans, and another from the Persian Gulf; both females.

The principal measurements of the first are \* :—

Length of mantle (lower surface) . . . . .	1·3	centim.
Breadth „ . . . . .	·95	„
„ „ attachment to neck . . . . .	·4	„
„ between fins . . . . .	·8	„
„ across eyes . . . . .	·7	„
„ of fin . . . . .	·4	„
Length of fin-attachment . . . . .	·4	„
„ from extremity of mantle to tip of dorsal arm .	2·4	„
Length of dorsal arm . . . . .	·8	„
„ dorso-lateral arm . . . . .	·10	„
„ ventro-lateral „ . . . . .	·11	„
„ ventral „ . . . . .	·7	„
„ tentacular „ . . . . .	2·1	„
„ „ club . . . . .	·5	„

The mantle is rounded at its apex. The round fins are attached about halfway up the mantle. The band uniting the mantle to the neck is narrower than in *In. Morsei*. The funnel has a small opening, and a wide base on which are l-shaped sockets. The two muscular bands which unite the base of the funnel above the sockets to the head are less prominent than in *Sepiola* or *In. Morsei*. There are glandular pads and a small valve inside the funnel.

The edge of the buccal membrane is notched, but the lobes are not distinctly marked.

The first two pairs of arms are rounded; the ventro-lateral arms are slightly keeled; the ventral arms are provided with a well-developed keel on the upper edge. They all bear two rows of round suckers, obliquely set on slender stalks rising from a swollen base. The opening of the sucker is wide; the horny ring has an ornamented surface and a smooth edge.

The tentacular arms are flattened, and a groove runs down the inner surface. The club is of great length, slightly enlarged, provided with a lateral membrane on both sides, and a large number of minute suckers in eight rows. Each sucker is nearly hemispherical, set obliquely on a long slender stalk (fig. 3). The papillary area of the horny ring is wide, and the edge armed with about 15 teeth (fig. 2).

The ground-colour of the first individual is pale brownish yellow, inclining to orange

\* In the following descriptions the terms “upper” and “lower” are used to denote the surfaces generally called “dorsal” and “ventral;” since, strictly speaking, they do not correspond to the morphological dorsal and ventral surfaces.

on the arms and upper surface of the mantle. Scattered over the mantle, more especially on the lower surface, are large brown chromatophores (fig. 1); similar chromatophores are seen on the upper surface of the fins, and on the head and arms. There is a conspicuous row of five between the eyes on the upper surface of the head.

The second specimen is of a duller tint and less well preserved.

This species appears to be more closely related to *Iniotenthis japonica* (Tilesius, MS.), Verrill, which also has two rows of suckers on the arms, than to *In. Morsei*, Verrill, which has four.

*INIOTEUTHIS MORSEI*, Verrill.

Seven specimens from the Andamans have been placed in this species.

Family SEPIARII, Stp.

Subfamily SEPIADARII, Stp.

*SEPIADARIUM KOCHII*, Stp.

Four specimens, all female. One from off the south coast of Ceylon, lat. 6° 6' 30" N., long. 81° 23' E., from a depth of 32 fathoms. The other three from the Andamans.

*SEPIA SINGAPORENSIS*, Pfeffer.

One female specimen from Singapore.

*SEPIA ACULEATA*, von Hasselt.

Ten specimens appear to belong to this species. One from the Irawaddy delta, at a depth of 20 fathoms; four from Port Blair, and five from the Andaman Sea.

*SEPIA SINGALENSIS*, n. sp. (Pl. 1. figs. 4, 5, 6, 7, & 8.)

Two male specimens; the first from Colombo, the second from off Point Galle (?).

The principal measurements of the former are:—

Length of mantle (above) . . . . .	16	centim.
"          "    (below) . . . . .	14.4	"
" from "    apex to mouth . . . . .	17.4	"
Breadth of "    at origin of fins . . . . .	4.9	"
"          "    halfway . . . . .	6.2	"
"          "    fin . . . . .	1.2	"
Length of dorsal arm . . . . .	7	"
"    dorso-lateral arm . . . . .	6.5	"
"    ventro-lateral " . . . . .	6.3	"
"    ventral " . . . . .	6.7	"
"    tentacular " . . . . .	12.7	"
"          "    club . . . . .	3.1	"
"    pen . . . . .	15.5	"
Breadth of " . . . . .	4.8	"

The mantle is of a narrow oval shape; the strong fins arise a little way below the mantle-margin, and do not join at the apex (fig. 4). The siphon is thick-walled, with a somewhat crescentic opening; it does not reach to the junction of the ventral arms.

The arms have broad compressed bases (especially the ventral arms, which are 23 mm. broad), without well-developed keels. The inner surfaces, bounded on either side by narrow lateral membranes, bear four rows of moderate-sized suckers, largest on the lateral arms, where they attain a diameter of 2 mm. On the distal half of the arms the suckers become extremely small. The horny ring of the arm-suckers has a narrow papillary area, and a margin smooth on the proximal two-thirds of its circumference, and armed with very irregular teeth on the distal third (fig. 8).

The stem of the tentacle is compressed, forming a sharp edge on the outer surface. The club is furnished as usual with a wide keel springing from the upper surface. Suckers of very unequal size are placed in four rows on the proximal region; the largest attain a width of 4 mm. in the two central rows, and are provided with smooth horny rings. The suckers diminish rapidly in size at either end; these and the suckers of the outer rows have horny rings armed all round with numerous sharp teeth (fig. 7). In the distal region the small suckers are closely packed in six or seven rows, and near the extreme apex two suckers stand out from the rest on the upper margin as if utilized for some special purpose (an arrangement I have noticed in *Sepia officinalis*).

The buccal membrane has seven lobes provided with a few suckers, the horny rings of which closely resemble those of the arm-suckers.

A small web is developed at the bases of the arms except of the ventral pair.

The mandibles are shown in fig. 6.

The long oval pen of this *Sepia* is very remarkable (fig. 4). Above, the rough calcareous surface raised in three slight ridges narrows anteriorly, and is bounded on either side by a broad expanse of the chitinous margin (*ch.m.*) (in places about 1 cm. broad). Below, the striated area formed by the loculi reaches far up (*loc.*), and is marked in the centre by a longitudinal groove. The margin of the inner cone is produced forwards and reflected over the posterior loculi, to which it is closely applied (*i.c.*).

The apical spine has unfortunately been broken off; it appears to have been small.

It is not without hesitation that I have placed these specimens in a new species, as they closely resemble *Sepia Rouxii*, d'Orb., described in d'Orbigny and Férussac's monograph from the Indian seas (5).

There are, however, several characters in which the two species differ. Whereas *S. Rouxii* is of a "forme générale racourcie," has very wide fins, and toothed rings to all the suckers of the tentacular club, *S. singalensis* is of narrow shape, with moderate fins, and smooth rings on the largest suckers. On the other hand, their pens are remarkably similar.

The ground-colour of the best specimen is pale brown, speckled with slate-coloured chromatophores on the lower surface, and conspicuously striped with broad dark bands on the upper surface of the mantle, head, and arms.

The hectocotylized region is short and situated about halfway up the left ventral arm.

At this point the suckers are small and resting on elevated transverse ridges. Scattered about the siphon of one specimen are spermatophores, conspicuous for the covering of black adhesive substance at the base (fig. 5).

SEPIELLA INERMIS (van Hasselt, MS.).

Among the 25 specimens referred to this species there is great variation as to general appearance, shape, width of the fins, and details of the structure of the pen. Nevertheless I have not been able to distinguish any modifications of specific importance. The differences in the soft parts seem to be due to varied preservation. Six specimens were captured near Madras, three near Bombay, five at Sandheads, one in the Chilka Bight, one at Mergui, two at Singapore, two at Penang, and five off the Ganjam coast at a depth of 10 fathoms.

Family LOLIGINEI.

SEPIOTEUTHIS INDICA, n. sp. (Pl. 1. figs. 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, & 19.)

Although the nine specimens in the collection belonging to the genus *Sepioteuthis* differ considerably in size and colour, I refer them all to one species. The best-preserved individuals are of a pale brownish-yellow ground-colour, sprinkled with slate-coloured chromatophores, very thickly on the upper surface of the mantle, head, and arms, more sparsely on the lower surface.

Seven specimens come from the Andamans, and two from Singapore.

Below are the principal measurements of a large male and of a large female:—

	Large Male. centim.	Large Female. centim.
Length of mantle (lower surface) . . . . .	15·5	18·3
Breadth „ near margin . . . . .	5·1	5·9
„ „ halfway . . . . .	5·1	6·1
„ fin 7 cm. from mantle-edge . . . . .	2·9	2·9
„ „ 10 cm. from mantle-edge . . . . .	3	12·5 em. from } mantle-edge } 3·6
Length of dorsal arm . . . . .	5·2	5·5
„ dorso-lateral arm . . . . .	6·3	6·5
„ ventro-lateral „ . . . . .	8	9
„ ventral „ . . . . .	7·4	8·6
„ tentacular „ . . . . .	13·5	15
„ „ club . . . . .	5·2	6·7
Length of pen . . . . ♂ 13 em.	♂ 20·5 cm.	12·7 cm.
Breadth of pen . . . . .	2·4	4
		3

From the outline figure given (fig. 9) it will be seen that the fins are perfectly rounded, while the mantle from about halfway tapers to a blunt point; the whole forming an almost perfect oval. In this respect this species resembles *S. Blainvilliana*, Fér., and *S. mauritiana*, Q. & G. The fins begin 3·5 cm. from the margin of the mantle and join

behind at the apex. The siphon presents no peculiarity. The olfactory fold below the eye is prominent, undulating, and with its two extremities turned forwards (fig. 13).

The buccal membrane is large (in one specimen extending 2 cm. beyond the mandibles), and provided with seven lobes bearing suckers. The horny ring of the latter is armed on its distal border with strong teeth (fig. 15). The jaws are shown in fig. 14. Adhering to the buccal membrane of this specimen (a large female) are spermatophores very similar to those of *Loligo indica* (Pl. 2. fig. 28), but slightly thicker.

The powerful arms are provided on both edges of the inner surface with a lateral membrane, strengthened by transverse muscular ridges springing from the base of the suckers. This membrane is especially well-developed on the lower edge of the second or dorso-lateral arm. A median outer keel is developed along the dorsal and ventro-lateral arms; a lateral keel on the outer lower edge of the dorso-lateral arm; and two lateral keels on the ventral arms, the upper one being large and membranous.

The suckers, closely set in two rows, are of moderate size, largest on the dorso-lateral arms, where they attain a diameter of .35 cm. The horny ring is armed with from 20 to 28 strong teeth (generally 21–22), rather larger on the distal border (fig. 17).

The stem of the tentacular arm is thick, and flattened near the base (13 mm. broad about 5 cm. from the base in the large female already mentioned), from the inner edge of which springs a membrane reaching down below the buccal membrane. The club is wide, provided with a keel on its outer edge and with a membrane on either side, and bears four rows of suckers of unequal size. The largest suckers, situated towards the centre of the club, reach a diameter of 5 mm.; their horny rings are armed usually with 15 teeth (figs. 18, 19) (sometimes with 16–18 teeth). The smaller distal and proximal suckers and the outer rows of suckers usually have 17 large sharp teeth on the distal border. At the tip of the club is a slightly spoon-shaped expansion, on which the suckers are modified, and arranged in two rows on either side enclosing a space (fig. 12). These suckers are highly specialized, being small, flat, and very short-stalked; the papillary area of the horny ring is very wide and beset with rows of conical teeth reaching the margin (figs. 11 & 12). Such a special group of suckers constitute what I shall call the apical set, an arrangement which has not, so far as I am aware, been noticed by previous observers in the Myopsida. It is found in both sexes, and reminds us strongly of a somewhat similar group in *Onychoteuthis*; the apical set of suckers, perhaps, forms a sort of "connective apparatus." It occurs also in *Loligo Pealei* and *L. indica*; on the other hand, it appears to be absent in *L. marmora* and in the genus *Loliolus*.

In the male the hectocotylized left ventral arm is modified from about the 23rd pair of suckers to the tip. In this region (fig. 16) the suckers are reduced to conical papillæ. The right arm, as noticed in other species by Steenstrup (7), is also slightly modified, the suckers near the tip being unusually small.

The pen is very like that of *Sepioteuthis Blainvilliana*, Fér., thin, lanceolate, convex above, with a strong, raised, convex ridge down the middle (fig. 10).

It is often very difficult to distinguish between the various species of this genus described by authors. *Sepioteuthis Blainvilliana*, Fér., and *S. mauritiana*, Q. & G. (5),

seem to be the nearest allies of this new species. From the former it is distinguished by the lesser number of teeth on the horny rings of the arm and tentacular suckers, by the presence of suckers on the buccal membrane, and by the undulation of the olfactory crest (?). From the latter, *S. mauritiana*, it is distinguished by the lesser number of teeth on the horny ring of the suckers and by the shape of the pen.

LOLIGO INDICA, Pfeffer. (Pl. 2. figs. 20, 21, 22, 23, 24, 25, 26, 27, & 28.)

To this species are referred eight specimens from Mergui, one from Camorta Harbour, one from Daley Sandheads (1887), and two from the mouth of the Mutlah River; also, with some hesitation, a large female from the Chilka Bight.

The first 12 specimens differ little in size; below are the measurements of a male and of the large female mentioned above:—

	♂.	♀.
	centim.	centim.
Length of mantle (upper surface) . . . . .	9·1	14
Breadth „ at beginning of fins . . . . .	1·9	3
Length of fin-attachment . . . . .	5	7·6
Breadth of fins combined . . . . .	4·3	7·65

Length of pen of a smaller ♂, 6·6 centim., breadth 1·2 centim.

„ „ the large ♀, 14 centim., breadth 2·7 centim.

I feel obliged to go into some detail concerning this species, since the figures and descriptions published by Mr. Hoyle of the ‘Challenger’ specimens (1) differ widely from Dr. Pfeffer’s original description (6).

Concerning the horny ring of the suckers of the arms, Pfeffer says, “Armringe mit 6 ziemlich grad viereckigen Zähnen; darauf folgt die erhabene Leiste, die vorn noch jederseits eine Einkerbung als Rudiment eines Zahnes zeigt.” This hardly agrees with Hoyle’s figures, but corresponds exactly to my figure of the horny ring of the female (fig. 26).

With regard to the horny ring of the suckers of the arms, I find that there is a well-marked sexual difference, for in the males these rings are armed with from 9 to 11 rounded teeth (fig. 20).

Again, concerning the horny ring of the tentacular suckers, Pfeffer says, “Grosse Tentakelringe mit etwa 21 spitz dreieckigen Zähnen, deren Basis schmaler ist, als die Zwischenräume.” While this description differs much from Hoyle’s figures, it agrees entirely with what I find (fig. 27). Although 21 is the usual number of teeth in these specimens, there are sometimes as few as 15 in the large female. Fig. 24 shows the horny ring armed with 6 strong teeth from one of the very small distal suckers of the club; while fig. 25 represents a portion of the horny ring from one of the suckers of the apical set at the tip of the club (cfr. *Sepioteuthis*, p. 6).

The lobes of the buccal membrane are provided with small toothed suckers, the horny ring of which is shown in fig. 21. I figure also a club-shaped spermatophore removed from the buccal membrane (fig. 28).

The hectocotylized arm of the male is strongly modified. On its proximal half are two rows of small suckers (fig. 22); on the outside of these the upper edge of the arm is drawn out into a wide thick flap (fig. 22, *fl.*). On the distal half of the arm the suckers are reduced to rounded projections (*m.s.* fig. 23) which bend over a groove. The outer and upper edge of the arm is developed into a lateral membrane of considerable width (*l.m.* fig. 23).

*LOLIOLUS INVESTIGATORIS*, n. sp. (Pl. 2. figs. 29, 30, 31, 32, 33, 34, 35, 36, & 37.)

Nine specimens, some of which are much mutilated. The specimen figured and one other come from the Mutlah River, five from the Yé River, one from Mergui, and one from Sangor. They vary considerably in size; the following are the principal measurements taken on the specimen figured, a male of average size:—

Length of mantle (upper surface) . . . . .	3·5 centim.
„ from apex of mantle to base of arms . . . . .	4 „
Breadth of mantle near edge . . . . .	1·3 „
„ across eyes . . . . .	1·35 „
„ „ combined fins . . . . .	2·9 „
Length of attachment of fins . . . . .	2·1 „
„ dorsal arm . . . . .	·8 „
„ dorso-lateral arm . . . . .	1·6 „
„ ventro-lateral „ . . . . .	2·1 „
„ ventral „ . . . . .	1·8 „
„ tentacular „ . . . . .	3·3 „

The mantle is of conical shape, with a rounded apex; its margin projects on the upper surface into a small point above the neck, and below on either side of the funnel (figs. 29 & 30). The fins have rounded anterior and lateral edges; the two together form a heart-like figure. They join and are continued beyond the mantle apex.

The head is large and provided with a transverse olfactory crest below the eye. The siphon possesses a valve, and muscular bridles hidden below the skin.

The three dorsal pairs of arms bear on their outer surface a median keel, especially well-developed on the 3rd pair. The ventral arms are somewhat square in section, and both the outer edges are drawn out into lateral keels. Small lateral membranes spring from the inner surface on the upperside of the 1st and 2nd pairs of arms, and on both sides of the 3rd and 4th pairs of arms. The suckers, in two rows, are obliquely set on their stalks (fig. 36); the horny ring is provided with three large blunt teeth (fig. 37).

The tentacular arms enlarge distally into small clubs, bearing an outer keel and four rows of suckers. The horny ring of these is armed with sharp teeth on its distal border (fig. 35).

A few small suckers are situated on the seven lobes of the buccal membrane; their horny ring strongly resembles that of the tentacular suckers, but there are only from four to six large teeth.

The mandibles are rather weak (fig. 34). The lower mandible has a sharp, hard, tooth-like point and a small basal tooth (*b.t.* fig. 34*b*).

The pen is lanceolate; narrow anteriorly, it broadens out to a thin blade behind (fig. 31).

In the male the left ventral hectocotylized arm is somewhat sickle-shaped (figs. 29 & 32). The upper outer edge is developed into a wide lateral membrane (*l.m.* fig. 33), and the suckers are more modified than in Steenstrup's species (7), the upper row being reduced to mere papillæ, and the lower row having almost entirely disappeared (fig. 33).

## OIGOPSIDA.

### Family ONYCHII.

*ABRALIA ANDAMANICA*, n. sp. (Pl. 2. figs. 38, 39, 40, 41, 42, 43, 44, & 45.)

Three specimens, captured at a depth of from 188 to 320 fathoms in the Andaman Sea, belong to this species. The following are the measurements of the largest specimen, a female (fig. 38):—

Length of the mantle (lower surface) . . . . .	3·8 centim.
„ from mantle-edge to base of arms . . . . .	1·2 „
„ of attachment of fins . . . . .	2·3 „
„ from mantle-apex to angle of fin . . . . .	2·7 „
Breadth of combined fins . . . . .	3·4 „
Length of dorsal arm . . . . .	1·7 „
„ dorso-lateral arm . . . . .	2 „
„ ventro-lateral „ . . . . .	1·8 „
„ ventral „ . . . . .	2 „
„ tentacular „ . . . . .	4 „
„ „ club . . . . .	·8 „

Length of pen of a male, 2·4 centim., breadth 35 centim.

The mantle is nearly conical, tapering gradually to the apex. At the free edge there is no pronounced dorsal point, but there is a small projection on each side of the funnel (figs. 38 & 39). The fins, rhomboidal in shape, reach about halfway up the mantle; their posterior edge is slightly concave, their anterior convex and more rounded.

The head is large, and fits closely on to the edge of the mantle. At the edge of the eyelid is a rudimentary sinus. On each side of the neck are two olfactory crests, the smallest being nearest the siphon. There is a well-developed valve in the funnel; and the socket at the base of the latter is I-shaped. The buccal membrane has 8 lobes; its inner surface is covered with papillæ of considerable size.

The first and second pairs of arms have a median external keel, and a small lateral membrane on the upper edge. The third, or ventro-lateral, pair has a large membranous keel (*k*, fig. 38), and a membrane along the lower edge. The ventral arms have the outer and upper edge drawn out into a lateral keel.

All these arms bear two rows of hooks for about three fourths of their length, and two rows of suckers on the distal quarter. On the ventral arm, for instance, 14 hooks and

12 suckers can be counted. These suckers are very obliquely set on short stalks (figs. 42 & 43), and of a compressed conical shape. The horny ring is studded with teeth, and the margin is armed with small teeth on the proximal side and large blunt teeth on the distal side.

The tentacular arms are scarcely at all enlarged to form the clubs (figs. 38 & 40). Each club bears a small keel externally, three hooks along the lower edge of the internal surface (*h*), and above these two rows of suckers. Beyond the hooks on the distal region small suckers are arranged in four rows. The horny ring of the suckers is furnished with small teeth round its margin (figs. 44, 45). Near the base of the club a set of three small short-stalked suckers alternating with three tubercles forms a connective apparatus (*c. app.* fig. 40).

Fig. 41 (*a* & *b*) shows the pen of a small male, the mantle of which is 3 cm. long; it is lanceolate, with a strong median ridge. This specimen has a large bundle of spermatophores in the mantle-cavity.

In colour the female is of pale yellowish-brown tinge, inclining to orange on the upper surface, covered with dark purple-brown chromatophores, most numerous on the upper surface of the mantle, head, and arms, and on the buccal membrane. The male is paler, the chromatophores being less numerous.

Both sexes are provided with a very large number of small dark tubercles, generally showing a white opaque lens in the centre, distributed over the lower surface of the mantle, head, funnel, and ventral arms (fig. 38).

These tubercles, no doubt luminous or phosphorescent organs, are evenly scattered over the lower surface of the mantle; on the siphon they are situated in six irregular longitudinal series; on the head there is a row round the lower half of each eye and nine rows between these. Three rows extend on to the base of the ventral arms, but only two are continued to their extremities.

*ABRALIA LINEATA*, n. sp. (Pl. 3. figs. 46, 47, 48, 49, & 50.)

Two specimens; one, a male, taken at a depth of 265 fathoms in the Andaman Sea, the other, a female, at a depth of from 90 to 100 fathoms off the Ganjam coast.

The principal measurements of the first specimen, which is the one figured, are given below:—

Length of the mantle (upper surface) . . . . .	1·5 centim.
„ „ (lower surface). . . . .	1·3 „
„ from mantle-apex to base of arms . . . . .	2 „
„ of attachment of fin . . . . .	·8 „
„ of posterior border of fin . . . . .	·9 „
Breadth of mantle . . . . .	·6 „
„ combined fins . . . . .	1·5 „
Length of dorsal arm . . . . .	·7 „
„ dorso-lateral arm . . . . .	1·0 „
„ ventro-lateral „ . . . . .	·9 „
„ ventral „ . . . . .	1·1 „
„ tentacular „ . . . . .	1·6 „

The short mantle tapers to a sharp point. The fins are rhomboidal, with anterior rounded border and nearly straight posterior border; they extend forwards more than halfway up the mantle beyond the point of attachment. The head, of about the same width as the mantle, is provided with large eyes, and fits less closely on to the mantle than in the preceding species (this may be due to differences in preservation). A small olfactory crest is situated behind the eye. The funnel has a valve, two well-marked bridles, and l-shaped sockets.

The buccal membrane has 8 lobes.

The three dorsal pairs of arms are rounded proximally and slightly keeled distally. The ventral arms have a lateral membrane on the upper side. Two rows of hooks are borne by all the arms along almost their entire length. The ventral arms appear to bear no suckers at all distally, but their tips are swollen, and provided in both sexes with three large convex pigmented organs forming a sort of club. These swellings are probably phosphorescent organs; they correspond exactly to the modified arms described by Pfeffer in *Enoploteuthis Hoylei*, Pfeffer, and considered by him to be due to hectocotyli- zation. The other arms bear, near their extremity, a small number of minute suckers, the horny ring of which is armed on the distal margin with large teeth (fig. 49).

The tentacular arm is slightly expanded to form a club, bearing in the middle region four hooks on the lower side, and three hooks alternating with suckers on the upper side (fig. 48). Beyond these are four rows of small suckers, with a wide ornamented papillary area and a smooth margin (fig. 50). At the base of the club is situated the connective apparatus of four suckers and tubercles (*c. app.* fig. 48).

The pen of the second specimen has been lost; the type-specimen figured I have not dissected.

The most striking characteristic of this pretty little Cephalopod consists in the distribution of the phosphorescent organs in regular rows on the lower surface of the mantle, funnel, head, and two ventral pairs of arms. The whole animal is of a creamy-white colour, with a few brownish chromatophores at rare intervals, more especially on the upper surface; two of these, of exceptional size, are situated on the upper surface of the head between the eyes (fig. 46). The eyes and buccal membrane are of a deep purplish-brown colour. The phosphorescent organs already mentioned are arranged in six longitudinal rows on the mantle, of which the two central rows are the widest; also on the funnel in six irregular rows (fig. 47). A row surrounds the lower half of each eye, and three rows extend between these. The median row bifurcates and runs up the two ventral arms, together with the lateral rows. The ventro-lateral arms are provided with one row of these organs, and a few are scattered along the edge of the mantle and over the neck. The ventral arms are abnormally long and slender, and it seems probable that the special organs already described at their tips are phosphorescent and used as search-lights.

#### ONYCHOTEUTHIS BANKSII, Leach.

I refer provisionally one male specimen from Sandheads, and one large female captured at a depth of 272 fathoms in the Bay of Bengal, to this species.

The latter only has an apical set of suckers to the tentacular club.

This genus is greatly in want of revision by some naturalist who could have access to the type-specimens.

### Family TAONOTEUTHI.

#### Subfamily CHEIROTEUTHIDÆ.

CHEIROTEUTHIS MACROSOMA, n. sp. (Pl. 3. figs. 51, 52, 53, 54, 55, 56, & 57.)

A single female specimen of this elegant Cephalopod was captured off the Kistna delta, lat. 12° 50' N., long. 81° 30' E., at a depth of 475 fathoms.

From figure 51 and the measurements given below, it will be seen that this new species of *Cheiroteuthis* is remarkable for the great length and graceful tapering of the mantle.

Length of body and arms (without tentacles) . . . . .	69 centim.
„ mantle (lower surface) . . . . .	36 „
„ „ (upper surface) . . . . .	38·5 „
Breadth of „ . . . . .	6 „
Circumference of mantle . . . . .	18 „
Length of attachment of fins . . . . .	14·8 „
Breadth of combined fins . . . . .	13 „
Length of mantle-apex beyond fins . . . . .	6 „
Breadth of „ „ „ . . . . .	2·5 „
Length from base of arms to posterior edge of funnel . . . . .	10 „
Length of funnel . . . . .	5 „
Aperture of funnel . . . . .	1·3 „
Diameter of external eyelid . . . . .	1 „
Length of dorsal arm . . . . .	14·25 „
„ dorso-lateral arm . . . . .	16 „
„ ventro-lateral „ . . . . .	22 „
„ ventral „ . . . . .	27 „
Maximum width of lateral membrane—	
On ventral arms . . . . .	1·2 „
On ventro-lateral arms . . . . .	1 „
On dorso-lateral arms . . . . .	·4 „
Length of pen . . . . .	40·4 „
Breadth „ . . . . .	·75 „

The colour of this specimen in spirit is of a dull purplish-brown, lighter and yellower on the lower surface, darker and inclining to heliotrope and blue on the upper surface of the mantle, head, and on the outer surface of the arms. The buccal membrane, inner surface of the arms and suckers are paler.

The mantle, as seen in the figure from the ventral surface, tapers gradually until the middle of the fin, where it is very narrow; it then enlarges slightly, and is produced beyond the fin at its apex (*ap.prol.*) very much as in *Cheiroteuthis Picteti*, a species

admirably described by M. Joubin (2). This apical prolongation of the mantle is shorter than in the latter species, and moreover is provided with a lateral fin on each side (*ap.f.*), a character which distinguishes the present species at once from any hitherto described. The mantle is laterally compressed, forming slight median longitudinal upper and lower ridges. Dorsally the mantle-edge is produced in a point above the neck; below it is raised opposite the funnel. The fins are wide, the outlines of the right and left together forming an almost perfect circle (*f*, fig. 51).

The funnel, provided with a large internal valve, is fixed to the head without distinct bridles, and at its posterior edge carries two sockets, each possessing two prominent lobes fitting into corresponding depressions in the mantle (fig. 56, *a* & *b*).

The head is small; the eyes moderately large and without sinus. About halfway between each eye and the attachment of the siphon is an olfactory papilla (*olf.p.*), about 2 mm. in length. The buccal membrane is well developed, with seven lobes and ridges. The mandibles are very sharp (fig. 54, *a* & *b*); the upper mandible has a basal tooth on either side (*bt.*, fig. 54*b*), corresponding to which are small teeth on the lower mandible. The radula consists of seven rows of teeth (fig. 57), closely resembling those of *C. Picteti*, Joubin (2).

All the arms are somewhat square in section, and are provided along the upper and outer edge with a membrane very narrow in the first two pairs, absent in the third, and very broad in the fourth (*m*). The third and fourth pairs have narrow membranes along the lower and outer edge\*.

Two rows of small suckers are placed rather far apart along each arm (rather more closely set on the dorsal than on the ventral arms). Each sucker is obliquely set on a slender stalk, and has a narrow opening, the horny ring of which is armed on the distal side with square teeth (fig. 55). The soft rim of the sucker is more or less raised up into a peak above the toothed horny margin (fig. 55). On the ventral arms, at the base of the outer row of suckers are convex pigmented patches, no doubt similar to the "vésicules réfringentes" described by Joubin in *Ch. Veranyi* (3).

The tentacular arms, which have unfortunately lost their clubs, are long and slender, bearing at intervals the modified flattened suckers characteristic of the genus.

The pen was somewhat injured owing to the contraction of the mantle. It is very long and narrow (fig. 52, *a* & *b*); the hollow cone reaches halfway up and opens by an oblique aperture. Diagrams of transverse sections of the cone and of the anterior region are given in figure 53, *a* & *b*. The pen thus closely resembles that of *Ch. lacertosa*, described by Verrill (9), and of *Ch. Picteti*; yet the portion in front of the cone is not tubular, as figured by Joubin for the latter species. *Ch. Veranyi*, on the other hand, has hitherto been described, by d'Orbigny and Férussac (5), and by Vérany (8), as possessing a pen flattened and expanded at both ends. On examining a specimen from the Mediterranean, I find, however, that its pen resembles in every essential that of *Ch. macrosoma* here figured; in the case of the works referred to, the artist probably flattened out the slender cone before drawing it.

\* These membranes correspond rather to the keels in other forms, as they do not spring directly from the sucker-bearing surface of the arm.

Of the four species\* of *Cheiroteuthis* hitherto known, two come from the Atlantic, one from the Mediterranean, and one from Amboyna. In general shape and size the present species approaches most nearly the latter, *Ch. Picteti*; yet it differs from it in the possession of a fin along the apical region of the mantle, in the beak, horny ring of the suckers, socket at the base of the siphon, and pen.

CHEIROTEUTHIS PELLUCIDA, n. sp. (Pl. 4. figs. 58, 59, 60, & 61.)

This small specimen, captured at a depth of 922 fathoms off the Vizagapatam coast, lat. 16° 11' 15" N., long. 82° 30' 30" E., was brought up alive on deck, when it appeared transparent, with dark purple chromatophores. In spirit it is still remarkably transparent, and the chromatophores (not represented in fig. 58) are very large and few in number, scattered at wide intervals over the body, fins, and arms.

The principal measurements are as follows:—

Length of the mantle (lower surface) . . . . .	4·8 centim.
Breadth           " . . . . .	·8   "
Length           "       to sudden constriction . . . . .	2·6   "
"       "       beyond fin . . . . .	·6   "
"       of fin-attachment . . . . .	2·1   "
Breadth of fin . . . . .	1·8   "
Length from mantle-edge to base of arms . . . . .	2·2   "
Breadth across eyes . . . . .	·7   "
Length of dorsal arm . . . . .	1·4   "
"       dorso-lateral arm . . . . .	1·8   "
"       ventro-lateral   " . . . . .	2·3   "
"       ventral           " . . . . .	4·5   "
"       tentacular       " . . . . .	8   "
"       "       club . . . . .	3   "

In general appearance this interesting little *Cheiroteuthis* reminds us strongly of *Dorotopsis vermicularis* (Rüppell) by its long and almost cylindrical mantle with a narrow apex, its long thick neck, and the great disparity in size between the ventral and remaining three pairs of arms.

The mantle, as already mentioned, is nearly cylindrical until it suddenly narrows down in the region of the fins to a narrow straight prolongation, which extends beyond the fins, forming a rounded spine (fig. 58). The fins themselves are broad and rounded (*f*), but the outline is less circular than in the preceding species. Dorsally the mantle projects over the neck in a small point.

The funnel is sharply recurved at its apex, and provided internally with a broad valve produced and thickened at the sides. The socket of attachment is shown in fig. 59.

The head is hardly wider than the neck; the eyes are somewhat prominent. Between these and the siphon are two olfactory papillæ (*olf.p.*). The buccal membrane is furnished with seven well-marked ridges and lobes.

Beyond the eyes the head narrows considerably, and enlarges again to support the

\* M. Joubin has lately described a new species from the Atlantic (4).

arms. The three small and dorsal pairs of arms bear two rows of suckers, and have no lateral membrane. The large ventral arms have a membrane on the upper side; toward the base they bear two rows of suckers, but about halfway up the suckers come to alternate in so nearly the same straight line that there appears here to be only one row. The horny ring of the suckers (fig. 60) is armed with rounded teeth on the proximal, and powerful sharp teeth on its distal side.

The tentacular arms are comparatively short, and provided at intervals with numerous flattened suckers. The long clubs bear four rows of small suckers, the outer row of which has the longest stalks. Round the margin of the club is a ribbed lateral membrane; the apex ends in thickened, deeply pigmented, and somewhat spoon-shaped knob. The horny ring of the suckers has a wide papillary area bearing sharp teeth, and characteristically notched on its distal border; the proximal margin of the ring is smooth, the distal margin armed with powerful sharp teeth (fig. 61).

I have not dissected out the pen; it appears to closely resemble that of the foregoing species.

Although, as the description shows, this specimen closely resembles *Doratopsis*, yet the structure of the tentacular arms shows that it undoubtedly belongs to the genus *Cheiroteuthis*.

HISTIOPSIS HOYLEI, n. sp. (Pl. 4. figs. 62, 63, 64, 65, 66, 67, 68, 69, 70, & 71.)

One specimen captured near the Andamans, at a depth of 490 fathoms.

Length of mantle to notch between fins (upper surface) . . . . .	2.2 centim.	
"          "          to apex (lower surface) . . . . .	1.9	"
Breadth          "          . . . . .	1.2	"
Length of fin-attachment to posterior notch . . . . .	.6	"
"          fin beyond mantle-apex . . . . .	.3	"
"          combined fins . . . . .	1.3	"
"          dorsal arm . . . . . (right)	3.5 centim.	(left) 3.3 centim.
"          dorso-lateral arm . . . . . "	3.4	" 3.7 "
"          ventro-lateral " . . . . . "	3.1	" 3.4 "
"          ventral          " . . . . . "	3	" 3.2 "
"          tentacular          " . . . . . "		" 7 "
"          pen . . . . .	2.1 centim.	
Breadth of " . . . . .	.6	"

The mantle swells out slightly midway, then tapers to a blunt point (figs. 62 & 66). Dorsally it projects above the neck; the lower margin is nearly straight. The fins are rounded, joined distally above the mantle-apex, beyond which they project.

The funnel is strongly recurved (*si.*, fig. 68); the two lips which bound its aperture are so applied to each other as to leave a narrow U-shaped opening. The sockets at the base of the funnel are I-shaped (*so.*); two small bridles bind it to the head. Inside we find a small valve prolonged into the upper portion of the 'funnel-organ,' which covers the upper or attached wall of the siphon, and into which fit two rounded flaps fixed on either side to the lower or free wall of the siphon. The whole arrangement closely

resembles that described and figured below in *Taonius abyssicola*. Mr. Hoyle makes no mention of the 'funnel-organ' in his species (1).

The head is wide and sharply marked off from the narrow neck. Below each eye is an olfactory papilla (*olf.p.*, fig. 64).

The eyes are large, with widely open eyelids (figs. 62 & 64); the left eye is injured and protrudes from the eyelid, it has been restored in the figure.

The arms, which differ somewhat in length on the right and left sides, appear to be in the following order of length: 2, 1, 3, 4. Unlike *H. atlantica* of Hoyle, the web at the base of the arm is quite rudimentary (fig. 63). The small suckers, placed in two rows on all the arms, are of a peculiar conical shape (figs. 69 & 70), with a wide opening furnished with a narrow horny ring armed round its margin with small sharp teeth.

The left and only complete tentacle enlarges at its extremity into a small club (figs. 62 & 65), bearing four regular rows of small suckers on its distal half, and as many as six irregular rows on its proximal half. At the widest region of the club the central suckers attain a large size (fig. 65). They have round shallow cups, set almost straight on short thick stalks (fig. 67); the margin of the horny ring is armed with numerous long straight pointed teeth. Near the base there is a connective apparatus consisting of a row of three alternating suckers and tubercles (*c.app.*, fig. 65); two or three small suckers are scattered down the stem.

The buccal membrane has seven lobes, with corresponding ridges extending on to the arms, as shown in figure 63.

The delicate little pen is lanceolate (fig. 71).

The colour of this specimen in spirit is pale yellowish-brown, covered with dark purplish-brown chromatophores, on the mantle, upper surface of the fins, head, buccal membrane, and arms (especially on their inner surface).

As seen in the figure, a large number of U-shaped pigmented organs, most probably phosphorescent (see Joubin, 3 & 4 *a*), are scattered in irregular transverse rows on the lower surface of the mantle, head, and arms; a few extend over to the upper surface, and one row surrounds each eye (fig. 64). The first three pairs of arms have one row each extending to their tips, whilst the larger ventral arms have three rows proximally, reduced to two distally.

The exact systematic position of this little Cephalopod is not very easy to determine. I have placed it provisionally in the genus *Histiopsis* of Hoyle, from whose specimen it differs in the absence of a distinct web at the base of the arms, in the horny rings of the suckers, in the buccal membrane, in the continuation of the fins beyond the mantle-apex, in the possession of one row only of pigmented organs on the first three pairs arms, and perhaps in the presence of the 'funnel-organ' (Verrill's organ).

The horny rings of the tentacular suckers are very like those of *Histioteuthis*, to which genus it is no doubt closely related.

#### CALLITEUTHIS REVERSA, Verrill.

One specimen of this widely distributed species was caught in the Andaman Sea at a depth of 265 fathoms.

TAONIUS ABYSSICOLA, n. sp. (Pl. 5. figs. 72, 73, 74, 75, 76, 77, 78, 79, & 80.)

Two specimens from the Laccadive Sea belong to this genus. The first, the large specimen shown in figure 72, comes from a depth of 902 fathoms. It is somewhat injured; the skin has been rubbed off the mantle, fins, and head, and the eyes have burst out of their lids. The second specimen, from a depth of 1370 fathoms, is very much smaller and in a less satisfactory state of preservation.

The principal measurements of the large specimen are as follows:—

Length of mantle (lower surface) . . . . .	7·6 centim.
Breadth „ near edge . . . . .	3·8 „
Length of fin-attachment . . . . .	2·4 „
Breadth across combined fins . . . . .	1·7 „
„ of head between eyes . . . . .	·7 „
„ across eyes . . . . .	2·8 „
Length of dorsal arm . . . . .	2·5 „
„ dorso-lateral arm . . . . .	2·8 „
„ ventro-lateral „ . . . . .	3·3 „
„ ventral „ . . . . .	2·8 „
„ tentacular „ . . . . .	4·2 „
„ „ club . . . . .	1·1 „

The mantle is loose, enclosing an ample cavity; it diminishes gradually to the origin of the fin, and then suddenly to the narrow apex. The outline of the fins is egg-shaped. The mantle is attached by a lozenge-shaped cartilaginous plate to the back of the neck, and on both sides to the base of the siphon.

The aperture of the funnel is covered by the sharply recurved upper lip (fig. 72). All previous observers have described the funnel of this species as destitute of valve.\* On slitting up the funnel of this specimen and turning aside the two sides as shown in figure 74, I found that the inner and upper wall is sharply bent inwards near the opening so as to form a deep pit where the siphon is fused to the head. On either side of this pit are the two cushions (*c*) noticed by Verrill (9), which in their normal position almost close up the lumen of the funnel. When these two cushions are pushed aside, a *well-developed valve* is disclosed rising from the bottom of the pit (fig. 74, *v.*). Behind the cushions, further down the funnel, are two triangular flaps, flattened and fastened by their base to the sides of the funnel (*t.fl.*, fig. 74); they appear to be of a glandular nature, and probably correspond to the lateral pads described in other forms by Weiss (10).

On the inner and upper wall of the siphon is a wide A-shaped plate—the funnel-organ—very similar in shape to that figured by Weiss in *Verania sicula*. In the present instance it was so loosely attached that it readily came off; it is represented in figure 75, and its position is indicated by a dotted line in figure 74. On the inner surface this plate is produced on either side into a triangular cap (*t.c.*), which fits closely as a glove

\* Since this was written M. Joubin (4) has described a small valve in the siphon of a new species of *Taonius* from the Atlantic.

on to the flaps already described lying opposite them.\* I have confirmed these observations on the second specimen.

Contrary to Verrill's observations in two other species (9), I find on either side between the eye and the funnel a truncated olfactory papilla (fig. 76). It is slightly expanded and flattened distally, the flat oblique surface being concave.

The head appears to have been narrow. The two eyes are very large and protrude from their sockets.

The arms are thick, and of considerable length for this genus. The three dorsal pairs are provided on both sides with a well-developed lateral membrane (largest in the third pair), springing from the inner edge and supported by muscular thickenings arising from the base of each sucker (fig. 73). The ventral arms are also provided with such a membrane on the lower edge; but it is rudimentary on the upper side, where on the contrary the outer edge of the arm is produced into a lateral keel. On all the arms we find two rows of suckers, largest on the third pair. The suckers (figs. 77, 78), very obliquely set on a short stalk, have a wide opening provided with a horny ring, armed on the distal margin only with about 14 squarish teeth. The papillary area is narrow.

The tentacular arms are thick-stemmed, the clubs only slightly enlarged and bearing a lateral membrane on either side similar to that of the arms. The suckers of the club are compressed and considerably injured in this specimen; they appear to be set in four rows, and of a peculiar conical shape (fig. 80). The stalk of the sucker swells gradually to the base of the cup, where there is a thickened ridge; it then narrows and expands again into a bell-shaped cup, with an oblique opening. The margin of the horny ring is armed with eight or nine strong curved teeth, extending round the distal two-thirds of the circumference. The striated outer margin is frayed out into a fringe, but this is probably artificial. From the club extending down the stem are small short-stalked round suckers, the horny margin of which is armed all round with blunt teeth (fig. 79). Distally at the base of the club these suckers are placed in four rows, which dwindle gradually to two rows proximally, where the suckers are very small and set in pairs on either side of a median groove.

The buccal membrane has seven ridges; the lobes are indistinctly marked.

Purplish-brown chromatophores colour the fragments of skin adhering to the head and arms, the lateral membranes between the ridges, and the buccal membrane.

The pen can be seen, without dissection, as a narrow ridge starting from the nuchal plate and expanding posteriorly into a thin plate, narrowing again to form a slender cone, as figured by Pfeffer for *Taonius (Megalocranchia) maximus* (6).

The second specimen is very much smaller, and is possibly a young individual of the same species; it is, however, not in a sufficiently good state of preservation to allow one to make certain of its specific identity.

\* In their normal position the points of the flaps are directed away from the middle line; in figure 74 they are directed inwards owing to the stretching open of the funnel.

## OCTOPODA.

## Family PTEROTI.

## CIRRHOTEUTHIS PACIFICA, Hoyle?

A small and mutilated specimen, captured at a depth of 265 fathoms in the Andaman Sea, has been referred to this species.

## Family OCTOPODIDÆ.\*

## OCTOPUS VULGARIS, Lam.

One large female from the Andamans, and one smaller male from Point Galle, Ceylon. These specimens resemble very closely our common Octopod, and I could find no important distinction between the European and Indian forms.

## OCTOPUS GRANULATUS, Lam.

Eleven specimens have been placed in this species. Three come from Port Blair, three from the Andamans, one from Great Cocos Island, one from Bombay, two from the Southern portion of the Malacca Straits, and one from Maskat in Arabia.

## OCTOPUS GLOBOSUS, Appellöf. (Pl. 5. fig. 81.)

One specimen from the Nicobars, one from the Kabusa Islands (Mergui Archip.), five from the Southern portion of the Malacca Straits, three from Bombay, and one from Point Galle, Ceylon—in all eleven specimens have been referred to this species. The extremity of the hectocotylized arm of a male is shown in figure 81.

OCTOPUS PICTUS (Brock), var. *fasciata*, Hoyle. (Pl. 5. fig. 82.)

One male specimen from Port Jackson, which agrees very closely with the specimen described by Hoyle in the 'Challenger' Report. The extremity of the hectocotylized arm, however, shown in fig. 82, differs considerably from that described by Hoyle in *Oct. maculosus* (Proc. R. Phys. Soc. Edinb. vol. viii. 1883), which he considers to be the same species. It seems probable that the var. *fasciata* may have to be separated as a distinct species.

## OCTOPUS JANUARI, Stp.

Three specimens appear to belong to this widely distributed and abyssal species. One, a female, comes from a depth of 193 fathoms in the Bay of Bengal (lat. 20° 17' 30" N., long. 88° 30' E.); the other two are males captured at a depth of 271 fathoms in the Andaman Sea.

The ridges on the hectocotylized tip of the arm in the male are more marked than in the figure given by Hoyle in the 'Challenger' Report (1), but in all essential respects these specimens agree with his description.

\* I must express my thanks to Mr. W. E. Hoyle for kindly examining some of these Octopods.

*OCTOPUS MACROPUS*, Risso.

With considerable doubt eight specimens have been referred to this species. Seven come from the Andaman Islands (three from Port Blair) and one from the Malacca Straits.

*OCTOPUS ACULEATUS*, d'Orb.

Ten specimens from the Andaman Islands (six from Port Blair), one from Colombo, and one from Little Cocos Island. It is with some doubt that these have been placed in this species, which is not very thoroughly defined.

*OCTOPUS LEVIS*, Hoyle?

One female specimen from Gopalpur, at a depth of 7 fathoms, has been provisionally placed in this species. It agrees closely, although not perfectly, with Hoyle's description.

*OCTOPUS MICROPHTHALMUS*, n. sp. (Pl. 5. figs. 83, 84.)

One female specimen from Port Blair, Andaman Islands (fig. 83).

This species is remarkable from the smooth cylindrical shape of the head and mantle, the eyes forming no prominence whatever on the surface of the head. The mantle ends obtusely, and fits closely on to the head; the mantle-opening, which is very narrow, reaches rather more than halfway from the siphon to the eye. The aperture of the eyelid is small. The funnel reaches to within 4 mm. of the edge of the web between the ventral arms; it is attached to the lower surface of the head along almost its entire length. The arms are rounded, and bear small somewhat conical suckers, which are arranged some distance apart. Although they are placed in two rows, the suckers are situated in zigzag fashion so as to approximate to the condition found in *Eledone*, for instance, where they are in one row. The mandibles are dark and strong (fig. 84, *a* & *b*).

The following are the principal measurements:—

Length of mantle and head to lower edge of web between ventral arms . . .	4.5 centim.
„ „ to mantle-edge . . . . .	2.7 „
Breadth of mantle . . . . .	2 „
„ head across eyes . . . . .	1.5 „
Length of dorsal arm . . . . .	8.6 „
„ dorso-lateral arm . . . . .	8.1 „
„ ventro-lateral „ . . . . .	6.9 „
„ ventral „ . . . . .	6.9 „

There is a small web at the base of the arms, reaching 1.6 cm. from the mouth between the dorsal arms, where it is longest (the inner surface of this web is the same between the bases of all the arms).

The colour is yellowish-brown, inclining to dark brown on the upper surface of the mantle, head, and outer surface of the arms.

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<i>a.</i> Arm.	<i>loc.</i> Striated region of loculi.
<i>ap.f.</i> Apical fin.	<i>l.olf.f.</i> Left olfactory fold.
<i>ap.prol.</i> Apical prolongation of the mantle.	<i>m.</i> Membrane.
<i>ap.s.</i> Apical set of suckers.	<i>mo.</i> Mouth.
<i>b.m.</i> Buccal membrane.	<i>m.s.</i> Modified sucker.
<i>b.t.</i> Basal tooth.	<i>mt.</i> Mantle.
<i>c.app.</i> Connective apparatus.	<i>olf.p.</i> Olfactory papilla.
<i>ch.m.</i> Chitinous margin.	<i>ph.org.</i> Phosphorescent organ.
<i>d.a.</i> Dorsal arm.	<i>pp.</i> Pigmented patch.
<i>e.</i> Eye.	<i>r.s.</i> Rudimentary sucker.
<i>e.l.</i> Eyelid.	<i>s.</i> Sucker.
<i>f.</i> Fin.	<i>si.</i> Siphon.
<i>f.l.</i> Lateral membrane developed into a flap.	<i>so.</i> Socket.
<i>h.</i> Hook.	<i>t.</i> Tentacular arm.
<i>hd.</i> Head.	<i>t.c.</i> Triangular cap.
<i>i.c.</i> Inner cone.	<i>t.fl.</i> Triangular flap.
<i>i.l.m.</i> Inner lateral membrane.	<i>v.</i> Valves.
<i>k.</i> Keel.	<i>v.a.</i> Ventral (4th) arm.
<i>l.m.</i> Lateral membrane.	<i>v.h.a.</i> Ventral hectocotylized arm.

## EXPLANATION OF THE PLATES.

## PLATE 1.

*Iniocteus maculosa*, n. sp.

- Fig. 1. View of lower surface, nat. size.  
 2. Enlarged view of the horny ring of a tentacular sucker.  
 3. Enlarged side view of a tentacular sucker.

*Sepia singalensis*, n. sp.

- Fig. 4. Outline of the mantle and fins, and figure of the pen (inner surface), nat. size.  
 5. Enlarged view of a spermatophore.  
 6. Upper (*b*) and lower (*a*) mandibles, nat. size.  
 7. Enlarged view of a portion of the horny ring of a small tentacular sucker.  
 8. Horny ring of a small sucker of an arm.

*Sepioteuthis indica*, n. sp.

- Fig. 9. Outline of the mantle and fins, reduced.  
 10. Figure of the pen of another specimen, reduced.  
 11. Enlarged view of a portion of the horny ring of an apical sucker of the tentacular club.  
 12. Enlarged view of the apex of the tentacular club.  
 13. Side view of the head, showing the olfactory fold, nat. size.  
 14. Upper (*b*) and lower (*a*) mandibles, nat. size.  
 15. Horny ring of a sucker of the buccal membrane, enlarged.  
 16. Portion of the left 4th arm of a male, enlarged.  
 17. Edge of the horny ring of a sucker of the 3rd arm, enlarged.  
 18. Large tentacular sucker,  $\times 4$  diam.  
 19. Portion of the edge of the horny ring of tentacular sucker, enlarged.

## PLATE 2.

*Loligo indica*, Pfeffer.

- Fig. 20. Edge of the horny ring of an arm-sucker of a male, enlarged.  
 21. Horny ring of a sucker of the buccal membrane, enlarged.  
 22. Lower view of the left 4th arm of a male, showing the hectocotylization, nat. size.  
 23. Portion of the hectocotylized region of the same, inner view enlarged.  
 24. Horny ring of a small tentacular sucker, enlarged.  
 25. Enlarged view of a portion of the horny ring of an apical sucker of the tentacular club.  
 26. Horny edge of an arm-sucker of a female, enlarged.  
 27. Enlarged view of a portion of a large tentacular sucker of the same.  
 28. Enlarged view of a spermatophore.

*Loliolus Investigatoris*, n. sp.

- Fig. 29. Upper view of a male, nat. size.  
 30. Outline lower view of the mantle and fins, nat. size.  
 31. Upper view of the pen, nat. size.  
 32. Lower view of the hectocotylized 4th left arm, nat. size.  
 33. Enlarged inner view of a portion of the same.  
 34. Enlarged views of the upper (*b*) and lower (*a*) mandibles.  
 35. Horny ring of a tentacular sucker, enlarged.  
 36. Side-view of an arm-sucker, enlarged.  
 37. Edge of the horny ring of the same, enlarged.

*Abralia andamanica*, n. sp.

- Fig. 38. Lower view, nat. size.  
 39. Outline upper view of mantle and fins, nat. size.  
 40. Enlarged view of the tentacular club.  
 41. Upper (*a*) and side (*b*) views of the pen of a smaller specimen, nat. size.  
 42 & 43. Front and side views of an arm-sucker, enlarged.  
 44 & 45. Front and side views of a tentacular sucker, enlarged.

## PLATE 3.

*Abralia lineata*, n. sp.

- Fig. 46. Upper view, nat. size.  
 47. Lower view, enlarged.  
 48. Enlarged view of the tentacular club.  
 49. Horny ring of an arm-sucker, enlarged.  
 50. Horny ring of a tentacular sucker, enlarged.

*Cheiroteuthis macrosoma*, n. sp.

- Fig. 51. Lower view, nat. size.  
 52. Upper (*a*) and side (*b*) views of pen, nat. size.  
 53. Diagram of a section of pen across anterior region (*b*) and cone (*a*), enlarged.  
 54. Upper (*b*) and lower (*a*) mandibles, nat. size.  
 55. Sucker of the ventral arm, enlarged.  
 56. Socket (*a*) at the base of the siphon, and cushion on the mantle (*b*), nat. size.  
 57. Teeth of the radula, enlarged.

## PLATE 4.

*Cheiroteuthis pellucida*, n. sp.

- Fig. 58. Lower view, nat. size.  
 59. Socket at the base of the siphon, enlarged.  
 60. Sucker of the arm, enlarged.  
 61. Tentacular sucker, enlarged.

*Histiopsis Hoylei*, n. sp.

- Fig. 62. Lower view, nat. size.  
 63. Enlarged view of the mouth, buccal membrane, and the base of the arms.  
 64. Enlarged view of the right side of the head.  
 65. Enlarged view of the tentacular elub.  
 66. Upper view in outline of the mantle and fins, nat. size.  
 67. Enlarged side view of a large tentacular sucker.  
 68. Enlarged left-side view of the funnel and mantle-edge.  
 69 & 70. Enlarged side and front views of an arm-sucker.  
 71. Upper view of the pen, nat. size.

## PLATE 5.

*Taonius abyssicola*, n. sp.

- Fig. 72. Lower view, nat. size.  
 73. Inner view of a portion of the dorsal arm, enlarged.  
 74. Enlarged view of the base of the head and siphon and mantle slit up along the median line and turned aside.  
 75. Funnel-organ, lower view, removed from its place on the wall of the siphon, indicated by a dotted line in fig. 74, enlarged.  
 76. Enlarged view of the olfactory papilla.  
 77. Side view of an arm-sucker, enlarged.  
 78. Horny ring of the same, enlarged.  
 79. Enlarged view of a portion of the horny ring of a small sucker at the base of the tentacular club.  
 80. Front (*a*) and side (*b*) views of a tentacular sucker.

*Octopus globosus*, Appellöf.

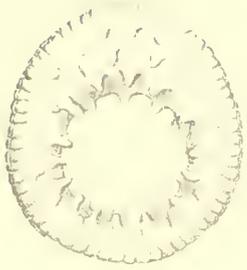
- Fig. 81. Enlarged view of the extremity of the hectocotylized arm.

*Octopus pictus* (Brock), var. *fasciatus*, Hoyle.

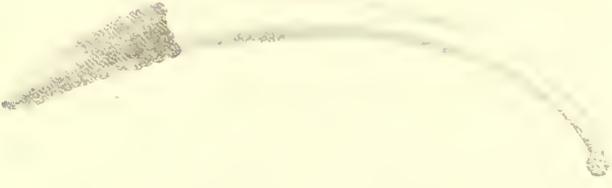
- Fig. 82. Enlarged view of the extremity of the hectocotylized arm.

*Octopus microphthalmus*, n. sp.

- Fig. 83. Lower view, nat. size.  
 84. Lower (*a*) and upper (*b*) mandibles, enlarged.



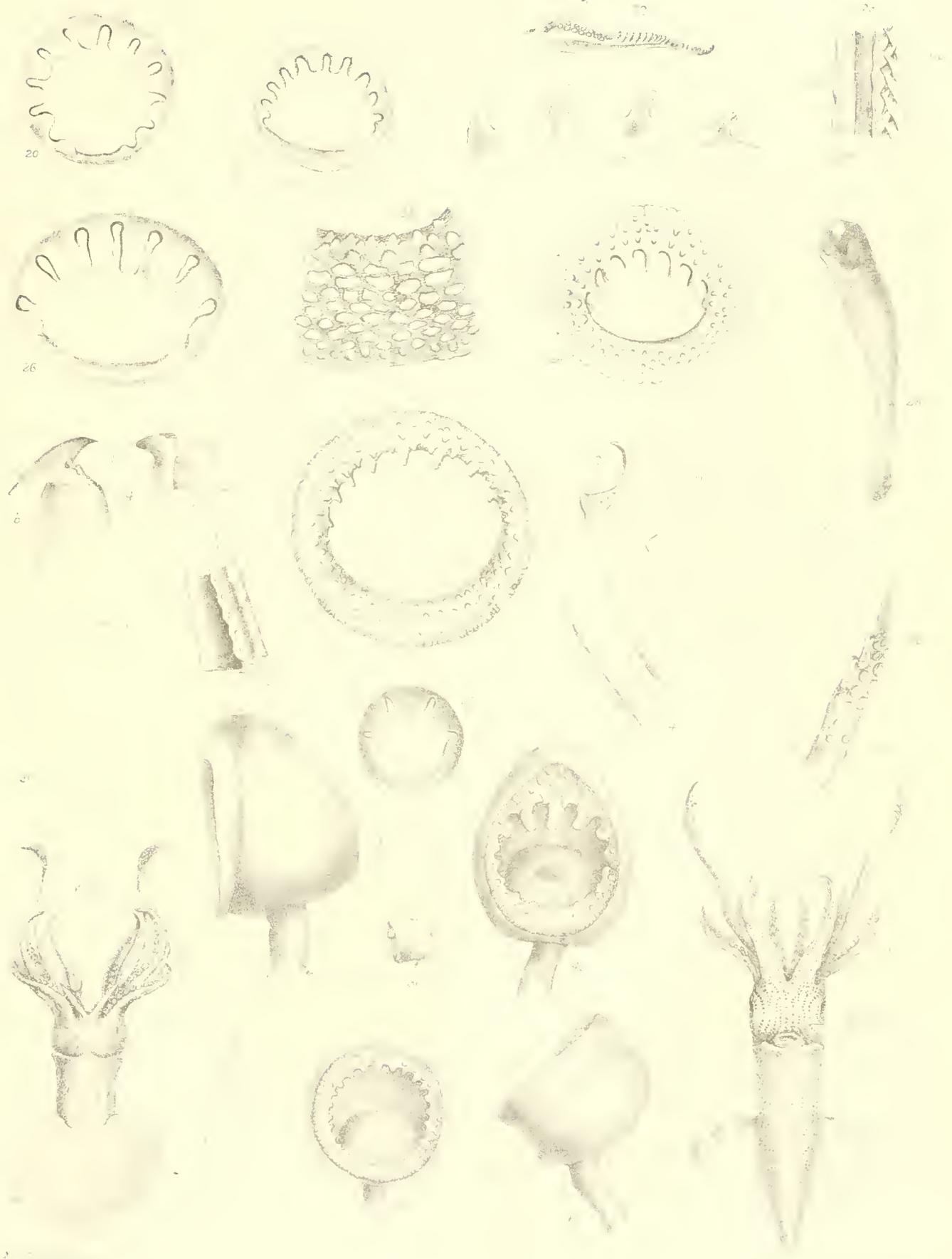
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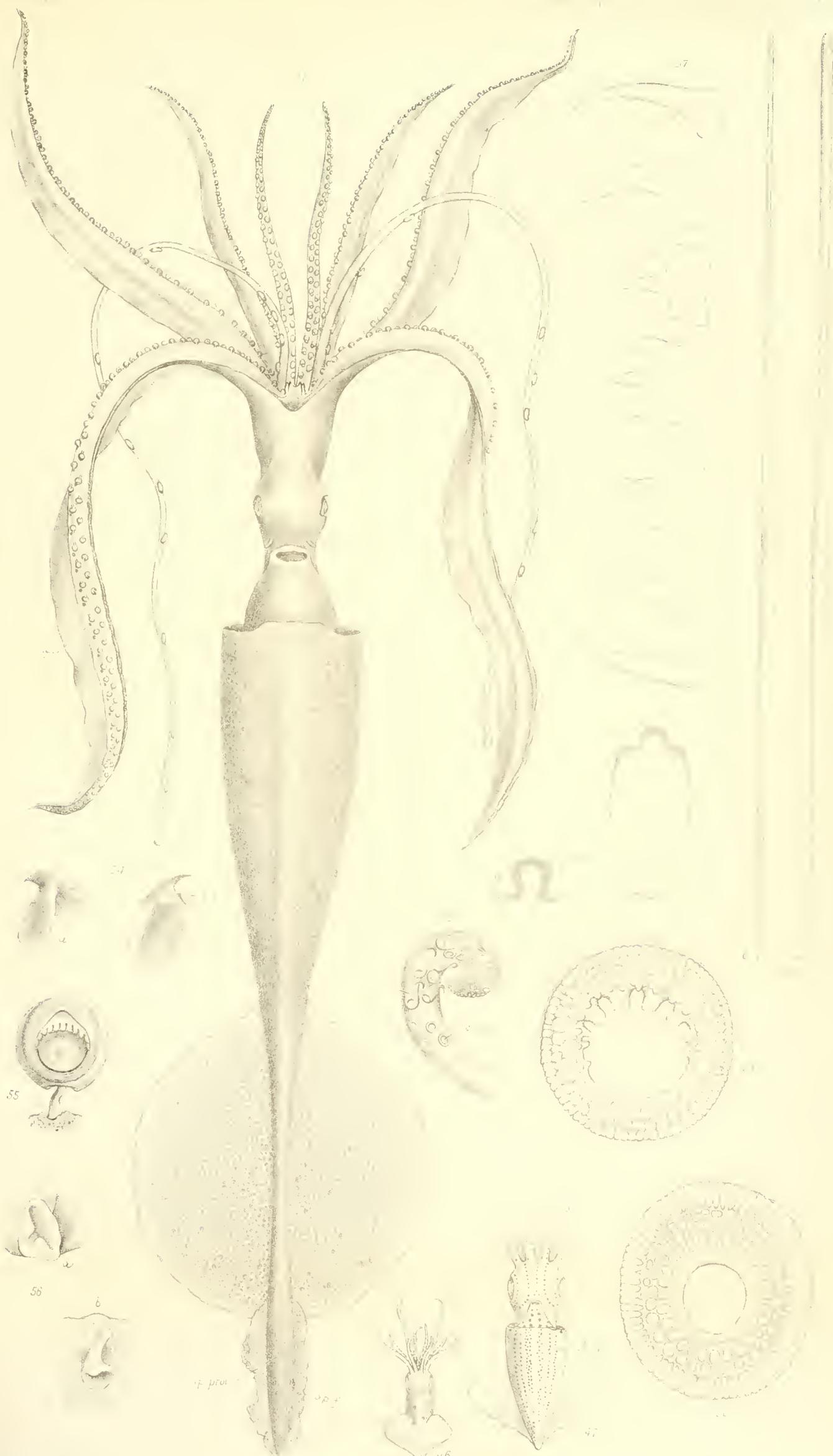
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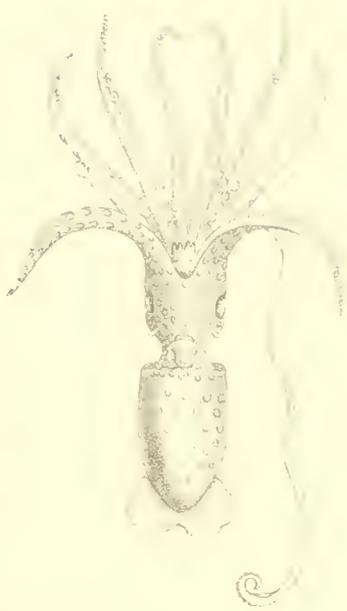














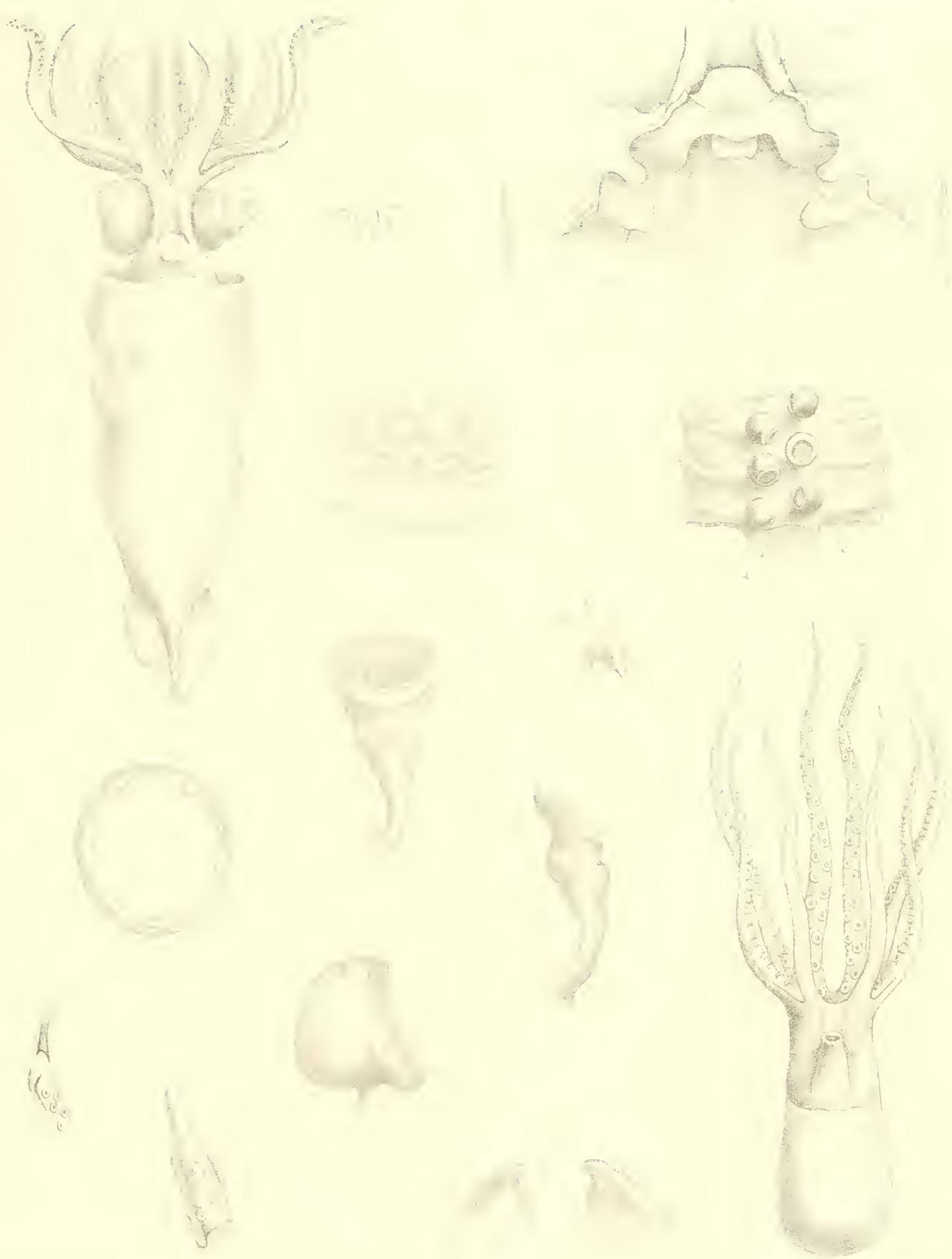


Fig. 1. *Physalia physalis* (Linn.) (Physalia)

Plate 10





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Part	IV. 1882. ....	0 7 6	0 5 6	Part	IV. 1890. ....	0 12 0	0 9 0
Part	V. 1882. ....	0 3 0	0 2 3	Part	V. 1890. ....	0 6 0	0 4 6
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Part	VII. 1883. ....	0 5 0	0 3 9	Part	VII. 1891. ....	0 6 0	0 4 6
Part	VIII. 1883. ....	0 3 0	0 2 3	Part	VIII. 1892. ....	0 8 0	0 6 0
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Part	XI. 1884. ....	0 10 0	0 7 6	Part	XI. 1894. ....	0 2 6	0 2 0
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Part	XIV. 1885. ....	0 6 0	0 4 6	Part	III. 1894. ....	0 10 0	0 7 6
Part	XV. 1885. ....	0 4 6	0 3 6	Part	IV. 1896. ....	1 4 0	0 18 0
Part	XVI. 1885. ....	0 5 0	0 3 9	Part	V. 1896. ....	0 10 0	0 7 6
Part	XVII. 1886. ....	0 3 0	0 2 3	Part	VI. 1896. ....	0 8 0	0 6 0
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THE  
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OF

THE LINNEAN SOCIETY OF LONDON.

AMPHIPODA FROM THE COPENHAGEN MUSEUM AND OTHER SOURCES

BY

THE REV. THOMAS R. R. STEBBING, M.A., F.R.S., F.L.S.



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*May* 1897.



II. *Amphipoda from the Copenhagen Museum and other Sources.* By the Rev.  
 THOMAS R. R. STEBBING, *M.A., F.R.S., F.L.S.*

(Plates 6-14.)

Read 19th November, 1896.

INTRODUCTORY REMARKS.

THE Zoological Museum at Copenhagen is rich in Amphipoda. It is rich also in living authorities on this group of Crustaceans, since Inspektor Dr. Meinert and Professor Lütken are two of its Directors, and Dr. H. J. Hansen is on the staff. This might well seem a happy concurrence of a fine collection in the hands of those well qualified to make its value known to the world. But the masters in science find their work continually expanding, while time remains remorselessly inelastic. Hence it is that these gentlemen, being themselves beset by other duties, have passed over to me the task of reporting on the Amphipoda of the Danish University.

In this first memoir on the subject some of the more striking rarities are described, together with one or two of a less uncommon type. As the collection is not local but cosmopolitan, the opportunity has been taken of bringing into notice certain other new or insufficiently known forms, in addition to those received from Denmark. For some of these I am indebted to Professor W. A. Haswell, D.Sc., of Sydney, New South Wales, and G. M. Thomson, Esq., F.L.S., of Dunedin, New Zealand. A specimen, which in the Report on the 'Challenger' Amphipoda was unavoidably presented without adequate ceremony, and which in consequence subsequently became the subject of misunderstanding, is now set forth with due illustration, and a specimen from the Clyde, some years ago described without figures, now in like manner makes a more formal appeal for acceptance as the representative of a valid species.

The range of the various specimens described extends from the shore to the deep sea, from Cuba to Ceylon, from the North Atlantic to the South Pacific, from the western coast of Scotland to the eastern coasts of Australia and New Zealand. Nine genera and ten species are discussed. Six of each are new. The species afford an illustration of two difficulties which not unfrequently arise in systematic natural history. Some of them are so like their previously known neighbours that a short-sighted person might think them not worth distinguishing. Others stand oddly apart, with so queer a combination of characters that more than one existing family must look at them askance, unwilling to embrace, reluctant to repulse, in truth not very well able either "to do with them or without them." Opinions will differ on the policy of promptly establishing new families for eccentric forms, or of postponing that responsibility to as late a date as

possible. In the amiable endeavour to oblige the partisans of either view, I offer tentatively a new family for one of these perplexing species, boldly assign one to an old family, and leave one for the present homeless.

Fam. ORCHESTIIDÆ.

PARHYALE, n. g.

*First antennæ* longer than the peduncle of the second.

*First maxillæ* with the palp one-jointed, not extending beyond the distal margin of the outer plate.

*Maxillipeds* with the palp four-jointed.

Both pairs of gnathopods subchelate, differing in the two sexes.

The third uropods carrying a minute inner ramus.

*Telson* bipartite.

The character of the Orchestiidæ has to be slightly modified for the reception of this genus, since in it the third uropods are not absolutely one-branched, but show a gradation towards the more normal biramous condition.

PARHYALE FASCIGER, n. sp. (Plate 6.)

Specimens in spirit are slightly iridescent. The skin has some minute setules scattered over it. The second and third pleon-segments are squared at the postero-lateral angles. The fourth segment almost reaches to the telson, overlapping the very short fifth segment, while the sixth is dorsally obsolete. The telson is divided to the base, its two oblong or sometimes somewhat triangular leaves standing nearly upright.

*Eyes* oval, dark, obliquely set near the top and front of the head; ocelli numerous.

*First antennæ.* The second and third joints together approximately equal in length to the much stouter first joint; the flagellum of ten or eleven joints is longer than the peduncle.

*Second antennæ.* The last two joints of the peduncle nearly equal in length; the flagellum not once and a half as long as the peduncle, with about twenty joints in the male and fourteen to sixteen in the female.

*Upper lip.* The apical margin is rounded and furred in the usual manner.

*Mandibles.* The cutting-edge has six teeth. The secondary plate on the left mandible is strong and quinque-dentate, on the right it is slighter, with comb-like, slightly concave edge; the spine-row on the left attains the number of six spines, which have the appearance of plumose setæ; the molar tubercle is strong, prominent, finely denticulate, with a hairy tuft at one corner, and a long feathered seta at the other. Above it and a little in advance is the articulating process.

*Lower lip.* The lateral processes are short.

*First maxillæ.* The inner plate is slender, surmounted by two feathered setæ, of which the inner is the shorter. The outer plate is rather broad, surmounted by nine spines

variously denticulate, in two rows, which are set so closely together that it is difficult to count and discriminate the spines. The palp is slender, tipped with a minute hair and small seta. There is often a slight constriction of the margins near the apex, as though a second joint were being thought of.

*Second maxilla.* The setæ round the apex of the outer plate are longer than those of the inner. The fringe on the inner plate is bounded by a seta conspicuously longer than the rest.

*Maxillipeds.* The inner plates have the usual setæ and three apical teeth. The outer plates reach but little beyond the first joint of the palp, and have their spinules set a little within the margin. Both the second and third joints of the palp are broadly lobed at the inner distal extremity. The third joint has a little rounded and shining process for the apex of its outer margin. On the inner surface there is a graduated row of spines, and in the male a dense tuft of setæ on the outer surface, from among which the sharp curved finger projects. The inner margin of the finger carries some spinules or small hairs.

*First gnathopods.* The side-plates are widened below, and have the front margin straighter than the hinder one. The fifth joint is distally widened, and has the projecting hind margin fringed with setæ. The hand or sixth joint is as long as the preceding, and in the male fully as wide, but narrower in the female. The hind margin has a central fringe of setæ, bounded by a slight contraction in the width of the hand. The palm is rather oblique, fringed with little hairs and setules, and carrying two unequal but stoutish spines at the extremity, against which the rather broad finger impinges. There are spines on the inner surface of both hand and wrist, and minute hairs on the inner margin of the finger.

*Second gnathopods.* The side-plates are oblong, with rounded corners below, but with the hind margin somewhat excavate above. The branchial vesicles of these limbs and the four following pairs have at the base a small vesicle accompanying the ordinary large one. The marsupial plates of the female are long, distally acute, and, at least in the distal part, closely fringed. As in the first pair, the second joint widens distally, the third is short, the fourth is of nearly uniform breadth, but having the hind margin longer than the front. The wrist in the male is almost triangular, with convex front border, and behind masked by the fourth joint, whereas in the female it protrudes a spine-fringed lobe between that joint and the hand. In the male the hand is massive, with very oblique palm, uniformly convex till near the distal end, bordered with numerous little spines, over which the long and broad finger closes tightly, sending its point into a little pocket on the inner surface of the hand, from which arises a small group of stoutish spines. The hind margin is almost smooth, but has a small indent similar to that in the first pair. In the female the hand is less massive, but still much larger than the wrist, with a very oblique palm, leaving a shorter hind margin, which is fringed with spines. In both sexes the finger has little hairs set at right angles to the inner margin.

*First pereopods.* The side-plates are a little broader than the preceding pair, but similarly shaped. The fourth joint is longer and much broader than the fifth or sixth.

The finger is short, curved, with a spinule from its inner margin curving towards the small but decided nail. The fingers are similarly shaped in all the peræopods.

*Second peræopods.* The side-plates are broader than the preceding pairs, with the hind margin doubly excavate above. The limbs closely resemble the preceding pair.

*Third peræopods.* The side-plates are broad, bilobed, not very deep. The second joint has the breadth and depth about equal, with the margins very slightly indented. The fourth joint is much broader, but not longer than the sixth, which is narrower but a little longer than the fifth. The fourth joint has spines on both margins, the apical groups being large. The same applies to the fifth joint, except that its hind margin is only armed at the apex. The sixth joint has spines along the front.

*Fourth peræopods.* These are similar to the preceding, but with the joints from the second to the sixth decidedly larger.

*Fifth peræopods.* The side-plates are not bilobed. The limbs are like the preceding pair, but larger.

*Pleopods.* There are two, or in some cases three, small coupling-spines. The spines of the inner margin of the first joint of the inner ramus have a distal thickening, but no cleft could be distinguished. The rami appear to be as nearly as possible equal in length, with about thirteen joints apiece, each carrying the usual pair of plumose setæ.

*Uropods.* The first pair are the longest, with peduncle longer than the rami, having spines on its upper margin and a large spine at the apex. The rami are of equal length, with one large and other small spines at the apex, the inner having two in addition on the upper margin. The second pair are much shorter, but similarly armed. The third pair are short, the peduncle not being so long as the telson. It carries some apical spines. So does the outer ramus, which is a little shorter. The inner ramus is conical, almost rudimentary, tipped with a minute seta.

*Length.* In the partially-folded position which seems natural to animals of this genus, the length of the specimens averages a quarter of an inch.

*Hab.* Harbour, Antigua, West Indies (specimens received from W. R. Forrest, Esq.). Specimens from the Copenhagen Museum were labelled "St. Thomas, Havnen, 1877. Eggers."

The specific name refers to the appearance presented by the extremity of the maxillipeds, which in the male is very striking.

#### Fam. LYSIANASSIDÆ.

##### LYSIANAX CINGHALENSIS, n. sp. (Plate 7 A.)

First three segments of pleon large, postero-lateral angles of third segment rounded.

The *eyes* large and black, occupying most of the surface of the head, on the top of which they meet.

*First antennæ.* First joint tumid, scarcely longer than deep, nearly twice as long as the second and third combined; flagellum six-jointed, shorter than first joint of peduncle; accessory flagellum three-jointed, less than half the length of the primary.

*Second antennæ.* In the male about two-thirds the length of the animal, the ultimate joint of the peduncle considerably longer than the penultimate, flagellum of about thirty-five slender joints.

*Mouth-organs* closely agreeing with the generic account given by Sars in 'The Crustacea of Norway.' The slender mandibular palp has the first joint characteristically elongate, and there are but few spines on the palp of the first maxillæ.

*First gnathopods.* The side-plates widened below, so that they are as wide as deep; the second joint as long as the four succeeding joints combined, the third larger than the fourth, the fifth much wider but rather shorter than the narrow, tapering sixth; the finger curved, small.

*Second gnathopods.* The second and third joints slender and elongate, the fifth as long as the third, the sixth more than half the length of the fifth, gradually widening distally, with short transverse palm, on which the finger closes tightly, without overlapping it.

*First and second peræopods.* The side-plates of the second pair are deeply and rather widely excavate behind. The second joint of the limbs comparatively short; the fourth, fifth, and sixth joints rather long, with some plumose setæ.

*Third peræopods.* The side-plates wider than deep, pretty evenly bilobed; the second joint as broad as long, smaller than the side-plates; the fourth joint rather broad, produced to an acute point.

*Fourth and fifth peræopods.* The second joint broader and much longer than in the preceding pair, roundly produced behind.

*Branchial vesicles* strongly pleated.

*Uropods* slender. First pair with the rami subequal, more than three-fourths as long as the peduncle, each with three marginal spines. Second pair, with subequal rami, almost as long as the peduncle; the outer ramus with four marginal spines, the inner constricted near the end, with a spine in the notch. Third pair with the peduncle longer than the rami, produced to a point at the outer angle; the inner ramus a little shorter than the outer, both with long setæ on the inner margin.

*Telson* oval, not reaching far along the peduncle of the third uropods, having a feathered setule on each lateral margin, and the apex smoothly rounded.

*Length* three-tenths of an inch.

Labelled "Trincomali (Ceylon), 3/89, surface. K. Fristedt," Copenhagen Museum.

LYSIANAX CUBENSIS, n. sp. (Plate 7 B.)

Lateral angles of the head considerably produced, broadly rounded. Postero-lateral angles of third pleon-segment quadrately rounded.

*Eyes* reniform, moderately large.

*First antennæ.* First joint large, longer than deep, not very much longer than second and third combined, neither of these being extremely short; flagellum six-jointed, shorter than the peduncle; accessory flagellum three-jointed, less than half the length of the primary.

*Second antennæ.* Last two joints of the peduncle (in the female) subequal; flagellum broken.

*Mouth-organs* of the character usual in the genus, but palp of first maxilla with the apex rather wide, carrying one little spine and six very distinct teeth.

*First gnathopods.* Side-plates widened below, deeper than wide. The second joint shorter than the four succeeding joints combined, the fifth rather stouter than the tapering sixth and quite as long; finger small.

*Second gnathopods.* The second and third joints rather long and slender, the fifth as long as the third, the sixth much more than half as long as the fifth, at first gradually but distally rather abruptly widened; palm transverse, finger very small.

*First and second peræopods.* Side-plates of the second pair broad, the excavation being moderate in breadth and depth. The joints of the limbs of moderate dimensions, fringed with smooth setæ or spines.

*Third peræopods.* Side-plates much wider than deep, the front lobe deeper than the hinder. Second joint much wider than deep, almost as large as the side-plate, the fourth joint little widened.

*Fourth peræopods.* Second joint longer than broad, front margin strongly bowed, hind margin sinuous, fourth joint scarcely widened.

*Fifth peræopods.* Second joint much larger than in the preceding pairs, very broad, but rather longer than broad; fourth joint scarcely widened.

*Marsupial plates* slender, branchial vesicles rather strongly pleated.

*Uropods.* First pair with the rami subequal, slender, carrying a few marginal spines, somewhat shorter than the peduncle. Second pair shorter than the first; peduncle scarcely as long as outer ramus, which has four marginal spines; inner ramus slightly shorter, stout, with two spines, then strongly constricted with a spine in the notch. Third pair much shorter than second; peduncle rather longer than the rami, with one lateral margin running out into a point, the other notched near the middle, the rami almost smooth, equal.

*Telson* reaching little beyond the sides of the sixth pleon segment, little longer than broad, boat-shaped, apex truncate.

Colour of specimen, in spirit, brownish. *Length* about three-tenths of an inch.

Specimen labelled "*Lysianassa* aff. Paa en Reise til Cuba." Copenhagen Museum, Studer Collection.

#### Fam. STEGOCEPHALIDÆ.

##### ANDANIOTES, n. g.

Head with small rostrum. First segment of peræon the longest. Sixth segment of pleon longer than the fourth or fifth. Each of the first three side-plates socketed in a groove on the underside of that next succeeding; the fourth very large, subequal in breadth and depth, with a wide shallow excavation behind, overlapping the fifth and in part the sixth. Eyes wanting. First antennæ with very thick first joint; flagellum tapering, the first joint very long, longer than the remaining three combined; the accessory flagellum small, one-jointed, tipped with a long spine. Second antennæ with the last joint of the peduncle shorter than the penultimate, flagellum short. Epistoma carinate. Upper

lip broader than deep, slightly bilobed. Lower lip with the front lobes wide apart, not larger than the hind lobes, and surmounted with a single spinule at the outer corner. Mandibles a slightly sinuous oblong in shape, with straight smooth cutting-edge; a tooth-like accessory plate on the left \* mandible. First maxillæ with inner plate rather large, bordered with 7-11 long plumose setæ; outer plate moderately broad, carrying nine slender spines and a tuft of setules; the palp one-jointed, nearly reaching the end of the outer plate, tipped with seven setæ or slender spines. Second maxillæ with inner plate very broad, with a fringe of 18 or 19 setæ, most of them plumose; the outer plate shorter and greatly narrower, tipped with nine setæ. Maxillipeds with inner plates very broad, the apical margin sloping outward, with three little spine-teeth; the outer plates not nearly reaching the end of the palp's second joint, fringed with 13 spine-teeth on the inner margin; the joints of the palp successively diminishing in size, the third and fourth slender and small. Appendages of the peræon nearly as in *Andania*. Uropods with the peduncles robust, much longer than the rami; both peduncles and rami successively diminishing. In the male, outer ramus of first pair thick, curved, smooth, inner rather shorter, straight, slender, each with two marginal spinules; rami of second pair slender, smooth, subequal; rami of third pair minute, the outer nearly twice as long as the inner, with a tiny second joint. In the female all the rami slender; those of the third pair not minute, subequal, nearly as long as the peduncles. Telson broadly oval, but ending almost acutely, cleft nearly to the middle, but without any dehiscence, shorter than the peduncles of the third uropods.

ANDANIOTES CORPULENTUS (Thomson). (Plate 8.)

1882. *Anonyx corpulentus* G. M. Thomson, Trans. New Zealand Institute, vol. xiv. p. 231, pl. 17. figs. 1 a-f.  
 1888. *Andania abyssorum* Stebbing 'Challenger' Amphipoda, p. 739, pl. 37.  
 1893. *Stegocephalus abyssorum* Della Valle, Gammarini, p. 629, pl. 59. fig. 38.

*Head* with lateral angles rounded and below them produced downward in long straight triangular lobes hidden under the first side-plates, below which the mouth-organs of the down-bent head are visible. Third pleon-segment with the postero-lateral angles narrowly rounded, the dorsal line distally bent abruptly downward, having (in the male) two little eminences below the bend, the distal margin somewhat squared; the fourth segment dorsally convex; the fifth depressed; the sixth long, dorsally convex, forming two longitudinal eminences, between which the telson is concealed in a lateral view.

*First antennæ.* The third joint of the peduncle is transversely oval; the first joint of the flagellum carries transparent filaments; the setiform spine at the apex of the accessory flagellum is longer than the joint.

*Second antennæ.* The flagellum is eight-jointed.

*First gnathopods.* The side-plates are roughly triangular. The second joint is long and broad, stronger in the male than in the female; the third joint longer than broad; the fifth joint in the male longer and much wider, in the female wider but only little

\* Not on the right, as stated in the 'Challenger' Amphipoda, p. 739.

longer than the sixth, with many setæ on both margins, those in front elongate; the sixth joint abruptly narrows distally, so as to leave no palm, carrying long setæ in front, more in the male than in the female, and a row of shorter ones at right angles to the hind margin; the finger is small, curved.

*Second gnathopods.* The second joint is slender, curved at the base, the third longer than the fourth, the fifth and sixth rather slender, subequal; the curved finger impinging against the sinuous hind margin of the sixth joint, which is armed with plumose setæ.

*Third peræopods.* The second joint is scarcely dilated; the fourth is not very wide, acutely outdrawn below.

*Fourth peræopods.* Second joint twice as broad as in the preceding pair, fourth joint also larger.

*Fifth peræopods.* Second joint longer and much broader than in the preceding pair, subequal in length to the rest of the limb, broadly overlapping the third joint; the fourth joint rather wide, but much shorter than in the preceding pairs.

*Pleopods.* Coupling-spines rather long.

*Length* nearly three-tenths of an inch.

*Hab.* New Zealand. A male and a female specimen received from G. M. Thomson, Esq., F.L.S., the first describer of the species. A female specimen was also taken by the 'Challenger' Expedition.

#### Fam. PHOXOCEPHALIDÆ.

##### PONTHARPINIA, n. g.

1880. *Urothoë* Haswell, Proc. Linn. Soc. N. S. Wales, vol. iv. p. 325.

1891. *Harpinia*? Stebbing, Trans. Zool. Soc. London, vol. xiii. pt. 1, p. 4.

Back very broad, tapering to the rostrum and telson. Third pleon-segment setose on the lower hind margin. Eyes small, lateral, set rather far back. First antennæ with first joint tumid, second more slender, setose, third short; accessory flagellum many-jointed, more than half as long as the primary. Second antennæ with the basal joints of the peduncle short and stout; the penultimate long, broad, and setose; the ultimate much shorter and narrower, but also carrying long setæ; the flagellum shorter than the peduncle. Upper lip distally rounded, wide. Lower lip quadrilobate. Mandibles with cutting-plate and left mandible's accessory plate small, divided into a few teeth; spine-row of 8-10 spines, the first on the right mandible conspicuously the largest (perhaps representing the accessory plate); molar small, prominent, tipped with a few unequal spinules; palp much longer than the trunk of the mandible, third joint rather shorter than second, with many long setæ near the base and the apex. First maxillæ: inner plate small, carrying three short setæ, outer with eleven spines, very slight in size and armature; second joint of palp with 4 spinules and 4 setules on truncate apex. Second maxillæ: inner plate shorter and narrower than the outer, its armature not occupying more than half the inner margin. Maxillipeds with the plates narrow and not very long; the outer scarcely reaching the middle of the long and broad second joint of the palp, fringed with half a score of graduated spines; the fourth

joint of the palp slender and curved, considerably longer than the third. Gnathopods apparently varying in the two sexes. First and second peræopods with the fourth joint much longer than the fifth or sixth; fifth much wider than the sixth, fringed with long spines at the hinder apex; the finger small, spine-like, scarcely so large as a knife-like spine on the apex of the sixth joint. Third and fourth peræopods with the second, fourth, and fifth joints greatly widened; fifth pair much smaller than the others, its second joint much expanded, widest distally, produced to the end of the fifth joint; third joint wider than those following, which are all narrow and small; the finger straight, acute. First uropods with a long spine at apex of peduncle, rami subequal, rather longer than peduncle, spinose; second pair short, rami equal, one spinose; third pair with lanceolate rami. Telson divided into two suboval plates.

*Marsupial plates* of the female narrow.

The generic name is intended to indicate the intermediate character of this genus between such forms as those in the genera *Urothoë* and *Haustorius* of the Pontoporeiidæ and *Harpinia* in the Phoxocephalidæ. By the character of the mandibles it is better placed in the latter family.

#### PONTHARPINIA PINGUIS (Haswell). (Plate 9 B.)

1880. *Urothoë pinguis* Haswell, Proc. Linn. Soc. N. S. Wales, vol. iv. p. 325, pl. 19. fig. 2.

1882. „ „ „ Catalogue of the Australian Stalk- and Sessile-eyed Crustacea, p. 240.

1891. *Harpinia*? *pinguis* Stebbing, Trans. Zool. Soc. London, vol. xiii. pt. 1, p. 4.

1893. *Urothoë irrostrata*? Della Valle, Gammarini, p. 667.

*Head* long, tapering from a broad base. First side-plates tending to quadrate, but widened below; fourth with rounded lower margin, widest just below the shallow excavation; fifth broad, not deep, the hinder lobe the deeper; seventh very small. Third pleon-segment with a very small produced point at the lower hinder angles, above which the hind margin is finely serrulate. The fourth segment appears dorsally to overlap the fifth and sixth.

*First antennæ.* Flagellum consisting of 15 joints, accessory flagellum of 10; in a female specimen of 9 and 7 respectively. A peculiarity of these joints is that the apical margin being oblique, they overlap one another. This is shown in Haswell's figure of the primary flagellum, though he does not mention it in his text.

*Second antennæ.* Last joint of peduncle narrow at base, thence a little widening; flagellum in female with 10 joints, shaped as in the first pair. Haswell's figure shows 21 joints.

*Upper lip* wider than deep. *Lower lip* with very small principal lobes.

The *mouth-organs* in general are small, except the palps of the mandibles and maxillipeds.

*First gnathopods.* ♀. Second joint reaching much beyond the side-plate; fifth nearly as long as second and rather wider, fusiform; sixth shorter and rather narrower, widening from a narrow base, then preserving an almost uniform width to the transverse slightly convex palm, which ends in a short tooth, the convex front margin of the widened part

fringed with many seta-like spines; the finger closely fits the palm and projects a very little beyond it.

*Second gnathopods.* ♀. Almost exactly like the first, but the sixth joint rather longer and more slender, with a smaller palmar tooth, and the finger not extending beyond the palm. The marsupial plate is as long as the second joint but much narrower, while the branchial vesicle is considerably longer and much wider; the side-plate is oblong, with the lower margin slightly convex, and like the side-plates in general partly fringed with setæ.

*Gnathopods.* ♂. The species now being described is assigned to Haswell's *Urothoë pinguis* on the supposition that the account given by Haswell refers to the male, and that in that sex the gnathopods are strikingly different from those of the female. Haswell's description says:—"Gnathopoda large; anterior pair with the carpus three-fourths of the length of the propodos; the propodos ovoid, swollen; the palm not defined; the dactylos half as long as the propodos; posterior pair longer than the anterior; carpus small, subtriangular; propodos ovate, palm defined by a prominent angle; dactylos rather more than half as long as the propodos."

*Third pereopods.* Second joint expanded, longer than broad, front margin sinuous, serrulate, carrying slender spines and setæ, hind margin smooth; fourth joint broader than long, with a long free upper margin armed with slender spines, hind margin cut into 5 teeth, this and the lower margin spinose; fifth joint narrower than fourth, but still very broad, breadth and length equal, fringed with many spines and setæ; sixth joint not longer, and less than half as broad; finger quite small.

*Fourth pereopods* similar to third, but larger; second joint broader in proportion to length; fourth very large and setose, with 7 teeth on hind margin, of which the lowest two are formed by deep incisions; fifth joint rather longer than broad, about twice as broad as the sixth.

*Fifth pereopods.* The large expansion of the second joint has a smooth front margin, the hind one serrate, the lower serrulate and fringed with setæ; the fifth joint is apically finely pectinate; the finger is more than half the length of the sixth joint.

*Pleopods.* The peduncles are short; the rami with about 21 rather broad joints.

*Uropods.* The rami of the first pair are slightly curved, each with a short stout nail; the rami of the second pair are straight; those of the third pair (at least in the male) lanceolate, long, plumose.

*Telson* with length and breadth equal, the apices rather divergent, each with a spinule in a small emargination, the outer margins (in the male) setose.

*Length* of male  $\frac{1}{10}$  inch, of female  $\frac{3}{10}$  inch.

"Bondi, New South Wales, east on the beach during a storm," is the source assigned for the specimen described by Professor Haswell; the specimen here described was contained in a gathering from Jervis Bay, kindly forwarded to me by the same author.

## Fam. LEUCOTHOIDÆ.

## LEUCOTHOË INCISA, Robertson. (Plate 10.)

1888. *Leucothoë furina* Chevreux (not Savigny), Bulletin de la Société d'études scientifiques de Paris, 11<sup>e</sup> année, 1<sup>er</sup> sem., Extr. p. 9.  
 1892. *Leucothoë incisa* Robertson, Transactions of the Natural History Society of Glasgow, vol. iii. p. 217 (sep. copy, p. 23).

The drawings of this species were made many years ago, but have waited till now for a suitable opportunity for publication. The species of *Leucothoë* are separated by rather fine distinctions. In 1860 Boeck named a new species *Leucothoë Lilljeborgii*, but in his later works he was willing to let this lapse as a synonym of the long known *Leucothoë spinicarpus* (Abildgaard). In 1889 Norman gave the name *imparicornis* to a form from Shetland, which Sars in 1892 determines to be the same as Boeck's *Lilljeborgii*, the latter name having priority. To this species, as figured and described by Sars, *Leucothoë incisa* makes a tolerably close approximation, yet it seems difficult to unite the two. In *incisa* the fourth side-plates have the front angle rounded, not acute; the first gnathopods have the tip of the process of the fifth joint strongly hooked, the inner margin of the hand not quite smooth but faintly crenulate, and the finger not very small; in the second gnathopods the palm is convex and faintly but broadly crenulate, the finger is not abruptly bent at the base; the telson, instead of being little longer than broad, is fully twice as long as broad, with the apex almost acute. As in *Lilljeborgii*, the inner margin of the wrist in the first gnathopods is serrate, and the postero-lateral angles of the third pleon-segment are sharply upturned, forming a sinus with the bulging hind margin. There is a tendency to this in the preceding segment. The mandibles have the cutting-edge divided into about eight teeth; the secondary plate on the left mandible is large, with ten teeth, that on the right is much slighter (Sars denies its existence in this genus); the second joint of the palp is not much longer than the narrower third. In the maxillipeds the first and second joints of the palp have the length and breadth subequal.

*Length* not quite three-tenths of an inch.

Taken off Cumbræ, in the Clyde, at low water and also in 20 fathoms, by Dr. David Robertson, LL.D., F.L.S.

## ANAMIXIS, n. g.

Head hood-like. First side-plates small, three following pairs very large. Eyes well developed. First antennæ attached below the apex of the head, with elongate peduncle and no secondary flagellum. Second antennæ remote from the first, shorter and thinner, with small flagellum. Mouth-organs (at least in the adult) degraded and abnormal. Maxillipeds with the full number of joints, the third simple. First gnathopods delicately chelate; second massive, complexly subchelate; the other limbs slight, normal. Branchial vesicles small, simple. Pleopods small. First and second uropods biramous, third at present unknown. Telson simple.

The shape of the head calls to mind the genus *Dulichia*, the situation of the antennæ *Platyischnopus*, the size of the side-plates *Metopa*, the massiveness of the second gnathopods *Microtopus*, the structure of both pairs of gnathopods and of the antennæ and

maxillipeds *Leucothoë*. In reference to this combination of characters the name of the genus has been chosen, from the Greek word *ἀνάμιξις*, mingling. Among existing families it stands nearest to the Leucothoidæ, but the extraordinary nature of the mouth-organs—whether due to a parasitic mode of life or to a marital stage of existence, or falling under any other explanation—so far isolates the species now to be described that it may have to be placed alone in a separate family, Anamixidæ, which would for the present bear the characters of the genus.

ANAMIXIS HANSENI, n. sp. (Plate 11)

The *head* is longer than any one of the pereon-segments, and is narrowed distally, with rounded apex, with no distinct lateral angles. The second pleon-segment has the postero-lateral angles acute, slightly produced; those of the third are a little blunted. The fifth segment is very short, scarcely distinguishable from the fourth; the sixth projects on either side of the telson, in a way to suggest that the missing third pair of uropods may be of a fairly large size.

The *eyes* are round, placed in the middle of the sides of the head, consisting of about eighteen short ocelli.

*First antennæ*. The first joint long and rather stout, the second nearly three-quarters as long as the first, but much more slender, the third about two-fifths of the second; the flagellum eleven-jointed, a little longer than the first joint of the peduncle. A sensory filament is present on several of the joints. These antennæ depend from the head, being inserted just below its apex.

*Second antennæ*. These are inserted at the other extremity of the head. The first two joints are very small, the third is little more than half as long as the first of the upper antennæ, the fourth is slightly longer than the second in the other pair, and the fifth is a little longer than the third joint of its own pair. The slender flagellum is four-jointed, less than half as long as the penultimate joint of the peduncle.

*Mouth-organs*. The underside of the head is slightly carinate, and apparently attached to the keel there projects from between the second antennæ a vertical plate, which may be called the oral lamina. Its truncate front edge has some minute microscopic teeth. With this curious and abnormal exception, no mouth-parts could be detected other than the pediform maxillipeds.

*Maxillipeds*. The second joint bulges slightly on the upper or inner side, while on the outer or lower side it has a shallow cleft, between two smoothly rounded apices, which just overlap the bases of the third joint. The third joint has no lobe or lamina, but in appearance is the basal joint of a five-jointed palp. Of the actual palp the first and second joints are about equal in length, the second the wider, carrying some setæ on the lower margin, the third joint is longer than either of the preceding, armed with several setæ, and having its surface minutely furred. The fourth joint or finger is slender, strongly curved, nearly as long as the third joint. Owing to the absence of plates from the joints of the protopod the palps are in close contiguity. The appearance is rather that of legs than of mouth-organs. In dissection the head came easily away, leaving the maxillipeds very firmly attached to the first gnathopods.

*First gnathopods.* The side-plates are small, triangular, with the apex to the rear. The second joint is slender, narrowest at the base. The small third joint is larger than the fourth. The fifth joint is very much wider and much longer than the second joint. It may be regarded rather as the hand than the wrist, its long and slender curved apical process, tipped with a slightly curved needle-like spine, forming the immovable finger of the chela, while the sixth and seventh joints form the movable finger. The sixth joint is slender, rather straighter than the process of the fifth, but otherwise very like it, and tipped with a similar spine, which must be regarded as the seventh joint. It might be supposed that the fifth joint in this remarkable form represented a coalescence of the wrist and hand, did not a comparison with the first gnathopods in *Leucothoë* make it reasonably certain that the chela is composed in the way just described.

*Second gnathopods.* The side-plates are very large, rounded in front, produced beyond the first segment. The second joint is narrow, distally somewhat widened, a little curved. The third joint is of stouter build than usual, apparently articulating with all the three following joints. The fourth joint is small, most of it lying flatly on the inner surface of the fifth joint, with which it seems to be in coalescence. The fifth joint is subequal to the second, but broadest at its base and apically pointed. The hand is broad and between three and four times as long as its breadth, the hind margin distally cut into three teeth. The finger, more than half the length of the hand, has a curved acute tip, and two slight projections on the inner margin. The complex clasper is formed by its impinging against the apex of the wrist and the denticulations of the hand. The peculiar arrangement of the third and fourth joints may be explained by the extraordinary massiveness of these limbs and especially of the hand, which is in striking contrast to that of the preceding pair as well as to the general structure of the other limbs.

*First pereopods.* The side-plates are as deep as the preceding pair, but of much less width. The branchial vesicles are all of remarkably small size. The second joint reaches a little below the side-plate. Of the other joints the fourth is the widest, the fifth is shorter than the sixth, the nail is slender and curved.

*Second pereopods.* The side-plates are rather wider than the preceding pair, with a faint emargination at the farther end of the lower margin and a very shallow excavation at the upper part of the hind margin. The limb differs but little from the preceding.

*Third pereopods.* The side-plates are bilobed, with the hinder lobe the larger. The second joint is not much longer than wide. The fourth joint has the hind margin slightly produced. The rest of the limb is missing. The spiny armature in these and the other limbs is insignificant.

*Fourth pereopods.* The side-plates are lobed behind. The second and fourth joints are rather larger than in the preceding and following pairs.

*Fifth pereopods.* The side-plates are small, rounded behind. The second joint is rather more strongly spined along its front margin than is the case in the other limbs.

*Pleopods.* The rami are small, five- or six-jointed, shorter than the peduncles.

*Uropods.* The first pair are the longer. In both, the inner ramus is a little longer and the outer considerably shorter than the peduncle. The third pair are missing.

*Telson.* This is a little longer than broad. The broadly rounded apex does not reach so far back as the projecting points of the preceding segment, which are in turn overlapped by the peduncles of the second uropods and these by the peduncles of the first pair.

The *length* of one specimen, with tail folded in, was less than a tenth of an inch, of the other rather more than a tenth.

*Hab.* West Indies. From *Goniastræa varia* Dana.

The name is given in compliment to my friend, Dr. H. J. Hansen, the accomplished naturalist by whom it was obtained.

#### Fam. PARDALISCIDÆ.

#### PARDALISCOIDES Stebbing.

1888. *Pardaliscoides* Stebbing, 'Challenger' Amphipoda, p. 1725.

1893. *Pardalisca* Della Valle, Gammarini, p. 691.

First antennæ longer than second, second joint of the peduncle longer than the first, both flagella many-jointed. Mandibles with broad cutting-edge; that on the left side having two blunt teeth above and two that are acute below, one of them small, the other large, a rather broad accessory plate with crenulate edge, and two plumose spines; that on the right having a similar cutting-edge minus the smaller acute tooth, no accessory plate, but three plumose spines; the three-jointed palp slender, fringed with setiform spines. First maxillæ with one seta on the small inner plate, seven very unequal spines on the inner plate, one of them plumose; the second joint of the palp broad, with many spinules about the apical margin. Second maxillæ with the plates slender, the outer carrying three, the inner seven setæ. Maxillipeds with inner plates very small, outer plates short and narrow, fringed with spinules, the supporting joint not very large; palp with first joint short, second robust and long, but scarcely longer than the third, the finger long and slender with minute setules on the inner margin. The triturating organs (anterior lateral gastric lobes) are armed with six long spines. The gnathopods are similar, simple, with the fifth joint robust, fusiform, the sixth and seventh slender, the seventh fringed with minute setules. The peræopods are slender, elongate. The second uropods have the rami unequal, the third have the rami foliaceous. The telson is deeply cleft.

#### PARDALISCOIDES TENELLUS Stebbing. (Plate 12.)

1888. *Pardaliscoides tenellus* Stebbing 'Challenger' Amphipoda, p. 1725.

1893. *Pardalisca abyssi* Della Valle, Gammarini, p. 692.

*Head* with acute rostrum. There appears to be a small dorsal denticle on each of the last two or three segments of the pleon.

*First antennæ.* The first joint stout, the third half the length of the second; of the flagellum thirteen joints remain, the first much the longest; of the accessory flagellum seven or eight joints remain, the first as long as that of the primary.

*Second antennæ.* Last two joints of the peduncle elongate, the last shorter than the preceding; the flagellum half the length of the peduncle, twelve-jointed.

*First and second gnathopods.* There are numerous spines of various sizes on and near the margins. On the hind margin of the wrist and hand, commencing at the narrowed distal end of the wrist, is a series of short spines which are plumose. The setules on the inner margin of the fingers are exceedingly small.

*First and second peræopods.* The fifth joint longer than the fourth or the sixth; the second pair rather longer than the first, and further distinguished by having the hind margin of the sixth joint fringed with about a dozen short blunt spines.

*Third peræopods.* Second joint very slightly expanded, fourth joint the longest; finger slender, acute.

*Fourth peræopods* like the third, but with rather longer joints.

*Fifth peræopods* considerably longer than the fourth, the second joint expanded above, narrowing downward, fourth joint very long. Branchial vesicle small, narrowly oval.

*Telson* much longer than broad, cleft three-fourths of the length, dehiscant, with a spinule at each apex and a setule on each lateral margin.

*Length* not quite a third of an inch.

*Hab.* South Pacific, lat. 37° 29' S., long. 83° 7' W. Taken by H.M.S. 'Challenger,' in tow-net at trawl, from a depth of 1775 fms.

#### Fam. EUSIRIDÆ.

##### EUSIROPSIS, n. g.

Head distinctly rostrate; body without dorsal projections; side-plates of pereon shallow. Antennæ of male with calceoli on peduncle and flagellum in both pairs; first antennæ shorter than the second, secondary flagellum one-jointed; the second antennæ of male with the last joint of the peduncle very elongate. Mouth-organs nearly as in *Eusirus*, but the mandibles have the molar feebly developed and the first maxillæ have the second joint of the palp narrower and scarcely longer than the first. Gnathopods nearly as in *Eusirus*, but with the backward projection of the carpus almost obsolete. First and second peræopods slender, with the finger ending obtusely and tipped with long setæ. The three following peræopods slender, elongate, plumose, with the fingers acute. The uropods of the first two pairs with outer branch much shorter than inner, the third pair very plumose in the male, the outer ramus shorter than the inner. The telson narrow, apically incised.

##### EUSIROPSIS RHISEI, n. sp. (Plates 13, 14.)

Head with triangular rostrum longer than broad; second, third, and fourth the shortest of the pereon-segments; first three segments of pleon large, with the posterolateral angles rounded, hind margin not serrate.

*Eyes* to all appearance entirely wanting.

*First antennæ.* First joint rather bulky, carrying eight tufts of setules on the lower margin; second joint rather shorter and much narrower than the first, with calceoli along the lower margin; third joint almost like a joint of the flagellum; the latter rather

stout, carrying a calceolus on each of the thirty-one joints remaining, the end being broken off. The secondary flagellum is minute and quite unobtrusive.

*Second antennæ.* The first three joints very short; the fourth stout, not so long as the first of the upper antennæ, furnished on the upper margin with nine tufts of setules; the fifth slender, longer than the whole peduncle of the other pair, armed above with many calceoli; the flagellum longer than the peduncle; of the forty-two joints twenty-seven carry each a calceolus on the upper side, the terminal fifteen, which are more slender and elongate than most of the others, having each a sensory filament. It may be supposed that the abundant armature of the antennæ compensates the animal for its want of eyes.

*Upper lip.* The apical margin is rounded, and the usual fringing moustache is strongly developed.

*Mandibles.* As in the neighbouring genus *Eusirus* the cutting-plate is scarcely dentate, the secondary plate on the left mandible is quinque-dentate, on the right it is more spine-like; the spine-row contains five or six small spines; the molar is very feeble and unobtrusive; the second joint of the palp is robust, the third is narrower but rather longer, fringed with many spinules.

*Lower lip.* The inner lobes are small.

*First maxillæ.* The inner plate is feeble, short, and seemingly not armed with any setæ; the outer plate carries ten spines, of which the two outermost are the largest, the rest are denticulate; the palp has a stout first joint, but the second is weak and tapering, scarcely longer than the first, tipped with five setæ.

*Second maxillæ.* The inner plate is broader than the outer, but its apical armature is shorter and very scanty.

*Maxillipeds.* The inner plates reach only to the base of the palp, and are not strongly armed, but have the usual apical teeth; the outer plates reach scarcely to the middle of the palp's second joint, and are fringed with not numerous setules. The palp's second joint is broad and carries a conspicuous row of setæ near the apex; the third joint is similarly armed; and the finger, which is long and strong, has a few small setules on its inner margin.

*First gnathopods.* The side-plates are very shallow, covering no part of the limb's second joint. The fourth joint is subequal to the third, its broad apex reaching almost to the base of the hand, and having the wrist attached to its front margin. The distal end of the wrist is attached to the front margin of the hand, not to the side as might be supposed from the drawings made from mounted and somewhat flattened dissections. On the inner side of the wrist there is a small process, probably homologous with the large one in *Eusirus* which intervenes between the fourth joint and the base of the hand. The hand is massive, distally widened, with long convex palm carrying setules, and ending in a spinigerous pocket, into which the long curved finger inserts its tip.

*Second gnathopods.* The side-plates are shallow, longer above than below. The branchial vesicles attached to these and the five following pairs of limbs have accessory lobes. The joints of the second gnathopod show scarcely any difference in shape from those of the first.

*First pereopods.* The side-plates have a curious sort of axe-head shape, the front

corner rounded, the hinder acutely produced. The whole limb is very slender, and, like all the other peræopods, is adorned with long plumose setæ. The second joint is elongate, with four or five setæ on the hinder margin and two on the front. The fourth joint has four setæ on the front margin; the fifth has one on the front and two on the hind margin; the sixth, which is rather longer than either of the two preceding, has two setæ of great length on the hind margin and two or three on the front. The seventh joint is not finger-like, less than half the length of the sixth, its apical margin not acute, fringed with six plumose setæ, mostly of great length.

*Second peræopods.* The side-plates are almost oblong, twice as long as deep, with the upper margin slightly excavate. The limbs are in near agreement with the preceding pair.

*Third peræopods.* The side-plates are bilobed, the hinder lobe the deeper. The second joint is expanded, rather deeply notched on the hind margin. The third joint is short. The remaining joints are all very elongate, armed with numerous spines and long plumose setæ on both margins, except in the case of the finger, which has the setæ only on the hind margin. The fourth, fifth, and sixth joints are severally much longer than the second, which is scarcely, if at all, longer than the straight acute finger.

*Fourth peræopods.* The hind lobe of the side-plates is rather long, the front one evanescent. The limb is like that of the preceding pair, but with a larger second joint, and the fifth decidedly shorter than the sixth.

*Fifth peræopods.* The side-plates are not bilobed. As already noticed, there are branchial vesicles. The second joint is rather longer than in the preceding pair, while the fifth and sixth are not quite so long. As in the two preceding pairs, the setæ fringing the margins of the sixth joint are of great length, and the hinder apex carries a remarkable tuft of these elongate appendages, which, together with those on the fingers, produce a striking effect.

*Pleopods.* There are three or four cleft spines on the first joint of the inner ramus, this ramus consisting of seventeen joints, while the outer, which is slightly longer, has nineteen.

*Uropods.* In the first pair the peduncle is nearly as long as the inner ramus, and carries some small plumose setæ on its outer, and spines on its inner margin. The outer ramus is a little more than half the length of the inner. Both have many spines along the margins, those on the inner margin of the inner ramus being small but very close-set. The peduncle of the second pair is about as long as the outer ramus, which is less than half the length of the inner. These rami are armed as in the preceding pair, which they a little exceed in length. In the third pair the peduncles rather exceed in length those of the preceding pair. The outer ramus is a little shorter than the inner of the second pair; it has spines at six points of the outer margin, and the inner fringed with spines and many long plumose setæ. The inner ramus is rather longer than that of the second pair, and is fringed on both margins with spines and long plumose setæ.

*Telson* longer than the peduncles of the third uropods, distally cleft for about a quarter of its length; a little way above the acute apices a notch on either outer margin carries a long seta, and there is another a little higher up than the top of the cleft.

*Length*, not including the antennæ, in the slightly curved position of the specimen figured, two-fifths of an inch.

*Hab.* Tropical Atlantic. The label accompanying the specimen figured contained the words "*Riisei* 55. Stud. Saml. ded. 1892." A second specimen, in less satisfactory condition, was labelled "22° N.B. 36° V.L. Hygom. Stud. Saml. ded. 1892." Copenhagen Museum.

The specific name was given in MS. by Professor Lütken in compliment to Herr Riise.

Fam. undetermined.

SANCHO, n. g.

Rostral point small. Peræon depressed, very broad at the centre; first segment short, seventh unusually long. Pleon narrow, much of it flexed. Eyes on the top of the head, separate. First antennæ with principal flagellum longer than peduncle; accessory flagellum small, one-jointed. Second antennæ with last joint of peduncle longer than the preceding joint. Upper lip not emarginate. Lower lip without inner lobes. Mandibles with cutting-edge, accessory plate, and spine-row small, but molar and three-jointed palp powerful. First and second maxillæ normal. Maxillipeds with outer plates smaller than, and scarcely reaching beyond, the inner; fourth joint of palp small. Gnathopods subchelate, the first pair in both sexes feeble; the second also feeble in the female, but in the male very long with very bulky sixth joint. Peræopods normal, the fifth pair the longest. Second uropods with peduncle scarcely shorter and rami much longer than those of the first, third with short peduncle but very long inner ramus; in all three pairs the outer ramus is shorter than the inner. Telson short, triangular.

The name is taken from a character famous in fiction.

SANCHO PLATYNOTUS, n. sp. (Plate 9 A.)

The second and third pleon-segments have the postero-lateral angles minutely produced; at the second segment the pleon is bent and the remainder closely adpressed to the ventral surface of the trunk.

*Eyes* round, separated by more than the diameter of either, composed of numerous ocelli, of which those of the outer ring appear to be larger than the rest. Specimens preserved in spirit have a light pinkish pigment.

*First antennæ.* First joint stout, about once and a half as long as broad, second much shorter and thinner, third about half the length of second; flagellum in male of forty-one joints, the first longer than the last of the peduncle, followed by many joints not longer than broad, to which succeed several much longer than broad.

*Second antennæ.* The basal joints short, the last joint of the peduncle rather long, longer and thinner than the penultimate, which has an apical tooth; the flagellum in the male similar in structure to that of the first antenna, but perhaps shorter; thirty-three joints in an example not quite perfect.

*Upper lip* with broad front, the margin little curved.

*Mandibles.* The cutting-edge small, little dentate, the molar massive; the third joint of the palp broad, distally fringed with spinules.

*First maxillæ.* Inner plate oval, tipped with two setæ, outer plate with the eleven apical spines very small, inconspicuously denticulate; second joint of the palp broad, with some apical setules.

*Second maxillæ.* The inner plate broader than the outer, both apically fringed with spines, which are longer on the outer plate.

*Maxillipeds.* The inner plates broad and with the inner margins protruding; the outer plates reaching scarcely beyond the end of the first joint of the palp, fringed with slender spines on the inner margin; the second joint of the palp rather large, fringed with long setæ, the third joint much narrower but not much shorter, the fourth both short and narrow, tipped with spines or setæ.

*First gnathopods.* Side-plate distally widened. The second joint is moderately long and narrow, unarmed; the fourth little longer than the third; the fifth in the male considerably longer and narrower than the sixth, both having the hind margin fringed with spinules; the sixth is rather longer than broad, with spinules at the front apex, and a small palm which matches the weak finger. In the female there is little difference in the length and breadth of the fifth and sixth joints.

*Second gnathopods.* Side-plates broader and of more uniform width than the preceding pair. In the male the second joint is narrowed at the point of attachment and broadest near the centre, though nowhere very broad; the fourth joint is longer than the third, but shorter than the fifth, all three being narrow; on the contrary, the sixth, besides being longer than the fifth, is from the very base enormously broader, its front margin nearly straight, the opposite curved, slightly crenulate, the broad, slightly sloping palm divided into three or four irregular teeth; the smooth, eurved, and rather massive finger closes down over the palm into a great pocket excavated in the thickness of the hand. In the female these limbs closely resemble the feeble first gnathopods, but with the fifth and sixth joints a little longer.

*First peræopods.* Side-plates with convex front and concave hind margin. The second joint moderately long, the sixth longer than the fourth or fifth, which are subequal; the finger short, acute, slightly eurved, having a spinule on the concave margin.

*Second peræopods.* Side-plates larger than the preceding, the hind margin excavate, serrate below the excavation. The limb resembles that in the preceding pair, but with the fourth and fifth joints a little longer.

*Third peræopods.* Side-plates not very large, pretty equally bilobed, the hind lobe produced below the front. The second joint tending to oval, the hind margin feebly serrate; the fourth joint rather strongly produced downward.

*Fourth peræopods.* Side-plates with hind lobe produced much below the front. The second joint more oblong than in the preceding pair, the hind margin nearly straight, fringed with long setæ; the fourth joint strongly produced.

*Fifth peræopods.* Side-plates small. Second joint larger than in the preceding pair, the straight hind margin more strongly produced downward; the fourth joint similar to that in the preceding pair, but with more numerous spines; the fifth and sixth joints

are narrow, elongate, subequal, with numerous marginal spines and spinules; the finger comparatively small.

*Pleopods.* Inner margins of the peduncles closely adjacent; coupling-spines small; rami with eleven or twelve joints, and two cleft spines on the first joint of the inner ramus.

*Uropods.* Of these little more can be said than is stated in the account of the genus. The short peduncle of the third pair has a dentate apex, to which the long inner ramus is perhaps very loosely attached, as it was wanting from the majority of specimens, notwithstanding the protection given by the folding of the pleon; in young ones not yet released from the maternal pouch it was well developed.

*Telson* not longer than broad, scarcely so long as the peduncle of the third uropods, the sides convex till near the apex.

*Length*, without the flexed portion of the pleon, from about a tenth to an eighth of an inch, or 3 mm.

*Locality.* Port Jackson, in Australia. Sent by Professor W. A. Haswell, M.A., D.Sc. The specific name is derived from  $\pi\lambda\alpha\tau\acute{\upsilon}\alpha$ , broad, and  $\rho\acute{\omega}\tau\alpha\alpha$ , a back.

#### EXPLANATION OF THE PLATES.

*a.s.*, upper antenna; *a.i.*, lower antenna.

*l.s.*, upper lip; *l.i.*, lower lip.

*m.*, mandible; *mx.* 1, 2, 1st and 2nd maxilla; *mxp.*, maxillipeds.

*gn.* 1, 2, 1st and 2nd gnathopods; *pp.* 1-5, 1st to 5th pereopods; *br.*, branchial vesicle.

*plp.*, pleopods; *ur.* 1, 2, 3, 1st, 2nd, and 3rd uropods.

*T.*, telson.

A line above the figure of a whole specimen indicates the natural size.

#### PLATE 6.

*Parhyale fasciger*, n. g. et sp.

The lateral view of the whole animal and the figures on the left hand and down the centre of the Plate are from male specimens, those on the right hand are from a female specimen.

The antennæ and appendages of the pereon and pleon have a uniform enlargement; so also, but on a higher scale, the mouth-organs, portions of the gnathopods of both sexes, the third uropods and telson of the male, second and third uropods and telson of the female, portions of the first maxilla and mandibles being still more highly magnified.

#### PLATE 7.

**A.** *Lysianax cinghalensis*, n. sp.

All the parts are magnified to the same scale, except a portion of *mx.* 1, which is more highly magnified than the rest.

**B.** *Lysianax cubensis*, n. sp.

The antennæ, limbs, uropods, and telson are drawn to the same scale, while still more magnified figures are given of the mouth-organs, part of the second gnathopod, second and third uropods, and telson in two positions.

## PLATE 8.

*Andaniotes corpulentus* (Thomson).

Antennæ, mouth-organs, uropods, and telson, more magnified than the limbs and figures of uropods and telson at foot of Plate. Mandibles seen from the outside, so that the accessory plate is not visible.

## PLATE 9.

*A. Sancho platynotus*, n. g. et sp.

Dorsal view of a male specimen, the last three joints missing in the third, fourth, and fifth peræopods. The mouth-organs, uropods, and telson (in both sexes) are magnified more highly than the other parts.

*B. Pontharpinia pinguis* (Haswell).

The mouth-organs and telson are more highly magnified than the other parts.

## PLATE 10.

*Leucothoë incisa* Robertson.

Antennæ, appendages of peræon and pleon, on a uniform scale, other parts more enlarged. *Pls.* 1, 2, 3, postero-lateral angles of 1st, 2nd, and 3rd pleon-segments. *plp.sp.*, coupling-spines from peduncle of pleopod.

## PLATE 11.

*Anamixis Hanseni* n. g. et sp.

In the lateral view of the animal the ends of the 3rd, 4th, and 5th peræopods are missing.

*a.s.A.*, *a.i.A.*, the antennæ of a second specimen.

*or.l.*, supposed oral lamina projecting vertically from underside of head.

*maxp.* (in middle line of Plate), maxillipeds as seen from within; *maxp. Δ.*, from a different specimen, the lower figure giving a lateral view, the upper an exterior one.

*gn.* 1, *gn.* 2, the figures on the left hand are from the inner side of the limbs, those on the right from the outer side. In the latter the finger and part of the hand of *gn.* 2 are missing.

## PLATE 12.

*Pardaliscoides tenellus* Stebbing.

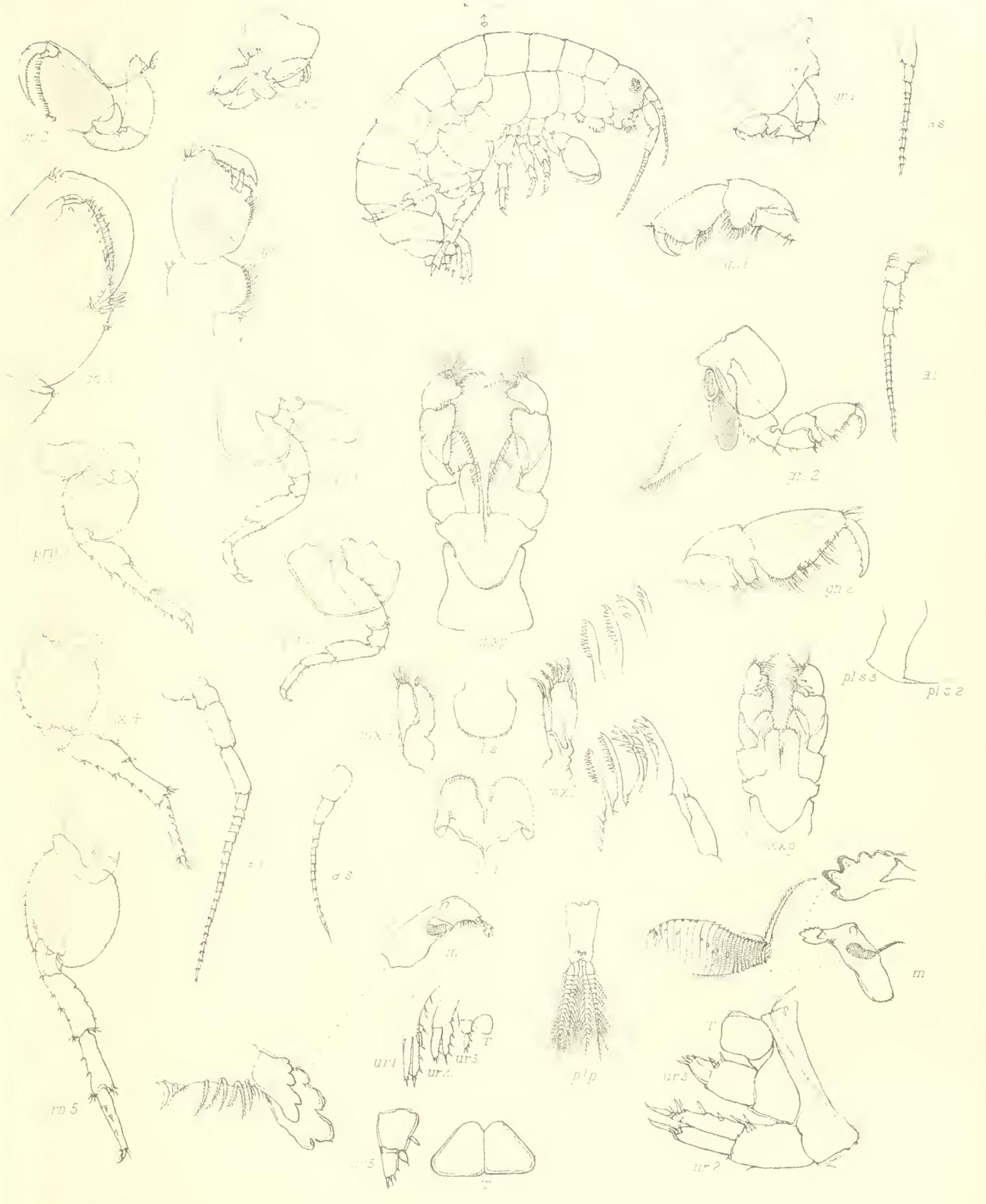
The mouth-organs are more highly magnified than the other parts.

## PLATES 13, 14.

*Eusiroopsis Riisei*, n. g. et sp.

In Plate 13 the first gnathopod is seen from the outer side, in Plate 14 from the inner side.





W. Stebbins, dc.

JTR:lh



A.



B.

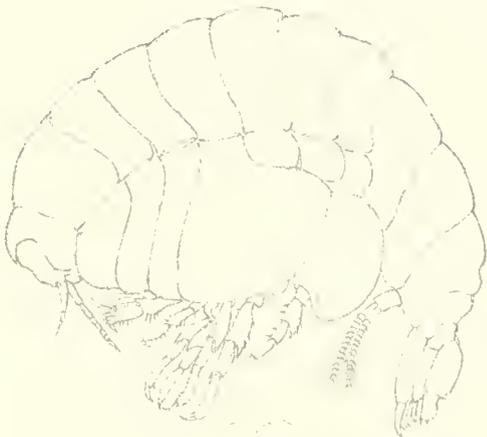


*Streblospio*

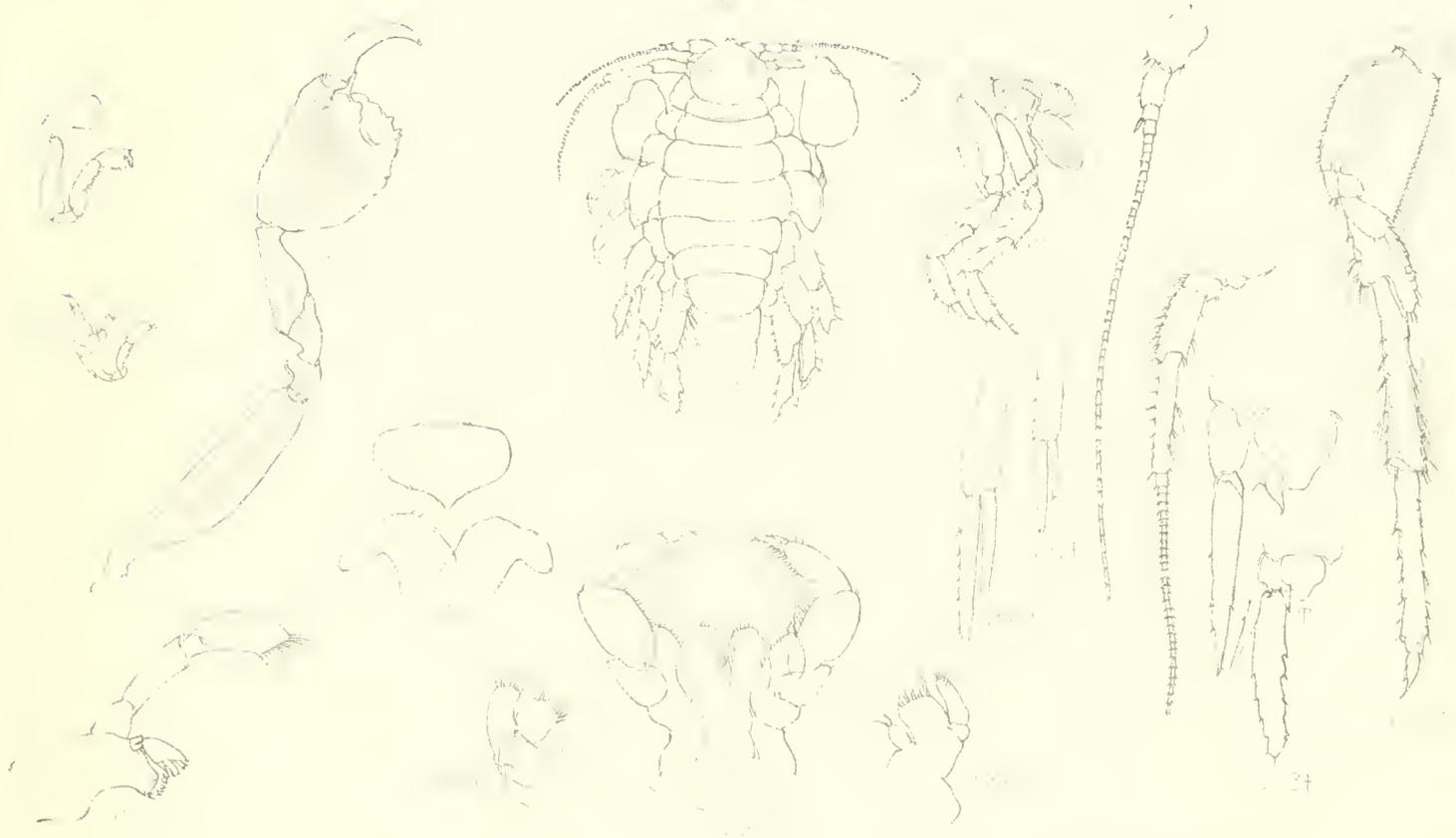
A. *Streblospio benedicti* (Stebbing)

B. *Streblospio benedicti* (Stebbing)

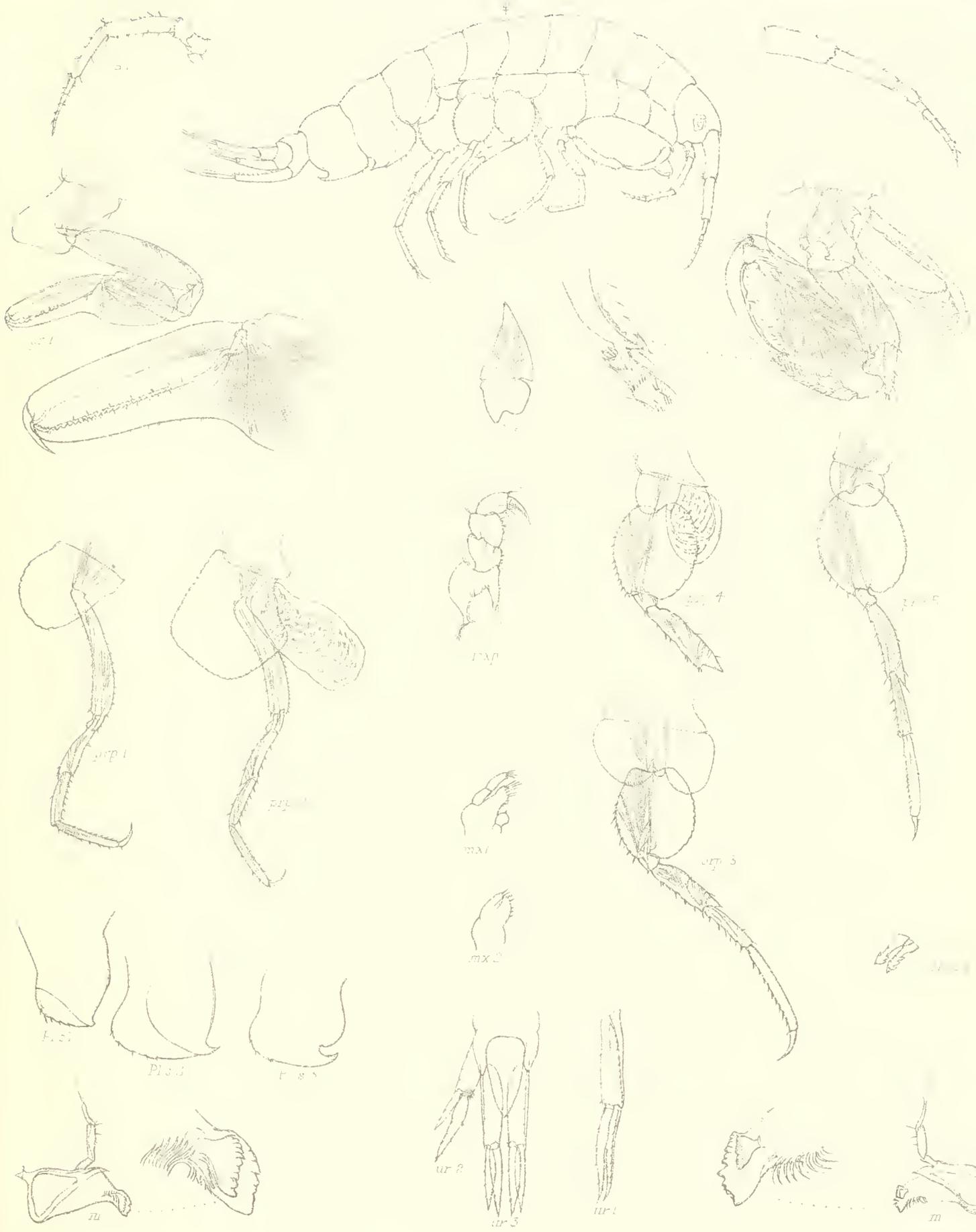








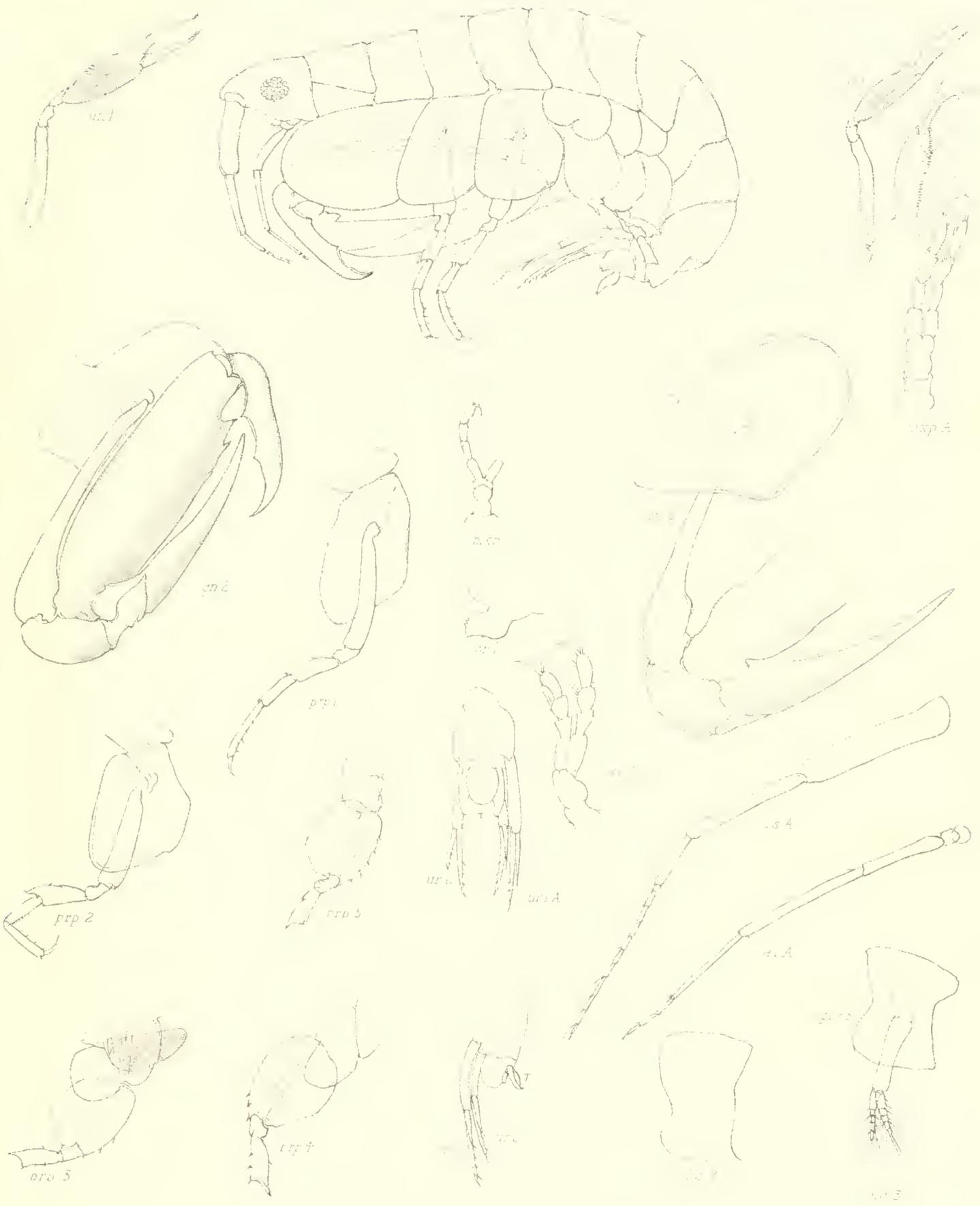




Rk. Stebbing del.

L. Kroyer



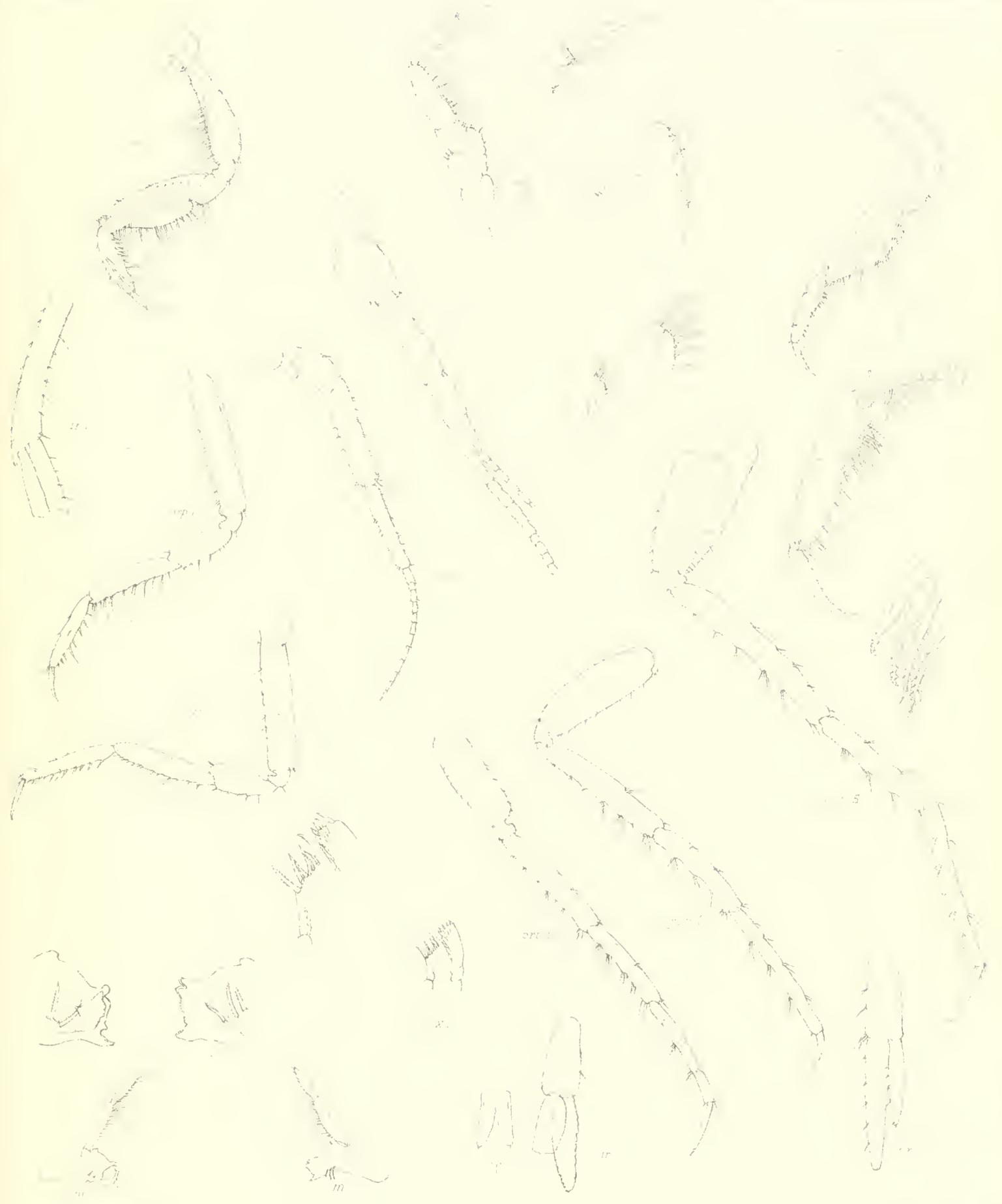


A. R. Scl. h. g. del.

A. P. Scl. h. g. del.

ANAMIRIS LANSENI NOV. GEN. ET SP.





*L. ...*

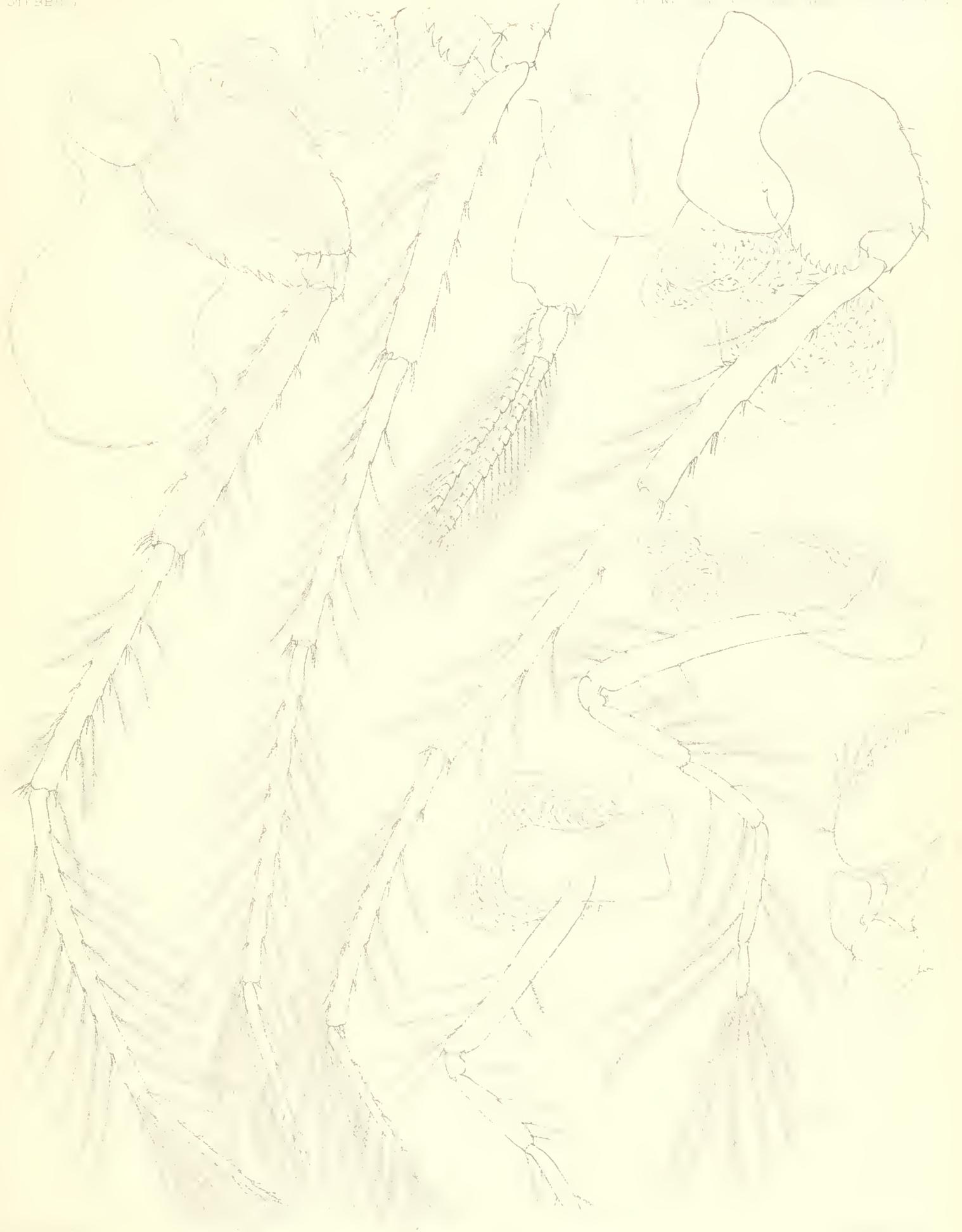
FAMILIA ... IDES TENEBRIONIDAE

*L. ...*













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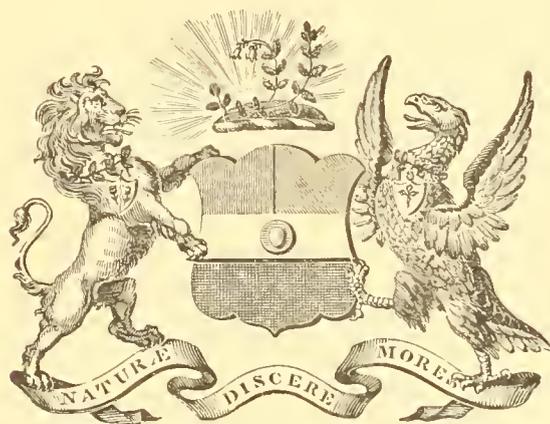
THE ORIGIN OF THE CORPUS CALLOSUM:  
A COMPARATIVE STUDY OF THE HIPPOCAMPAL REGION OF THE CEREBRUM  
OF MARSUPIALIA AND CERTAIN CHEIROPTERA.

BY

G. ELLIOT SMITH, M.D., CH.M. (SYDNEY),

"JAMES KING" RESEARCH SCHOLAR OF THE UNIVERSITY OF SYDNEY; ST. JOHN'S COLLEGE, CAMBRIDGE.

*(Communicated by Prof. G. B. Howes, Sec. Linn. Soc.)*



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III. *The Origin of the Corpus Callosum: a Comparative Study of the Hippocampal Region of the Cerebrum of Marsupialia and certain Cheiroptera.* By G. ELLIOT SMITH, M.D., Ch.M. (Sydney), "James King" Research Scholar of the University of Sydney; St. John's College, Cambridge. (Communicated by Prof. G. B. HOWES, Sec. Linn. Soc.)

(Plates 15 & 16.)

Read 21st January, 1897.

IT is now a generally recognized fact that the dorsal commissure of the Metatherian is not strictly homologous to the similarly-situated commissure of the Eutherian cerebral hemispheres. For while the dorsal commissure of the Marsupial springs mainly, if not wholly, from that peculiar cortical formation which we know as "*hippocampus*," its topographical representative in the more highly-organized mammal is derived from a much wider cortical area, of which the hippocampus constitutes a part—and in the great majority of cases only a relatively very small part. In other words, the dorsal commissure of the Metatherian is essentially "hippocampal," while that of the Eutherian cerebrum is partly "hippocampal" and partly "non-hippocampal." These "non-hippocampal" fibres of the dorsal commissure of Eutheria are derived from the general or typical cortex which Sir William Turner calls "*pallium*."

It will be found that in higher mammals, such as the Primates, the Cetacea, the Carnivora and Ungulata, the "pallial" element forms the main bulk of the dorsal commissure. But if we compare a large series of mammalian cerebra we find that, speaking generally, there is a rapid decrease in the extent and importance of this "pallial" factor as we descend the Eutherian scale. The "pallial" or "non-hippocampal" factor shows a rapid actual decrease, while the hippocampal factor takes a continually increasing share in the constitution of the dorsal commissure. From such considerations, and from the knowledge that the "pallial" factor was wanting altogether in the Marsupialia, it seemed likely that some Eutherian form might be found in which the newer "non-hippocampal" element might be so slightly developed as not to interfere with or destroy the resemblance of its dorsal commissure to that of the Marsupial. And if such a transitional form could be found we ought to be able to decide the exact relation of the newly-developed "pallial" fibres to the pre-existing "hippocampal" fibres, and hence form some accurate conception of the nature of this new commissure, which in its highly-developed state in man we know as the "*corpus callosum*."

The desired "connecting links" I have had the good fortune to find in certain Cheiroptera—*Nyctophilus Timoriensis* and *Miniopterus Schreibersii*—both of which, but more especially the former, realize the conditions above stated.

In this contribution I propose to compare the commissures and certain neighbouring

cortical areas of these bats with the Marsupial type, in order to find out the distinctive mode of arrangement of the former. Having determined the nature of the dorsal commissure of the bat and its relation to the pre-existing type, I shall attempt, by means of comparison with more highly-developed Eutherian forms, to indicate the true lines along which the evolution of the corpus callosum proceeds in the Mammalia.

For a considerable time I have been aware of the fact that Zuckerkandl, in his remarkable work upon the olfactory centre ('Ueber das Riechcentrum,' 1887), had grouped together the brains of Monotremes, Marsupials, and certain small Cheiroptera on the ground that they presented in common certain features in which they differed from all other mammals.

These distinctive features were stated in the following terms:—(1) that the Randbogen [or Randwindung—*Gyrus marginalis* \*] retains its embryonic form, *i. e.* that it is in all parts equally broad, and extends up to the Ammonsfurche \*, and is continuous with the mesial wall of the hemisphere anteriorly; (2) that the corpus callosum is rudimentary; and (3) that the Balkenwindung \* is wanting.

From the fact that Zuckerkandl uses the term Randbogen instead of hippocampus we might infer that he did not definitely recognize the dorsal part of the Randbogen as hippocampus—an inference which is borne out by his reference to the corpus callosum. If any other evidence were needed to show that Zuckerkandl quite failed to appreciate the most salient features of the Monotreme and Marsupial cerebrum, it is provided in his remarks upon the cerebrum of *Echidna*, where he speaks of the fascia dentata as "der ventrale Schenkel des Randbogens." This clearly indicates that he did not recognize the dorsal limb of the Randbogen as fascia dentata or hippocampus. [It is only right to mention that Zuckerkandl's work appears to have been purely macroscopic.]

Thus Zuckerkandl reduces the cerebrum of the Marsupial and Monotreme to the conventional Eutherian type, possessing a true corpus callosum, and with a hippocampus practically limited to the descending limb of the lateral ventricle. Such being the case, until quite recently I paid little heed to his remarks concerning the resemblance of *Vespertilio murinus* (the bat of which he examined the brain) to the Marsupial type; for, having reduced the Marsupial to conformity with a simple Eutherian type, it seemed very natural to group an actual example of such a type (which the bat provides) with the Marsupial.

But quite recently, upon examining the brain of a common Australian bat (*Nyctophilus Timoriensis*), I was struck by the remarkable resemblance which its hippocampus (Zuckerkandl's Randbogen) and cerebral commissures present to the Metatherian type. It appeared to be a case of reducing the bat to the Metatherian condition rather than advancing it to the Eutherian status, as Zuckerkandl's researches would appear to indicate. In the course of this communication we shall see how far this appearance is justified by the histological examination of *Nyctophilus* and *Miniopterus*.

The object of this paper being to consider phylogenetically the origin of the true corpus callosum (as distinct from the hippocampal commissure), we are solely concerned with the transition from the condition found in the Proto- and Metatheria, in which

\* These terms will be explained subsequently.

the true corpus callosum is wanting, to the Eutheria, in which alone that structure is found. This relieves us from the necessity of discussing the writings of Osborn and many others who have based their researches primarily upon the examination of some sub-mammalian form, and from this treacherous standpoint have advanced hypotheses to include the Mammalia.

Since Flower ('Philosophical Transactions,' 1865) compared the cerebral commissures of the Marsupial with those of certain lowly-organized Eutheria, in order to determine the nature of the former, no one, so far as I know, has dealt with the subject from this comparative standpoint. But while Flower compared the two series in order to throw light upon the Marsupial, I am instituting the reverse process of comparing the Cheiroptera with the more distinctly defined Metatherian type.

Within the last three three years the labours of Blumenau \*, Marchaud †, and Paul Martin ‡ have added considerably to our knowledge of the process of development of the corpus callosum in the higher mammals. And it is very instructive to compare the progress of the developing commissure in man or the cat with the stages of its phylogeny with which this contribution deals.

The following statements concerning the ontogenetic process are a free translation of certain of Martin's conclusions (*loc. cit.*):—A thickening takes place in the lamina terminalis, which later disappears; but before the disappearance the first fibres of the corpus callosum appear in the dorsal part of the thickening. [Martin throughout uses the term corpus callosum (Balken) in the sense of the whole dorsal commissure, including the hippocampal commissure. This will be apparent from the next statement.] The first "callosal" fibres spring from the posterior columns of the fornix. The ventral part of the corpus callosum [the psalterium] consists of fibres which run in the inner Randbogen. The splenium is composed of fibres which extend from the inner and outer Randbogen to the other side. The body and genu of the corpus callosum consist of fibres passing through the outer Randbogen. The cavum septi pellucidi is formed during the disappearance of the thickened lamina terminalis, partly in the place of the disappearing thickening, but mainly by the inclusion of a part of the longitudinal fissure of the cerebrum by the corpus callosum. For a long time it is open nasally-ventrally. Upon the ventral side of the corpus callosum a gradual "soldering" of the hemisphere-walls takes place in the situation of the cavum septi. The corpus callosum increases by intussusception as well as by apposition of fibres. The striæ longitudinales are formed in part by the upper Randbogen. The thickened lamina terminalis contributes towards the formation of the caudal part of the striæ mediales.

In the subsequent consideration of the results of our comparison we will see the extent to which the ontogenetic process recapitulates the phylogenetic history. At the

\* "Zur Entwicklungsgeschichte und feineren Anatomie des Hirnbalkens," Archiv für mikroskopische Anatomie, Bd. xxxvii. 1891, pp. 1-14, Taf. i.

† "Ueber die Entwicklung des Balkens im menschlichen Gehirn," Archiv für mikroskopische Anatomie, Bd. xxxvii. 1891, pp. 298-334, Taf. xv., xvi.

‡ "Bogenfurche und Balkenentwicklung bei der Katze," Jenaische Zeitschrift für Naturwissenschaft, Bd. xxix. 1895, pp. 221-252, Taf. ii. and 13 figures in text.

same time we will see how the latter explains much that is apparently meaningless and purposeless in the ontogenetic process.

From the foregoing remarks concerning the scope of this investigation, it must be evident that we are mainly concerned with the hippocampal region of the two types of cerebrum. In other words, we are going to study and compare the dorsal commissure of the Marsupial, which is "hippocampal," with its topographical representative in the bat, which is mainly "hippocampal." It is therefore necessary to have a clear and definite idea of disposition of the hippocampal region of the Metatherian cerebrum; and we may first of all consider the hippocampus of *Perameles nasuta*, which exhibits very clearly the distinctive features of the Marsupial brain (mainly by means of sections stained by the Weigert method).

I have not yet been fortunate enough to get specimens of the brain of *Nyctophilus* in a condition suitable for the application of the Weigert stain. But the resemblance to the Marsupial type is so great that with the aid of the lithium carmine stain quite sufficient detail can be made out to reveal the distinctive features of the region with which we are concerned. I hope soon to be able to supplement these notes by a fuller paper on the brain of *Nyctophilus*, studied by more specialized neurological methods\*.

My friends Mr. James P. Hill and Mr. J. Macpherson, of the University of Sydney, very kindly placed at my disposal four brains of *Nyctophilus* which were in a good state of preservation, though hardened only in alcohol. My friend Dr. R. Broom, who was at Taralga working at the organ of Jacobson in *Miniopterus*, kindly gave me the brain from one of his specimens. Mr. Robert Grant, the able assistant in the Physiological Laboratory at Sydney, stained and cut series of coronal, sagittal, and oblique sections from these specimens. To these gentlemen I acknowledge my deep gratitude and great indebtedness.

This work was done mainly in the Anatomical Department of the University of Sydney, and has been completed—so far as such an unfinished work can be said to be—in Cambridge.

#### *The Hippocampal Region in the Marsupial.*

The mesial wall of the descending limb of the lateral ventricle of the cerebrum of the Marsupial presents a marked prominence, which extends in the long axis of the ventricle. This is the *hippocampus*—the homologue of the *hippocampus major* of the Primate brain. In its histological structure and in the disposition of its constituent parts this region of the Metatherian cerebral hemisphere agrees exactly with the corresponding part of the Eutherian, so that in seeking for distinctive features of the two types of brain it may be neglected. We will therefore begin the study of the brains under consideration at a point just in front of the place where the lateral ventricle begins to curve downward to form its descending cornu.

The first figure (Pl. 15. fig. 1) represents a coronal section through the forebrain of

\* Since this was written I have confirmed, by means of preparations stained by Weigert's method, all the observations concerning *Nyctophilus* which are here recorded.

*Perameles nasuta* at about the junction of body and descending limb of the lateral ventricle. This corresponds to a situation almost immediately behind the commissures of the hemispheres, as we shall see later.

In this section the 'tween-brain—a somewhat square-shaped mass with rounded corners—will be seen to occupy the ventral mid-region. The basal part of the thalamic region lies upon the optic tract (*o.tr.*), which may be seen extending into the furrow between the hemisphere (the region of the *nucleus amygdalæ, n.a.*) and the 'tween-brain. The two halves of the optic thalamus are connected by means of a broad bridge of grey matter—the *commissura mollis (c.m.)*—and above and below the latter portions of the third ventricle may be observed. The small recess of the third ventricle lying above the soft commissure is roofed by a somewhat dome-shaped epithelial fold, which is attached on either side to a ridge containing a longitudinal band of medullated fibres—the *stria medullaris thalami (s.m.l.)*.

Upon its lateral aspect the thalamic region fuses with the corpus striatum of the cerebral hemisphere, and a mass of medullated fibres, cut either transversely or obliquely, indicates the place of union. The corpus striatum consists of two parts, which are separated one from another by the internal capsule (*c.i.*). A smaller grey mass, lying above the internal capsule and projecting into the lateral ventricle, is the *nucleus caudatus (n.c.)*. A larger grey mass lying below the internal capsule is the *nucleus lenticularis (n.l.)*. The ventral part of the nucleus lenticularis (*n.a.*) is the homologue of the grey mass known in human anatomy as the *nucleus amygdalæ*. It is directly continuous with a cortical area of distinctive structure known as the *pyriform lobe (py.l.)*, from which the nucleus lenticularis in its upper part is separated by a layer of medullated fibres (the *external capsule, c.e.*).

Along its dorsal border the pyriform lobe is separated from the general cortex (which Turner calls "*pallium*," *p.*) by the shallow *rhinal fissure (f.r.)*. Above the corpus striatum, where the lateral wall and roof of the ventricle are formed by this general cortex or *pallium*, the inner lining of the latter is formed by a mass of medullated fibres—the *corona radiata (c.r.)* of writers. If the cortex be traced in a mesial direction its edge will be found to present those peculiarly distinctive features which we at once recognize as *hippocampus*. Thus if the mesial wall of the hemisphere be traced downward in the section (fig. 1, Pl. 15) we reach a deep indentation—the *hippocampal fissure*, and corresponding to this fissure a marked prominence into the lateral ventricle forming the hippocampus (*hip.*). Below the hippocampal fissure the characteristic features of the *fascia dentata (f.d.)* (which we shall consider subsequently) are immediately recognizable. And extending into the deep depression between the nucleus caudatus (*n.c.*) and optic thalamus is the prominent *fimbria (f.)*, spur-like in transverse section. [In order to avoid an unnecessary confusion in the figure, the choroidal fold of the lateral ventricle which is attached to the fimbria has not been represented.]

Having thus seen how the "hippocampal formation" constitutes the edge of the cortex cerebri, I propose to carefully examine the series of changes which this peculiar formation undergoes as we trace it forward in a series of coronal sections of the cerebrum of the bandicoot (*Perameles*).

A coronal section through the cerebrum, just in front of that represented in the first figure, presents a marked change in the appearance of the hippocampal region, which is represented upon an enlarged scale in fig. 2. The hippocampus itself, as well as the fascia dentata, have undergone practically no change, but a huge bundle of medullated fibres from the upper part of the fimbria is now exposed in the act of crossing the middle line. This is the posterior extremity of what—to avoid confusion of terms—will for the present be termed the *commissura dorsalis* (c.d.).

It would be foreign to the scope of this work to describe in detail the histology of the hippocampal formation, seeing that the minute structure of the Metatherian hippocampus is identical with that of the Eutherian, which Sala, Schaffer, Ramon y Cajal, and von Kölliker\*, among many others, have so carefully and minutely described within recent years. But I wish to call attention to certain features which are intimately associated with the evolution of the structure we are primarily considering.

Lying upon the upper surface of the “*dorsal commissure*” (c.d.) there is a complicated epithelial fold the outline of which is roughly triangular, and which projects upward into the great cleft between the two cerebral hemispheres. The fascia dentata (*f.d.*) lies in contact with this epithelial (choroidal) fold on either side, and may be easily recognized by certain distinctive features. Thus it possesses a very thickly-packed column of small cells—the *stratum granulosum* (*s.gr.*)—the nuclei of which stain very deeply, lying parallel to the surface, from which they are separated by a clear layer almost devoid of cells—the *stratum moleculare*. The fascia dentata—consisting of stratum granulosum and stratum moleculare—is folded in a peculiarly characteristic manner. Its mesial extremity is completely bent upon itself, so that the stratum moleculare or superficial layer rests upon the dorsal aspect of the *dorsal commissure*. The lateral extremity of the fascia dentata undergoes a corresponding bending, the concavity of which is directed toward the mesial plane. It would appear that the fascia dentata had continued to increase in breadth whilst its mesial and lateral extremities were relatively fixed, and, to accommodate itself to these conditions, it had bulged out into a pouch, as it were, and at the same time become flattened by the resistance of the general cortex lying immediately above it. Such factors, in reality, seem to have been at work, as I have recently pointed out †. The fissure which separates the fascia dentata from the general cortex where their respective superficial layers come into contact is the *fissura hippocampi* (*f.h.*).

The concavity of this pouch of fascia dentata is occupied by scattered nerve-cells, many of which give origin to the brush of medullated fibres which are to be seen in the figure, collecting near the inner margin of the fascia dentata, to lose themselves in the huge mass of medullated fibres lying immediately below.

The hippocampus proper projects as a large rounded swelling into the lateral ventricle. This swelling is covered by a thick layer of medullated fibres—the so-called *alveus* (*alv.*). These fibres almost all pursue an oblique course, so that in a coronal section only short pieces of fibre are seen massed together. In the first figure most of the fibres of the

\* ‘Gewebelehre des Menschen,’ Bd. ii. zweiter Hälfte, 1896.

† “The Fascia Dentata,” Anatomischer Anzeiger, xii. Bd. Nr. 4 und 5, 1895, p. 119.

alveus are tending towards the fimbria, but in the section under consideration many fibres of the alveus, as well as fibres coming from the "pouch" of the fascia dentata, proceed directly into the *commissura dorsalis* along with many fibres of the fimbria which have come from more caudally situated regions of the hippocampus. It will be noticed, however, in the figure that as yet only the upper part of the fimbria is contributing fibres to the commissure. The tip of the fimbria, which contains fibres coming from the most distant parts (temporal pole) of the hippocampus, is yet undisturbed and has given no contribution to the dorsal commissure. Between the alveus and the curved lateral part of the hippocampal fissure there is a broad, more or less definitely stratified region. Slightly nearer to the alveus there is a very uniform and clear layer (in specimens stained by Weigert's method). This is the layer of "pyramidal cells," and consists of a closely-packed column of large cells, which stain moderately with ordinary stains. Between the layer of pyramids (*pyr.*) and the alveus (*alv.*) there is a stratum containing scattered polymorphous cells and very abundant medullated nerve-fibres—the *layer of polymorphous cells*. The space between the hippocampal fissure and the layer of pyramids is usually divided by writers into three zones—a broad clear layer next to the layer of pyramids (*stratum radiatum, s.r.*), a thin superficial layer (*stratum zonale*), and an intermediate layer very rich in medullated nerve-fibres (*stratum lacunosum, s.l.*).

A large number of fine medullated fibres (*x*) extend from the region of the layer of pyramids through the stratum radiatum into the stratum lacunosum. These fibres are very distinct in the region bordering upon the fascia dentata (*vide* fig.). In the stratum lacunosum many of these fibres end by means of free branching in relation to the processes of the pyramidal cells, which extend through the stratum radiatum into the more superficial regions. But a considerable number of medullated fibres assume a longitudinal direction (*i. e.* in the long axis of the hippocampus) as soon as they reach the stratum lacunosum (*s.l.*). These fibres, which may be called "*longitudinal association fibres of the hippocampus*," appear in transverse section (*s.l.*) as rounded bundles immediately surrounding the lateral or deeper part of the hippocampal fissure.

In the general cortex (*p.*) the cells are scattered throughout the whole thickness of the cortex, whereas in the hippocampus (leaving out of account the fascia dentata) the great majority of the nerve-cells are crowded together into the regular row of pyramids. The transition-region from typical cortex to typical hippocampus is generally known as the *subiculum cornu ammonis* (*sub.*). Whether the "subiculum" ought to be grouped with the general cortex or with the hippocampus is a question to which we shall have to refer subsequently. The deepest layer of the general cortex consists of a mass of medullated fibres—the *corona radiata*. It will be noticed at a glance that while the fibres derived from the hippocampus and "subiculum" proceed into the alveus, those derived from the general cortex proceed away from the alveus, *i. e.* towards the external capsule. At the point of meeting of alveus and corona radiata there is obviously a commingling of fibres, but it is equally clear that any passage of fibres from the alveus into the "corona" or *vice versâ* is either non-existent or extremely slight and practically negligible. In the adjoining regions there are groups of longitudinal fibres belonging respectively to the two distinct formations, and it is quite possible that an interchange between these two

series *may* take place. The longitudinal series belonging to the margin of the general cortex or pallium is the so-called *cingulum* of higher forms (figs. 6 & 11, *cing.*, *cing.*!). There are, however, definite bonds of union between hippocampus and general cortex which are found in their junction. Thus from the stratum zonale and stratum lacunosum of the hippocampus fibres extend not only into the "neutral ground," so to speak, of the "subiculum cornu ammonis" but well into the molecular layer of undoubtedly true cortex. This is a definite association bundle between hippocampus and pallium, which may be called *tractus hippocampi ad pallium* (fig. 2, *y*).

As the hippocampal region is successively examined in a series of coronal sections, the main features of the hippocampal formation itself remain unchanged for some time, but its commissure—the *commissura dorsalis*—undergoes marked changes.

Thus the depth of the commissure rapidly increases at the same time that the prominence of the fimbriæ is diminishing (fig. 3). The meaning of this is that an increased number of fibres from the fimbria are crossing in the dorsal commissure. The scheme (fig. 4) of the commissures as they are seen in sagittal section explains the meaning of these changes.

In figure 5 a new factor for the first time becomes evident. Upon the lateral aspects of the commissure, more especially upon the right side of the figure, a mass of grey matter (*s*) will be observed to enclose the dorsal commissure and to become continuous ventrally with a mass enclosing a second commissure—the *commissura ventralis*. This grey mass enclosing the two commissures will for the present be distinguished as the "*commissure-bed*." On either side it will be noticed to become continuous by a narrow bridge of grey matter with the *corpus striatum* (*c.st.*). In this narrow bridge there are a number of longitudinally-coursing nerve-fibres (*s.t.*). These are the uncrossed fibres of the *stria terminatis*, the other fibres of which may be seen entering the ventral commissure (*s.t.*) in figure 3 to cross to the other side. In figure 5 the dorsal commissure has reached its greatest depth.

Figure 6 shows the appearance which is presented by a section after all the commissural fibres of the fimbria have crossed. The thin *commissura dorsalis* (*c.d.*) is derived from the corresponding region of the hippocampal formation. The huge *commissura ventralis* (*c.v.*) appears to become continuous with the *capsula externa* (*c.e.*), which, after being joined by fibres of the *capsula interna* (*c.i.*), becomes the *corona radiata*. The dorsal and ventral commissures lie *in* the large mass of grey matter which forms the *commissure-bed*. A thin lamina (*i*) of this grey mass may sometimes be distinguished upon the dorsal aspect of the *commissura dorsalis*. This may be distinguished as the "*indusium verum*."

The "*commissure-bed*" (*s*) contains large numbers of uncrossed fibres (*d.f.*), which are derived from the alveus of the hippocampus (which is situated above them) and from the fimbria. These fibres are divided into two groups by the ventral commissure. The *postcommissural fibres* (*columna fornicis*, *c.f.*) collect upon the dorsal aspect of the ventral commissure and incline backward and downward to enter the thalamic region. The *precommissural fibres* proceed downward and forward in front of the ventral commissure.

As we proceed forward in the examination of coronal sections, the dorsal commissure will be found to become gradually thinner and finally disappear altogether, while the *descending fornix-fibres* remain unchanged. The ventral commissure disappears in about the same coronal plane. The "*commissure-bed*" extends a slight distance further forward before the hemispheres become separated one from another.

Figure 7 represents (about four times the natural size) the appearance of a coronal section immediately in front of the place where the hemispheres become separated from each other.

In this figure the hippocampus is again easily recognizable, although its conformation has become greatly simplified. The *fissura hippocampi* (*f.h.*) is much shallower, and the hippocampal projection into the ventricle less prominent. The fascia dentata is much narrower, and consequently much less folded. The thin alveus may be seen proceeding directly into the mass of *descending fornix-fibres* which occupy the superficial portions of the grey mass which we may call the "*corpus præcommissurale*"\*, but which is really only the anterior continuation and homologue of the grey mass which further back has been called "*commissure-bed*." The other features of the section do not concern us in considering the hippocampal formation. The only other point to which I wish to call attention is that the "*corpus præcommissurale*" is directly continuous below the lateral ventricle with the corpus striatum, where the latter is capped by the peculiar cortex which Ganser calls the "*cortex of the head of the corpus striatum*," and which corresponds to the "*tuberculum olfactorium*" (*t.o.*)—such a prominent feature upon the ventral aspect of this brain.

If we were to trace these various structures forward in a series of coronal sections, we should find that the hippocampal fissure would become gradually shallower until it eventually disappeared, the prominence in the ventricle disappearing *pari passu*. The fascia dentata, now placed entirely upon the surface, becomes narrower and less clearly differentiated, until at last we fail to recognize any distinguishing feature of a hippocampus. But by the time this has occurred we have arrived almost at the olfactory peduncle. In certain Marsupial brains (*Dasyurus viverrinus*) it is even possible to distinguish the hippocampal formation as far forward as the olfactory peduncle, so that here we have the "*precommissural area*" completely cut off from the general cortex or pallium (*p.*) by a hippocampal band, as semi-schematically represented in figure 8 (*hip.* & *f.d.*). This is the primitive condition of the hippocampus, which is found (although recognized with difficulty) in the Reptile, and which I have already described in the foetal *Ornithorhynchus* (Qu. Jour. Micr. Sci. vol. xxxix. pp. 181-206).

Figure 9 represents the appearance which this region presents in *Perameles* when viewed from its mesial aspect.

In this figure the optic nerve (*opt.*) is seen extending towards the lamina terminalis, at the inferior extremity of which is the oval section of the optic tract (*o.tr.*). Extending upward from the optic tract is the thin ventral portion of the lamina terminalis—the *lamina cinerea* (*l.c.*). At its upper part this lamina expands to enclose the large

\* By "*corpus præcommissurale*" is meant that grey mass the mesial surface of which is the "*precommissural area*" (*p.a.*).

*commissura ventralis* (c.v.), oval in section and placed obliquely. Extending upward from the ventral commissure there is a thick mass of grey matter—the “*commissure-bed*” (*s*)—which contains in its upper part the *commissura dorsalis* (c.d.), shaped somewhat like an inverted obliquely placed V with the dorsal limb nearly horizontal.

Above the dorsal commissure the *fascia dentata* (*f.d.*) is easily recognizable and is separated from the general cortex (*p.*) by the *fissura hippocampi* (*f.h.*). Anteriorly the hippocampal fissure gradually becomes shallower until it can no longer be traced, so that the fascia dentata, the stratum zonale of the hippocampus, which now of course lies upon the surface (compare figure 8, *hip.*"), and general cortex (*p.*) are indistinguishable. Upon its ventral side the fascia dentata becomes directly continuous with the extensive pale region which constitutes the “*precommissural area*” (*p.a.*). In the forward direction the “*precommissural area*” is directly continuous with the mesial wall of the extremely short olfactory peduncle, which connects the hemisphere with the olfactory bulb (*o.b.*). Upon its ventral side the “*precommissural area*” becomes continuous with the grey boss generally known as the “*tuberculum olfactorium*” (*t.o.*).

By means of this representation of the anterior portion of the mesial wall of the hemisphere of *Perameles* (fig. 9), and the semi-schematic representation of the corresponding region in *Dasyurus* (fig. 8), we obtain a good general idea of the anatomy of the commissural region.

In *Dasyurus* it will be observed that the *dorsal commissure* is not so distinctly bilaminar as it is in *Perameles*; and in *Phascogaleos* (Pl. 16. fig. 10) it can hardly be called bilaminar. Thus we have in the Marsupial all the intermediate stages between the rounded dorsal commissure of *Ornithorhynchus* and *Echidna* and the distinctly bilaminar form found in most mammals. There are certain important features of this region which can only be demonstrated by sagittal section, which we will consider almost immediately. But before leaving the consideration of figure 8, I wish to call attention to the possible consequences of elongation of the *commissura dorsalis*.

The “*commissura dorsalis*” is contained in the mass of grey matter which I have called the “*commissure-bed*,” the separate anterior prolongations of which in the two hemispheres are formed by the “*corpora precommissuralia*”—the grey masses corresponding to the surface-region of each hemisphere, which is distinguished as “*precommissural area*.” Now this combined grey mass—“*commissure-bed*” and “*corpus precommissurale*”—is separated from the general cortex (pallium) above it by the hippocampus; and the dorsal limb of the commissure separates the “*commissure-bed*” from what we may call the “*supracommissural hippocampus*,” while the “*corpus precommissurale*” becomes directly continuous with what we may call the “*precommissural hippocampus*.” Now it is clear that if the dorsal commissure elongates in the forward direction it must cut off part of this “*precommissural*” body from the *precommissural hippocampus*, which becomes “*supracommissural*.” The structure lying upon the ventral aspect of such an elongated dorsal limb of the *commissura dorsalis* must be either “*commissure-bed*” or “*corpus precommissurale*.”

Figure 10 represents the appearance of a sagittal section through the corresponding region in the brain of *Phascolarctos cinereus*, after staining by the Weigert method. Between the small *commissura dorsalis* (c.d.) and the large elliptical *commissura ventralis* (c.v.) a large number of non-crossing fibres will be noticed in the "commissure-bed" and "precommissural area." Of these the postcommissural form the *columna fornicis* (c.f.). The precommissural area contains various sets of fibres. The largest group ( $\alpha$ ) connect the alveus hippocampi and the basal region of the brain just behind the tuberculum olfactorium (t.o.). In *Ornithorhynchus* I distinguished these fibres as the "hippocampo-basal association bundle" \*. Other fibres ( $\beta$ ) pass backward below the ventral commissure to enter the subthalamie region, where they become lost. Fibres entering into the constitution of these two series may be seen in the precommissural area (in the region marked *p.a.*), proceeding from the most anterior part of the hippocampus. Fibres may also be seen proceeding directly from the olfactory peduncle (and probably bulb) to enter the fascia dentata (*f.d.*). This is the *olfactory bundle of the fascia dentata* ( $\gamma$ ). Other fibres belonging to the same series ( $\delta$ ) may be seen proceeding backward above the dorsal commissure as a well-defined tract, probably homologous with the nerve-fibres of the *stria medialis Lancisii* of the higher mammalian brain.

In the Marsupial, a typical hippocampal formation lies upon the dorsal aspect of the commissura dorsalis. In this hippocampal formation there are two important series of longitudinal fibres, which are displayed most clearly in a horizontal section. Such a section of the cerebral hemisphere of *Trichosurus vulpecula* is represented in fig. 11. In this figure (as also in fig. 2) a large series of longitudinal association bundles are visible in the *stratum lacunosum*. Secondly, in the region of the subiculum (and possibly in other regions of the hippocampus) large numbers of longitudinal fibres are contained in the alveus, but in transverse section are not recognizable in the mass of oblique fibres.

Upon the ventral aspect of the hippocampus in its anterior part we have had occasion to refer to a large mass of grey matter, the anterior paired region of which we have known as the "corpus præcommissurale," and its posterior region as the "commissure-bed." This region has been the great source of confusion to comparative anatomists, more especially those working at reptilian and amphibian forms, and it therefore demands a very careful study. Most writers call the whole mass the "septum."

A study of figs. 5, 6, and 9, which are all from *Perameles*, shows that the "commissure-bed," or matrix of the commissures, extends across the median plane uninterruptedly, becomes continuous upon its dorsal aspect with the hippocampus of both sides, and upon its ventral aspect with that thin band (*l.c.*) of the lamina terminalis which extends from the ventral commissure to the optic tract (*o.tr.*). It is connected also in the median line above with the thin epithelial roof of the third ventricle (a structure not shown in the figures). It is clear, therefore, that this matrix, which includes the two commissures, occupies the situation of the dorsal part of the lamina terminalis, and in part bounds the third ventricle anteriorly.

\* Journal of Anatomy and Physiology, vol. xxx. p. 480.

If we examine a series of transverse and sagittal sections of a reptilian brain, it will be found that both ventral and dorsal commissures lie *in* the easily recognizable lamina terminalis. This lamina contains in the median plane a minimal amount of grey matter. But on either side of the median plane this thin bridge of grey matter becomes continuous with a huge mass of grey matter which we readily recognize as the backward continuation of the "precommissural body." Thus in the Reptile the "commissure-bed" consists of the posterior extremities of the "precommissural area" united by the thin grey lamina formed by the lamina terminalis.

In the mammal it is evident that either the grey mass of the "precommissural area" has invaded, and thus thickened, the lamina terminalis, which becomes a continuous grey mass across the mesial plane, or, on the other hand, the mesial surfaces of the two posterior regions of the precommissural area may have become "glued" together. One or other event must have occurred; and the evidence, I believe, points to a gradual thickening of the lamina terminalis by the invasion of grey matter from the adjacent "precommissural area." However the thickening is brought about, we know that the two cerebral commissures of the Marsupial lie *in* the "commissure-bed," which is morphologically a thickening of the lamina terminalis. Yet we are equally sure, both from its topographical relations to surrounding structures and from its minute structure, that the "commissure-bed" is morphologically part of the same sheet of grey matter as the "precommissural area."

If the hippocampal region be studied where it bulges in the descending limb of the lateral ventricle in any Eutherian brain, a considerable variety of the form and relative sizes of its constituent parts will be apparent. In the Marsupial brain equally great variations are found in the corresponding region of the hippocampus. But if we examine the supra-commissural part of the hippocampus in a series of Marsupials, the greatest variety and most varied degrees of complexity are demonstrated. In *Notoryctes*, and less markedly in *Dasyurus*, the formation is very simple. In *Macropus* it is much more complex. *Perameles* is an example of a highly-developed type. Both Monotremes present in the supra-commissural region a more complicated form of hippocampus than is found in any other mammal. But the anterior extremity of the hippocampus undergoes the same process of unfolding and simplification in all Marsupials and Monotremes which I have so briefly described in *Perameles*. Hence, should we find a difference in the relative degree of development of various parts of the hippocampal formation in the brains of two different animals, we must not lay much weight upon such differences as an indication of the systemic position of their possessor.

#### *The Hippocampal Region in the Bat.*

The cerebrum of the bat may now be studied in the same manner as that of the bandicoot. Beginning with a coronal section through the hippocampal region of *Miniopterus* immediately behind the region of the commissures, one cannot fail to notice the great similarity between the two forms (figs. 12 and 1). What differences do occur, apart from those of absolute size, point to a less complex form of structure in *Miniopterus* (fig. 12) than in *Perameles* (fig. 1). This simplification consists of a diminished depth of

the hippocampal fissure (*f.h.*), a less prominent hippocampal eminence in the lateral ventricle, and a less broad and slightly less convoluted fascia dentata (*f.d.*). These variations in the *form* of the hippocampus are of little moment, for, as I have before remarked, great variations are found in any order. Moreover, it is noteworthy that in very small Marsupials like *Notoryctes* one finds a simplicity of hippocampal formation similar to that which the minute *Miniopterus* presents (compare fig. 6 of my paper on *Notoryctes* \*).

In the next section, which passes through the posterior extremity or *splenium* of the dorsal commissure (Pl. 16. fig. 13), we have a condition which recalls that presented by the corresponding section through the brain of *Perameles* (Pl. 15. fig. 2).

But if we compare the hippocampus in figs. 12 and 13, a distinct simplification will be noticed in the foremost section (fig. 13). The fascia dentata (*f.d.*) is narrower, the layer of pyramidal cells (*pyr.*) is shorter, and the hippocampus as a whole is distinctly flatter. In fig. 12 there is a very sharp angle between the alveus and the corona radiata, while in fig. 13 the angle has become rounded off. It is possible that fibres coming from a wider cortical field may round off the angle, but the carmine stain does not permit us to definitely decide this. But in the next section (fig. 14) there is no question, even with the carmine stain, of the much wider field of origin of the dorsal commissure.

If we are undecided whether any fibres other than hippocampal are passing to the dorsal commissure in fig. 13, we have in fig. 14 a very distinct demonstration of the existence of a very considerable bundle of fibres arising from the general cortex and forming part of the superior commissure. In fact, the insignificant flattened band of grey matter which now represents the hippocampus can contribute but a very small share towards the formation of the thick commissural tract (C.D.) upon which it lies. The hippocampus is now much more insignificant and more flattened than it was in the last figure. The regular row of nuclei immediately above the dorsal commissure belongs to the layer of pyramidal cells of the hippocampus (*pyr.*), and the group of closely-aggregated smaller nuclei which cap the mesial end of the layer of pyramids represents the stratum granulosum of the fascia dentata. In fig. 15 the region of the fascia dentata from fig. 14 has been represented upon a larger scale, and in figs. 12, 13, 14, and 15 the stratum molleculare of the fascia dentata has been shaded in order to render its recognition more easy.

It will be noticed, if we compare figs. 13 and 14, that the commissural fibres of the general cortex pursue their new course through the alveus of the hippocampus. In other words, the alveus of the "dorsal hippocampus" of the bat consists of a mixture of fibres derived from the hippocampus, which we might call "true alveus," and commissural fibres derived from the general cortex—"false alveus." Our "false alveus" is the corpus callosum proper. From the examination of this series, therefore, we may infer that *the fibres of the corpus callosum proper reach the mesial plane by passing through the alveus of the dorsal part of the hippocampus.*

\* "The Cerebrum of *Notoryctes typhlops*," Transactions of the Royal Society of South Australia, vol. xix, pl. viii. (1895).

As we proceed forward the supra commissural hippocampus becomes more and more rudimentary. Had we not been tracing these structures in a series of sections, we should never recognize in the few cells situated above the commissures in fig. 16 the representatives of the fascia dentata (*f.d.*) and the rest of the hippocampus (*hyp.*).

If we were to examine a series of sections further forward we should find, after the anterior extremity of the dorsal commissure had been passed, that at the junction of the precommissural area and general cortex (pallium) a few small cells would be found to represent the hippocampus which is present in the marsupial (fig. 7).

Now that we have seen how the hippocampus is disposed in transverse sections, it will complete our ideas concerning the commissural region if we study its disposition in sagittal section. The transverse sections which I have figured were those of *Miniopterus*. The two series of sections of the brain of *Nyctophilus*, which would have served our purpose even better, were not exactly transverse, and therefore might be confusing. It may be remarked, however, that the "non-hippocampal" element in the dorsal commissure is even less developed in *Nyctophilus* than it is in the single specimen of *Miniopterus* which I have examined. I have made several series of sagittal sections of the brain of *Nyctophilus*, and, for illustration, a section slightly to the side of the middle line has been chosen in order to show the relation of the hippocampus to the "*splenium*" of the dorsal commissure. A section passing through the mesial plane presents no difference in the appearance of the commissures from that presented in fig. 17.

In this section (fig. 17) we cannot fail to be struck with the resemblance to the Marsupial. The relatively enormous size of the ventral commissure (c.v.) and the shape and proportions of the dorsal commissure (c.d.) are strongly suggestive of the Metatherian structures. Yet in no Marsupial are the two limbs of the commissure so broadly expanded. For the ventral limb (c.v.) is nearly vertical, and the dorsal limb (c.d.) nearly horizontal, so that the angle included between the two limbs is not far short of 90°. Of the two limbs the ventral is the larger. Both limbs become thicker as they are traced towards their place of union, where they form a massive "*splenium*." Immediately behind the *splenium* in this section we see the fascia dentata (*f.d.*) cut very obliquely, and extending forward from the concavity of the pouch formed by the stratum granulosum the layer of pyramidal cells of the hippocampus (*hyp.*) immediately above the dorsal commissure.

The "commissure-bed" (*s*) enclosing both commissures fills up the great interval between the two limbs of the *commissura dorsalis* and the *commissura ventralis*.

In the dorsal limb of the *commissura dorsalis* (c.d.) I have represented by means of dots the position which a study of transverse sections leads me to regard as approximately those occupied by the commissural fibres which do not spring from the hippocampal formation, *i. e.* by the fibres of the corpus callosum proper. From this we see that the anterior extremity of the dorsal limb is almost purely "callosal"—if we may use such a term. The transition from purely "callosal" to purely "hippocampal" parts of the commissure is a very gradual one, "hippocampal" and "non-hippocampal" fibres being intimately mixed one with another at the place of junction.

*Thus it would appear that in this bat commissural fibres arising from a very restricted area of the dorso-mesial cortex above the supracommissural region of hippocampus, instead of passing by the circuitous route via the external capsule and through the central commissure, pass through the alveus of the supracommissural hippocampus to reach the opposite hemisphere through the dorsal limb of the dorsal commissure. In other words, fibres which do not arise in the hippocampal formation pass through the alveus of the hippocampus to become commissural, and, as a result of the consequent atrophy of the invaded region of hippocampus, the invading fibres usurp the place previously occupied by the anterior part of the hippocampal commissure.*

The "usurping fibres" are the "corpus callosum, and the atrophic hippocampus forms part of the "indusium" and "striae Lancisii."

The relation of the rudimentary corpus callosum to the hippocampus, to the "commissure-bed," and to all the surrounding structures is identical in every respect with that which the corresponding part of the hippocampal commissure presents in the Marsupial. We have no reason to regard the "commissure-bed" in the bat in any other light than as the strict homologue of the structure which we have designated by that name in the bandicoot. For even though the large mass of hippocampal cortex is wanting upon the dorsal aspect of the commissure, it cannot have been absorbed into and swell the mass of the "commissure-bed," for its vestiges are clearly and indubitably present, as we have just seen, upon the *dorsal* aspect of the "commissura dorsalis." Since our new commissure or corpus callosum lies entirely upon the ventral aspect of the hippocampus, it must be still contained in the "commissure-bed" (or possibly the "corpus præ-commissurale") just as in the Marsupial.

#### *General Considerations.*

We have now contrasted the hippocampal region of a typical Marsupial cerebrum with that of certain Cheiroptera as types of an extremely low grade of Eutherian organization. I propose now to briefly discuss the significance of the differences observed, and their special bearing upon the question of the origin of the corpus callosum.

Fig. 1 (p. 63) represents in a schematic manner the position which the hippocampus occupies in the mesial wall of the hemisphere of a Marsupial. This hippocampus may be roughly divided into three segments:—(a) a "precommissural segment" (*hip''*), which lies in front of the commissures and separates the precommissural area (*p.u.*) from the general cortex (*p*); (b) a "supracommissural segment" (*hip'*), which lies above the dorsal commissure, whose dorsal limb separates it from the "commissure-bed" (*s*); and (c) a "postcommissural segment," which constitutes the greater part of the hippocampal formation and possesses a true fimbria (*f*).

These three segments of the hippocampus form an extensive arc, reaching from the olfactory bulb (*o.b.*) in front to the tip of the temporal pole (*t*) behind and below. The "commissura dorsalis" derives its fibres from this extensive arc. [The few fibres springing from the precommissural body which probably enter into the constitution of the dorsal commissure may be disregarded in this discussion.] The commissural fibres

derived from the precommissural and supracommissural segments form the dorsal limb, and those derived from the postcommissural segment form the splenium and ventral limb of the "commissura dorsalis."

Now, we have seen that in the brain of the bat commissural fibres arise from a small area of the mesial cortex, which is distinctly not hippocampal, but which is placed above the hippocampus, and that, after passing through the alveus of the supracommissural hippocampus, they cross the mesial plane intimately intermingled with the hippocampal fibres of the dorsal limb of the "commissura dorsalis." Coincidentally with this invasion of the alveus, and possibly as a direct result of it, retrogressive changes occur from before backward in the "precommissural" and "supracommissural" segments of the hippocampus. So that soon these parts of the hippocampus (*hip'* and *hip''*) are reduced to mere vestiges, which, however, may still retain their characteristic histological elements. These vestiges are the so-called striæ Lancisii (mesial and lateral) and the associated film of grey substance. It is natural to suppose that with the retrogressive changes in the supracommissural hippocampus the hippocampal factor in the dorsal limb of the dorsal commissure wanes, so that the usurping pallial fibres remain practically if not actually unmixed with hippocampal fibres, to constitute the dorsal limb of the dorsal commissure.

This change is so gradual, and the pallial invasion so insidious, that at first the appearance of the commissures is unchanged, as in *Nyetophilus*, from our Marsupial type, and we are apt to overlook the fact that there has been thus introduced "the greatest modification exhibited by the brain in the whole series of vertebrated animals," as Huxley has said. It is unnecessary to discuss the question of the homology of these pallial fibres in the dorsal commissure; for, in the 'Transactions of the Linnean Society of New South Wales,' I have already (October 1894) called attention to the fact that while in the Marsupial the whole pallium is bound to its fellow of the opposite hemisphere by means of fibres of the ventral commissure, in the Eutherian hemisphere part of the homologous pallium sends its commissural fibres by the much shorter route which the commissura dorsalis provides. Therefore we cannot regard the corpus callosum as an entirely new group of commissural fibres, but rather *as fibres the undoubted homologues of which are found in the ventral commissure of the Metatherian cerebrum.* The passage of these pallial fibres through the dorsal commissure is an adaptive feature which is obviously advantageous to the organism, since the new route provides a very considerably shorter and more direct path for the commissural fibres of the rapidly-increasing dorsal part of the pallium. It is not at all surprising, therefore, to find a great and rapidly-growing demand upon this advantageous pathway *viâ* the dorsal limb of the dorsal commissure. Thus quite early this dorsal limb becomes completely transformed from a practically purely "hippocampal" to a practically purely "pallial" structure. (In fig. 1, p. 63, this reconstructed limb of the commissure has been darkly shaded.) But the continued crowding in or intussusception of new commissural fibres soon expands the bulk of the dorsal limb not only in thickness, but also in length. At first the increase in length is most noticeable in the caudal direction, in correspondence with the rapid backward growth of the hemisphere. This backward extension of the commissure takes place in the

plane in which the dorsal limb already lies. Now this plane is directed backwards and upwards, as indicated by an arrow in fig. 1.

What are the effects of such a backward extension upon the hippocampus? The

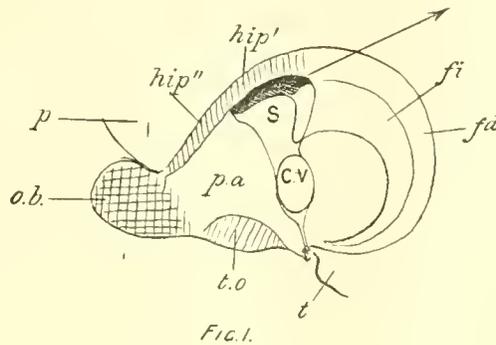


FIG. 1.

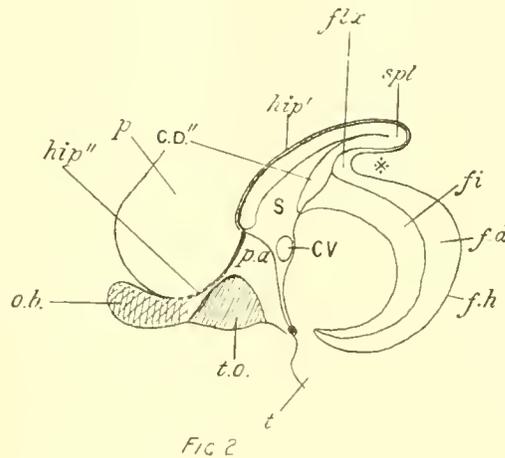


FIG. 2.

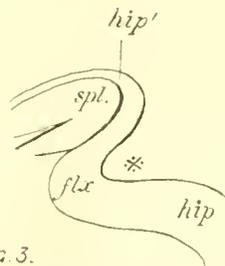


FIG. 3.

Fig. 1.—Scheme to show the arrangement of the hippocampus in the mesial wall of the hemisphere of a Marsupial.

The darkly-shaded part represents the first corpus callosum, such as is found in *Miniopterus*, and the arrow indicates the line of its backward extension in the higher Mammals.

Fig. 2.—Scheme of the corresponding region of a more highly developed cerebrum, such as that of *Pteropus*.

Fig. 3.—The "spherical" region from fig. 2 on a larger scale.

remains of the hippocampus which cover the dorsal aspect of the corpus callosum are stretched, and thus further attenuated, by the lengthening commissure. The backward growth of the commissure, owing to its obliquity, soon indents the hippocampal formation just at the junction of the atrophic "supracommissural" segment with the

unaltered "postcommissural" segment. This indentation soon increases and becomes a very extensive bend, the portion of the hippocampus which surrounds the posterior extremity of the dorsal commissure being carried backward and greatly stretched (fig. 2). In this way the obliquely-directed commissure first of all pushes upward and backward the hippocampus at the junction of supra- and postcommissural parts, stretching and carrying back the part of hippocampus that invests it *above the rest of the postcommissural hippocampus*. The "postcommissural hippocampus" (fig. 3, *hip*) thus appears to become subcallosal and to be separated in the vertical plane from the splenium of the dorsal commissure (*spl*) and the circumsplenic portion of the hippocampus (*hip'*) by a process of pallium (figs. 2 and 3, \*) upon which Zuckerkandl has laid so much stress under the confusing name "Balkenwindung." (It will be remembered that it was the lack of this feature which, in part, led him to group a bat with Marsupials and Monotremes).

As a result of the operation of the above-mentioned factors, therefore, a somewhat reversed S-shaped bending is produced in the hippocampus at the junction of its middle and posterior segments. The upper part of the S with its concavity looking forward is formed by the attenuated hippocampus (fig. 3, *hip'*) surrounding the splenium (fig. 3, *spl*), while the lower part of the S, which is convex in front, is formed by a "subsplenic" bending of a plumper hippocampal region, which I have distinguished as the "*hippocampal flexure*" (*fl.*).

Throughout all these changes the main mass of the ventral limb of the dorsal commissure (c.d.) has remained unchanged.

In the Marsupial and in a large number of lowlier Eutheria the plump ventral limb extends obliquely upwards to meet the dorsal limb in a thick splenium. But when the dorsal limb extends further backward, the main mass of the ventral limb is left in its old position (fig. 2, c.d.), its postero-superior extremity becoming greatly stretched and correspondingly thinned by the backwardly-extending corpus callosum.

The fimbria maintains its position unchanged (figs. 1 and 2, *f*) and always lies upon the posterior or inferior aspect of the corpus callosum. In its backward growth the corpus callosum carries back its matrix or "commissure-bed," in which it always lies.

But although the elongation of the corpus callosum is most obvious in the backward direction, it also grows forward towards the anterior extremity of the brain.

In the Amphibia and certain Reptiles, where the olfactory bulb is placed in front and is not overlapped by the hemisphere, the "corpus præcommissurale" extends forward as a horizontal band from the lamina terminalis to the mesial wall of the olfactory peduncle. It is bounded upon its dorsal aspect by the homologue of the hippocampus. In the Marsupials with small pallia the upper margin of the precommissural body is slightly oblique (Pl. 15. figs. 8 and 9). As the pallium increases in extent it bulges over the olfactory bulb (figs. 1 and 2, p. 63) more and more, and consequently the "precommissural" hippocampus (*hip''*) becomes more and more oblique, because it always extends towards the olfactory peduncle. Thus the hippocampus comes to bend downward in front of the commissures. Now it is obvious that the dorsal limb of the commissura dorsalis (fig. 1), if it extends forward, must indent this precommissural segment of the

hippocampus as I have represented in fig. 2. This anterior portion of indented hippocampus is the "*gyrus geniculi*" of Zuckerkandl.

It is apparent from this that *the dorsal commissure, which in the Marsupial lies within a well-defined arc formed by the hippocampus (fig. 1), never breaks through this hippocampal arc even in its much more extended and reconstructed form as a corpus callosum, but pushes the dorsal part of the arc before it as it elongates in both directions (fig. 2).*

We have seen that in the Marsupial a large mass of grey substance, containing both commissures and formed by the "corpus præcommissurale" and "commissure-bed," is situated upon the ventral aspect of this hippocampal arc. Since the hippocampal formation may be recognized surrounding the corpus callosum even in the brains of the ox, the monkey, and man, it is clear that the matrix of this commissure can be formed of no other structure than the "precommissural body" and the "commissure-bed." This introduces us to the problem of the nature of the "septum pellucidum."

We have already seen that the first "callosal" fibres replace the hippocampal fibres of the dorsal limb of the "commissura dorsalis," and in every respect present the same relations as the fibres, the places of which they usurp. The first "callosal" fibres, therefore, must lie in the structure which is exactly homologous to what we have called, in the Marsupial, the "commissure-bed."

In discussing the nature of the "commissure-bed" we came to the conclusion that with the increasing dimensions of the commissures the dorsal part of the lamina terminalis became thickened or invaded by the posterior parts of the "corpora præcommissuralia," so that a bridge of grey matter—the "commissure-bed"—was formed, connecting the two hemispheres, and forming a matrix for the two cerebral commissures. This secondary thickening appears to take place gradually in the ontogeny of each individual, and cannot be regarded as a mere mechanical fusion of the precommissural area of the two hemispheres. We may therefore safely say that the dorsal commissure of the Metatherian and (for the reasons stated above) of the early Eutherian cerebrum is contained in a matrix which is formed by a thickening of the dorsal part of the lamina terminalis at the expense of the "corpora præcommissuralia." As new commissural fibres crowd in and the commissure increases in length and depth, this matrix becomes extended, but I believe it always continues to enclose the dorsal commissure, even in its most extended form.

Paul Martin says that in the cat the cephalic extremity of the corpus callosum or genu is formed by the apposition of fibres in front of those which are situated in the thickened lamina terminalis. It must be evident (if we glance at fig. 1) that if these apposed fibres grow in a "secondary fusion of the walls of the hemisphere," such a fusion must consist of a "soldering" of the two "precommissural hippocampi" (*hip*). But such a "soldering" does *not* take place, because in the *gyrus geniculi* we have seen the representative of the "precommissural" hippocampus pushed before the advancing corpus callosum. There seems to be no other alternative which could be for a moment maintained but that the corpus callosum is contained in its original matrix or "commissure-bed," which has become enormously but gradually elongated. This conclusion is strongly forced upon us by comparison, in the order mentioned, of such a series of

cerebra as those of the *Iguana*, *Ornithorhynchus*, *Phascoglossus*, *Perameles*, *Nyctophilus*, *Dasyurus*, and *Talpa*, with more highly-developed forms.

In this process of forward extension the dorsal commissure has carried forward its own matrix, derived from the original "commissure-bed." It is obvious that if this takes place without a corresponding growth of the bridge of grey matter (*s*) which lies between the dorsal and ventral commissures, we shall have part of the great longitudinal fissure (bounded on either side by the precommissural area) roofed in by the corpus callosum (contained, of course, in its proper matrix). This roofed space will be bounded posteriorly by the ventral limb of the "commissura dorsalis." This enclosed part of the great longitudinal fissure is the so-called "fifth ventricle," or "*carum septi pellucidi*."

By means of the accompanying five schemes (in which the commissure-bed is shaded) I have graphically represented different stages in this process. From these schemes it will be readily recognized how the backward extension of the dorsal commissure (fig. 5) stretches not only the matrix in which it lies but also the sheet of the "precommissural body" (*p.a.*) which fills up the large angle between the two limbs of this commissure. Thus a portion of the precommissural body of each hemisphere becomes one of the leaves of the septum pellucidum. In his valuable memoir Paul Martin speaks of a fusion taking place (in the brain of the cat) between the opposed walls of the hemisphere on the ventral side of the corpus callosum. In this manner, in the more highly-developed macrosomatic Eutherian cerebra, the massive corpora præcommissuralia below the corpus callosum may meet and fuse in the median plane so as to obliterate the cavum septi. But the commissure itself is *not* situated in any such secondary fusion of the hemisphere walls, so that it does *not* affect the main argument advanced above.

But though the corpus præcommissurale thus takes an important share in the formation of the septum pellucidum, part of it always remains distinct in the higher mammalian cerebrum as a vertical band, lying parallel to the lamina terminalis and separating the latter from the general pallium. This band is the "gyrus subcallosus" of Zuckerkandl. In order to show the last stage which this process reaches, I have represented in Pl. 16. fig. 18 this region of the cerebrum

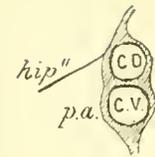


FIG. 4.

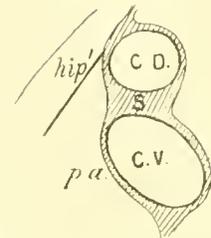


FIG. 5.

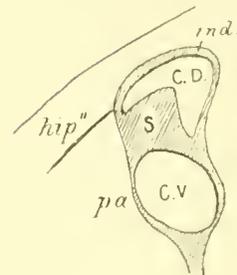


FIG. 6.

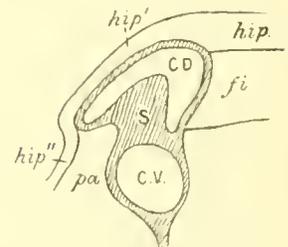


FIG. 7.

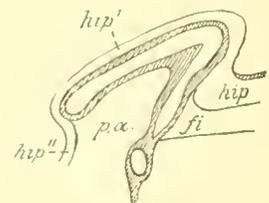


FIG. 8.

Figs. 4-8.—Schemes to explain the evolution of the "septum pellucidum."

Fig. 4 is a type of a Reptile.

" 5 " " Monotreme.

" 6 " " Marsupial.

of an adult man. The anterior extremity of the corpus callosum has become so bent that its rostrum (*r.*) becomes continuous with the remains of the "commissure-bed," which still surrounds the ventral commissure (*c.v.*). In this way the septum pellucidum (*sept.*) becomes surrounded by a complete ring of the matrix of the commissures and cut off from the gyrus subcallosus, which is the remainder of the precommissural area. This gyrus subcallosus extends down to the base of the cerebrum immediately in front of the ventral commissure and lamina cinerea (*l.c.*). Its line of separation from the pallium is indicated in the figure by a dotted line (*a.l.*). The gyrus subcallosus is traversed by a well-marked vertical depression—the *fissura prima* (*fiss.pr.*),—which has no important morphological significance.

With the knowledge which we have acquired of the process of phylogenetic development of the region of the commissures, it is extremely instructive to study the beautiful figures with which Marchand, in man, and Paul Martin, in the cat, represent (*op. cit.*) the process of ontogenetic development.

In the Marsupial we have a *fissura arcuata* or *hippocampi*, extending from the tip of the temporal pole right round the mesial wall of the hemisphere towards the olfactory peduncle; so, in the foetal child or kitten, we find the Bogenfurche (which we might, with Mihalkovics, appropriately call "Ammonsfurche") following a similar course and shading away towards the cephalic pole of the hemisphere. And it is necessary to remark, in passing, that the so-called part of the "vordere Bogenfurche," which His calls "fissura prima," has nothing whatever to do with the true Bogenfurche or fissura arcuata, if we regard the latter as the primitive fissura hippocampi.

In the early stages of the cat, the lamina terminalis becomes thickened and invaded by the commissural fibres of the fornix (Paul Martin), so in phylogeny we have the corresponding stages in the adult Monotremes and Marsupials.

Then, as the commissural fibres increase in number, the grey mass or thickening of the lamina terminalis is invaded by so many white fibres that the grey substance seems to disappear, but it is in reality being gradually extended by the swelling commissure.

The backwardly-extending commissure produces exactly the same series of changes—the same hippocampal flexure—in our phylogenetic series as it does in the developing brain of the cat and man (see Martin and Marchand's figures).

Thus, for all the stages in the developing brain of the cat, we can find almost exact prototypes among the more lowly-developed mammals.

The great feature which far more than any other distinguishes the mammalian brain from that of all submammalia is the possession of a definite pallium—distinct alike in its histological features and its morphological relations—giving rise to a definite internal capsule of projection-fibres and well-defined and fully-medullated commissural fibres. At first, in the Monotremata and Marsupialia, this pallium (like the parent mass of the basal ganglion from which it appears to have sprung) is united to its homologue of the opposite hemisphere by means of the "commissura ventralis"—"the commissure of the cerebral hemisphere" *par excellence*.

But the rapid growth in extent and complexity of this general cortex or pallium is accompanied by a richer and more abundant commissural system. This growing commissural system from the dorsal part of the enormous pallium not only finds in the

“*commissura dorsalis*” a shorter path, but a clearer scope for longitudinal extension than the ventral commissure provides. And thus we have pallial fibres invading and subsequently superseding the dorsal limb of what was previously the hippocampal commissure.

“Pallial” commissural fibres probably first make their appearance in Reptiles and form a very insignificant constituent of the ventral commissure. In Monotremes and Marsupials these fibres become extremely abundant, and swell the proportions of the ventral commissure enormously. But in Eutheria a rapidly increasing proportion of these fibres forsake the *commissura ventralis* and form the new “dorsal commissure of the pallium”—the corpus callosum,—which throws the “parent” commissure into insignificance. The remnant of the *commissura ventralis* is known in man by the somewhat misleading name “anterior commissure.”

#### EXPLANATION OF PLATES 15 & 16.

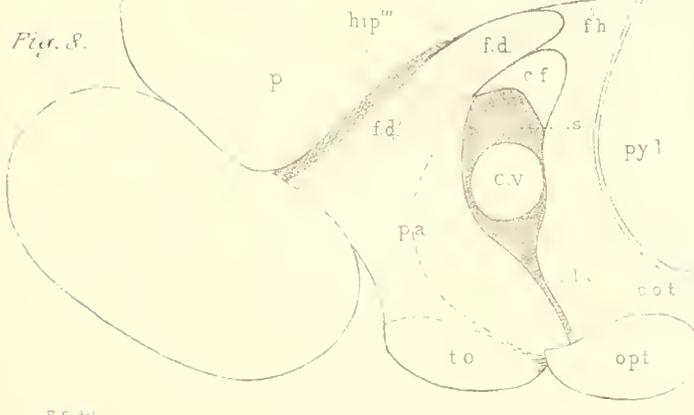
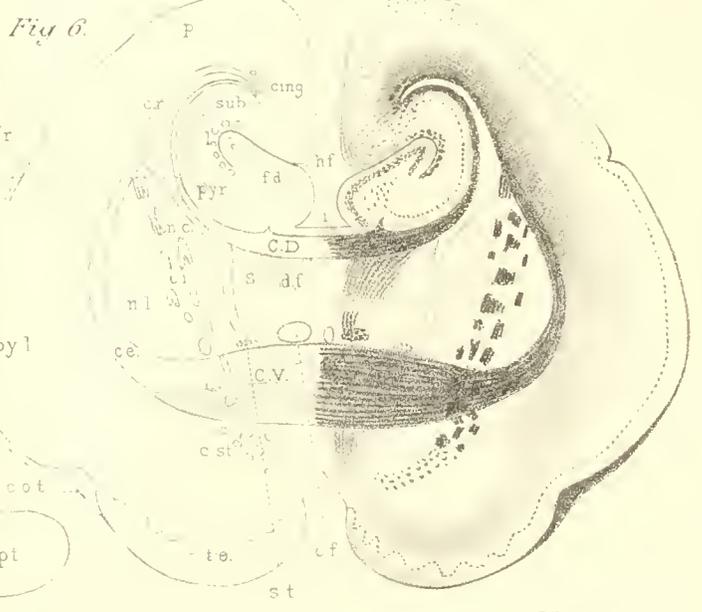
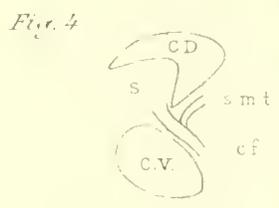
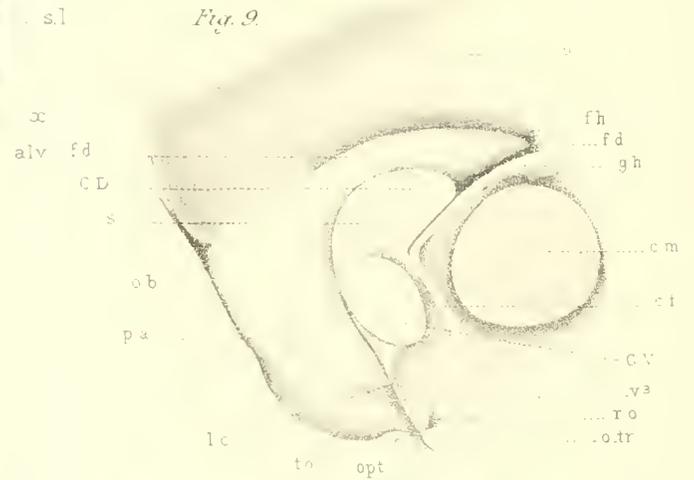
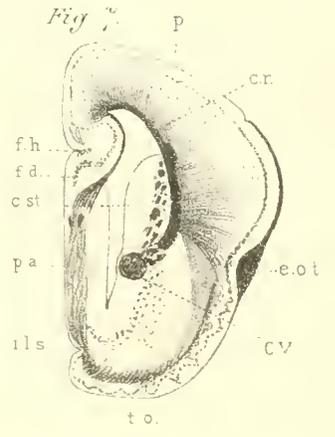
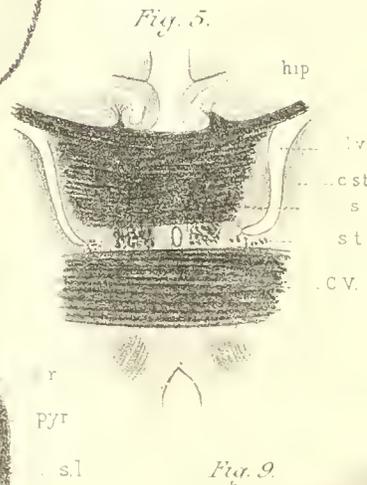
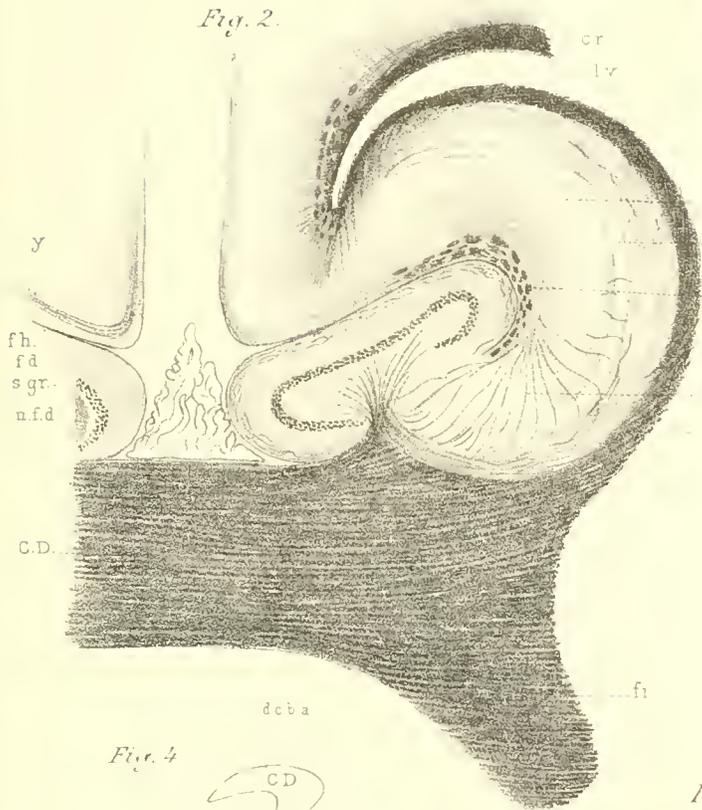
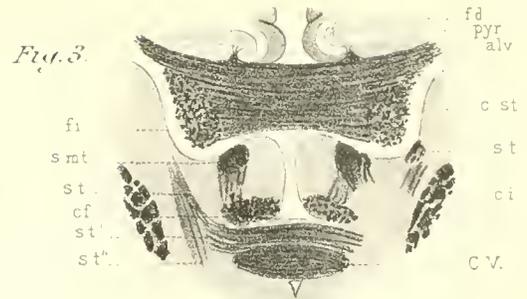
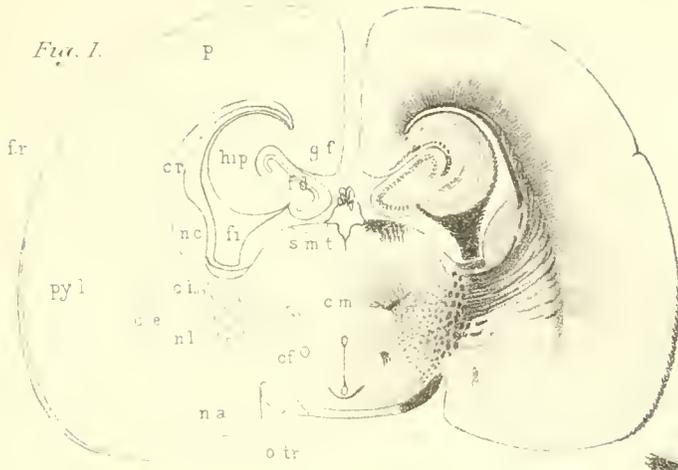
- Fig. 1. Coronal section through the forebrain of *Perameles nasuta*. Stained by Weigert's method.  $\times 4$ . The section passes just behind the commissures.
2. Coronal section through the hippocampal formation and the posterior extremity of the “*commissura dorsalis*” in *Perameles*. Weigert stain. Fascia dentata represented as it appears after nuclear staining.  $\times 20$ .
- Figs. 3 & 5. Coronal sections of the “*commissura dorsalis*” of *Perameles*, a short distance in front of fig. 2.  $\times$  about 6.
- Fig. 4. Representation of the commissures of *Perameles* (as seen in a mesial sagittal section) to show the planes in which the sections represented in figs. 2 (*a*), 3 (*b*), 5 (*c*), and 6 (*d*) were cut.
6. A coronal section of the cerebral hemispheres of *Perameles*, to show the general arrangement of the commissures. Weigert stain.  $\times$  about 6.
7. Coronal section of the right cerebral hemisphere of *Perameles* immediately in front of the cerebral commissures. Weigert-Pal and carmine stains.  $\times 4$ .
8. Semi-schematic representation of the anterior part of the mesial wall of the cerebral hemisphere of *Dasyurus viverrinus*.  $\times$  about 4. To show that, as a result of the unrolling of the hippocampus anteriorly, the whole of its *morphologically* superficial layer now *actually* forms part of the visible surface. Thus the surface of the hippocampus proper (*hip.*) appears above the fascia dentata (*f.d.*!).
9. Anterior portion of the forebrain of *Perameles*, exposed in a mesial sagittal section.  $\times 4\frac{1}{2}$ . The bulbous olfactorius only represented in part and in outline.
10. Sagittal section through part of the anterior portion of the mesial wall of the cerebral hemisphere of *Phascogaleus cinereus*. Weigert stain.  $\times 6$ .
11. Horizontal section through the left hemisphere of *Trichosurus vulpecula*, a short distance above the commissures.  $\times 2$ . *ant.mes.*, the antero-mesial angle.
12. Coronal section through the right hippocampal formation of a bat (*Miniopterus Schreibersii*), to compare with the hippocampal region of fig. 1. Lithium-carmine stain.  $\times$  about 20.
13. Coronal section of *Miniopterus*. Compare fig. 2.
14. Coronal section of right hemisphere of *Miniopterus*.  $\times$  about 20. Compare with fig. 6.
15. The fascia dentata and adjacent parts. Enlarged from fig. 14.
16. Coronal section of the hippocampal region of *Miniopterus*, a short distance in front of fig. 14.
17. Sagittal section of the commissures and adjacent parts of brain of *Nyctophilus* near the mesial plane.  $\times$  about 40.
18. Drawing of the “gyrus subcallosus” of a human brain.

*Explanation of reference-letters in the figures.*

The significance of the reference-letters *a, b, c, d, z, β, γ, δ* is explained in the text.

- a.l.* Anterior limit of the "gyrus subcallosus."  
*alv.* Alveus hippocampi.  
*cing.* Cingulum.  
*cing<sup>l</sup>.* Longitudinal fibres in the alveus hippocampi adjacent to the cingulum.  
*c.d.* "*Commissura dorsalis.*"  
*c.d.<sup>l</sup>* Dorsal limb of the "*commissura dorsalis.*"  
*c.d.<sup>v</sup>.* Ventral limb of the Metatherian type of "*commissura dorsalis.*"  
*c.e.* Capsula externa.  
*c.f.* Columna fornicis.  
*c.i.* Capsula interna.  
*c.m.* Commissura mollis.  
*c.r.* Corona radiata.  
*c.st.* Corpus striatum.  
*c.v.* "*Commissura ventralis.*"  
*d.f.* Descending hippocampal or fornix-fibres.  
*e.* Epithelial fold roofing the third ventricle.  
*e.o.t.* External olfactory tract.  
*f.d.* Fascia dentata.  
*f.h.* Fissura hippocampi.  
*fi.* Fimbria.  
*fl.* The remains of the fimbria intermingled with fibres of the commissura dorsalis.  
*flx.* The "subsplenial hippocampal flexure."  
*f.r.* Fissura rhinalis.  
*g.h.* Ganglion habenulae (and stria medullaris thalami).  
*hip.* Hippocampus.  
*hip<sup>l</sup>.* "Supracommissural hippocampus."  
*hip<sup>h</sup>.* "Precommissural hippocampus."  
*hip<sup>h</sup>.* Stratum zonale of the "precommissural hippocampus" lying upon the surface immediately above the stratum zonale (*vel* moleculare) of the fascia dentata (*f.d.<sup>l</sup>*).  
*i.* "*Indusium verum.*"  
*i.l.s.* Internal limiting sulcus of the tuberculum olfactorium (*t.o.*).
- l.* "Longitudinal association bundles" of the hippocampus.  
*l.c.* Lamina cinerea.  
*l.v.* Lateral ventricle.  
*n.a.* Nucleus amygdalæ.  
*n.c.* Nucleus caudatus.  
*n.f.d.* Nucleus fasciæ dentatæ.  
*n.l.* Nucleus lenticularis.  
*o.b.* Olfactory bulb.  
*opt.* Optic nerve.  
*o.tr.* Optic tract.  
*p.* General cortex or pallium.  
*p.a.* "*Precommissural area*" or "*corpus præ-commissurale.*"  
*py.l.* Pyriform lobe.  
*pyr.* Layer of pyramidal cells of the hippocampus.  
*r.o.* Recessus opticus.  
*s.* "Commissure-bed."  
*sept.* "Septum pellucidum."  
*s.gr.* Stratum granulosum of the fascia dentata.  
*s.l.* Stratum lacunosum of the hippocampus.  
*s.m.t.* Stria medullaris thalami.  
*spl.* Splenium of the corpus callosum.  
*s.r.* Stratum radiatum of the hippocampus.  
*s.t.* Stria terminalis.  
*s.t<sup>l</sup>.* The crossing fibres of the stria terminalis entering the "*commissura ventralis.*"  
*s.t<sup>h</sup>.* The uncrossed part of the stria terminalis.  
*sub.* Subiculum cornu ammonis.  
*t.* "Temporal pole" of the cerebral hemisphere.  
*t.o.* Tuberculum olfactorium.  
*v.3.* Third ventricle.  
*x.* Medullated nerve-fibres going to the stratum lacunosum.  
*y.* "*Tractus hippocampi ad pallium.*"





- E.S. del.

F. Huth, Lith. Edin.



Fig 10.

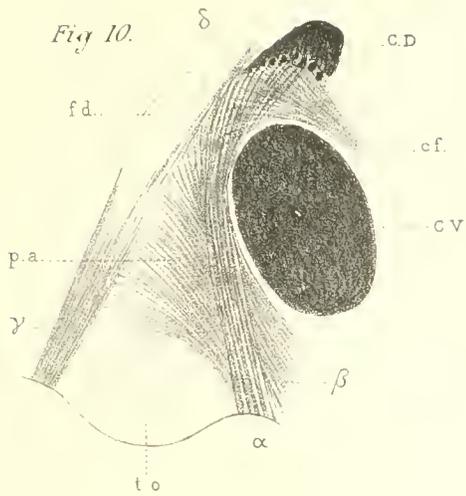


Fig 11.

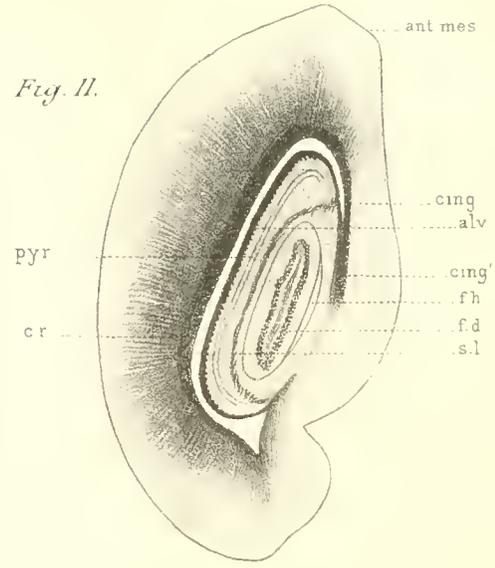


Fig 12.

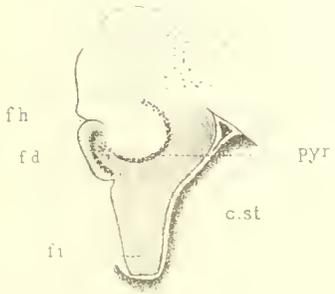


Fig 13.

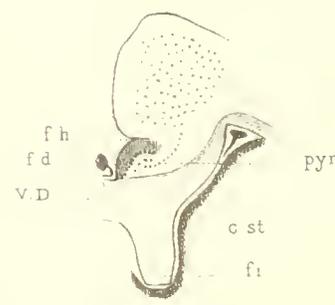


Fig 17.

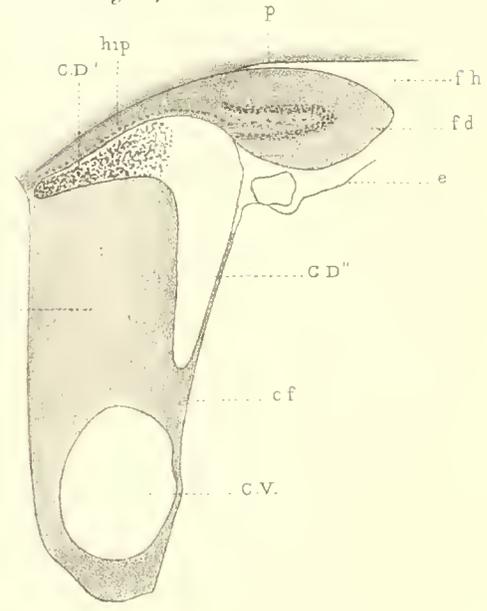


Fig 15.

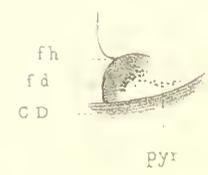


Fig 14.

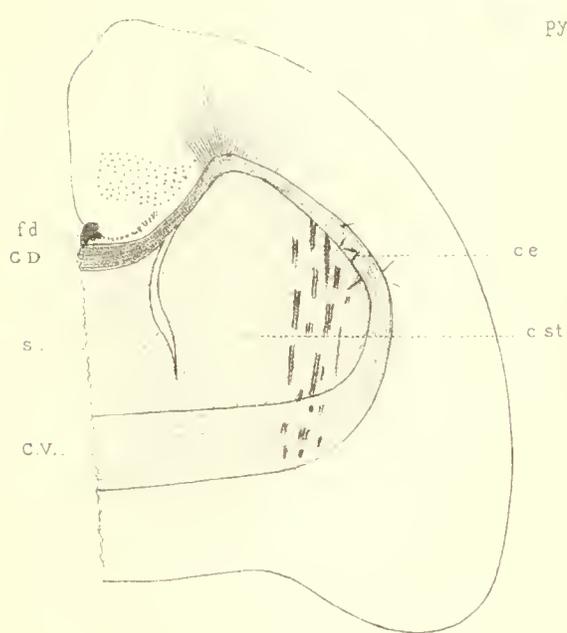


Fig 16.

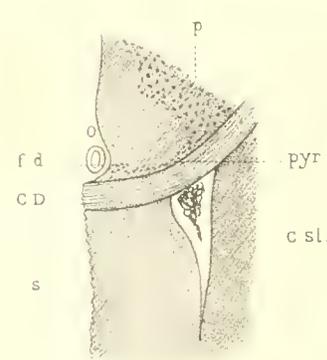
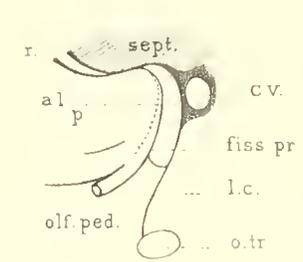


Fig 18.







# LINNEAN SOCIETY OF LONDON.

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Part	VII. 1883. ....	0 5 0	0 3 9	Part	IX. 1892. ....	0 12 0	0 9 0
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Part	XI. 1884. ....	0 10 0	0 7 6	Part	II. 1894. ....	1 11 0	1 3 3
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Part	XV. 1885. ....	0 4 6	0 3 6	Part	VI. 1896. ....	0 8 0	0 6 0
Part	XVI. 1885. ....	0 5 0	0 3 9	Part	VII. 1896. ....	0 12 0	0 9 0
Part	XVII. 1886. ....	0 3 0	0 2 3	Part	VIII. 1897. ....	0 2 6	0 2 0
Part	XVIII. 1888. ....	0 2 6	0 2 0	VII. Part	I. 1896. ....	0 10 0	0 7 6
III. Part	I. 1884. ....	1 14 0	1 5 6	Part	II. 1897. ....	0 12 0	0 9 0
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THE

TRANSACTIONS

OF

THE LINNEAN SOCIETY OF LONDON.

ON THE MUSCULAR ATTACHMENT OF THE ANIMAL TO ITS SHELL  
IN SOME FOSSIL CEPHALOPODA (AMMONOIDEA).

BY

GEORGE CHARLES CRICK, F.G.S., F.Z.S.,

OF THE BRITISH MUSEUM (NATURAL HISTORY).

(Communicated by the President, Dr. A. GÜNTHER, M.A., F.R.S.)



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June 1898.



IV. *On the Muscular Attachment of the Animal to its Shell in some Fossil Cephalopoda (Ammonoidea).* By G. C. CRICK, F.G.S., F.Z.S., of the British Museum (Natural History). (Communicated by the PRESIDENT.)

(Plates 17-20.)

Read 3rd February, 1898.

INDICATIONS of the muscular attachment of the animal to its shell have been figured in not a few Nautiloids, but comparatively few Ammonoids have been recorded in which what has been believed to be the remains of this attachment has been figured and described. Of these the best known are Opper's figures of three examples of *Ammonites steraspis*\* from the Lithographic Stone of Bavaria, published in 1863, in which the body-chamber of each is shown to be traversed by a fine curved line, the relation of which to the animal was not, however, indicated by the author.

In 1870, Trautschold † figured a specimen of *Ammonites bicurvatus*, exhibiting what he considered to be the impression of the muscular attachment of the animal, but this figure differs considerably from Opper's figures.

In the following year, Dr. W. Waagen ‡ published his important paper, "Ueber die Ansatzstelle der Haftmuskeln beim Nautilus und Ammonoiden," in which he expressed his opinion that the "shell-muscle" in the Ammonoidea was attached to the inner (umbilical) portion of the lateral area of the whorl. He believed the curved line figured by Opper on the body-chamber of *Ammonites steraspis* to be a trace of the "annulus," and probably also of the shell-muscle, and, reproducing one of Opper's figures, he completed by a dotted line what he considered to be the form of the shell-muscle. This interpretation of Opper's figures has been accepted by most authors.

In 1879, Eck § figured and described a small septate fragment of *Ceratites semipartitus* from the Upper Muschelkalk of Schwieberdingen, near Stuttgart, which he thought showed not only the appearance of the surface of the mantle (the so-called "epidermids"), but also the impression of the annulus. The specimen was merely an internal cast of five chambers, and on the surface of the cast of each chamber there was a depressed zone with a finely-pitted surface, occupying on the siphonal region the middle two-thirds, and becoming much narrower on the side of the whorl; in two of the chambers a groove was also present on the antisiphonal area.

\* Pal. Mittheil. p. 251, pl. lxxix. figs. 1, 2, & 6 (1863).

† Bull. Soc. Nat. Moscou, vol. xliii. pp. 301-306 (1870).

‡ Palaeontographica, vol. xvii. pp. 185-210, pls. xxxix. & xl. (1871).

§ Zeitschr. deutsch. geol. Gesell. vol. xxxi. p. 276, pl. iv. figs. 5 a-d (1879).

In his large works on the Triassic Cephalopoda, Dr. E. von Mojsisovics\* has figured several species of Ammonoids bearing on the internal cast of their body-chamber a groove or grooves (extending in some examples from the umbilicus on one side, over the periphery, to the umbilicus on the other side), which he considered to be the impression of the homologue of the muscular attachment of the recent Nautilus.

Dr. O. Jaekel †, in 1889, figured a Ceratite from the Trias of Rüdersdorf, near Berlin, bearing a groove precisely similar to those figured by Dr. E. von Mojsisovics, and although he doubted this indicating the position of the homologue of the annulus and of the shell-muscle in the recent Nautilus, he was unable to give any explanation of its nature. After an examination of Oppel's original specimen, this author says the line which Oppel figured and which has been regarded as indicating the position of the anterior boundary of the annulus and of the shell-muscle can scarcely be followed with certainty, and he is inclined to doubt the correctness of the interpretation.

In his 'Vorläufige Mittheilung über die Organisation der Ammoniten' ‡, Dr. Steinmann evidently does not agree with Dr. Waagen's interpretation of Oppel's specimens (although he seems to make no special reference to them), a fact which is clearly brought out in the 'Elemente der Paläonfologie' (1890) by himself and Döderlein, where (p. 351, fig. 102) one of Oppel's figures (Pal. Mittheil. pl. lxxix. fig. 2) is reproduced, and the curved line on the body-chamber completed in the manner suggested by Waagen, but in the explanation of the figure this line is thus described: "(?) vordere Grenze des Haftbandes."

At the meeting of the Geological Society of London which was held on March 25th, 1891, a communication was read from Mr. S. S. Buckman, entitled "Notes on Nautili and Ammonites." Only an abstract of the paper was published §. Nautili and Ammonites were exhibited in illustration of the paper, and, according to the abstract, "Two specimens exhibited show long spatulate depressions more or less parallel to the periphery for about half the length of the body-chamber. It was suggested that these impressions indicated the position of the shell-muscles."

So far, then, as I have been able to ascertain, no satisfactory examples exhibiting the form and position of the muscular attachment of the Ammonoid animal to its shell have yet been figured and described either to confirm or to contradict the explanation which Waagen gave of Oppel's figures.

The Ammonite animal may have been, and probably was, attached to its shell at the edge of the last septum, as in the living Nautilus, but from my own observations it is

\* Abhandl. d. k.-k. geol. Reichsanst. Wien, Bd. vi. Theil i. Heft i. (1873) pl. xvi. f. 3 (*Phylloceras occultum*); pl. xix. f. 1 (*Pinacoceras transiens*); pl. xix. ff. 2, 3, 4 & pl. xx. ff. 8 & 9 (*Pinacoceras humile*); pl. xx. ff. 2, 3, 5, & 7 (*Pinacoceras insectum*); pl. xxii. ff. 7, 8 (*Pinacoceras myophorum*); *ibid.* Bd. vi. Hälfte ii. (1893) pl. cxxxiv. f. 1 (*Choristoceras ammonitiforme*); *ibid.* Bd. x. (1882) pl. liii. f. 2 (*Megaphyllites sandalinus*); pl. liii. f. 3 (*Megaphyllites obolus*).

† "Ueber einen Ceratiten aus dem Schammkalk von Rüdersdorf und über gewisse als Hafttring gedeutete Eindrücke bei Cephalopoden," Neues Jahrb. 1889, ii. p. 19, pl. i.

‡ Berichte der naturforschenden Gesellschaft zu Freiburg, Bd. iv. Heft 3, pp. 31-47 (1889).

§ Abstr. Proc. Geol. Soc. London, Session 1890-91, p. 165 (Quart. Journ. Geol. Soc. vol. xlvii.).

quite clear that it was furnished with shell-muscles and an annulus like the recent *Nautilus*, and it is the object of the present communication to record the indications of these structures in various Ammonoids. It is not proposed here to record every Ammonoid in which these impressions have been observed—this I hope to be able to do subsequently—but to describe the form and position of these impressions so far as I have been able to observe them in the different forms which the Ammonoids assume, *e. g.* in *Baculites*, *Hamites*, *Crioceras*, *Ancylloceras*, *Macroscaphites*, *Scaphites*, and *Turrilites*, the group of the Ammonites (ranging from very evolute to almost entirely involute forms), as well as in *Clymenia* and the group of the Goniatites.

It may be well at the outset to refer to the indications of the shell-muscles and of the annulus as they exist in the shell of the recent *Nautilus*, and for this purpose it will probably suffice among the many figures which have been published of the muscular attachment of the recent *Nautilus* to call attention to the figures accompanying Dr. Waagen's paper already alluded to (p. 71)\*. I may, however, here remark that in the recent *Nautilus* the shell-muscles are ear-shaped and situated upon each side of the animal; they are connected both on the dorsal and on the ventral side by a narrow band—the annulus. The shell-muscles are not inserted into the shell-substance, but are merely applied to the inner surface of the test with the intervention of a thin layer of conchiolin; and all that is usually preserved in the interior of the shell to indicate the form and position of the muscular attachment is a fine, generally raised line, corresponding to the anterior boundary of the annulus and of each shell-muscle; it is only rarely that there are any indications of the posterior boundary of these structures. On an internal cast this raised line would be represented by an incised line, and since in fossils the remains of the muscular attachment are preserved almost always on internal casts, they therefore exist as incised lines. Such structures have been described and figured in not a few fossil Nautiloids, including the genus *Nautilus* itself. In the fossil forms any record of the form and position of the muscular attachment would, when present, usually be preserved upon the surface of the natural internal cast of the body-chamber, and hence raised lines on the inner surface of the original test would appear on the internal cast as incised lines, and *vice versa*.

In order to observe in the recent *Nautilus* the exact position of the muscular attachment with relation to the edge of the last septum, an artificial cast of the shell of *Nautilus pompilius* was made by filling a sagittal section of a recent shell with paraffin wax, and then dissolving away the shelly matrix with hydrochloric acid. The anterior boundary of the muscular attachment alone was indicated by a very finely incised line.

To show the usual position of the muscular attachment in Ammonoids, and for the better understanding of the less perfectly preserved examples, it is proposed first to describe the impressions of the "muscular scars" in the specimen on which they have been most clearly seen, and then the specimen in which the remains of the annulus have been most clearly observed. The former is an example of *Crioceras* from the

\* See also the recently-published paper by L. E. Griffin, "Notes on the Anatomy of *Nautilus pompilius*," Zool. Bull. vol. i. no. 3, pp. 147-161; with bibliography.

Specton Clay, and the latter an Oxfordian Ammonite, now referred to the genus *Cardioceras*. Then it is proposed to describe the form and position of the scars and of the annulus (when seen) in various forms of Ammonoids, ranging from the straight (in the adult) from *Baculites*, through *Iamites*, *Crioceras*, *Ancyloceras*, *Macroscaphites*, *Scaphites*, and *Turrilites* to the group of the Ammonites; then in *Clymenia* and the group of the Goniatites.

The very fragmentary character, and consequently imperfect determination, of some of the specimens must be mentioned; but, bearing in mind the position of the shell-muscles in the Ammonoid, viz. on the inner portion of the whorl, it will be at once evident that the traces of the muscular attachment are more likely to be found in fragmentary specimens, principally on natural internal casts of the body-chamber.

#### *Muscular Scars.*

The muscular scars have been best observed in a fragment of *Crioceras quadratum*\*, n. sp., which I obtained from the Specton Clay of Yorkshire (Pl. 17. figs. 10, 11). It consists merely of the base of the body-chamber, and is about 38 mm. long. The greater part of the test, which was in a very soft, white, friable condition, has been removed by a stiff brush, so as to expose the surface of the internal cast of the body-chamber without scratching it. The section of the whorl is subquadrate, the outer area being somewhat narrower than the inner; at the last septum the height of the whorl is 29 mm., and its greatest thickness 27 mm. On the inner (dorsal) area of the internal cast, and near the posterior extremity of the body-chamber, there are two oval areas, one on either side of the median line, the major and transverse diameters of each being 14 mm. and 11 mm. respectively. The longer diameter of each is placed transversely, but not quite at right angles to the median line, the inner end of this diameter being slightly in advance of the outer extremity. The two impressions are nearly in contact, being only about 0.5 mm. apart at the inner or anterior end of their respective longer diameters; their posterior borders are only slightly in advance of the last septum. Each impression is very slightly roughened, and consequently distinct from the surrounding and somewhat polished surface of the cast. An incised line forms its boundary on the inner, anterior, and outer sides, being deepest on the anterior side, while its posterior boundary is marked by a faint, somewhat irregular and imperfectly-defined line. No trace of the portion of the annulus surrounding the base of the body-chamber, and connecting the muscular impression on the one side with the muscular impression on the other side, can be seen. In the triangular space between the two impressions, and 3 mm. posterior to the point where they are nearest together, there is near each incised line a very small, shallow, double pit, each pair of pits being disposed longitudinally; these doubtless were connected with the muscular attachment of the animal to its shell.

\* This is really a Bean MS. name. Some of the examples of this species in the British Museum Collection bear this name in Bean's handwriting, and I have adopted the name, since, so far as I know, the species has not yet been described.

*Annulus.*

The impression of the annulus has been observed in several specimens, but in the British Museum Collection (No. C. 6801) there is an example of *Cardioceras excavatum* (J. Sowerby)\* from the Oxford Clay, but the locality is not recorded, in which the form of the muscular attachment, and particularly that of the annulus, is remarkably well displayed (Pl. 18. fig. 8). The specimen is apparently complete, and shows the aperture of the shell, which is provided with a narrow, ventral (or peripheral) apophysis. Its dimensions are:—Diameter of shell 120 mm.; width of umbilicus 24 mm.; height of outer whorl 58 mm.; ditto above preceding whorl 40 mm.; thickness of outer whorl about 43 mm. The body-chamber occupies the last half of the outer whorl, its base being 14 mm. high and 29 mm. wide or thick. The whorl is subsagittate in transverse section; its inner margin slightly overhangs the umbilicus, so that the width of the umbilicus, measured at the umbilical margin, is less than that measured at the suture of the shell. A greater part of the test is preserved, and this is mostly in a soft friable condition. Some of it had been removed from the left † side of the specimen, so as to expose a portion of the internal cast of the base of the body-chamber. By means of a small stiff brush the rest of the test was carefully cleared from both sides of the base of the body-chamber, and the form of the muscular attachment of the animal was displayed very clearly, especially on the left side, the attachment on the right side being precisely similar, but a little less distinct. On the left side the impression of the anterior boundary of the shell-muscle crosses the umbilical margin 5 mm. in advance of the last septum, and passes as a very narrow band of a thin film backward and outward in a flat forwardly-convex curve as far as the middle of the second lateral lobe, at which point, and 1.5 mm. posterior to it, there is seen to be another similar band which passes from the umbilicus immediately above the saddle on the margin of the umbilicus; these two bands, continuing at about the same distance apart, pass over the lateral saddle into the first lateral lobe and, then diverging slightly, pass over the peripheral or external saddle forward and outward towards the periphery in a flat forwardly-convex curve, but becoming very indistinct before reaching the periphery. These two very narrow filmy bands appear to be the remains of the anterior and posterior boundaries of the annulus respectively.

Remains of the annulus are visible also on the right side, but much less distinctly; they are, however, sufficiently clear to confirm the structures which have been mentioned as existing on the left side.

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Having described the usual form of the muscular scars and of the annulus, I now proceed to describe their remains in various forms of Ammonoids, commencing with the genus *Baenlites* and proceeding in the order already indicated (*ante*, p. 73).

\* J. Sowerby, Min. Con. vol. ii. p. 5, pl. cv. (1815).

† The terms "right" and "left" are used in a strictly morphological sense, the periphery (or siphonal area) of an Ammonoid being ventral, and the antiperipheral (or antisiphonal) area dorsal.

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## BACULITES, Lamarek.

*Baculites ovatus*, Say.—An example of this species in the British Museum (No. C. 5415 *a*) from the Fox Hill beds (Upper Cretaceous) of Horse-head Creek, South Dakota, U.S.A., displays the impression of the shell-muscle very clearly. The specimen consists of the natural cast of nearly the whole of the body-chamber, the cast of the last loculus and of a portion of the penultimate loculus. The test has been almost entirely removed from the posterior part of the body-chamber (Pl. 17. figs. 1, 2, & 3). The shell in this species is laterally compressed, and tapers very slowly. The length of the specimen is 290 mm. or about  $11\frac{1}{2}$  inches; its transverse section is oval, the greatest thickness being a little nearer the antisiphonal (dorsal) than the siphonal (ventral) area. Of this length the body-chamber occupies 215 mm., but the aperture is not preserved. The ventro-dorsal and transverse diameters of the base are 38 and 25.5 mm. respectively. The two muscular impressions are at the base of the body-chamber and on the antisiphonal (dorsal) area; the inner, anterior, and outer portions of their boundaries can be distinctly traced as a faint, shallow, depressed (not sharply-incised) line. On the antisiphonal area the suture-line has a small antisiphonal lobe separating the two portions of a broad saddle, each portion corresponding to the second lateral saddle in an ammonite; each of these halves is followed by a rather broad lobe (the second lateral) which separates it from the saddle occupying nearly the middle of the lateral area, *i. e.* the first lateral saddle. The median line of the antisiphonal area is occupied by a very shallow longitudinal groove. The inner boundaries of the two muscular impressions seem to meet in the middle line at about 2.5 mm. in advance of the most anterior part of the saddle, adjoining the antisiphonal lobe. Starting from this point, the boundary of the impression passes forward and outward until it is 8.5 mm. from the same part of the suture-line; then, turning backward and still maintaining its course outward, it passes along the outer side of the second lateral lobe, close to the inner side of the first lateral saddle. The boundary of the other impression has a precisely similar course. The impressions are somewhat oval, their longer diameters making an angle of about 45° with the median line of the antisiphonal (or dorsal) area. At a point slightly below the level of the most anterior part of the adjoining saddle (the first lateral) the outer boundary of each impression is a little angular. On one (the right) side of the specimen no trace of the annulus can be seen, but on the other (the left) side a line is seen to pass from the angular portion of the impression outward and upward over, and about 1 mm. distant from, the adjoining saddle; although it can be traced only for a short distance, owing to the roughness of the surface here, it doubtless represents the anterior boundary of a portion of the annulus.

At a distance of 5 mm. in front of the boundary of the impression on the right side, there is another line having precisely the same curvature. It is not nearly so distinct as the one just described, but most probably indicates the anterior boundary of the same shell-muscle. Possibly the posterior line denotes the position of the shell-muscle during the formation of a septum, and therefore during a period of rest, when the muscle would

become firmly attached to the shell. The anterior faintly-impressed line may have been the last attachment of the anterior boundary of the shell-muscle during the gradual growth of the animal upward prior to the formation of a new septum. The corresponding line on the left side is obscured by the shelly matter adhering to the cast.

On the median portion of the peripheral area the septum possesses a rather broad (median) saddle, on either side of which is a small lobe—the two halves of the peripheral lobe. This is followed by the peripheral or external saddle. Anterior to the septum and on the central portion of the same area there is a feebly-incised line having the form of half an ellipse (Pl. 17. fig. 3); it arises close to the outer portion of the external (or peripheral) saddle, *i. e.* at about 7 mm. from the median line of the siphonal (ventral) area; then curves upward and towards the median line, attaining its greatest height at about 8.5 mm. in front of the median saddle, or about 5.5 mm. from its commencement. The line seems then to pass on to the other side without interruption, but the surface of the cast is not sufficiently well preserved to enable this to be stated with certainty. Its anterior portion is about on the same level as the anterior portion of the boundary of the muscular impression. About 6 mm. in front of this curve there is a similarly-curved feebly-impressed line, which most probably is comparable with the faint curve on the opposite (antisiphonal) surface.

Although the annulus is not well shown in this example, there is another specimen [C. 5415 *b*] in the British Museum, from the same horizon and locality (Pl. 17. fig. 4), which displays the muscular impression less distinctly, but clearly shows the anterior boundary of a portion of the annulus. This leaves the muscular impression at the "angle" mentioned in the previous description, and, passing upward over the adjoining saddle at a distance of about 1.5 mm. from the suture-line, crosses the next lobe in a shallow depression, and again rises over the next saddle at about the same distance from it as before. This depression, however, is seen only with difficulty and by turning the specimen about in a fairly good light. There can, I think, be no doubt that the annulus was in the form of a simply-waved band, being elevated at the saddles and very feebly depressed in each lobe just as in the example of *Cardioceras excavatum* already described (p. 75). The total length of the specimen is 245 mm., the body-chamber (the aperture of which is not preserved) occupying 165 mm., the diameters of the base of the body-chamber being 44 and 31.5 mm. respectively. The other side of the cast of the body-chamber is obscured by fragments of the test.

*Baculites vagina*, Forbes.—A portion of the muscular impression has also been seen in an example of this species in the British Museum Collection [one of the specimens numbered S3624] from the Upper Cretaceous of Pondicherry, India (Pl. 17. fig. 5). It is merely the internal cast of the greater portion of the body-chamber, about 60 mm. long, anteriorly incomplete, but fairly perfect posteriorly. Its transverse section is oval, the diameters of its anterior end being 24 and 14.5 mm.; those of the posterior end being 19 and 12.5 mm. The antisiphonal surface is broad and slightly flattened, the siphonal being narrow, flattened, and with subangular borders. On the broad antisiphonal surface the feebly convex boundaries of the two muscular scars (indicated by a feebly-incised line

on the internal cast) meet nearly in the middle line in an obtuse backwardly-directed point which is 3.25 mm. in advance of the saddle on either side of the antisiphonal lobe, these two saddles occupying a large portion of the antisiphonal area. From this point each boundary passes forward and outward for a short distance, then turns backward and sweeps over on to the lateral area in a broad anteriorly-convex curve which gradually disappears before reaching the last septum; if continued to the septum it would meet the large lateral lobe on its antisiphonal side. It would seem therefore that, just as in the *Baculites* already described, the muscular scar on either side occupied the space between the central line of the antisiphonal area and the antisiphonal side of the large lateral saddle. There is no trace of the annulus in this example.

#### HAMITES, Parkinson.

*Hamites maximus*, J. Sowerby\*.—In the British Museum Collection (No. C. 6802) there is an example of this species, from the Gault of Folkestone, which displays the form of the muscular scars exceedingly well (Pl. 17. figs. 6, 7). It is only a fragment, *i. e.* one portion (the larger) of the terminal hook, and consists of the internal cast of the last loculus and of a portion of the body-chamber; its length, measured on the periphery, is about 55 mm. The whorl is subcircular in section, only slightly compressed, its ventro-dorsal diameter (excluding the ribs) at the base of the body-chamber being 16 mm., and its transverse diameter (also excluding the ribs) 15.5 mm. The impressions of the muscular scars are seen on the inner (dorsal) surface of the cast of the base of the body-chamber, one on either side of the median line and disposed somewhat obliquely, just as in the example of *Crioceras quadratum* already described in this paper (*ante*, p. 74). Each scar is elliptical in outline, and enclosed by a very faintly-incised line; its longer axis is inclined to the median line of the dorsal surface of the body-chamber at an angle of about 45°; its posterior boundary is only about 1.5 mm. anterior to the antisiphonal saddle of the last septum. Anteriorly the impressions are 1 mm. apart. The longitudinal and transverse diameters of each scar are 12 and 10 mm. respectively. At about the middle of the outer portion of the boundary there is a slight angularity, which doubtless indicates the position of the commencement of the anterior border of the annulus, but no other traces of the annulus have been observed. In another example which is figured (Pl. 17. figs. 8, 9) each muscular scar bears a small roughened patch, and there are indications of a narrow band connecting the scars.

#### CRIOCERAS, Lèveillé.

*Crioceras quadratum* †, n. sp.—The muscular impressions in this genus have been best observed in two examples of *Crioceras quadratum* from the Speeton Clay, Yorkshire. One of these has already been described (see p. 74). The other forms part of the British Museum Collection (No. S9102). It consists of the natural cast of the body-chamber with

\* J. Sowerby, *Min. Con.* vol. i. p. 138, pl. lxii. (1814).

† See footnote, *ante*, p. 74.

only fragments of the test adhering to it. At the base of the body-chamber the whorl is subquadrate in section, its height being 35 mm., and its greatest width 31 mm. (Pl. 17. figs. 12, 13). The impressions are not so complete as in the example just described. The anterior margin of each is indicated by a sharply-incised line; both lines almost meet each other in the median line of the inner (dorsal) area at about 10 mm. anterior to the summit of the innermost portion of the saddle on either side of the antisiphonal lobe. Disappearing posteriorly, each passes forward and outward for a length of about 10 mm., when each is about 5 mm. in advance of its origin; then, turning abruptly backward, each gradually disappears at a distance of about 9 mm. from its point of origin and about 14 mm. from the median line. The posterior extremity of each has a tendency to turn outward, and at a short distance from the extremity the line gives off a very faint branch which turns inward, but can be traced only for a short distance. Without doubt the faint line turning inward represents the boundary of the impression of the shell-muscle, and that continuing in an outward direction indicates the position of the anterior border of the adjacent portion of the annulus.

#### ANCYLOCERAS, d'Orbigny.

*Ancyloceras Matheronianum*, d'Orbigny.—In the genus *Ancyloceras* what is believed to be the impression of the muscular attachment of the animal has been best seen in an example of *Ancyloceras Matheronianum* in the British Museum Collection (No. C. 5322). It is a natural internal cast from the Neocomian of Cassis (Bouches-du-Rhône), France (Pl. 17. figs. 14, 15, 16). The coiled part of the septate portion is wanting, but the rest is fairly well preserved, although much waterworn. The body-chamber, measured along the centre of the periphery, is 380 mm. long; the cross section of its base is oval, the dorsal (or inner) portion being somewhat wider than the ventral (or outer); the ventro-dorsal diameter (or height) of the base is 75 mm., the transverse diameter (*i. e.* the thickness) 54 mm. (excluding the tubercles). What I regard as the impressions of the boundaries of the two muscular scars are seen on the inner or dorsal area. The two scars are not quite symmetrical, that on the right side extending about 15 mm. further forwards than that on the left. These boundary-lines are incised, but they are much coarser than usual. This, however, is probably due to the waterworn condition of the specimen, for the septal sutures, instead of being finely-incised lines as usual, are fairly deep and wide, and indeed have quite the appearance of having been considerably waterworn; and this condition of the septal sutures supports the opinion that the lines about to be described are really the impressions of the boundaries of the muscular scars. That on the right commences at about 3 mm. to the right of the median line and about 20 mm. in front of the large saddle adjoining the antisiphonal lobe; passing forward for about 35 mm. and approaching nearer the median line, it then turns outward, but still continues forward until at about 50 mm. from the last septum, when it turns still more outward and then disappears. That on the left appears to arise about 43 mm. in front of the most anterior portion of the saddle adjoining the antisiphonal lobe, and about 6 mm. from the boundary on the right side; passing forward and outward for nearly

20 mm., it is then at about 58 mm. from the last septum; then with a broad curve it turns backward until it is about 40 mm. from its commencement, when it appears to rapidly die out. Although the impressions of these boundaries may perhaps be more properly termed grooves, their form and position agree so well with what I have observed in somewhat similar forms that I think there can be no doubt as to their nature. I have not been able to observe any trace of the annulus in this example.

#### MACROSCAPHITES, Meek.

*Macroscaphites gigas*, J. de C. Sowerby, sp.—In the genus *Macroscaphites* what I regard as the anterior boundary of the muscular scar has been observed in an example of *Macroscaphites gigas*, J. de C. Sowerby, sp., in the British Museum Collection (No. 32608). The specimen is stated to be from the Lower Greensand of the Isle of Wight, but its matrix and state of preservation suggest rather the Kentish Rag (Lower Greensand) in the neighbourhood of Maidstone (Pl. 17. figs. 17, 18, 19). It is a much-compressed internal cast; the greatest diameter of its septate portion is 180 mm.; the length of its body-chamber measured along the centre of the periphery and over the coarse ribs is 350 mm., the height of the base of the body-chamber is 68 mm., the thickness (including the ribs) being reduced by compression to 22.5 mm. On the right side, at about 15 mm. above the most anterior part of the last septum and 20 mm. from the inner margin of the whorl when viewed laterally, a very fine incised line arises and passes thence as a flat arc forward and towards the inner margin, which it crosses at about 45 mm. in front of the last septum; it then curves backward and comes to within about 10 mm. of the septum, where it is in the middle line of the compressed and somewhat distorted dorsal area. From this point another line, making an acute angle with the line just described, passes forward and outward for rather more than 30 mm., when it curves outward still more and then disappears. These two curved lines we take to be the anterior boundary of the right and left muscular scars respectively; no traces of the annulus have been observed in this example. The material of this natural internal cast is very coarse, and the specimen is so much crushed that the very faint lines bounding the muscular scars can only be followed with difficulty; the boundary is preserved partly as an incised line and partly as a line of colour.

#### SCAPHITES, Parkinson.

*Scaphites binodosus*, A. Roemer.—The muscular impression can be traced in an example of this species contained in the British Museum Collection (No. C. 5182). It is from the Lower Senonian (Granulaten-Kreide) of Broitzen, near Brunswick. The specimen is a fairly well-preserved, but somewhat distorted internal cast. Its greatest length is 43 mm., and the greatest diameter of the septate portion is 26.5 mm. (Pl. 17. figs. 20, 21). At the posterior end of the body-chamber the whorl is 13.5 mm. high and 10.5 mm. thick (excluding the tubercles). The whorl is somewhat crushed obliquely, so that its sloping inner area is much more clearly seen on one (the left) side. On this side a feebly-incised (partly double) line arises almost close to the last septum, and at a distance of 5 mm.

from the inner edge of the whorl; passing forward in a broad, flattened, forwardly-convex curve, it gradually approaches and finally crosses the inner edge of the whorl at about 7.5 mm. in front of the last septum. Passing on to the dorsal (or concave) portion of the whorl, it turns backward, and in a rather broad forwardly-convex curve nearly reaches the centre of this area, where it appears to be joined by the corresponding impression on the opposite side. The boundary of the impression on the opposite side is not quite so distinct, and on the sloping inner area of the whorl it appears to be a little nearer the inner edge of the whorl than on the opposite side, but this is doubtless due in great measure to the oblique crushing to which the specimen has been subjected. At the base of the body-chamber it is only 2.75 mm. from the inner edge of the whorl; passing forward it gradually approaches and finally crosses the same at about 7.5 mm. in advance of the last septum. Passing thence in a forwardly-convex curve, it joins its fellow at about the centre of the dorsal surface of the whorl.

The lines here described are probably the boundaries of the muscular scars. I have not seen any indications of the annulus in this specimen.

*Scaphites aequalis*, J. Sowerby.—The muscular attachment of the animal has also been observed in an example of *Scaphites aequalis*, J. Sowerby, in the British Museum Collection (larger of the two specimens, No. 89113). The specimen is an exceedingly well-preserved and almost perfect natural internal cast from the Lower Chalk of Dorset. The greatest length of the specimen is 29 mm.; the greatest diameter of the septate part (which is at the base of the body-chamber) is 15.5 mm., the whorl here being 9 mm. high and 11 mm. wide (excluding the tubercles). The mouth-border is well preserved. The anterior border of the muscular attachment is preserved on the lateral area as a very faint line arising (on the left side) almost close to the last septum and at about 1.5 mm. from the edge of the whorl, and passing forward and towards the edge of the whorl crosses this edge somewhat obliquely at about 6.5 mm. in advance of the last septum. Fortunately a portion of the body-chamber can be removed so that the course of this line can be satisfactorily traced. Continuing still forward it passes into a fairly wide shallow groove 4 mm. in front of the most anterior portion of the septate part of the shell, the groove being disposed across the floor or concave portion of the body-chamber in a flat forwardly-convex curve, with a very slight backward depression at the centre of the area. A similar fine line can be somewhat less distinctly traced on the right side of the specimen, passing into the same groove on the floor of the body-chamber. About 3.75 mm. posterior to the groove just mentioned there is another similar but narrower groove. From my examination of other specimens it is not unlikely that this will prove to be the posterior boundary of the shell-muscles, which seem to have been united on the concave portion of the body-chamber into a fairly wide band. The shell-muscles then appear to have been almost confined to the concave area of the body-chamber, only a narrow portion extending on to the lateral area.

In the British Museum Collection (No. C. 6800) there is also a fragmentary example of the same species (Pl. 17. fig. 22), from the concave portion of the body-chamber of which the matrix has been removed as carefully as possible. There is a similar line on the lateral

area, passing into a shallow groove on the concave portion of the body-chamber, but the part of the latter between the groove and the anterior impressed line produced by the ornaments of the septate part of the shell is covered with a thin, yellowish, powdery layer, quite unlike the rest of the concave portion of the body-chamber. This in all probability indicated the place of attachment of the shell-muscles.

I have not observed the remains of the annulus in any example of this species that has come under my notice.

#### TURRILITES, Lamarek.

*Turrilites tuberculatus*, Bosc.—An example of this species in the Museum of Practical Geology (No. 6372) from the Lower Chalk of Cliffe Anstey, Wilts, displays the anterior border of the muscular scars exceedingly well (Pl. 18. figs. 1, 2). The specimen is a natural internal cast of about five whorls, the smallest of which is somewhat imperfect, and the rest fairly well preserved. Two of the upper whorls show that the siphuncle (*s*) is situated at about one-sixth of the height of the whorl below the suture of the shell. Unfortunately the suture-line is not well shown, so that it is not possible to say exactly where the body-chamber commences. The aperture is fairly well preserved. The height of the last whorl (from the lowest of the three rows of small tubercles to the suture of the shell) is about 52 mm.; the width of the whorl (*i. e.* the distance across the specimen) being 108.5 mm. The anterior border of the muscular attachment is well shown on the last whorl as a well-marked narrow groove. Viewing the specimen with the aperture away from you and directed downward, the course of this groove may be thus described:—Commencing somewhat below the centre of the whorl it passes for a very short distance (about 2 mm.) downward and to the right; then, turning still more to the right, it passes for a distance of about 13 mm. with a bold convex curve to within 12.5 mm. of the lowest row of smaller tubercles; then turning again still more to the right it passes under the uppermost row of small tubercles. Just beneath the tubercle to the left of the one under which this groove passes there are indications of a septal suture; this is believed to be the last septum, and therefore to indicate the commencement of the body-chamber. Passing still to the right and downward in a broad feebly-convex curve, and at the same time becoming deeper, the groove crosses the two lower rows of small tubercles at about 30 mm. from the last-mentioned bend; it is continued on to the surface below the tubercles until at about 10 mm. below the lowest row it curves round in a broad curve and passes to the left for a short distance; then at about 21 mm. below the lowest row of tubercles it makes an angular bend, passes downward and to the left for a distance of 11 mm., when it curves upward and passes into the umbilicus; this upward portion can be traced for about 24 mm., when it is obscured by matrix. With the exception of the 15 mm. first described, probably the whole of this incised line represents the anterior boundary of the two muscular scars.

*Turrilites Mantelli*, Sharpe.—An imperfect example of this species in the Museum of Practical Geology (No. 6373), from the Lower Chalk of the Isle of Wight, also shows a portion of the anterior border of one of the muscular scars (Pl. 18. fig. 3). The specimen

consists of the natural cast of only two whorls. The aperture is not preserved, but a portion of the last whorl without doubt formed part of the body-chamber. The larger whorl is 30 mm. high (*i. e.* from the lowest row of tubercles to the suture of the shell), and measures 65 mm. from side to side. The anterior border of the muscular impression occurs as an impressed line very near the anterior end of the specimen. Viewing the specimen with the large whorl downward, this line commences a little below the middle of the whorl, and, crossing the uppermost of the three rows of small tubercles, turns somewhat abruptly to the right, becomes more deeply impressed, and with a bold anteriorly-convex curve crosses the other two rows of small tubercles and passes on to the sloping surface below the tubercles, being intercepted at about 11 mm. below the lowest row of tubercles by the broken anterior end of the specimen.

Although the impression in this specimen is very incomplete, it serves to confirm the structure which has just been described in *Turrilites tuberculatus*.

Subg. HETEROCERAS, d'Orbigny.

*Turrilites (Heteroceras) polylocus*, Roemer.—It is exceedingly interesting to have been able to recognize any indications of the muscular attachment in this subgenus of *Turrilites*, since here the shell is coiled in the opposite direction to that of the genus *Turrilites*, and hence a corresponding inversion of the muscular attachment was to be expected. The example of *Turrilites (Heteroceras) polylocus*, Roemer, in which the attachment has been seen forms part of the British Museum Collection (No. 46154) and is from the Upper Cretaceous rocks of Haldem, Westphalia (Pl. 18. fig. 4). The specimen consists of about one and a half whorls. The aperture is exceedingly well preserved, but the suture-line is not shown, so that the base of the body-chamber cannot be thereby recognized. The form of the right side of the attachment is seen in fig. 4. Viewing the specimen as represented in the figure, the line indicating the anterior boundary of the muscular attachment is seen as an impressed line to commence on the lateral area of the whorl just to the right of the tubercle, which is above and somewhat to the left of the aperture; passing downward it turns to the left immediately under the tubercle, and continues to pass downward for rather more than 20 mm.; having turned upward very slightly, it continues as a line of colour in a broad sweep, nearly parallel to the outer curve of the whorl, to within about 60 mm. of the border of the aperture, when it again becomes a finely-incised line; then, turning upward and still passing forward for about another 20 mm., it curves somewhat abruptly backward, continuing for about 20 mm.; this last portion of the line enclosing an oval area, open posteriorly, the diameters of which are 20 and 12 mm. respectively. This area I regard as one of the muscular scars, and the line leading up to it as being partly the boundary of the shell-muscle, and partly the boundary of the annulus. It is much to be regretted that in developing the specimen its surface was somewhat scratched and rubbed, so that it is not possible satisfactorily to follow the course of the impression on the other side of the whorl.

## AMMONITES\*.

AMALTHEIDÆ, P. Fischer.

OXYNOTICERAS, A. Hyatt.

*Oxynoticeras?* *sp.*—The example (Pl. 18. figs. 5, 6) apparently referable to this genus, in which the form of the muscular attachment has been observed, is from the Great Oolite (Stonesfield Slate) of Stonesfield, Oxfordshire, and forms part of the British Museum Collection (No. 36710). It has been labelled "*Ammonites discus*, J. Sowerby," but it is probably not referable to Sowerby's species †, although its state of preservation does not allow an accurate determination. It is a crushed, poorly-preserved, internal cast lying loose on a piece of matrix. The greater part of the specimen is septate; the body-chamber has been broken across obliquely, but fortunately the posterior portion is preserved. When complete the specimen probably was quite 1.45 mm. in diameter, and its umbilicus about 22 mm. wide. The last half-whorl at least was occupied by the body-chamber, the base of which is 52.5 mm. high and about 10 mm. thick. The anterior border of the muscular scar and of the annulus can be traced across each side of the specimen, but it is more distinct on that side (fig. 5) lying upon the matrix. Here the anterior border arises from the suture of the shell at a distance of 11.5 mm. in advance of the last septum; after passing forward and outward for a short distance it turns backward in a rather broad curve, and passes uninterruptedly across the body-chamber in a fairly straight line, which is almost parallel to the general direction of the last septum, being in advance of the septum 15.5 mm. on the inner portion of the lateral area and 21 mm. near the periphery, where it seems to turn backward a little, but this appearance may be due to the much-compressed state of the fossil; it has no depressions corresponding to the lobes of the suture-line. The portion of the border to a distance of about 13 mm. from the inner edge of the whorl is indicated by a well-marked depressed line, and the rest of the border is indicated by the anterior boundary of a band of colour about 4.5 mm. wide, the posterior boundary of which is not sharply defined. The inner portion, bounded anteriorly by the depressed line, doubtless represents the muscular scar, and the broad band of colour the annulus; the scar exhibits distinct lines of growth.

On the opposite side the muscular scar and annulus are less clearly defined. The muscular impression appears to be somewhat nearer the last septum, for its anterior boundary arises as a faintly-incised line at a point only 8.5 mm. in advance of the last septum, and passes outward and backward as far as the septum, which it meets at a distance of 8.5 mm. from the inner edge of the whorl. Before reaching the septum, *i. e.* at a distance of 3.5 mm. from the septum, this boundary gives off a branch (indicated by a line of colour) which can be traced as a slightly-waved line across the body-chamber to the periphery, where it meets the anterior boundary on the opposite side. The portion of the annulus adjoining the muscular impression on this side is only about

\* The nomenclature and grouping of the Ammonites here adopted are those given by Prof. Dr. K. A. v. Zittel in his 'Grundzüge der Paläontologie,' 1895.

† J. Sowerby, *Min. Con.* vol. i. p. 37, pl. xii. (1813).

1.5 mm. wide for a length of about 8.5 mm.; it then expands somewhat rapidly to a width of 4.5 mm., a width which it maintains across the rest of the body-chamber, joining the band on the opposite side, the portion near the periphery being, however, somewhat less distinct than the rest.

The discrepancy in the position of the two impressions is doubtless due in a great measure, if not entirely, to the crushing which the specimen has undergone during fossilization.

#### AMALTHEUS, Montfort.

*Amaltheus spinatus*, Bruguère, sp.—The muscular impression has been observed in an example of this species in the British Museum Collection (No. C. 4919), the locality of which is not recorded. The specimen consists of the well-preserved septate portion of the shell, together with a natural cast of one side of the dorsal (or inner) part of the posterior portion of the body-chamber (Pl. 18. fig. 7). The dimensions of the specimen at the base of the body-chamber are:—diameter of the shell 57 mm.; width of umbilicus 24 mm.; height of outer whorl 19 mm.; ditto above preceding whorl about 17 mm.; thickness of outer whorl (excluding ribs) 19 mm.; ditto (including ribs) 22 mm. A portion only of the anterior boundary of the muscular impression is preserved. This, which appears as an impressed line, arises almost close to the suture (of the shell) 9 mm. in front of the anterior part of the small saddle belonging to the last suture-line that is situated on the edge of the umbilicus; it curves outward and backward for a distance of about 5 mm. where it is about 4 mm. from the suture (of the shell); then, passing backward nearly parallel to the inner edge of the whorl, it appears to divide just before meeting this small saddle, one part passing on the inner (dorsal) side of the small saddle situated on the edge of the umbilicus and then disappearing, the other passing on the outer side of the same saddle and then also disappearing. Posterior to this distinctly-impressed line there are several very faint lines concentric with it.

#### CARDIOCERAS, Neumayr & Uhlig.

*Cardioceras excavatum*, J. Sowerby, sp.—In the description of the annulus, which has already been given, I have described the muscular attachment in an example of this species (see *ante*, p. 75).

Another example of this species is also figured which shows the course of the anterior boundary of the muscular scar on the dorsal or impressed portion of the whorl (Pl. 19. figs. 1, 2).

*Cardioceras* aff. *excavato*, J. Sowerby, sp.—The muscular impression is also shown in an example of *Cardioceras* in the British Museum Collection (No. 50098), but its locality is not recorded (Pl. 18. figs. 9, 10). It is, however, allied to *Card. excavatum*, but is more compressed and more widely umbilicated than that species. The dimensions of the specimen are:—diameter of shell 54 mm.; width of umbilicus 18.5 mm.; height of outer whorl 20 mm.; thickness of outer whorl 12 mm. The test has been removed

from the greater part of the body-chamber, and the latter can fortunately be removed from the rest of the specimen. The whorl is carinate, subquadrangular in transverse section, its sides much flattened and nearly parallel to each other; at the base of the body-chamber it is 13.5 mm. high and 10 mm. thick. On the left side of the specimen (Pl. 18. fig. 9), near the base of the body-chamber a feebly-impressed (on the internal cast) line arises from the suture of the shell (*i. e.* the inner edge of the whorl) 4.5 mm. in front of the last septum; it extends outward and backward almost as far as the septum, nearly reaching the same at the inner side of the second (or inferior) lateral lobe; it then turns outward, as if to pass over the adjoining saddle, and soon disappears. When the body-chamber is detached (Pl. 18. fig. 10) this incised line is seen to be continued on to the impressed zone, being also indicated by a difference of colour, the portion posterior to the boundary being much lighter than the rest of this surface. From the edge of the whorl this boundary passes a little backward in an *f*-shaped curve nearly to the central line of the impressed area, when, turning abruptly backward, it passes nearly parallel to the median line of this area as far as the small saddle adjoining the antisiphonal lobe. The corresponding line on the other side of the impressed area has the same form, so far as it can be traced, but the edge of the whorl on this side is somewhat imperfect. A line of colour appears to indicate that the median space between the two boundaries was bridged over anteriorly. The form of the muscular attachment just described on the impressed area of the outer whorl is confirmed by its appearance on the inner surface of the dorsal portion of the test of the body-chamber, which remains attached to the preceding whorl.

The muscular scar on the right side of the body-chamber is not preserved, the inner portion of the base of the body-chamber having been broken off.

On the middle of the left lateral area there is a linguiform space, 8 mm. long and 4 mm. broad, enclosed by a very faint line, open behind and convex anteriorly (Pl. 18. fig. 9). Its lateral boundaries are nearly parallel to the inner and outer margins of the whorl respectively, the inner being 4.5 mm. distant from the inner margin, and the outer at the same distance from the periphery of the whorl. The inner boundary passes just into the inferior lateral lobe along its outer side, and the outer boundary just passes into the superior lateral lobe along its inner side. There is a similar linguiform area on the middle of the right side of the body-chamber, 9.5 mm. long and 6 mm. wide, open behind, and with a convex anterior boundary. Its inner boundary passes just into the inferior lateral lobe at its outer side, whilst the outer boundary passes just into the superior lateral lobe along its outer boundary, and not its inner, as on the opposite side of the body-chamber. Hence the linguiform area on this side is somewhat broader than that on the left side, the inner boundary being at about the same distance from the inner edge of the whorl, while the outer is nearer the periphery than on the opposite side.

Only in this one specimen have these linguiform areas been observed; but, as they are so distinctly displayed on both sides of the fossil, it is just possible that they are connected with the attachment of the animal to its shell. This example seems to support the figure given by Trautschold.

*Cardioceras Sutherlandia*, J. de C. Sowerby, sp.—The position of the anterior boundary of the shell-muscle is exceedingly well shown in a large example of this species from the Oxfordian of Scarborough, Yorkshire. It forms part of the British Museum Collection (No. S2369). It is a large internal natural cast, about 370 mm. (or nearly  $14\frac{3}{4}$  inches) in diameter, the umbilicus being 85 mm. in diameter, and having almost perpendicular walls. Nearly one-half of the outer whorl is occupied by the body-chamber, the base of which is obtusely cordate in section, 132 mm. (or nearly  $5\frac{1}{4}$  inches) high and 210 mm. (or rather more than  $8\frac{1}{4}$  inches) wide, the inner area being 45 mm. wide and nearly perpendicular to the plane of symmetry of the shell. The anterior boundary of the muscular impression, represented by a well-marked groove, crosses the umbilical margin 60 mm. (or about  $2\frac{2}{3}$  inches) in front of the last septum, and passing outward and backward becomes much less distinct at about 52 mm. from the last septum, and at about the same distance from the umbilical margin. It appears, however, to be continued across the whorl by a faint, somewhat irregular groove, which, originating some 6 mm. posterior to the groove just described, crosses the whorl in a flat forwardly-concave curve which is only 15 mm. from the anterior portion of the lateral saddle, and nearly touches the anterior part of the external saddle; this we regard as the anterior boundary of the annulus. Passing inward from the umbilical margin, the boundary of the shell-muscle is indicated by a distinct groove which curves somewhat backward, but can be traced only about halfway across the inner area of the whorl.

*Cardioceras funiferum*, J. Phillips, sp.—A similar boundary of the shell-muscle has been observed in several examples of this species which are contained in the British Museum Collection. It is well shown in an example (No. 50447) from the Oxford Clay of Trowbridge, Wiltshire. This is 167 mm. in diameter and 68 mm. thick, the umbilicus being almost closed and its margin rounded. About one-half of the outer whorl is occupied by the body-chamber, the base of which is acutely cordate in section, 64 mm. wide and 72 mm. high. On the left side of the specimen the anterior border of the shell-muscle is indicated by a groove which crosses the umbilical margin at 9 mm. anterior to the last septum; passing backward and outward as a fairly wide groove for about 10 mm., it then becomes shallower and wider. The posterior boundary of the muscular scar is represented by a slightly raised ridge, which, passing from the umbilical margin just above the last septum outward and forward, meets the lower boundary of the anterior groove at a point 12 mm. from the umbilical margin. The anterior groove appears to be continued across the whorl (*i. e.* to within 5 mm. of the periphery) as an exceedingly faint groove, which indicates the position of the anterior border of the annulus; this is 8 mm. anterior to the lateral saddle, 10 mm. anterior to the external saddle, and is depressed at each lobe. On the outer half of the lateral area of the whorl this boundary is partly indicated by remains of the test.

On the right side of the specimen there are similar indications of the anterior boundary of the muscular scar, but no traces of the annulus.

*Cardioceras* sp.—Indications of the muscular attachment are well displayed in a small Ammonite from the Upper Jurassic of Kintradwell, Sutherland, which forms part of the British Museum Collection (No. C. 4389). Although the specimen is fairly well preserved, I have not been able satisfactorily to determine the species, but it seems to be referable to the genus *Cardioceras* (Pl. 19, figs. 3, 4). Its dimensions are as follows:—diameter of shell 23.5 mm.; greatest thickness 8.5 mm.; width of umbilicus 7 mm.; height of outer whorl 8 mm. The last two-fifths of the outer whorl are occupied by the body-chamber; the test having been removed from the left side and from the periphery of this portion of the whorl, the internal cast is well displayed. Unfortunately only a small portion of the last suture-line can be made out, the rest being obscured by the test. The portion of the last septum adjacent to the suture of the shell is obscured, but on the internal cast of the body-chamber, at a short distance anterior to the last septum, a very fine incised line arises from the suture of the shell, passes inward in an almost radial direction for about 2.5 mm., then turns backward for about 0.5 mm., and again resumes its radial direction across the whorl, being feebly depressed as it passes over each lobe, and slightly raised in passing over each saddle; it is about 0.5 mm. above the lateral saddle and almost touches the most anterior portion of the external saddle. As it approaches the periphery it turns forward to join a somewhat peculiar-shaped roughened scar represented in fig. 4, the posterior inflated portion of which is rather rougher than the rest. Unfortunately the opposite side is obscured by matrix. The periphery of the posterior portion of the body-chamber seems to be somewhat deformed, and to possess a feeble keel with a shallow sulcus on either side; this deformation may account for the median division of this scar, which probably was originally horseshoe-shaped, as observed in several other Ammonoids.

The portion of the incised line near the suture of the shell doubtless represents the position of the anterior border of one of the shell-muscles, the rest of the line indicating the position of the anterior boundary of the annulus, there having been, in addition, a firm attachment at the centre of the periphery.

#### NEUMAYRIA, Nikitin.

*Neumayria catenulata*, Fischer, sp.—In the British Museum Collection there is an example of this species exhibiting the form of the muscular attachment. It is a badly-crushed internal cast from the Portlandian of Choroschowo, near Moscow, Russia. The specimen is 119 mm. in diameter, the width of the umbilicus (from suture to suture) being 18 mm., the height of the outer whorl 58 mm., and its thickness 26 mm. The inner area of the whorl slopes towards the umbilicus and at the base of the body-chamber is 6 mm. wide, the height of the whorl here being 43.5 mm., and its greatest thickness, which is at a short distance from the umbilical margin, 15.5 mm. The last two-thirds of the outer whorl are occupied by the body-chamber. The whorl is sagittate in cross section. The muscular impression is well shown on one side, but the crushed condition of the specimen has obliterated it on the other side. Arising from the suture at about 7 mm. from the base of the body-chamber, the boundary of the impression, in the form of a faintly-indent

line, passes outward and backward in a curve, which nearly meets the last septum at about 11.5 mm. from the suture, and thus encloses a subtriangular area on the inner side of the base of the body-chamber. Just before this outer line reaches the last septum it gives off a very faint branch which passes outward towards the periphery, but can be traced for a very short distance only. This is, without doubt, an indication of the anterior boundary of a portion of the annulus. Within and parallel to the outer boundary of the impression there are one or two very faintly indented lines.

TISSOTIA, Douvillé.

*Tissotia Ewaldi*, v. Buch, sp.—The muscular impression is shown in an example of this species in the British Museum Collection (No. C. 4810 *a*) from the Chalk (Senonian) of Mezab-el-Mesai, Algeria (Pl. 18, fig. 11). The specimen is a natural cast, 88.5 mm. in diameter; rather more than one-fourth of the outer whorl is occupied by a portion of the body-chamber, but this latter is somewhat imperfect on one side, so that the dimensions of the specimen can best be taken at the base of the body-chamber. Here its dimensions are as follows:—diameter of shell 84.5 mm.; width of umbilicus 8.5 mm.; height of outer whorl 42 mm.; greatest thickness of same (at a short distance from the umbilicus) 4.7 mm. The whorl is obtusely cordate in transverse section, rather wider than high, and indented to rather more than one-half of its height by the preceding whorl. The anterior border of the muscular impression is represented by a feebly-incised line. It cannot be traced quite as far as the suture of the shell, but on the narrow inner area of the whorl it is 4 mm. from the last septum; passing thence forward and outward on to the lateral area, it attains its greatest distance from the last septum (viz. 8.5 mm.) at 4 mm. from the edge of the whorl. Then, curving backward, it passes on the umbilical side of, and at a distance of 1.5 mm. from, the first (counting from the umbilicus) large lateral saddle, and, turning forward, sweeps round in an anteriorly-concave curve immediately about the small saddles occupying the margin of the umbilicus and soon disappears. The muscular scar thus bounded appears to have been an oval about 10 mm. by 7 mm., its longer axis being placed nearly in a radial direction but slightly inclined backward. From the anterior portion of the boundary of this impression a feebly-depressed line passes backward and outward in a broad forwardly-convex curve to within about 2.5 mm. of the outer portion of the first (counting from the umbilicus) large lateral saddle, then in a forwardly-concave curve crosses the adjacent lobe, and disappears just above the next lateral saddle. This line may indicate a portion of the anterior boundary of the annulus.

The opposite side of the body-chamber has been so much eroded that the muscular impression is not preserved.

## LYTOCERATIDÆ, Neumayr, emend. Zittel.

## LYTOCERAS, Suess.

*Lytoceras cornucopia*, Young & Bird, sp.—The impression of one of the shell-muscles has been observed in an example of this species in the British Museum (No. 37851) from the Upper Lias of Whitby, Yorkshire (Pl. 19, figs. 15, 16, 17). The dimensions of the specimen are:—diameter 22 mm.; width of umbilicus 8 mm.; height of outer whorl 8 mm.; greatest thickness of the outer whorl 8.5 mm. Rather more than one-half of the last whorl is occupied by the body-chamber, the base of which is nearly circular, its dorso-ventral and transverse diameters being each 6 mm. The amount of indentation by the preceding whorl is very small. At the base of the body-chamber, and on the inner area of the whorl, there is an oval impression (fig. 16), truncated on the inner side by the edge of the “impressed zone.” The diameters of the portion that can be seen are 1.75 mm. and 2.0 mm. respectively, the longer diameter being placed transversely on the whorl. The anterior and the posterior boundaries are both visible, the latter being almost close to the first auxiliary saddle; but no trace of the annulus can be seen.

On the peripheral area there is an elongated linguiform impression (fig. 17), which is rounded and submucronate anteriorly, but is open posteriorly, each limb being situated in each half of the siphonal (peripheral) lobe. Its anterior portion is a little in advance of the most anterior part of the siphonal saddle; its posterior portion is slightly contracted. Its length is 3.25 mm. and its width (between the limbs) .75 mm.

In the British Museum Collection there is also a portion of the natural internal cast of the body-chamber of another example of this species (Pl. 19, figs. 13, 14), from the Upper Lias of Whitby, which exhibits the impression of the boundary of the right muscular scar surrounded anteriorly and laterally by a dark-coloured, longitudinally-elongated, oval area, a portion of which is slightly rougher than the rest. Its form is shown in fig. 13. Only the right side of the base of the body-chamber is preserved, the height of the whorl here being 35 mm. At about 4.5 mm. anterior to the last septum, the incised line indicating the position of the boundary of the muscular scar passes from the suture of the shell—*i. e.* the edge of the impressed zone—in a radial direction for about 7 mm.; then, turning abruptly backward nearly at right angles to its former course, it is continued as far as the last septum. At the suture of the shell the boundary of the oval dark-coloured area is 3.5 mm. anterior to the incised line just mentioned; after proceeding forward in an anteriorly-concave curve for about 2 mm., it passes in an anteriorly-convex curve forward and outward for about 7 mm.; then, after curving gently backward for about 5 mm., it can be traced nearly as far as the last septum, having a direction nearly parallel to the edge of the impressed zone.

*Lytoceras fimbriatum*, J. Sowerby, sp.—The muscular impression is also shown in a fragmentary example of this species in the British Museum (No. 20837) from the Middle Lias of Kilsby Tunnel, Northamptonshire. The specimen consists of nearly half a whorl, and is a natural cast of part of the body-chamber of a shell having approximately the

following dimensions:—diameter 120 mm.; width of umbilicus 49 mm.; height of outer whorl 44 mm.; greatest thickness of ditto 41 mm. The posterior portion of the body-chamber is preserved; one side is much crushed, but the rest is fairly complete. A portion of the test still adheres to the cast. The specimen, measured along the median line of the periphery, is 165 mm. long; its transverse section is ovate, the greatest thickness being at about two-fifths of the height of the whorl from the inner edge; at its posterior end the height of the whorl and its thickness (allowing for the crushing) are 30 mm. and 27 mm. respectively. The impression of one shell-muscle is well shown, but only the inner portion of the other (Pl. 19. figs. 11, 12). The whorl is very slightly impressed by the preceding whorl. In shape the impression is truncated-oval, its longer diameter being transverse and the truncated end towards the median line of the dorsal surface. Arising a little in advance of the saddle on the side of the antisiphonal lobe, the boundary of the impression passes forward for about 5 mm. nearly parallel to the median line of the dorsal or antisiphonal surface, and at 1.5 mm. from its fellow on the opposite side; then, curving outward, it extends for about 10 mm. in a direction almost at right angles to its previous course; bending rather abruptly backward, it passes for a short distance nearly parallel to the boundary of the impressed zone; then, curving inward and backward, it speedily disappears. The greatest width (transverse) of the impression is 12 mm. There is no trace of the annulus. The boundary of the impression is indicated by a depressed line, which is rather deeply incised on the inner and outer portions, but somewhat less so on the anterior portion. The portion of the surface of the cast bounded by the impression is a little rougher than the rest. Owing to the crushed condition of the whorl, only the inner portion of the other impression is preserved. The impression is so situated that in a lateral aspect of the whorl only a very small portion of it can be seen (fig. 12).

*Lytoceras quadrisulcatum*, d'Orbigny, sp.—One example of this species, collected by Dr. J. W. Gregory in East Africa, exhibits a portion of the muscular impressions. It is a crushed fragment of a natural cast of the posterior part of the body-chamber. The inner portion of the whorl is badly crushed, but exhibits on either side a part of the muscular scar. At the base of the body-chamber the whorl is 30.5 mm. high and 30 mm. thick, the greatest thickness being a little within the central portion of the lateral area; the transverse section is therefore nearly circular. The muscular scars are somewhat darker than the surrounding surface of the cast, and present a slightly roughened appearance. That on the left is the better shown, but its inner portion is obscured so that the whole of its anterior border is not visible. Its boundary is usually a feebly-indented line, but sometimes a slightly-raised line. The anterior boundary of this impression appears to commence at about 7.5 mm. in advance of the most anterior part of the last septum, and about 8 mm. from the central line of the impressed zone; it passes thence slightly forward and outward for a distance of about 2 mm.; then, curving backward at about 10.5 mm. from the median line, it passes for a short distance nearly parallel to the median line; then, at about 4.5 mm. in advance of the last septum,

curving rather abruptly inward but still passing backward, it disappears at about 5.5 mm. from the median line, exhibiting, however, a tendency to again turn forward. The portion of the scar which is visible has a pyriform shape; its axis is at an angle of about 45° with the median line of the dorsal area of the whorl, the "stalk" being directed outward and backward; its length is about 8.5 mm., and its greatest width about 5 mm.

The other scar is truncated by a fracture crossing it obliquely, so that only the posterior portion of the impression is seen. It is somewhat darker than the surrounding surface, and bounded anteriorly and laterally by a very slightly-raised line. Commencing from the fracture at about 9 mm. in advance of the most anterior part of the last septum, and at the same distance from the median line of the dorsal area, the anterior boundary passes backward and very slightly outward; then, curving round, comes to within 2 mm. of the suture-line; then, curving inward and forward, it is again intercepted by the fracture at about 4 mm. from the median line. The anterior and outer boundaries of the impression are sharply marked by a feebly-incised line, but the posterior boundary is not quite so sharply defined.

There is a very shallow and rather broad depression on the peripheral area about 5 mm. in front of the summit of the siphonal (peripheral) saddle; on either side of the median line of the periphery, and at a distance of 3 mm. apart, a very faint line curves forward and towards the median line of the periphery, nearly meeting its fellow at about 3 mm. anterior to the depression just mentioned. This possibly represents the anterior border of the peripheral portion of the annulus.

#### ÆGOCERATIDÆ, Neumayr, emend. Zittel.

##### ARIETITES, Waagen, emend. Zittel.

*Arietites obtusus*, J. Sowerby, sp.\*—The muscular impression is well shown in an example of this species from the Lower Lias of Lyme Regis, that was kindly lent to me by Mr. G. F. Harris, F.G.S. The specimen is a fairly-complete internal cast, almost entirely denuded of the test. Its dimensions are:—diameter of shell 101 mm.; width of umbilicus 43 mm.; height of outer whorl 32 mm.; ditto above preceding whorl 29 mm.; greatest thickness (excluding ribs) 30 mm.; ditto (including ribs) 33 mm. The dimensions of the base of the body-chamber are:—height of whorl 26 mm.; thickness (excluding ribs) 22 mm.; ditto (including ribs) 25 mm. The body-chamber is complete and occupies the last half-whorl. The muscular impression is situated at the base of the body-chamber and occupies the inner area of the whorl (Pl. 19. figs. 8, 9, 10). Its anterior boundary, represented by a fine incised line, is convex, its anterior portion being 16 mm. in front of the anterior portion of the second lateral saddle of the last septum. Passing backward its outer boundary is nearly parallel to, and at a distance of 6 mm. from, the suture (of the shell). It can be traced backward for a distance of

\* Min. Con. vol. ii. p. 151, pl. clxviii. (1817)=*Asteroceras obtusum* (J. Sowerby): *vide* Hyatt, 'Genesis Arietidæ,' 1889, p. 201.

11 mm., beyond which point the surface of the cast is fractured. About 2 mm. behind this line, and nearly concentric with its anterior portion, there is another very faint line, evidently marking a former attachment of the shell-muscle. On the inner area of the whorl there are three or four fine, faint, longitudinal grooves, extending over three-fourths of the length of the body-chamber; one of these, 2 mm. from the suture (of the shell), extends the whole length of the body-chamber.

On the periphery, on either side of the median line, there is a feebly-impressed sigmoidal line (fig. 10), the anterior portion of which is about 11 mm. in advance of the anterior portion of the external (peripheral or siphonal) saddle. Each line arises about 2 mm. from the median line of the periphery; it passes away from this line, and backward to about 8 mm. from the most anterior portion of the external (peripheral or siphonal) saddle, and then disappears. These lines may indicate the position of the attachment of the animal to this part of its shell, but no connection can be seen between these lines and the impressions on the inner area. A line drawn from the centre of the shell to the most anterior part of these lines on the periphery crosses the inner edge of the outer whorl at a point 7.5 mm. posterior to the anterior boundary of the impression which is seen on the inner area.

Posterior to these lines on the peripheral area there is a horseshoe-shaped marking with nearly parallel sides, each of which passes posteriorly into each half of the siphonal lobe. It is rounded anteriorly, and crossed in its length by several lines parallel to the anterior border. Its length (above the small median saddle) is 14 mm., and its width 5 mm. This may, or may not, be connected with the muscular attachment of the animal, but similar impressions have been observed in other forms. (See *Egoceras capricornum*, p. 95.)

*Arietites raricostatus*, Zieten, sp.\*—In the British Museum Collection there is an example of this species (No. C. 4882) showing the muscular impressions (Pl. 20. figs. 10, 11). The locality of the specimen is not recorded, but, judging from the matrix, it came probably from the Lower Lias of Somersetshire. The specimen is a well-preserved natural cast with the following dimensions:—diameter 51 mm.; width of umbilicus 33 mm.; height of outer whorl 10 mm.; greatest thickness of outer whorl (excluding ribs) 14 mm.; ditto (including ribs) 16 mm. The body-chamber occupies the whole of the last whorl, and its posterior part (*ab*) can be removed from the rest of the fossil; its transverse section is transversely oval, its thickness (excluding the height of the ribs) being 10 mm., and its height 7 mm.; it was only slightly indented by the broad periphery of the preceding whorl. The greater part of the muscular impressions is on the concave dorsal area, *i. e.* on the impressed zone. On either side of the median line of this area (fig. 11) there is a subtriangular impression, having its broadly-rounded apex directed forward. These impressions are about 1 mm. apart, that on the right side of the shell being the more nearly complete. Each is bounded by a faint double line. Commencing

\* F. Zieten, Verstein. Würt. p. 18, pl. xiii. f. 4 = *Caloceras raricostatum* (Zieten), *vide* Hyatt, Gen. Arietidæ, p. 144.

at the most anterior part of the antisiphonal (or antiperipheral) saddle and at a point 0·5 mm. from the median line, the boundary of the more nearly complete impression passes forward and outward until it is 3 mm. in advance of the last septum and about 2·5 mm. distant from the median line; then, turning backward and passing still outward, it approaches the last septum, and nearly (but not quite) meets the inner portion of the lateral saddle, where it disappears, its place of disappearance being 4·5 mm. from the median line of the dorsal area or of the impressed zone. The outer boundary of the muscular impression is on the edge of the umbilicus, and therefore in a lateral view of the Ammonite only the outer backwardly-directed portion of the impression can be seen. There is a corresponding and similar impression on the other side of the specimen, but it is not so complete, owing to a fracture of the fossil. There are no traces of the annulus.

*ÆGOCERAS*, Waagen, emend. Zittel.

*Ægoceras capricornum*, Schlotheim, sp.—A portion of the impression of the muscular attachment of the animal has been observed in an example of this species from the Lias of Cheltenham, that forms part of the British Museum Collection (No. 67929). The specimen is a well-preserved natural cast, bearing portions of the test in a soft, white, friable condition (Pl. 20, fig. 2). By removing this with a stiff brush from near the base of the body-chamber, the muscular impression is well shown on either side. The dimensions of the specimen are as follows:—Diameter of shell (including ribs) 47 mm.; ditto (excluding ribs) 44 mm.; width of umbilicus 20 mm.; height of outer whorl (including ribs) 15 mm.; ditto (excluding ribs) 14·5 mm.; thickness of whorl (including ribs) 17 mm.; ditto (excluding ribs) 14·5 mm. At the base of the body-chamber the height and thickness of the whorl are respectively 11 and 13 mm. including the ribs, or 10 and 10·5 mm. excluding the ribs. The outline of the muscular impression is seen on either side at the base of the body-chamber and quite close to the suture of the shell. It is convex anteriorly, its anterior boundary being 6 mm. in front of the most anterior portion of the second lateral saddle; its outer boundary is nearly parallel to, and at a distance of 2 mm. from, the edge of the impressed zone, and passes posteriorly on to the outermost branch of the second lateral saddle. Its anterior boundary exhibits a tendency to curve forward at the suture of the shell. In the middle of the peripheral area there is a tongue-shaped scar, which is rather more than twice as long as wide, has nearly parallel sides, and is rounded anteriorly; each side of it just touches the boundary of the siphonal lobe. The scar seems to have been covered with a thin film of shelly matter, for part of this has been broken away from the anterior portion so as to expose a black layer beneath. This scar would be situated in the immediate neighbourhood of the siphuncle, and may or may not have had anything to do with the muscular attachment of the animal. Its length above the extremity of the small median saddle is about 6 mm., and its width is 1·5 mm. A precisely similar scar has been observed in *Arietites obtusus*\*.

\* See *ante*, p. 93.

The outline of the muscular impression is also well shown in another example of this species from the Lower Lias, near Whitby, in the collection of F. L. Bradley, Esq., F.G.S., of Alderley Edge, Cheshire, to whom I am greatly indebted for the loan of the specimen. The impression has the same form and position as that already described in the example from the Lias of Cheltenham, which is in the British Museum Collection (No. 67929). The specimen is in the centre of a nodule; its dimensions, so far as can be ascertained, are as follows:—diameter of shell 65 mm.; width of umbilicus 31 mm.; height of outer whorl 16 mm.; ditto at base of body-chamber 13 mm. The last half-whorl is occupied by the body-chamber, the exposed portion of which is almost completely denuded of the test; at its base and on the inner portion of the whorl the outline of the muscular impression can be seen. The anterior convex boundary of the impression is 5.5 mm. in advance of the last septum, the width of the impression from the suture of the shell being 2 mm.

There is no trace of the annulus, and the peripheral portion of the fossil is obscured by matrix.

*Ægoceras laqueolum*, Schloenbach, sp.\*—In an example of this species from the Lower Lias of Harbury, Warwickshire, in the British Museum Collection (No. C. 6619), one of the muscular scars is well displayed. The specimen consists of about three-fourths of a whorl 165 mm. in diameter, and is a natural cast of part of the body-chamber. The base of the body-chamber is complete: it is 24 mm. high; 30 mm. wide including the ribs, or 29 mm. excluding the ribs. The muscular scar, which is clearly seen at the base of the chamber, is situated partly on the lateral area and partly on the impressed zone (Pl. 20. figs. 3, 4). The faintly-incised line bounding the scar arises from the last septum at a point 4.5 mm. from the inner edge of the whorl; then, passing forward for a length of about 9 mm. nearly parallel to the inner edge of the whorl, it turns towards the impressed zone, becomes much more distinct, and crosses the inner edge of the whorl 13 mm. in advance of the last septum; passing on to the impressed zone with a rather broad sweep, it gradually disappears, but the form of the scar is indicated by a difference in colour, the impression being a little darker than the surrounding surface. The impression did not quite reach the middle of the impressed zone; it appears to have been elliptical in form, about 15 mm. long and 11 mm. wide, the larger portion being situated on the impressed zone. On the anterior portion of that part of the scar which is situated on the impressed zone there is an exceedingly faint line, concentric with the anterior border of the scar, which evidently marks a former attachment of the anterior border of the shell-muscle.

Only a very small portion of the other scar is visible; this is on the impressed zone. The greater part of the impression is obscured by matrix.

There is no trace of the annulus.

\* Palæontogr. vol. xiii. pl. xxvi. f. 1 = *Caloceras liasicum* (d'Orbigny), *vide* Hyatt, Gen. Arietidae, p. 139.

*Ægoceras Portlockii*, Wright.—An example of this species from the Boulder Clay of Ireland (exact locality unknown) was sent to me by Dr. A. H. Foord for determination. It was in a reddish matrix. It is a natural cast of the posterior portion of the body-chamber, showing not quite the complete suture-line at its base, and bearing only fragments of the inner portion of the test. The length of the fragment measured on the periphery is just over 70 mm.; the whorl is much compressed, nearly twice as high as wide; the transverse section of the whorl is elongate-oval, its greatest thickness being at about one-third of the width of the lateral area distant from the suture (of the shell). The impressed zone on the inner side of the specimen shows that the indentation by the preceding whorl was very slight, and that the periphery of the preceding whorl was more acutely convex than that of the outer whorl. At the base of the body-chamber the height of the whorl is 33.5 mm., and the greatest thickness about 18 mm. Any indication of the muscular attachment that may be preserved on the surface of the impressed zone is obscured by portions of the test, but on each side of the inner portion of the lateral area of the posterior portion of the cast the impression of this attachment is to be seen. Its anterior boundary commences at a point on the edge of the impressed zone about 14 mm. in advance of the most anterior portion of the suture-line, *i. e.* the main or inner branch of the siphonal saddle; it passes outward and backward for a length of about 5 mm., then for a short distance runs nearly parallel to, and at about 5 mm. from, the suture. After passing backward for a distance of nearly 10 mm. from its commencement, the line divides into two principal portions, one being continued almost parallel to, and only slightly approaching, the edge of the impressed zone, the other curving towards, and apparently reaching, the same edge at a distance of 14 mm. from its commencement. A fracture of the specimen prevents the former of the two lines being traced any further. About 1 mm. anterior to the incised line just described, there is a much fainter depressed line which, after extending backward for about 5 mm., nearly parallel to the incised line already described, appears to turn outward towards the periphery, and then quickly to disappear, while posterior to the line already described, and also parallel to it, there are two or three much fainter lines. On the other side of the whorl there are lines corresponding to the principal incised line, and the line about 1 mm. anterior to it, but these can only be traced backward some 6 mm., owing to the crushed state of this side of the specimen.

Near the base of the body-chamber, and slightly on the right side of the median line of the periphery, there is a horseshoe-shaped incised line having its convexity directed forward. Its anterior portion is 12 mm. in advance of the anterior portion of the outer branch of the siphonal (or peripheral) saddle. It is about 6 mm. long, 5 mm. wide in the anterior part, and 3.5 mm. wide in the posterior part. Each limb appears to be continued backward as far as the posterior end of the specimen, which is at about the level of the anterior portion of the *outer* branch of the peripheral (or siphonal) saddle, as a somewhat irregular, shallow, very faintly-impressed groove or grooves, each being almost parallel to the central line of the periphery. The posterior termination

of each limb is rather more deeply impressed than the rest. Within this horseshoe-shaped impression, and occupying the median line, is a very fine incised line, which extends backward from about 1 mm. posterior to the anterior boundary of the impression for a distance of about 6.5 mm. Doubtless this horseshoe-shaped impression had to do with the muscular attachment of the animal to its shell, for it has been observed in other forms, but the present specimen does not enable us to trace any connection between this impression and the marks of the muscular attachment seen on the inner edge of the whorl.

#### SONNINIA, Bayle.

*Sonninia sp.*—In the British Museum Collection there is an example (No. C. 5188) of *Sonninia sp.* from the Inferior Oolite of Yeovil, Somerset, in which the impression of the shell-muscles can be seen (Pl. 20, fig. 12). The test has been removed from the internal cast of the whole of the body-chamber, and the impression of each shell-muscle is displayed near the base of the chamber. The specimen has the following dimensions:—diameter of shell 91 mm.; width of umbilicus (from suture to suture) 28 mm.; ditto (from margin to margin) 37 mm.; height of outer whorl 36.5 mm.; greatest thickness (almost close to the umbilical margin) 24 mm., excluding thickness of test. The body-chamber occupies one-half of the last whorl; at its base the whorl, or more correctly the internal cast of the whorl, is 27 mm. high and 19 mm. thick. The whorl is subquadrate in section, with nearly parallel sides and well-defined inner area, the latter at the base of the body-chamber being about 6 mm. wide and sloping towards the umbilicus, making an angle of about 140° with the lateral area. The boundary of the muscular impression is indicated by an incised line which appears on the inner area of the whorl at a point 10.5 mm. anterior to the last septum; it passes outward and backward, just crossing the subangular umbilical margin, on to the lateral area, being at about 6 mm. distant from the suture of the shell, and appears to almost touch the saddle of the last septum that is situated on the subangular umbilical margin. On the area enclosed by this incised line, and concentric with it, there are several very faint lines, similar to those seen in the impression of the shell-muscles in the recent *Nautilus*. The surface of the cast anterior and also exterior to this incised line bears a number of shallow and irregular indentations, which may have had something to do with the muscular attachment, but the incised line just described appears to have been the impression of the anterior and exterior boundary of the shell-muscle. A similar line and similar adjacent indentations are present on the opposite side of the cast, but no indications of the annulus have been observed in this specimen.

#### HARPOCERATIDÆ, Neumayr, emend. Zittel.

##### HECTICOCERAS, Bonarelli.

*Hecticoceras hecticum*, Reinecke, sp.—In the British Museum Collection there is an example (No. 22309 a) from the Brown Jura  $\epsilon$ , Dettingen, Würtemberg, which displays the impression of the muscular attachment on both sides of the body-chamber

(Pl. 20, figs. 5, 6, 7). It is a natural cast, and has the following dimensions:—Diameter of shell 18·5 mm.; width of umbilicus 7·5 mm.; height of outer whorl 6·5; greatest thickness 4 mm. At the base of the body-chamber the whorl is 5·5 mm. high and 3·5 mm. thick. The shell is somewhat compressed, the inclusion very slight, and the umbilicus wide and shallow. The body-chamber occupies rather more than one-quarter of the last whorl, its inner (dorsal) edge subtending a chord of 8 mm. on one side and a little less on the other side. From the fractured anterior end of the body-chamber a double feebly-impressed line passes backward at a distance of 1 mm. from the suture (fig. 6); then, diverging slightly, the two lines cross the whorl in a rather deep forwardly-concave curve, their greatest distance from each other being rather more than 1 mm. Approaching each other slightly, but without touching, they curve forward at the periphery, each forming a submucronate point before passing on to the other side. It is to be noted that these points are not in the median line of the periphery, but slightly on one side (fig. 7). The posterior of the two lines crosses the lateral area about 1 mm. in advance of the anterior portion of the first lateral saddle. On the left side of the anterior end of the body-chamber (fig. 5) the double line just described curves slightly towards the periphery, but the opposite side, being a little shorter, does not exhibit this curvature. This double line probably represents a portion of the anterior boundary of the shell-muscle, the two lines on the lateral and peripheral areas indicating the position of the anterior and posterior boundaries respectively of the annulus.

#### ÆCOTRAUSTES, Waagen.

*Æcotraustes crenatus*, Bruguière, sp.—Two examples in the British Museum Collection (No. 8968), from the Oxfordian of Doubs, France, exhibit what appears to be the muscular impression. Both are natural casts.

One (Pl. 20, fig. 9) of these (No. 8968 *b*) has the following dimensions (exclusive of the spines on the periphery):—diameter 11 mm.; width of umbilicus 3 mm.; height of outer whorl 5 mm.; thickness of ditto 3 mm. At the base of the body-chamber the height of the whorl is 4 mm., and its thickness 2·5 mm. The septate part of the shell and the extreme base of the body-chamber are of a reddish-brown colour, while the rest of the body-chamber is of a much darker shade, a dark and very distinct line marking the division near the base of the body-chamber. This line appears to be the anterior border of the muscular attachment of the animal. It commences from the suture only a short distance in advance of the last septum, and crosses in a radial direction the inner half of the lateral area until reaching the lateral saddle where it is 0·75 mm. in advance of the suture-line; it then curves slightly backward, making a very shallow curve, until it reaches a point about 1·25 mm. from the median line of the periphery, where it turns somewhat abruptly forward, and reaches the median line of the periphery, 2·25 mm. in advance of the summit of the outer (or peripheral) saddle, thus forming on the periphery a subtriangular projection. A precisely similar line is seen on the opposite side of the cast, but in this species there does not appear to be any forward prolongation near the

inner area of the whorl such as has been observed in *Distichoceras Baugieri* (see below) and *Hecticoceras hecticum* (see p. 98).

The other specimen (No. 8968 *a*) has the following dimensions, exclusive of the peripheral spines, which in this example are comparatively small:—diameter of the shell 11 mm.; width of umbilicus 2 mm.; height of outer whorl 5.5 mm.; thickness of ditto 2.5 mm. At the base of the body-chamber the height of the whorl is 4.25 mm. (excluding spines), and the thickness 2.5 mm. The state of preservation of this specimen is quite similar to that of the one just described; the dark line near the base of the body-chamber, which is most probably the anterior boundary of the muscular attachment, is very like that in the previous specimen, but is slightly more waved on the lateral area. In this example also there does not appear to be any forward prolongation of the muscular impression on the inner (*not* impressed) area of the whorl.

The lack of any forward prolongation in this species seems to be confirmed by a specimen (No. 19536 *e*) in the British Museum Collection, from the Drift of Braunston, Northamptonshire, in which there is an indication of the anterior boundary of the muscular attachment near the suture of the shell, and in this example also it is only a short distance anterior to the last septum.

#### DISTICHO CERAS, Munier-Chalmas.

*Distichoceras Baugieri*, d'Orbigny, sp.—In the British Museum Collection there are two examples (No. 5140 *a, b*) of this species which clearly display the form and position of the muscular attachment of the animal to its shell. The species occurs in the Oxfordian, but the locality of these specimens is not recorded.

In the larger example (No. C. 5140 *a*) rather more than one-half of the last whorl is occupied by the body-chamber (Pl. 20, fig. 8). Its dimensions (not including the spines on the edges of the periphery) are:—diameter 17 mm.; width of umbilicus 4.5 mm.; height of outer whorl 8 mm.; greatest thickness (which is at a very short distance from the umbilicus) 4.5 mm. At the base of the body-chamber the height of the whorl is 5 mm., and its thickness 3.5 mm., the transverse section being sublanceolate. Measured along the curve of the inner portion of the lateral area, the anterior boundary of the muscular attachment can be seen as much as 6.5 mm. in advance of the last septum. After passing backward at a distance of 1.75 mm. from, and parallel to, the inner edge of the whorl for a distance of about 5 mm., the boundary then passes outwards in a shallow curve towards the periphery, just before reaching which it turns slightly forward. There does not appear to be a definite line at the anterior extremity of the forward prolongation of the impression, but the area included between the boundary of the muscular attachment and the inner edge of the whorl is a little roughened, the surface of the specimen outside this line being smooth and polished. Where the boundary turns outward there are several fine incised concentric lines. It is to be observed that the boundary of the forward prolongation of the muscular attachment does not coincide with the longitudinal groove running along the middle of the lateral area, but is situated between the inner margin of the whorl and this groove.

The smaller example (No. C. 5140 *b*), which exhibits the muscular attachment, has the following dimensions (excluding both the height of the peripheral spines and the inflated terminal portion of the body-chamber):—diameter 15 mm.; width of umbilicus 4 mm.; height of outer whorl 6.5; thickness 4 mm., the whorl at the base of the body-chamber being 4.5 mm. high and 3 mm. thick. In this specimen the outer boundary of the forward prolongation of the muscular attachment is slightly more distinct than in the example already described, and appears to be continued backward as a dark (not incised) line into the second lateral lobe on one side of the specimen and on to the second lateral saddle on the opposite side, but at about 2.5 mm. from the last septum it gives off a branch which curves outward towards the periphery, where it is bent slightly forward. The width of the forward prolongation of the impression is 1.5 mm., the most anterior part of the impression being 5 mm. from the last suture-line.

The form and position of the muscular attachment in this species are also exhibited by a specimen \* (No. 22267) in the British Museum from the Brown Jura  $\zeta$ , Beuren, Würtemberg; it agrees with that already described in the example C. 5140 *a*.

In this species, then, the shell-muscle seems to have been attached to the long flattened surface on the inner area of the body-chamber. The anterior border of the shell-muscle and of the annulus agrees almost precisely with that described and figured by Oppel in his well-known figures of *Ammonites* [= *Oppelia*] *stereaspis* from the Lithographic Stone of Solenhofen, Bavaria, a fact which supports Prof. Zittel's arrangement of the genera *Distichoceras* and *Oppelia* in the same subfamily (*Oppelinae*).

#### STEPHANOCERATIDÆ, Neumayr, emend. Zittel.

##### STEPHANOCERAS, Waagen.

*Stephanoceras Banksii*, J. Sowerby, sp.—There are indications of the muscular attachment of the animal in Sowerby's type-specimen, which forms part of the British Museum Collection. It is a natural internal cast from the Inferior Oolite of the West of England, but the precise locality is not recorded. Its diameter is about 230 mm. (about 9 inches) and its thickness about 150 mm. (or nearly six inches). One-third of the outer whorl is occupied by the body-chamber, the base of which is 50 mm. high and 130 mm. wide. The inner area of the whorl is convex and slopes considerably towards the umbilicus. On the inner area, and arising from the suture of the shell at a point 43 mm. in advance of the last septum, there is a faint impressed line which passes backward and outward across the inner area, crossing the umbilical margin at about 30 mm. posterior to its point of origin and 25 mm. from the suture of the shell. Arising from the suture of the shell, and at a point 20 mm. posterior to the line already described, there is another groove which is rather more distinct and passes backward (more quickly than the anterior line) and outward for rather more than 10 mm., then, with a forwardly-concave curve, passes

\* A peculiarity about this specimen is that the chambers are arranged as if were in pairs, a large loculus being succeeded by a small loculus. This is certainly the case with the last sixteen chambers.

to about the middle of the inner area, and then turning backward again it disappears in the broken surface of the specimen. The anterior line probably indicates the position of the anterior boundary of the shell-muscle, and the posterior line possibly the posterior boundary of the same; I think the latter cannot indicate the position of a former attachment of the anterior boundary, for it is not parallel to the anterior line. The other side of the specimen is too badly preserved to show the muscular impression. I have not observed any indications of the position of the annulus in this specimen.

#### PERISPINCTES, Waagen.

*Perispinctes Achilles*, d'Orbigny, sp.—The lateral aspect of the muscular impression in this species is clearly shown in an example in the British Museum Collection (the smaller of the two specimens, No. 37017) from the White Jura of Randen, near Schaffhausen (Pl. 19, fig. 5). The example is a natural internal cast, almost completely denuded of the test. Its dimensions are:—diameter of shell 69 mm.; width of umbilicus 28 mm.; height of outer whorl 24.5 mm.; greatest thickness (almost close to the umbilicus) 16 mm. The whorl is much compressed, and not much indented by the preceding whorl; the body-chamber, measured along the median line of the periphery, is about 80 mm. long. The incised line marking the boundary of the muscular impression is plainly visible at the base of the body-chamber. At the inner edge of the whorl it is 5.5 mm. in advance of the most anterior part of the last septum; passing backward and outward for a short distance, it is then continued backward as an exceedingly faint line as far as the last septum in a direction nearly parallel to the inner edge of the whorl. The width of the impression from the suture of the shell is 2.25 mm., of which only about one-half is visible in the lateral aspect of the shell. The boundary of the anterior portion of the scar is more deeply incised than the rest.

The impression on the other side is similar, but not quite so distinct.

There is no trace of the annulus.

#### ASPIDOCERATIDÆ, Zittel.

##### PELTOCERAS, Waagen.

*Peltoceras* sp.—The impression of both shell-muscles is well seen on an example of *Peltoceras* sp. that was found in the Amptill Clay at Amptill Tunnel, and that formed part of my late father's collection (Pl. 20, fig. 1). The specimen, a mere fragment of the natural cast of a large shell, consists of the posterior part of the body-chamber; it is about 150 mm. long. It is quadrangular in transverse section, and at the base of the body-chamber is 73 mm. high, 65 mm. thick (excluding the ribs), and 72 mm. thick (including the ribs). An antiperipheral, antisiphonal, or dorsal aspect of the fragment displays two longitudinally-elongated oval scars, somewhat pointed anteriorly and bounded by a faintly impressed line. The outer boundary of each area terminates immediately above the inner branch of the lateral saddle, while the inner boundary passes down close to the outer side of the antiperipheral (or antisiphonal) saddle on the same side. The anterior extremity

of each impression is situated on the edge of the impressed zone, so that about one-third of the width of the impression is on the impressed zone, the other two-thirds being on the inner area of the whorl. The two impressions are nearest together at about half their length; they are here 19 mm. apart, while the posterior extremities of their inner boundaries are 32 mm. apart. The length of each impression (measured from the anterior extremity of the inner branch of the lateral saddle) is about 50 mm.; the greatest width being 17 mm. No traces of the annulus have been observed in this specimen. In the middle of the peripheral area, and extending a short distance into the peripheral lobe, there is a broad, faint, longitudinal depression about 25 mm. long and 3.0 mm. wide, slightly wider anteriorly than posteriorly. Possibly this had something to do with the muscular attachment of the animal to its shell. On one side of this there is a narrower, shorter, and less distinct longitudinal depression.

#### ASPIDOCERAS, Zittel.

*Aspidoceras* sp.—Among the specimens which Dr. J. W. Gregory collected from “below Chamgamwe, opposite Mombasa Island,” East Africa, there is a fragment of an *Aspidoceras* which displays the muscular impression; it is merely the natural cast of the posterior part of the body-chamber, and this is incomplete on one side (Pl. 19, figs. 6, 7). The section of the base is obtusely cordate, and measures about 43 mm. in width and 34 mm. in height. The impression is seen on the inner area of the whorl as a faintly-impressed line, which, arising from the edge of the impressed zone (corresponding to the suture of the shell) at a point about 15 mm. in advance of the base of the body-chamber, passes outward, describing a curve slightly convex forward, and when at a distance of 9.5 mm. from the edge of the impressed zone passes backward nearly parallel to this edge for a distance of at least 10 mm. It then seems to divide into several very faint grooves which are continued backward nearly to the base of the body-chamber. No indications of the annulus can be seen. Unfortunately the cast is very imperfect on the opposite side.

#### COSMOCERATIDÆ, Zittel.

##### PARKINSONIA, Bayle.

*Parkinsonia Parkinsoni*, J. Sowerby, sp.—The muscular impressions are well shown in a well-preserved example of this species in the British Museum Collection (No. 9) from the Inferior Oolite of Bayeux (Calvados), France. Fully two-thirds of the outer whorl are occupied by the body-chamber; the test having been removed from the greater part of this chamber, the internal cast is well displayed. The dimensions of the specimens are:—diameter of shell 243.5 mm.; width of umbilicus 58 mm.; height of outer whorl 49 mm.; greatest thickness of ditto 32.5 mm. The body-chamber appears to be fairly complete; its length measured along the median line of the periphery is 287 mm.; and the dimensions of its base are:—height 31.5 mm., greatest thickness (which is at about one-third of the height of the whorl from the inner edge) 22.5 mm. The muscular impression on each side can be seen. At the suture of the shell the

anterior border, an incised line, is 9.5 mm. in advance of that portion of the lateral saddle of the last suture-line which is close to the umbilical margin; it passes thence outward and backward nearly parallel to the suture and almost as far back as the last septum, when it appears to turn outward and pass over this portion of the lateral saddle as a feebly-depressed rather than an incised line. This last-mentioned portion of the boundary may have been produced by the anterior border of the annulus. The greatest width of the portion of the impression that is visible is 5 mm., and it is confined to the somewhat sloping inner area of the whorl. Its surface is a little roughened, and the impression seems to have occupied the lobe which is situated on the inner area of the whorl. An irregular, wavy, depressed line passes over the siphonal lobe on each side of the body-chamber, and this most probably indicates the position of a further portion of the anterior border of the annulus.

PRIONOTROPIDÆ, Zittel.

SCHLÆNBACHIA, Neumayr.

*Schlœnbachia Goodhalli*, J. Sowerby, sp.—The remains of the muscular attachment are exhibited by an example of this species in the British Museum Collection (No. 46491). The specimen is from the Greensand of Blackdown, Dorset. It consists of a segment of two adjacent whorls, the outer of which exhibits at about its mid-length the basal portion of the body-chamber, which on the left side is entirely denuded of the test. The whorl is carinated, much compressed laterally, and its sides nearly parallel; at the base of the body-chamber it is 80 mm. high and 45 mm. wide or thick, the inner area being concave, sloping towards the umbilicus, and 12 mm. wide. On the left side, on the internal cast of the body-chamber, the anterior boundary of the muscular scar is seen as an incised line arising at the suture of the shell at about 30 mm. in advance of the corresponding portion of the last septum; passing obliquely backward and outward across the inner area, it crosses the umbilical margin at about 22 mm. in advance of the corresponding part of the last septum; it continues outward and backward for a short distance, and then divides; one part passes backward and outward for a very short distance and then disappears; the other passes backward nearly parallel to, and at a distance of 4 mm. from, the umbilical margin, and disappears shortly before reaching the suture-line of the last septum. The branch which passes outward is probably the commencement of the anterior border of the annulus, the other being the outer boundary of the muscular scar. Arising from the suture of the shell, 13 mm. posterior to the line already described, and crossing the inner area nearly parallel to the same line, there is another very feeble groove, which scarcely crosses the umbilical margin before reaching the last suture-line. From the appearance of the inner surface of the piece of the test which fits on to this portion of the specimen, it seems most probable that this feeble groove indicates the position of the posterior boundary of the muscular scar. The opposite side of the whorl is too imperfect to exhibit any trace of the muscular attachment.

At a point 29 mm. in advance of the small median saddle, the periphery is crossed by an incised line which on the left side passes inward and backward for about 8 mm., then passing backward nearly parallel to, and at a distance of 8 mm., from the median line of the periphery until it meets the external saddle. Traces of a precisely similar line can also be seen on the right side. This I believe to have also been part of the anterior boundary of the annulus.

#### CLYMENIA, Münster.

*Clymenia undulata*, Münster.—The muscular impression in the genus *Clymenia* has been best observed in an example of this species in the British Museum Collection (No. 81826). It is from the Clymenien-Kalk (Upper Devonian) of Schübelhammer, Bavaria (Pl. 20, figs. 13, 14). This specimen, the outer whorl of which is somewhat imperfect, has the following dimensions:—Diameter of shell 48·5 mm.; width of umbilicus 20·5 mm.; height of outer whorl 16 mm.; greatest thickness of ditto 12 mm. Nearly one half of the outer whorl is occupied by the body-chamber, its length, measured along the periphery, being 65 mm.; its anterior portion is flattened for a distance of nearly 20 mm., the width of the flattened portion being 3 mm. It may be remarked that in this genus the siphuncle is on the inner side of the whorl, and is relatively much larger than in the rest of the Ammonoidea. The internal cast of the posterior part of the body-chamber and of two or three of the succeeding loculi is denuded of the test. The base of the body-chamber is 12·5 mm. high and 10 mm. thick, the periphery here being quite rounded. One side of the basal portion is well-preserved, but the other is somewhat imperfect. On the well-preserved side (fig. 13) a curved feebly-incised line arises almost close to the suture of the shell and at a distance of 2 mm. from the last septum; passing backward nearly parallel to the inner half of the lateral portion of the suture-line, it just clears the most anterior portion of the latter and then passes straight on to the periphery, being at the centre of the latter about 2 mm. anterior to the last septum. It appears to cross the periphery without interruption, but unfortunately the line here is somewhat obscured, and it is not impossible that the line here may be bent backward into a very minute V-shaped sinus.

Another feebly-incised line proceeds from the suture of the shell and passes backward almost close to the last septum for some distance into the lateral lobe; then turning forward it meets the anterior line, already described, at the most anterior point of the lateral portion of the suture-line. At a short distance from this junction and a little nearer the periphery, the anterior line gives off a branch which gradually recedes from it and crosses the periphery about 1 mm. posterior to it. At the central portion of the periphery this line, like the anterior one, is somewhat obscured, but appears to cross the periphery without interruption, although it is not impossible that at the middle of the periphery this line may have had a very small V-shaped bend forward.

It would seem, therefore, that the shell-muscle occupied the space between the suture of the shell and the outer side of the lateral lobe, and that the annulus extended from

the outer side of the lateral lobe across the periphery as a narrow band having its greatest width at the centre of the periphery.

Unfortunately, the opposite side of the body-chamber is not sufficiently well-preserved to show the muscular impression.

Near the anterior end of the body-chamber the internal cast exhibits a wide and fairly deep groove, which crosses the lateral area in a curve which is concave forward, and projects considerably forward near the periphery. The lateral portion of the groove is fully 6 mm. wide, but shallow, while the portion near the periphery is 4 mm. wide and deeper than the rest. The opposite side of the specimen is broken here, and does not show the groove. This groove, however, seems to have nothing to do with the muscular attachment of the animal, but is here mentioned for comparison with the groove which has been depicted in some Ammonoids (e. g. *Pinacoceras*\*) as the anterior boundary of the muscle and of the annulus.

## GONIATITES.

### GLYPHIOCERAS, Hyatt.

*Glyphioceras crenistria*, J. Phillips, sp.—Among the Goniatites the form of the attachment of the animal to its shell is well seen in an example† of this species from Bolland, Yorkshire (Pl. 20. figs. 15, 16). It forms part of the British Museum Collection (No. C. 5080). It is a well-preserved example, having the following dimensions:—Diameter of shell 43 mm.; width of umbilicus about 4.5 mm.; height of outer whorl 21.5 mm.; thickness of ditto 27.5 mm. The body-chamber occupies five-sixths of the outer whorl, and, being denuded of the test, its internal cast is well displayed. The muscular attachment is so well preserved that it can be traced from the umbilicus on one side across the whorl to the umbilicus on the other side. As seen in a lateral aspect (fig. 15) the muscular scar is almost confined to the inner area of the whorl, and is depressed (on the internal cast) a little below the surrounding surface. The most anterior portion of its anterior boundary is a little more than 2 mm. in advance of the last septum. Passing backward and outward, this boundary just crosses the umbilical margin and reaches to within about 1 mm. of the septum, when, turning abruptly outward, it is continued as a very fine raised line at this distance from the septum, until passing into the lateral lobe, when it recedes very slightly from the suture-line. It crosses the lobe in an obtuse point 3.75 mm. from the point of the lobe, and, then passing up the other side of the lobe, it gradually approaches the suture-line and, just clearing the pointed external saddle, passes into the external lobe at about 1 mm. from the septum (fig. 16), at the same time separating into two very minutely-waved lines; at 5 mm. from the apex

\* Dr. E. v. Mojsisovics, 'Das Gebirge um Hallstatt,' i. pl. xx. figs. 2 & 3 (*Pinacoceras insectum*); pl. xx. figs. 8 & 9 (*P. humile*).

† This is the specimen from which the suture-line figured in Cat. Foss. Ceph. British Museum, pt. iii, p. 161, fig. 76, was drawn.

of the external saddle these lines diverge, assume a direction at right angles to the plane of symmetry of the shell, and cross the external lobe with only a very slight V-shaped depression at the median line of the periphery. Nearly at the centre of the periphery there is a small circular pit on the posterior line. On the opposite side of the lobe, at about 1 mm. from the suture-line, these lines turn abruptly forward, approach and coalesce, the resulting line having the same course as that on the opposite side. At the umbilical margin this line passes into the boundary of the muscular scar, which also has the same form as that on the opposite side. At the centre of the periphery and immediately behind the lines already described there is a feebly-depressed double line in the form of a horse-shoe, each side of which passes quite close to the outer side of each half of the small median saddle; the enclosed area is about 2 mm. wide. At a short distance anterior to the raised line already described there is a rather broad shallow groove, which first makes its appearance in the lateral lobe, becomes more distinct all around the external saddle, and disappears in the external lobe. Almost in the median line of the periphery, and slightly in advance of the apex of the external saddle, there is a minute, shallow, oval depression. A fairly-prominent "normal line" extends some 7 or 8 mm. in advance of this depression, whilst the surface of the east behind this depression and in front of the anterior boundary of the annulus bears numerous fine longitudinal raised lines.

The depressed surface on the inner area of the whorl I regard as a portion of the muscular scar, and the faint line proceeding therefrom across the whorl I consider to be the impression of the annulus. The latter then seems to have been over a portion of its extent merely a line of attachment, but to have been 1 mm. wide on the periphery.

In the present specimen the boundary of the muscular scar cannot be traced on to the inner or dorsal portion (=impressed area) of the whorl, but this has been partially observed in another example of the same species in the British Museum Collection (the larger of the specimens No. C. 283). The diameter of the shell is 50 mm., the outer whorl (at the end of the septate part of the shell) being about one-half of the diameter. The specimen is entirely septate (Pl. 20. figs. 17, 18), the last septum being the base of the body-chamber. A portion of the test that formed the floor of the body-chamber still adheres to the preceding whorl, and on this the border of the muscular scar can be traced for a short distance. In this example the anterior border of the scar passes on to the floor of the body-chamber at about 3.5 mm. in advance of the last septum; for a short distance it is nearly parallel to the septum, but at about the middle of the lateral saddle it turns towards the septum and seems to disappear; unfortunately the test here has been broken away, and only a few fragments of the test remain on the opposite side of the whorl, so that its direction cannot be definitely traced further. On the floor of the body-chamber (fig. 18) there is also a strong raised line following the lobes and saddles of the last septum, and about 1 mm. in front of the same; near the umbilicus it gradually approaches and then passes into the angle between the septum and the wall of the shell. This seems to have been a line of attachment of the body of the animal; but, so far as can be made out from this example, it does not appear to have been continuous

with the anterior border of the muscular scar. It may have been the line of attachment of the posterior portion of the body just prior to the formation of a new septum.

*Glyphioceras truncatum*, J. Phillips, sp.—An example of this species from the Carboniferous Limestone of St. Doulagh's, co. Kildare, Ireland, which has been lent me by Dr. A. H. Foord, F.G.S., also exhibits the anterior boundary of one of the muscular scars very distinctly (Pl. 20. figs. 19). The specimen consists of about five-sixths of a whorl, the whole constituting part of the body-chamber, the base of which is fortunately preserved. Its dimensions are:—diameter 75 mm.; height of outer whorl 36 mm.; ditto above preceding whorl 20 mm.; greatest thickness (which is at about the middle of the lateral area) 27 mm.; width of umbilicus 10 mm. On one side of the specimen the anterior boundary of one of the muscular scars is preserved as an impressed line (on the internal cast of the body-chamber), which arises from the suture of the shell at about 4 mm. in advance of the last septum and curves gently outward and backward. It can only be traced for a length of about 6 mm., when it is obscured by the test; at about one-half of this length it is 4.5 mm. from the suture of the shell.

#### *Summary.*

As in the recent Nautilus, so in the Ammonoids, the shell was external and the animal was attached to its shell by means of "shell-muscles" and an "annulus."

In the Ammonites and such allied forms as *Baculites*, *Hamites*, &c. the shell-muscles were attached to the dorsal portion of the shell; they frequently either approximated or met each other in the median line of this region; when they did not quite meet they were doubtless united by a more or less narrow band corresponding to the dorsal portion of the annulus in the recent Nautilus.

My observations support the conclusion expressed by Dr. Waagen that the line figured by Oppel on the body-chamber of *Ammonites steraspis* indicated the position of the anterior boundary of the annulus and of the shell-muscles, the latter being situated, as he supposed, upon the inner or umbilical portion of the lateral area of the whorl. It is, however, not a little strange that in the species figured by Oppel the form of the muscular attachment differs somewhat considerably from that in the majority of the Ammonites which I have examined. It would seem that another interpretation is necessary for the figures which have subsequently been given purporting to be the remains of the muscular attachment.

In the earlier stages of development and in the general form of the shell as well as in the aperture of certain species, affinities have been recognized between the Ammonoids and the Dibranchiates. From the foregoing it is clear that the Ammonoid animal possessed a muscular attachment quite similar to that of the living Nautilus, the only recent genus of the Tetrabranchiates.

Indications of the muscular attachment of the Ammonoid animal, instead of being rare, seem to be fairly common. There appears to be some ground for believing that its form is in part due to the shape of the transverse section of the whorl and to the

length of the body-chamber, but I venture to believe that it will prove to be due to other causes, and also afford an important character for the purposes of classification. Thus, among the forms of muscular attachment described in the present paper, the shell-muscles in *Distichoceras* and *Oppelia* seem to have been relatively much longer than those of the other forms herein described; and hence one should expect these two genera to be closely related. This affinity seems to be supported by their other characters, for they have been placed in the same subfamily, viz. the *Oppelinae* \*.

Not only was the Ammonoid animal, like the Nautilus, at least at some periods, attached to its shell by means of the lobes and saddles of the posterior portion of the body (corresponding to those of the edge of the septum of its shell), but it seems from the foregoing descriptions that it was further provided with an annulus in addition to shell-muscles as in the recent Nautilus. It would appear, therefore, as if the provision of an annulus were an absolute necessity to the animal in addition to the shell-muscles, and most probably Dr. Waagen's explanation of its occurrence is the correct one, viz., that the annulus and shell-muscles served not merely to hold the animal to its shell, but formed also an air-tight band around it, fastening the mantle to the shell.

In conclusion, I desire to express my obligations to those who have in any way assisted me in my observations. To Dr. Woodward I am greatly indebted for valuable suggestions and much kind help, while to Mr. B. B. Woodward I am especially indebted for the advice which he has ever been most willing to give me. My thanks are also due to my colleague Mr. Edgar A. Smith for giving me every facility in the examination of the recent Cephalopoda under his charge. For the loan of specimens I have to thank Mr. F. L. Bradley, Mr. G. F. Harris, and the authorities of the Jermyn Street Museum. To Messrs. Sharman, Newton, and Allen, of that Museum, I am under deep obligations for all their kind help during the examination of the specimens under their charge. To Professor Howes, whose interest in my work has been a source of great encouragement to me, I desire to present my cordial thanks.

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#### EXPLANATION OF THE PLATES.

The figures are of the natural size unless otherwise stated.

× indicates the last septum.

—→ marks the remains of the muscular attachment.

#### PLATE 17.

*Baculites ovatus*, Say (p. 77).

Fig. 1. Dorsal aspect of fragment of body-chamber, showing anterior boundaries of muscular scars.

2. Right lateral aspect of same, showing on the left the boundary of the right muscular scar, and on the right the incised line on the ventral area.

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\* See Prof. Dr. K. A. v. Zittel, 'Grundzüge der Paläontologie,' p. 420.

Fig. 3. Ventral aspect of same, showing incised line on median portion.

4. Right lateral aspect of fragment of another example, showing anterior boundary of right muscular scar and of a portion of the annulus.

*Baculites vagina*, Forbes (p. 78).

Fig. 5. Dorsal aspect of portion of body-chamber, showing near the base the anterior boundary of the two muscular scars.

*Hamites maximus*, J. Sowerby (p. 79).

Fig. 6. Dorsal aspect of body-chamber, showing the two muscular scars near the base.

7. Left lateral aspect of the same.

8. Dorsal aspect of another example.

9. A portion of the same enlarged, showing the two scars, each bearing near its anterior border a small roughened patch, and also traces of a narrow band connecting the scars.  $\times \frac{7}{1}$ .

*Crioceras quadratum*, n. sp. (pp. 74 & 79).

Fig. 10. Dorsal aspect of a fragment of the body-chamber, exhibiting the two scars.

11. Left lateral aspect of the same.

12. Dorsal aspect of a fragment of another example in which the anterior boundaries of the two scars nearly meet in the median line.

13. Left lateral aspect of the same.

*Ancylloceras Mathersonianum*, d'Orbigny (p. 80).

Fig. 14. Left lateral aspect, showing portion of anterior boundary of left muscular scar.  $\times \frac{1}{4}$ .

15. Right lateral aspect of a portion of the same, exhibiting the termination of the anterior boundary of the right muscular scar.  $\times \frac{1}{4}$ .

16. Dorsal aspect of a portion of the same, showing the anterior boundaries of the two muscular scars, that on the right being much higher than that on the left.  $\times \frac{1}{4}$ .

*Macroscaphites gigas*, J. de C. Sowerby, sp. (p. 81).

Fig. 17. Right lateral aspect.  $\times \frac{1}{4}$ .

18. Left lateral aspect of a portion of the same, showing part of the boundary of the two scars.  $\times \frac{1}{4}$ .

19. Dorsal aspect of a portion of the same, also showing the anterior boundary of the two scars.  $\times \frac{1}{4}$ .

*Scaphites binodosus*, A. Roemer (p. 81).

Fig. 20. Left lateral aspect.

21. Dorsal aspect of a portion of the same, with part of the body-chamber removed.

*Scaphites equalis*, J. Sowerby (p. 82).

Fig. 22. Dorsal aspect of a fragment of the body-chamber. The curved lines at the lower part of the figure are the impressions of the ornaments of the septate part of the shell; the anterior border of the muscular attachment is indicated by the arrow.

## PLATE 18.

*Turrilites tuberculatus*, Bose (p. 83).

- Fig. 1. Lateral aspect, two of the upper whorls exhibiting the siphuncle (*si*), and the body-chamber showing the muscular attachment.  $\times \frac{1}{2}$ .  
 2. Dorsal aspect of body-chamber of same, showing the muscular attachment.  $\times \frac{1}{2}$ .

*Turrilites Mantelli*, Sharpe (p. 83).

- Fig. 3. Lateral aspect of fragment, the lower whorl of which exhibits a portion of the boundary of the muscular attachment.  $\times \frac{2}{3}$ .

*Turrilites (Heteroceras) polyplocus*, Roemer (p. 84).

- Fig. 4. Lateral aspect of terminal portion.  $\times \frac{1}{2}$ .

*Oxynoticeras?* *sp.* (p. 85).

- Fig. 5. Left lateral aspect of part of an example showing the muscular scar and the annulus.  $\times \frac{2}{3}$ .  
 6. Right lateral aspect of same.  $\times \frac{2}{3}$ .

*Amaltheus spinatus*, Brugnière, *sp.* (p. 86).

- Fig. 7. Left lateral aspect of imperfect specimen, exhibiting on the inner portion of the whorl (opposite the arrow) the boundary of the muscular scar.

*Cardioceras excavatum*, J. Sowerby, *sp.* (pp. 75 & 86).

- Fig. 8. Left lateral aspect, showing the muscular scar and the annulus.  $\times \frac{1}{2}$ .

*Cardioceras* aff. *excavato*, J. Sowerby, *sp.* (p. 86).

- Fig. 9. Left lateral aspect, exhibiting the anterior boundary of the muscular scar on the inner portion of the whorl opposite the arrow, and a linguiform impression on the middle of the lateral area.  
 10. Dorsal aspect of posterior portion of the body-chamber of the same, showing near the base the course of the anterior boundary of the muscular scar on the dorsal area of the whorl.

*Tissotia Ewaldi*, v. Buch, *sp.* (p. 90).

- Fig. 11. Left lateral aspect, showing close to the umbilicus (opposite the arrow) one of the muscular scars, and, passing from it towards the periphery, a portion of the anterior boundary of the annulus.  $\times \frac{2}{3}$ .

## PLATE 19.

*Cardioceras excavatum*, J. Sowerby, *sp.* (p. 86).

- Fig. 1. Right lateral aspect.  $\times \frac{2}{3}$ .  
 2. Sagittal section of the natural internal cast of the body-chamber of the same specimen, showing anterior boundary of muscular scar on dorsal portion of whorl.  $\times \frac{2}{3}$ .

*Cardioceras* *sp.* (p. 89).

- Fig. 3. Left lateral aspect, showing anterior boundary of scar and of annulus.  $\times \frac{1}{4}$ .  
 4. Ventral view of the same, exhibiting the impression on the central portion of that area.

*Perisphinctes Achilles*, d'Orbigny, sp. (p. 102).

Fig. 5. Left lateral aspect. The boundary of the muscular scar is seen on the inner portion of the outer whorl opposite the small arrow.

*Aspidoceras* sp. (p. 103).

Fig. 6. Dorsal aspect of a fragment of the body-chamber.  
7. Right lateral aspect of the same.

*Arietites obtusus*, J. Sowerby, sp. (p. 93).

Fig. 8. Left lateral aspect of a portion of a specimen, showing the muscular scar on the inner portion of the outer whorl opposite the arrow.  
9. Right lateral aspect of the same.  
10. Ventral aspect of the same, showing the linguiform impression on the central portion, and anterior to it an *f*-shaped incised line in the depression on each side of the keel.

*Lytoceras fimbriatum*, J. Sowerby, sp. (p. 91).

Fig. 11. Dorsal aspect of the posterior portion of the body-chamber, exhibiting the left and a portion of the right muscular scar.  
12. Left lateral aspect of the same.

*Lytoceras cornucopiæ*, Young & Bird, sp. (p. 91).

Fig. 13. Dorsal aspect of the posterior portion of the body-chamber.  
14. Right lateral aspect of the same.  
15. Right lateral aspect of another specimen, showing the small oval scar on the inner part of the outer whorl opposite the arrow.  
16. Portion of same enlarged, showing muscular scar.  $\times \frac{2}{1}$ .  
17. Ventral aspect of portion of same enlarged, exhibiting the linguiform impression.  $\times \frac{2}{1}$ .

## PLATE 20.

*Peltoceras* sp. (p. 102).

Fig. 1. Dorsal aspect of fragment, showing the two elongated muscular scars.  $\times \frac{1}{2}$ .

*Ægoceras capricornum*, Schloth., sp. (p. 95).

Fig. 2. Right lateral aspect. The muscular scar is the small white patch on the inner portion of the outer whorl opposite the arrow.

*Ægoceras laqueolum*, Schloenbach, sp. (p. 96).

Fig. 3. Dorsal aspect of fragment of body-chamber, showing the left muscular scar and part of the right.  
4. Left lateral aspect of the same.

*Hecticoceras hecticum*, Reinecke, sp. (p. 98).

- Fig. 5. Left lateral aspect.  $\times \frac{3}{2}$ .  
 6. Right lateral aspect of same.  $\times \frac{3}{2}$ .  
 7. Ventral aspect of portion of same.  $\times \frac{3}{2}$ .

*Distichoceras Baugieri*, d'Orbigny, sp. (p. 100).

- Fig. 8. Right lateral aspect.  $\times \frac{2}{1}$ .

*Æcotraustes crenatus*, Brugnière, sp. (p. 99).

- Fig. 9. Right lateral aspect.  $\times \frac{2}{1}$ .

*Arietites varicostatus*, Zieten, sp. (p. 94).

Fig. 10. Left lateral aspect of entire specimen.

11. Dorsal aspect of the portion *ab*, which is a natural internal cast of part of the body-chamber, showing at the base the remains of the two muscular scars.

*Sonninia* sp. (p. 98).

Fig. 12. Left lateral aspect, exhibiting the muscular scar on the inner portion of the outer whorl opposite the arrow, and also the adjacent indentations.

*Clymenia undulata*, Münster (p. 105.)

- Fig. 13. Right lateral aspect.  
 14. Peripheral aspect of the same.

*Glyphioceras crenistria*, J. Phillips, sp. (p. 106).

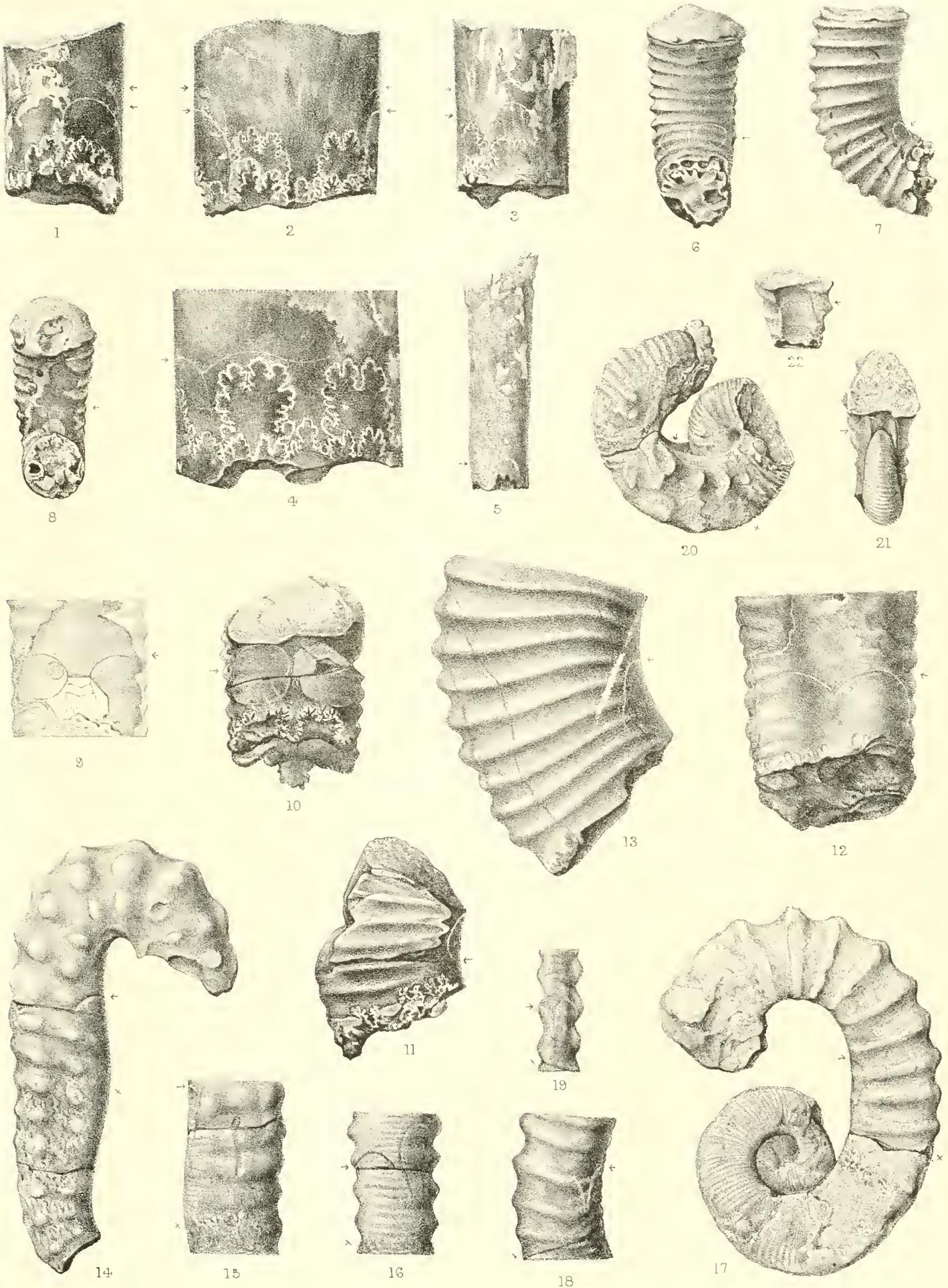
Fig. 15. Left lateral aspect. The fine white line opposite the arrow is the boundary of the annulus; the subtriangular patch into which it passes near the umbilicus is the left muscular scar, the black line posterior to it is the edge of the last septum, the lighter portion near it being the broken edge of the test.

16. Front view of the same, the arrow pointing to the line indicating the annulus.  
 17. Left lateral aspect of another example. The anterior septum is the base of the body-chamber. The muscular scar is indicated by the light patch (opposite the arrow) on the piece of the test, one layer of which is part of the floor of the body-chamber.  
 18. View of same from above; the raised line on the piece of test which is part of the floor of the body-chamber being indicated by the white line marked *a*.

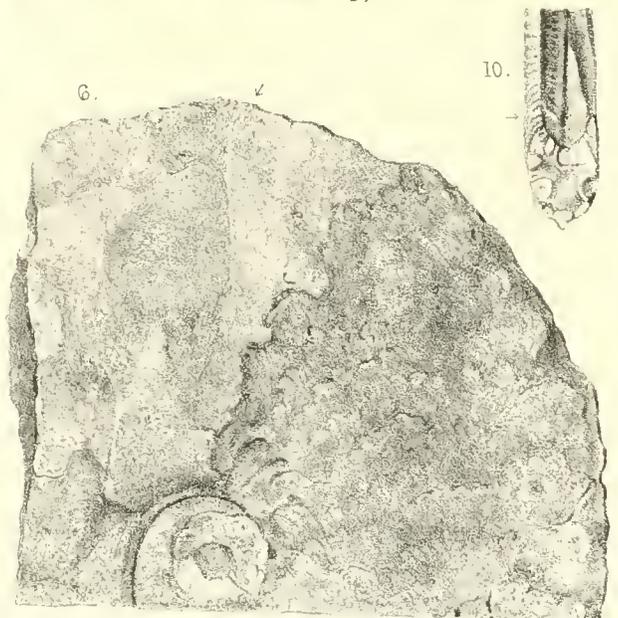
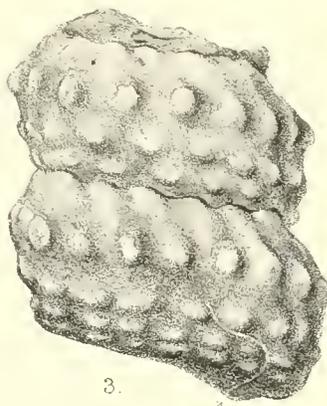
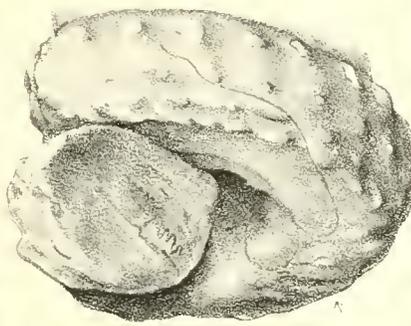
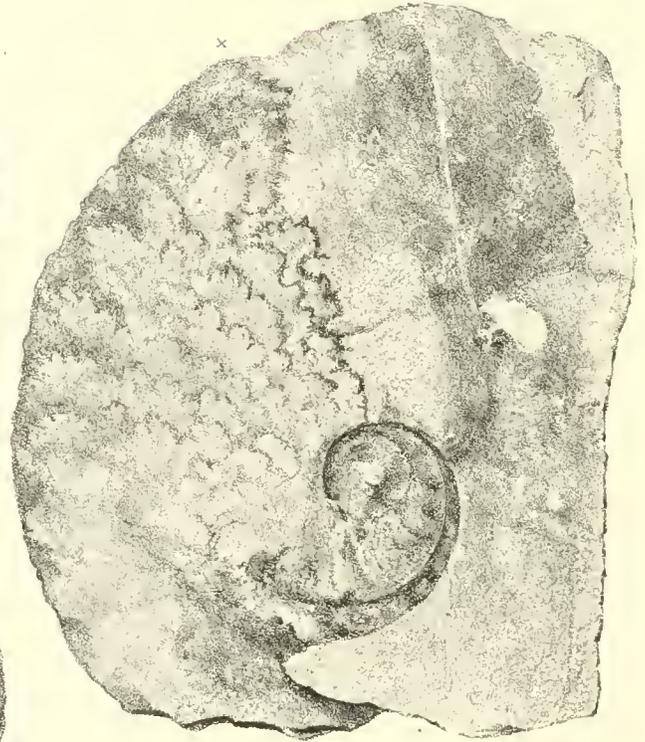
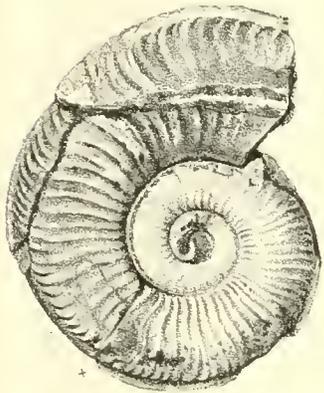
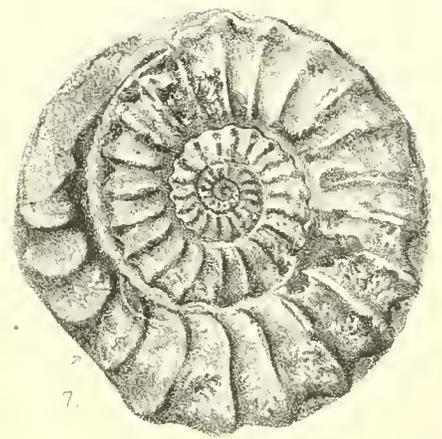
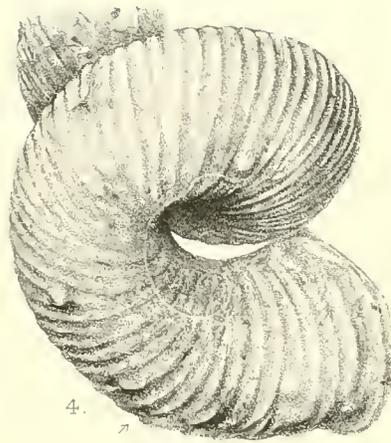
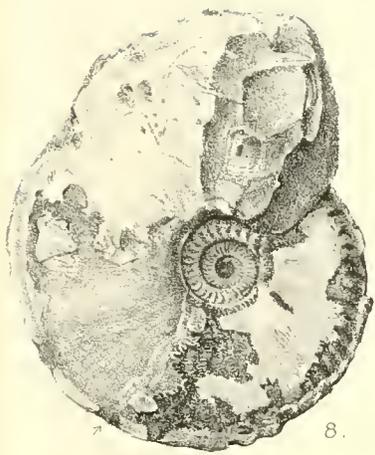
*Glyphioceras truncatum*, J. Phillips, sp. (p. 108).

- Fig. 19. Left lateral aspect.  $\times \frac{2}{3}$ .

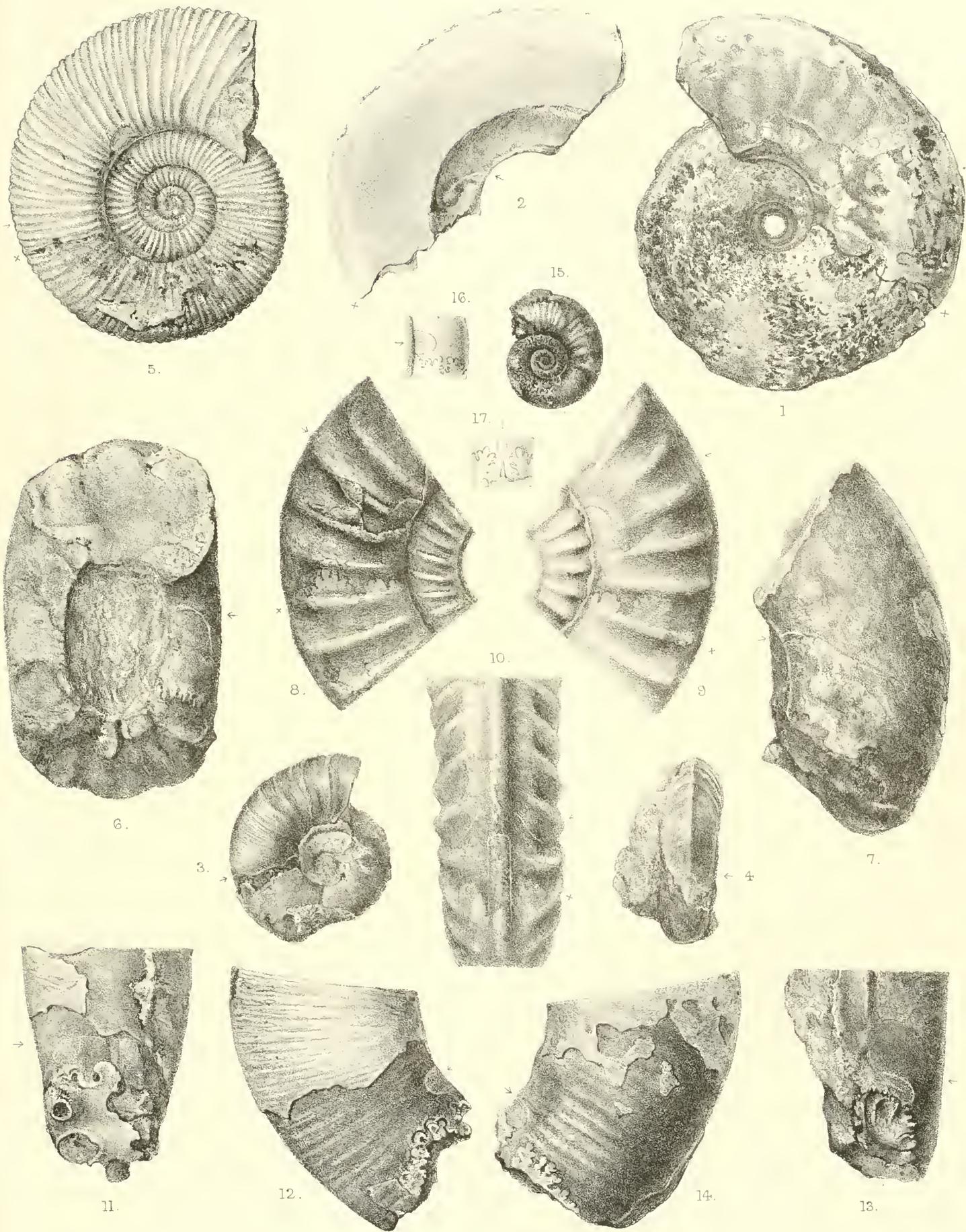




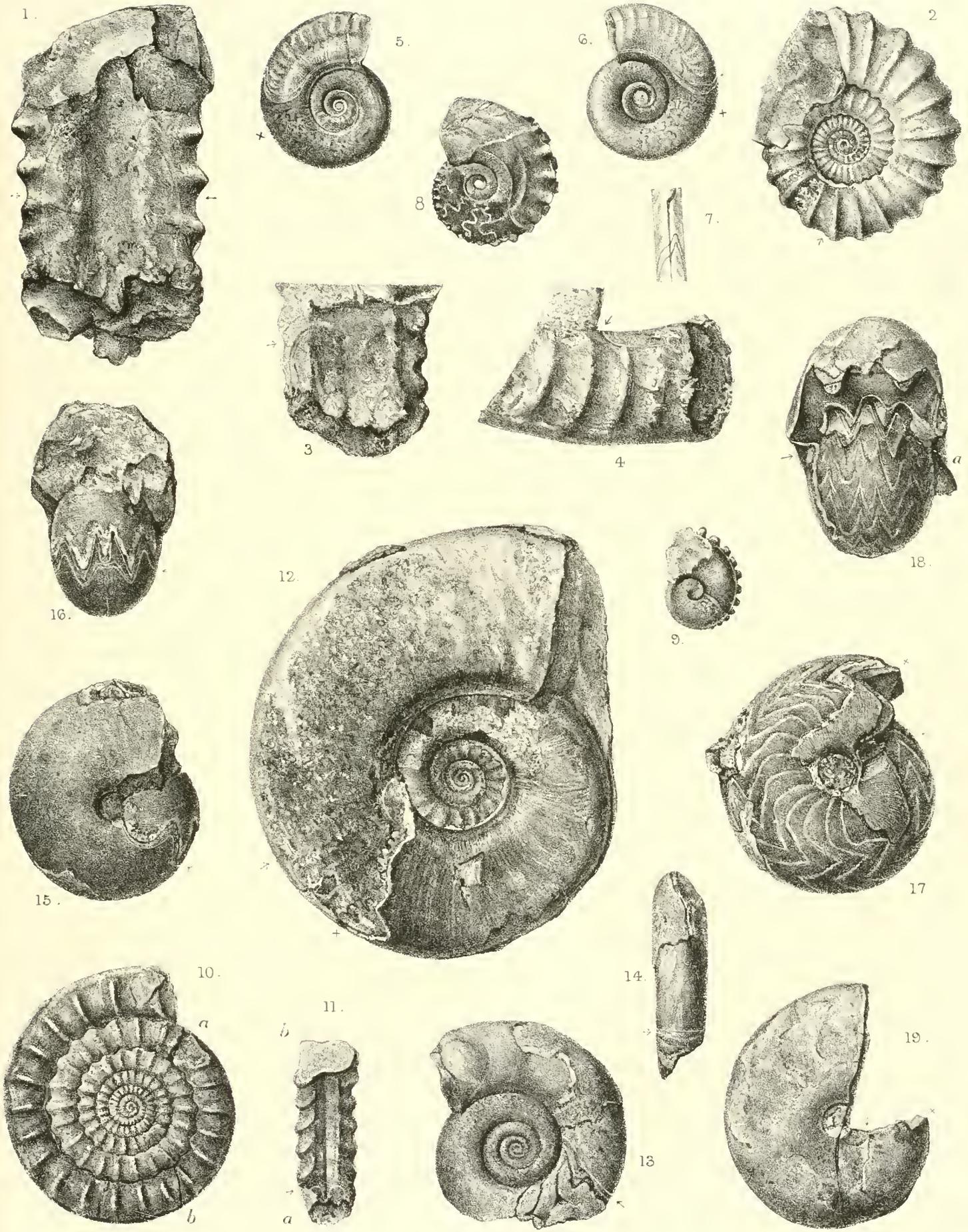
















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I. Part	I. 1875. ....	1 4 0	0 18 0	III. Part	V. 1887. ....	0 8 0	0 6 0
Part	II. 1875. ....	0 6 0	0 4 6	Part	VI. 1888. ....	0 6 0	0 4 6
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Part	VII. 1883. ....	0 5 0	0 3 9	Part	X. 1893. ....	1 8 0	1 1 0
Part	VIII. 1883. ....	0 3 0	0 2 3	Part	XI. 1894. ....	0 2 6	0 2 0
Part	IX. 1883. ....	0 3 0	0 2 3	VI. Part	I. 1894. ....	2 0 0	1 10 0
Part	X. 1884. ....	0 4 6	0 3 6	Part	II. 1894. ....	1 11 0	1 3 3
Part	XI. 1884. ....	0 10 0	0 7 6	Part	III. 1894. ....	0 10 0	0 7 6
Part	XII. 1885. ....	0 6 0	0 4 6	Part	IV. 1896. ....	1 4 0	0 18 0
Part	XIII. 1884. ....	0 6 0	0 4 6	Part	V. 1896. ....	0 10 0	0 7 6
Part	XIV. 1885. ....	0 6 0	0 4 6	Part	VI. 1896. ....	0 8 0	0 6 0
Part	XV. 1885. ....	0 4 6	0 3 6	Part	VII. 1896. ....	0 12 0	0 9 0
Part	XVI. 1885. ....	0 5 0	0 3 9	Part	VIII. 1897. ....	0 2 6	0 2 0
Part	XVII. 1886. ....	0 3 0	0 2 3	VII. Part	I. 1896. ....	0 10 0	0 7 6
Part	XVIII. 1888. ....	0 2 6	0 2 0	Part	II. 1897. ....	0 12 0	0 9 0
III. Part	I. 1884. ....	1 14 0	1 5 6	Part	III. 1897. ....	0 6 0	0 4 6
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Part	III. 1885. ....	1 10 0	1 2 6				
Part	IV. 1885. ....	0 8 0	0 6 0				

64.2

THE

TRANSACTIONS

OF

THE LINNEAN SOCIETY OF LONDON.

OBSERVATIONS ON THE STRUCTURE AND MORPHOLOGY OF THE  
CRANIAL NERVES AND LATERAL SENSE ORGANS OF FISHES;  
WITH SPECIAL REFERENCE TO THE GENUS *GADUS*.

BY

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(Communicated by Prof. W. A. HERDMAN, D.Sc., F.R.S.)



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(Plates 21-23.)

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## A. INTRODUCTION.

THIS investigation was first suggested to me as a desirable study by my former teacher, Professor J. C. Ewart, F.R.S., some years ago. I had at the time contemplated working at a Pleuronectid fish—allured by the problems which the asymmetrical head affords; but it was pointed out that I should be better equipped for such difficult work were I to study a modern symmetrical Teleostean first, and that in fact it were almost an impossibility to understand the former without having first investigated the latter. I therefore abandoned my first project, and decided to work out the anatomy of the lateral line system and its nerves on the common Codfish. That this work was necessary, and indeed essential to the proper understanding of this complicated system, is very obvious from a perusal of the literature. In spite of the enormous bulk of the latter, and the ponderous theses and memoirs that have been written on the subject of the present communication, we still know very little about the fine anatomy of the lateral line system, and very few authors have taken the trouble to grapple with the literature and to conduct their investigations on a strictly logical and scientific basis. To Mr. Edward Phelps Allis, who must be regarded as the pioneer in this work, vertebrate morphology owes much. He was not only the first to make a complete study of the topographical development of the lateral canals, and to give a correct and detailed account of their innervation, but many important morphological deductions have been directly inspired by his work. This author has recently completed his work on *Amia*. It is a completion upon which I may be permitted to cordially congratulate the author, and to express the hope that he will continue on other forms the studies he has pursued with such conspicuous success on *Amia*. Ewart has followed Allis with an account of his skilled dissections of the very complex lateral line system of *Læmargus* and *Raia*, and Pollard has added some details on the ancient Siluroid Teleosteans. Pinkus has very largely filled in a gap by an able account of the nerves of *Protopterus*, and the writer has published a description of the system in *Chimæra*. The most pressing want, therefore, was an investigation of the details in a modern specialised Teleostean, and the present memoir is largely an attempt to supply this deficiency in our knowledge of this interesting apparatus in *Gadus*.

The experience gained whilst working under Professor Ewart, and afterwards in investigating *Chimæra*, has been most valuable in the interpretation of the nerves of the Codfish. That the skeleton of this creature represents a very specialised condition is a palæontological fact, and it is hence not surprising to find its nerves in an equally advanced stage. My previous work on the simpler cartilaginous fishes (most of which has yet to be published) has prevented me from going astray in the interpretation of the nerves, and has enabled me to see in the specialised Cod the disguised form of the primitive cartilaginous fish. The separation of the components in the Cod has necessarily been effected with the microscope, and one cannot urge too strongly the importance of this instrument in the elucidation of cranial nerve morphology. Investigations based solely on microscopic or naked-eye anatomy often contain gross but pardonable errors; and whilst, on the other hand, a combination of the two methods does not indeed remove

the possibility of error, it certainly reduces mistakes to within a somewhat reasonable limit. Had I relied entirely upon sections, I should (as Pollard actually did) have described the lateralis accessorius as a modified lateral line nerve; whilst, had I confined myself to naked-eye dissection, the very interesting condition of the "facial ganglion" would have entirely escaped observation.

Figure 1 (Pl. 21) and the description of the sensory canals themselves (pp. 122-129) are based on the dissection of a single specimen, which, as shown in the Plate, had its anterior and posterior narial openings abnormally fused together. The right side, however, was normal in this respect. This specimen measured 237 mm. from the snout to the anterior extremity of the dorsal fin\*, 210 mm. from the snout to the dorsal attachment of the opercular fold, and 80 mm. from the barbel to the apex of the mid-ventral angle formed by the fusion of the two opercular folds. Its girth from the anterior extremity of the dorsal fin to the dorsal border of the base of the pelvic fin was 195 mm.

The young *Gadus virens* used in the microscopic part of the work were obtained at St. Andrews, where, on this as on many other occasions, Professor W. C. McIntosh, F.R.S., very kindly placed a table in his admirable new laboratory at my disposal. I also have to thank him for collecting the material and keeping it alive in the tanks when the exigencies of teaching left little time at my disposal. The smallest specimen I brought away from St. Andrews was 35 mm. long, but those sectioned were larger than that. They may therefore be described as young adults.

To Professor G. B. Howes, F.R.S., I am indebted for much kindly assistance and encouragement, and indeed both to him and to my valued chief, Professor W. A. Herdman, F.R.S., I owe "many acts of kindness that I can never repay, and have no wish to, for I prefer continuing the obligation." The preparation of the bibliography, of which a section is printed at the end of this paper, and which will be published separately when completed, has necessarily laid me under obligations to many librarians, as well as to Professor Howes. Of these I should like to mention Mr. A. W. Kappel, of the Linnean Society; Mr. F. H. Waterhouse, of the Zoological Society; Mr. A. H. White, of the Royal Society; and Mr. B. B. Woodward, of the Natural History Museum. To these gentlemen, who freely placed their knowledge and time at my disposal, I must express my heartiest thanks,

#### B. HISTORICAL (*GADUS*) †.

The first reference I find to the sensory canals and cranial nerves of the Cod is contained in the work of Monro (144) published in 1785. Monro considered the lateral canals glandular organs (*i. e.* "mucous canals"), and gives a large but superficial figure of *Gadus* in plate v., which shows the supra-orbital commissure and the median unpaired tubule, but which overlooks the supra-temporal canal. This author was the

\* The point of extension forward of the dorsal fin is extremely variable even in the same species, as may readily be seen by comparing common Cod placed side by side in a fishmonger's shop.

† I purposely omit references to text-books that are in constant use, such as T. J. Parker's 'Zootomy,' &c. [Since this section was written, several other *Gadus* references have been encountered, but these will be fully treated in my complete Bibliography.]

first to discover the nerve-supply of Lorenzini's ampullæ in Selachians. In 1825 Desmoulins and Magendie (60) gave a figure of the brain and roots of the nerves of the Cod, whilst Giltay in 1834 (88) figured and described the sympathetic nervous system, of which more presently. Leuret and Gratiolet, in a fine work (1839-1857, 119) treat of some Invertebrate nervous systems, and give a brief account of the central nervous system and cranial nerve roots of a few fishes, including the Cod, as also does Alcock (3, 1839).

In 1842 Stannius (198) commenced his studies on the peripheral nervous system, and published a careful description of the nerves of "*Gadus callarias*" (= *G. morrhua*). The results obtained on this form were included in his well-known general treatise published in 1849, which will be discussed elsewhere. In the same year he wrote a short note on the lateral canals of fishes (197), in which he briefly but accurately describes the lateral canals of "*Gadus callarius*." He corrects Monro's mistake *re* the supra-temporal canal, and devotes a few lines to the nerve-supply, remarking that the supra-temporal lateral line nerve is homologous with the Ramus auricularis vagi of higher Vertebrates. This homology can, of course, be maintained no longer.

Bonsdorff, in 1846 (30), gives us one of an admirable series of papers on cranial nerves, and treats of the trigeminus and cephalic sympathetic of "*Gadus lota*" (= *Lota vulgaris*). He gives a good figure of the brain and nerves, but in his interpretation of the latter was greatly misled by comparing them in too much detail with the Mammalian nervous system. Stannius's monograph (1849, 199) is concerned largely with *Gadus*, and will be discussed further in the text. Besides giving a fine figure of the lateralis accessorius, and showing further its connection with the spinal nerves (in "*Gadus callarius*"), he gives a further figure of the cephalic sympathetic and arteries in the same animal. Leydig (1850, 120) was the first to describe the histology of the lateral sense organs in *Lota vulgaris*, and shows the lateral line ossicle with its sense organ and perforating nerve. In Swan's beautiful atlas (1864, 205) there are several good figures of our type, but the accompanying text is unfortunately very meagre. The figure of the Cod's brain and nerves here given has been copied into several text-books, and may be seen in the first volume of Owen's 'Vertebrates,' p. 298.

In Traquair's work on the asymmetry of the Pleuronectidæ (1865, 207), the first accurate account of the topography of the sensory canals of *Gadus* and their relations to the bones of the skull is given. A figure (tab. 32. fig. 1) is published indicating the approximate position of the various canals (omitting details), and Dr. Traquair puts to brilliant use the lateral line system in sustaining his views on the Pleuronectid skull. Owen (1866, 149) makes some references to the nerves of the Cod, but his statements and figures are compiled from the works of Swan, Alcock, and Cuvier and Valenciennes. The histology of the brain of "*Gadus lota*" has been treated of by Stieda (1868, 201), who examined the nerve-tracts in the brain and spinal cord, and devotes a few notes to the roots of the nerves.

A very important work, historically, which has hitherto been overlooked, and to which I shall refer in some detail later on, was published in 1879 by A. Friant (73). This author describes and figures the brain and nerves of many bony fishes, including

"*Gadus carbonarius*" (= *G. virens*) (pl. v.) and "*Gadus lota*" (pl. vi.), and his work is remarkably accurate for the time it was published, and must certainly be regarded as a pioneer research. Cunningham (1890, 55) says (p. 77): "In the Cod, which may be taken as exhibiting pretty nearly the original condition of the cephalic tubes of the Sole and other flat fishes, there are no superficial sense-organs on the head, and the tubes of the two sides are symmetrically arranged." Omitting the last, I cannot acquiesce to any of these statements. The lateral sense organs have undoubtedly advanced *pari passu* with the development of the skull and the evolution of the asymmetry of the Pleuronectidæ. Cunningham's figure of the sensory canals of the Cod is copied "with slight modifications" from the figure given by Traquair in his Pleuronectid paper. Traquair's figure, as far as it goes, is perfectly accurate, and I must confess that Cunningham's modifications are somewhat unfortunate—especially the one that connects the hyomandibular with the lateralis canal. Further, the statement as to the absence of superficial sense organs is a curious oversight, especially as the mandibular line of pit organs is more obvious than these organs are in any other fish I am acquainted with.

Allis, in his last *Amia* paper (1897, 6), makes some passing references to *Gadus*, which he states are based on work being done in his laboratory by Dr. Dewitz and Mr. Samuel Mathers. On p. 631 he says:—"In *Gadus* there is a line of surface organs on the outer surface of the opercular bones immediately behind the preoperculum. They are all innervated by a special branch of the mandibularis externus facialis, and are therefore of the character of pit organs, and unquestionably represent in *Gadus* one of the cheek-lines of *Amia* or a similar line not found in *Amia*." Again, on pp. 632-633:—"In *Gadus* a line of surface organs is found along the lower edge of the mandible, parallel to the mandibular canal, and it is innervated by a long branch of the externus facialis, which first runs forward through the adductor mandibulæ, to the hind edge of the infraorbital canal behind the eye, and there turns downwards and reaches the mandible. A nerve in *Esox* corresponding in position to this nerve in *Gadus* innervates a line of surface organs lying on the upper jaw immediately below the infraorbital canal." Respecting the innervation of the latter organs he says (p. 637):—"This nerve [*i. e.* a branch of the externus facialis] in *Silurus* may be a branch corresponding to the one which in *Amia* innervates the mandibular line of pit organs, and in *Gadus* innervates a mandibular line of the slit like organs peculiar to that fish."

Finally Goronowitsch (1897, 90) has given an admirable account of the trigemino-facial complex of *Lota vulgaris*, in which the histology of the medulla and the nerve tracts of the ganglionic complex are ably elucidated and described.

It is thus seen that our knowledge of the lateral sense organs and their associated nerves in *Gadus* is still of a very imperfect description, and in fact all the work of any pretension was done before the lateral line system was properly understood, and before the researches of Allis, Ewart, and Strong had placed our knowledge of this interesting system on a secure basis of carefully ascertained fact and logical deduction. It is the purpose of the present communication to supply this defect, to add some new facts to our knowledge of the lateral organs, and perhaps to elucidate many points that are still somewhat obscure. I find with Allis that "as the work has progressed it has repeatedly

been found necessary to study details, and to include in the investigation whole subjects not contemplated in the beginning." The more important additions are the sections on the lateralis accessorius (which I trust is here correctly understood for the first time), the phylogeny of the lateral canals, the relations of the latter to the auditory organ, the metamerism of the lateral sense organs, and the morphology of the "facial" ganglion and Jacobson's anastomosis. Hence the somewhat comprehensive title of the present communication.

### C. SENSORY CANALS IN GENERAL.

The sensory canals of the Cod differ in no essential respect from those of the typical form. Indeed the uniformity that exists in this connection, even amongst fishes of widely different classification, is one of the most remarkable incidents in the history of this remarkable system. The same fundamental plan may be seen in all, whether we take an Elasmobranch, a Holocephalan, a Dipnoan, a "Ganoid," or a "Teleostean." Even in the Palaeozoic Coccosteans and Asterolepids, we see, thanks to the admirable and laborious researches of Traquair, the same generalised type. In *Coccosteus*, for example, we may consider the horizontal canal traversing the anterior dorso-lateral, the external occipital, and the central plates, as the lateral or body canal. This, after a break, gives rise to a supra-orbital canal, traversing the central and pre-orbital plates, and an infra-orbital, situated on the central, post-orbital, and maxillary ossicles. There is also a supra-temporal commissure situated on the two centrals, and this probably marked the anterior extremity of the lateral canal. The hyomandibular series is represented by canals on the post-orbital, marginal, and maxillary, and perhaps by the other canals in this region. In *Pterichthys*, again, the sensory canals are very simplified, being reduced to representatives of the lateral and infra-orbital canals, the former being connected anteriorly on the median-occipital plate by the supra-temporal commissure. Here the practical absence of a supra-orbital canal is perhaps correlated with the curious condition of the orbits in the Asterolepid fishes.

As I have elsewhere maintained (46, p. 181), and as the pioneer researches of Allis must be held to have established, the sensory canal systems of fishes, both recent and fossil, may be reduced to a common type. Pending the production of weighty evidence to the contrary, this must be considered as one of the best-established conclusions attained by the careful study of these organs by many able observers. This common type may be summarised as follows:—

(1) A supra-orbital canal passing, as its name implies, over the eye. Innervated by the superficial ophthalmic lateral line nerve. Anteriorly may anastomose with the infra-orbital canal or end blindly; posteriorly anastomoses either with the infra-orbital or lateral canal, but more often with the former.

(2) An infra-orbital canal coursing underneath the eye. Innervated by the buccal + otic lateral line nerves. Anteriorly may anastomose with the supra-orbital canal or end blindly; posteriorly anastomoses either with the lateral canal only or with both the supra-orbital and lateral canals (usually).

(3) A hyomandibular or operculo-mandibular canal. Developed in connection with the lower jaw, and may be represented by one or more canals. Innervated by the external mandibular lateral line nerve. Ventrally may anastomose with its fellow or fellows of the opposite side, but usually ends blindly; dorsally usually anastomoses with the infra-orbital canal, may in some cases do so with the lateral canal, may anastomose with both these canals, or may remain independent of any.

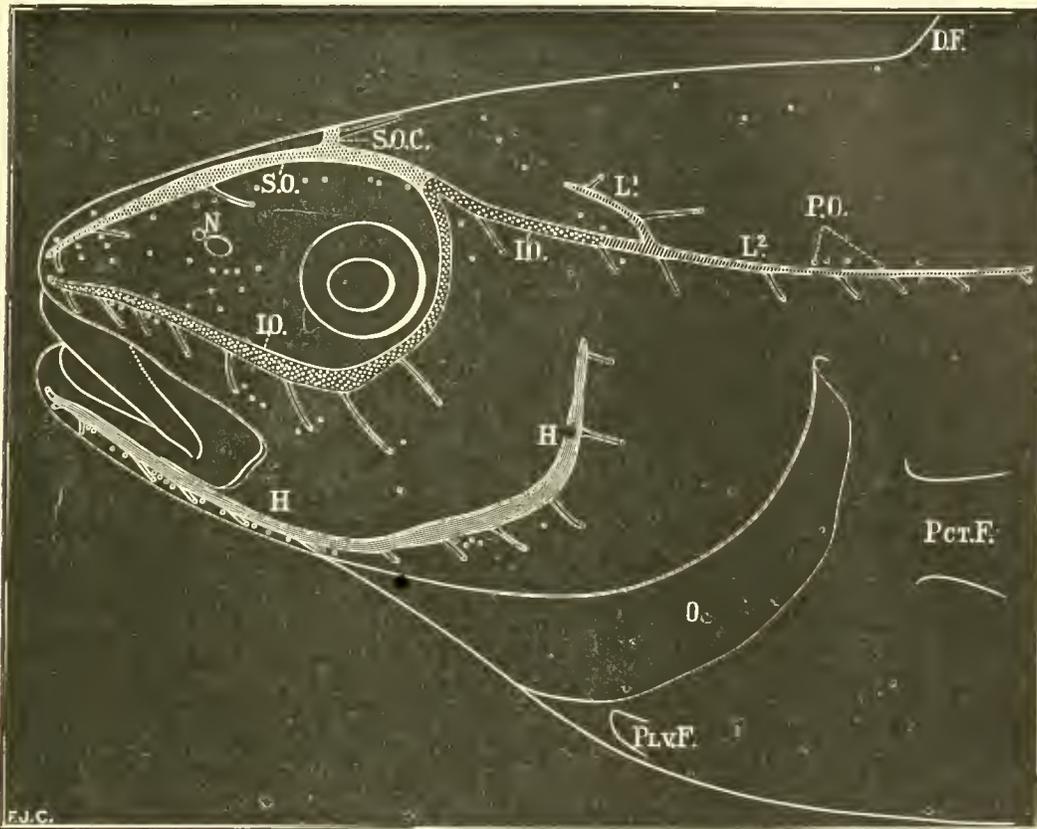


Figure of *Gadus virens*, half natural size, showing the sensory canals and their innervation—the latter indicated by the different kinds of shading. *D.F.* anterior extremity of dorsal fin; *L¹*, supra-temporal portion of lateralis canal; *L²*, lateral portion of lateralis canal; *N.* anterior and posterior narial openings; *O.* opercular fold; *Pct.F.* pectoral fin; *Plv.F.* pelvic fin; *P.O.* pit organs (innervated by the lateral line nerves); *S.O.C.* supra-orbital commissure.

- (1) Supra-orbital canal, *S.O.* Innervated by superficial ophthalmic lateral line nerve—cross-hatched.
- (2) Infra-orbital canal, *I.O.* Innervated by buccal + otic lateral line nerves—dotted.
- (3) Hyomandibular or Operculo-mandibular canal, *H.* Innervated by external mandibular lateral line nerve—longitudinal shading.
- (4) Lateralis canal, *L¹* and *L²*. Innervated by lateralis lateral line nerve—oblique shading.

(4) A lateral canal situated at the side of the body. Innervated by the lateralis lateral line nerve. Anteriorly anastomoses usually with the infra-orbital canal only, but may also do so with the supra-orbital canal; posteriorly ends blindly at the tail. The canal known as the supra-temporal or occipital commissure (=Commissural canal of Ewart) has somewhat variable relations, and is perhaps not homologous in all fishes.

Strictly speaking, and arguing from its condition in those fishes in which its innervation has been carefully ascertained, it should form a dorsal connection between the *anterior extremities* of the lateral canals. It may, however, interpolate itself, as it does in *Chimæra* and other recent fishes, and perhaps also in *Pterichthys*, between the two orbital canals, so that these do not anastomose posteriorly, but both arise from the lateral canal. But, however this may be, no canal can be considered a supra-temporal canal which is not innervated by the lateralis nerve, and which therefore is not a portion of the lateral canal.

I hence propose to describe the sensory canals of *Gadus morrhua* in the following order:—(1) Supra-orbital canal; (2) Infra-orbital canal; (3) Hyomandibular canal; (4) Lateralis canal. All these canals will be described from before backwards.

#### D. SENSORY CANALS OF *GADUS MORRHUA*. (Pl. 21, fig. 1.)

##### (1) *Supra-orbital Canal*.

The supra-orbital canal commences blindly at the anterior extremity of the nasal bone, and therefore of course at the extremity of the snout. This blind extremity appears very late in the ontogeny of the system, and is not seen in sections of young Gadids—the canal here being directly continuous with the first dermal tubule (I propose to designate as “dermal tubules” those small tubes by which at intervals the main sensory canals communicate with the surface\*). The supra-orbital canal on the nasal bone pursues a slightly sigmoid course obliquely inwards, upwards, and backwards, and measures whilst on this bone about 40 mm. long. The nasal is deeply grooved to receive the base of the canal, and its inner edge is partly turned outwards to form a rough tube—imperfect, however, dorsally and externally. Anteriorly the bony nasal furrow is imperfect ventrolaterally, in order that the first dermal tubule may enter the supra-orbital canal (see Pl. 21). The second dermal tubule enters the supra-orbital canal 25 mm. from the posterior extremity of the nasal, and lies in a backwardly-directed oblique furrow situated on the lateral wing of the nasal.

The canal now leaves the nasal and for a distance of about 5 mm. has no bony floor, but only a ligamentous one. An internal wall and roof are, however, *partly* supplied by a forward projection of the frontal. The third dermal tubule enters the canal at this region, but somewhat nearer the frontal than the nasal.

The remainder of the supra-orbital canal on the frontal is more conveniently described from behind forwards. In front of its anastomosis with the infra-orbital it courses inwards and forwards for a distance of about 20 mm. It then enters by a lateral foramen a canal bored in the substance of the frontal. The median portion of this canal forms a perfect tube, but posteriorly the roof is imperfect owing to the presence of a

\* The dermal tubules and sense organs of the lateral canals are enumerated in order from before backwards, in full knowledge of Allis's important proof of the relation between the sense organs and the tubules. Any scientific enumeration of these structures in the case of the Cod is, however, impossible until the development of both has been investigated, and any attempt therefore to do so here would be purely arbitrary and misleading.

long, laterally compressed, oval median fontanelle, which measured 12 mm. long in the present specimen. The posterior extremity of this fontanelle represents the nearest approach which the supra-orbital canal makes to the mid-dorsal line, the two supra-orbital canals being only separated at this region by a cylindrical bony basal projection or septum 3 mm. wide. It is here that the two supra-orbital canals communicate by a well-marked transverse commissure, very obvious in sections of young Gadids, but apt to be overlooked in dissections of adults. In front of this region the canal at once begins to course obliquely outwards, and continues to do so as far as its anterior extremity. The bony septum above referred to becomes wide at the anterior extremity of the fontanelle, where it is nearly 5 mm. wide. The median closed portion of the tube is a little over 10 mm. long, in front of which the next 14 mm. of the canal are imperfect externally, becoming more and more so anteriorly. The course of the supra-orbital canal from the posterior extremity of the median fontanelle up to the anterior edge of the frontal has been slightly obliquely outwards and forwards.

The fourth *unpaired* dermal tubule, which is the longest of those opening into the supra-orbital canal, enters it at the short transverse commissure. The surface pore in adults is, in all the specimens that I have examined, slightly to the left of the median dorsal line, whilst the tubule itself opens precisely at the centre of the commissure, although I have seen it also somewhat to the left. In sections of young Gadids, however, both the surface pore and the internal opening are exactly median—another instance of the slight disturbance of the symmetry of the lateral line organs which takes place in the adult. It may be mentioned here that this is the only unpaired dermal tubule in the Cod.

### (2) *Infra-orbital Canal.*

This will be described under the headings of the various bones which support it.

*First Sub-orbital or Lachrymal Bone* \*.—The infra-orbital canal arises blindly a little in front of the lachrymal near the mid-dorsal line at the extremity of the snout. The blind extremity exists from the very beginning, and is obvious both in sections of young forms and in dissections of the adult. The anterior extremity of the lachrymal is grooved to receive this part of the infra-orbital canal. The lachrymal itself is roughly triangular, with the apex directed forwards. Its length is about 60 mm., and breadth at the base over 35 mm. The base may be divided into two concave portions, separated by a median

\* The synonymy of the bones of the Teleostean skull is, it is hardly necessary for me to point out, a somewhat obscure subject. I have endeavoured as far as possible to steer a middle course, and therefore hope that no objection can be taken to any of my terms. It is, perhaps, necessary to explain that Allis (6) and other authors consider the first sub-orbital and lachrymal to be two separate bones. No reasonable objection, however, can be brought against the view advocated by McMurrich (136), that the lachrymal is a modified sub-orbital plate, and I therefore describe it as the first sub-orbital. We may note in this connection that the Teleostean lachrymal has been erroneously termed by some authors the pre-frontal. The correct homologue in the Teleosts of the Ganoid pre-frontal is, however, the lateral ethmoid (=the parathmoid). For the rest, sphenotic and pterotic are undoubtedly synonyms of post-frontal and squamosal respectively (but see p. 132). The confusion in the nomenclature of the bones of the fish's skull has arisen partly by the misuse of some terms and partly by the unnecessary introduction of others.

prominence, the ventral portion bearing a facet for the articulation of the second sub-orbital. The sensory canal passes along the middle of the bone, marking it into two almost equal halves. The dorsal border of the canal is slightly sigmoid, and anteriorly it approaches the border of the upper jaw, whilst the direction of the whole canal is distinctly downward. A thin bony lamina (see below) projects downwards from above and forms a roof and an external border for this portion of the infra-orbital canal, leaving it open, however, ventrally. About 35 mm. from the posterior extremity of the lachrymal this bony lamina is seen to be broken, thus forming a sort of notch and leaving this portion of the infra-orbital canal without any external boundary, and with only a portion of its roof. The first four dermal tubules open into the infra-orbital canal on the lachrymal, the first at the anterior extremity of the bone, and the third at the notch mentioned above.

The articulation of the lachrymal with the second sub-orbital is somewhat peculiar and may here be described. As mentioned above, and as is the case with the other sub-orbitals, the lachrymal sends down externally a bony lamina the function of which is to protect the external wall of the infra-orbital canal. With the posterior extremity of the imperfect tube thus formed the dorsal portion of the anterior convex extremity of the second sub-orbital becomes fitted or wedged in. Ventral to the external bony lamina the second sub-orbital simply overlaps the lachrymal, and the large facet thus formed at the posterior extremity of the latter bone measures 6 mm. antero-posteriorly.

*Second Sub-orbital.*—The direction of this ossicle is backwards and downwards. Its length dorsally at the sensory canal is about 20 mm., and its greatest width 22 mm. The anterior articular surface is convex, and is connected with the lachrymal in the way above described. Posteriorly there is an oblique articulation with the third sub-orbital. The second sub-orbital is a large semi-cartilaginous plate, the dorsal border of which is turned over so as to form a stout support for this portion of the infra-orbital canal. As, however, the dorsal border does not fuse on to the large body of the plate ventral to the sensory canal, the tube is imperfect ventrally, and is, in fact, only completed by the ligamentous sheath of the ossicle. The dermal tubules 5 and 6 open into the infra-orbital canal on this ossicle—the former at the anterior extremity, where it overlaps the lachrymal, and the latter near its posterior border.

*Third Sub-orbital.*—This ossicle continues the downward direction of its predecessor, but is somewhat more horizontal. The infra-orbital canal is still passing backwards and downwards. The length of the third sub-orbital is 15 mm., and its width 16 mm. The anterior and posterior articular surfaces are oblique and roughly parallel, but the anterior is much the longer. An imperfect tube for the lodgment of the sensory canal is formed in the same way as in the second sub-orbital. The seventh dermal tubule opens into the canal at the posterior extremity of the third sub-orbital.

*Fourth Sub-orbital.*—The infra-orbital canal now begins to take an upward turn, and, in consequence, the direction of this ossicle is upwards and backwards. It is further midway between the vertical and horizontal sub-orbitals, and measures 14 mm. in length and 7 mm. in width. The sub-orbitals thus narrow from before backwards. The sensory canal tube is formed similarly to those on the preceding sub-orbitals, but it must be noted

that as the sub-orbitals become narrower, so the edge turned over to form the tube approximates more and more to the ventral or posterior edge, the tendency thus being for the *whole* of the sub-orbital ossicle to be used up in the formation of the protective sensory tube. The eighth dermal tubule opens at the dorsal or posterior extremity of the ossicle, the latter tapering off to receive it.

*Fifth Sub-orbital or First Post-orbital.*—The infra-orbital canal has by this time taken a sharp upward curve, so that the fifth sub-orbital is not far removed from the perpendicular. Its length is 17 mm., and the anterior edge almost approximates to the posterior in the formation of the tube for the infra-orbital canal. The ninth dermal tubule is received by the infra-orbital canal between the fifth and sixth sub-orbitals. This tubule is not represented in *Gadus virens*.

*Sixth Sub-orbital or Second Post-orbital.*—This, the last and most posterior sub-orbital, articulates ventrally with the fifth sub-orbital, and dorsally with the postero-lateral region of the frontal, and also slightly with the post-frontal or sphenotic. Its direction is as near as possible perpendicular, and the portion of the infra-orbital canal that it lodges is of course directly continuous with that on the frontal. The length of the canal on the sixth sub-orbital is 14 mm., and it is protected in a precisely similar manner as on the fifth sub-orbital—the anterior and posterior edges not quite approximating.

*Frontal.*—The infra-orbital canal is now on the frontal. Situated on the upper surface of the postero-external angle of the frontal is a triangular fossa with the apex directed inwards and forwards. The base of the triangle forms a portion of the posterior edge of the frontal. The infra-orbital canal comes first along the *outer* side of the triangle (a distance of about 14 mm.), and arriving at the apex first of all anastomoses with the supra-orbital canal, and then turns sharply backwards, edging the *inner* side of the triangle (about 15 mm.). The canal, therefore, at this region turns first inwards and forwards, and then outwards and backwards. The two sides of the triangular fossa on the frontal are depressed so as to form slight furrows for the reception of the base of the infra-orbital canal. Further, the inner side of the triangle is raised up and arches outwards, thus forming a roof for this portion of the infra-orbital canal. As, however, elsewhere, the tube is imperfect externally.

*Post-frontal or Sphenotic.*—The sphenotic now comes to the surface and lodges the next 5 mm. of the infra-orbital canal, the latter still pursuing the downward and backward direction of the portion immediately preceding it on the frontal. The sphenotic, however, only supports the floor of the infra-orbital canal, an inner wall and roof being here formed partly by a backward projection of the frontal and partly by a forward prolongation of the pterotic. Externally the sensory canal is only protected by ligament. The tenth dermal tubule enters the canal at about the middle of the sphenotic, and in front of the canal in that bone transmitting the otic branch of the outer buccal nerve.

*Squamosal or Pterotic.*—The infra-orbital canal, leaving the sphenotic and still passing backwards and somewhat downwards, enters on the pterotic, which supports it for the last 30 mm. of its length, until, between the pterotic and the succeeding supra-temporal, the infra-orbital canal anastomoses with the lateral or body canal. A more or less perfect

tube is formed on the pterotic by a latero-external process being sent down. Posteriorly this process only forms an imperfect tube, but anteriorly it usually almost completely encloses the canal, yet does not fuse ventrally with the floor of the ossicle. The tube is thus imperfect for the whole of its length, but less so anteriorly than posteriorly. The last or eleventh dermal tubule of the infra-orbital canal opens into it between the pterotic and the adjoining supra-temporal, but the greater part of the aperture is on the pterotic.

### (3) *Hyomandibular Canal.*

The hyomandibular canal arises on the dentary at its anterior extremity near the symphysis, its length, whilst on this bone, being about 80 mm. The direction of the canal depends, naturally, on the position of the lower jaw. When the jaw is closed the canal has a strong upward incline. Its relations with the articular portion of the canal are, of course, fixed, and do not vary with the gape of the jaw. The hyomandibular canal fits into a deep groove on the ventral surface of the dentary which is continued almost to the anterior symphysis. This groove is widely open ventrally, and gradually tapers towards its anterior extremity. The first five dermal tubules open into the hyomandibular canal whilst on the dentary, the sixth opening at the junction of the dentary and articular, but rather on to the dentary.

Leaving the dentary the hyomandibular canal passes on to the articular, and then begins the upward curve which carries the canal on to the pre-operculum. Strong dorsal and ventral ridges form a stout protection for the canal, which is only exposed externally. The hyomandibular canal is 15 mm. long on the articular.

Owing to an inward shelving on the part of the articular and pre-operculum, the next 10 mm. of the canal have no bony support, but are protected only by a ligamentous sheath. This, of course, is developed in connection with the movement of the lower jaw. There is also a strong upward curve on the part of the canal to meet the succeeding portion on the pre-operculum. The seventh dermal tubule opens on to the canal at about the middle of this ligamentous section.

Having reached the pre-operculum, the hyomandibular canal lies at first somewhat horizontally. It then takes a graceful curve upwards, so that the posterior portion of the canal is practically vertical. Whilst on the pre-operculum the hyomandibular canal has a length of about 80 mm. A thin bony lamella projects downwards anteriorly and backwards posteriorly, forming an external lateral wall for the canal, but, however, leaving it open ventrally in front and posteriorly behind. Commencing at about 11 mm. from the posterior extremity of the canal, a ridge of bone 8 mm. long is seen to be thrown up, which forms a posterior wall for the canal. At this region the anterior bony lamina forming the external lateral wall of the canal tapers down, otherwise the hyomandibular canal would in this region be completely enclosed in bone. The tube then is here also incomplete externally, but is more perfect than it is at any other part of the pre-operculum. The hyomandibular canal ends blindly 10 mm. below the dorsal extremity of the pre-operculum. The dermal tubules eight to twelve open on to the

canal at the pre-operculum, the eleventh below and the twelfth above the ridge of bone just mentioned.

It is thus seen that the hyomandibular canal is perfectly independent of any of the others, and does not anastomose either with the infra-orbital or lateral canals.

#### (4) *Lateralis Canal.*

##### *First or Supra-temporal Portion.*

As with the infra-orbital canal, it will be most convenient to describe the lateral canal under the headings of its various supporting ossicles.

*First Supra-temporal or Extra Scapula.*—The supra-temporal canal commences blindly in both *G. morrhua* and *G. cirens* at the anterior extremity of the first supra-temporal ossicle. Its direction is markedly inwards and forwards. The greatest length of the ossicle is 17 mm., and its greatest breadth 6 mm. It is free anteriorly, that is, it has no articulation with any other bone, but its extremity is attached by a ligament to the dorsal spiny process of the parietal overhanging the foramen transmitting the so-called "cutaneous branch of the Vth."\* Posteriorly the ossicle articulates by means of an oblique convexity with the second supra-temporal. The first supra-temporal consists of an internal plate, having its dorsal edge turned over somewhat considerably to protect the supra-temporal canal. Anteriorly the portion turned over tapers down to admit of the entrance into the canal of the first or proximal dermal tubule.

*Second Supra-temporal or Extra-scapula.*—Supports the distal or basal portion of the supra-temporal canal, and consists of an internal plate, the two edges of which have more or less become opposed to form a tube. Posteriorly this apposition is complete, so that the tube is here perfect, though the two edges in question have not fused, such not being a characteristic of the Cod. Anteriorly, however, the tube, as in most of the other lateral line ossicles, is imperfect, but this is to enable the second dermal tubule to enter the canal. The upper posterior border of the ossicle bears a semicircular notch, which fits into the upper or epiotic limb of the post-temporal. The internal face of the second supra-temporal also rests on this limb of the post-temporal. The greatest length of the second supra-temporal is 17 mm., and its greatest width about 11 mm. Anteriorly it presents a concave border for articulating with the first supra-temporal, whilst posteriorly it articulates with two ossicles: *a*, by a long, slightly convex, ventral facet with the third supra-temporal; *b*, by a backwardly directed posterior facet (slightly concave) with the fourth supra-temporal. Posteriorly the supra-temporal portion of the lateralis canal takes a downward curve and becomes confluent with the lateral or body portion.

##### *Second or Lateral Portion.*

The first 20 mm. of this section of the lateral canal are supported partly by the third supra-temporal, but also partly by the ventral portion of the second (see Pl. 21. fig. 1). This fact must be taken into consideration when reading the description of the former ossicle.

\* = the R. lateralis accessorius (see Section N, p. 166).

*Third Supra-temporal or Extra-scapula.*—The third supra-temporal is a somewhat long bone supporting the anterior extremity of the lateral canal as it passes downwards and backwards from the pterotic. Its greatest length is 22 mm., and its greatest width 9 mm. It consists of a plate slightly convex internally, the dorsal edge of which is turned over, but not very markedly, to form an imperfect tube. Its ventral border is quite straight, whilst its dorsal border is somewhat irregular. Anteriorly it articulates by means of an oblique and well-marked concavity with the pterotic, the dorsal border of the third supra-temporal being prolonged forwards so as to fit into a corresponding shelving on the pterotic. Ventrally the latter presents a large triangular facet 10 mm. in length from base to apex, on which the ventral portion of the anterior extremity of the third supra-temporal rests and articulates. This articulation is very compact and strong. Posteriorly the articulation is with two ossicles: *a*, by a long dorsal and slightly concave facet with the second supra-temporal; *b*, by an oblique concavo-convex facet with the fourth supra-temporal. The third dermal tubule opened into the lateral canal near the posterior extremity of the third supra-temporal, and slightly posterior to the entry of the supra-temporal canal into the lateral. This tubule was present on the left side of the fish, but not on the right.

*Fourth Supra-temporal or Extra-scapula.*—This consists of a flat internal plate 11 mm. across at its widest part, and with a maximum length of 16 mm. Its dorsal edge is turned over so as to form an external process protecting the sensory canal. Anteriorly it has a close ligamentous articulation with two ossicles: *a*, by a convexo-concave ventral facet with the third supra-temporal; *b*, by a slightly convex dorsal facet with the second supra-temporal. The latter facet is internal to the first and passes back at an angle to it. Posteriorly the fourth supra-temporal rests on and overlaps the angle formed by the two forks of the post-temporal. The fourth dermal tubule opens into the lateral canal near the centre of the fourth supra-temporal.

*Post-temporal or Supra-scapula* \*.—The angle formed by the union of the two limbs of the post-temporal now comes to the surface of the skull and supports the next 9 mm. of the lateral canal. It is here that the lateral canal commences to approach the surface of the body and to take up that position in which it is to be found immediately under the skin. The fifth dermal tubule opens just at the posterior extremity of the post-temporal, and almost between that bone and the first lateral line ossicle.

Behind the post-temporal the lateral canal loses the support of the bones of the skull and pectoral girdle, and is only protected at intervals by the lateral line ossicles, which themselves diminish posteriorly as the canal approaches the skin and decreases in size.

At about the middle of the fish the lateral canal lies immediately under the skin, and is situated at the side of the body, its position being indicated by the modified scales lying immediately over the canal. In the specimen from which the above description has been written, it was about 55 mm. ventral to the anterior extremity of the dorsal fin. It is supported behind the post-temporal by a series of imperfect bony cylinders, the

\* The supra-clavicle of some authors (*e.g.* McMurrich, 136, and Gegenbaur). It is impossible, however, to homologise the bones usually termed post-temporal and supra-clavicle.

so-called "lateral line ossicles." The anterior extremity of each "lateral line ossicle" is placed just posterior to the internal opening of a dermal tubule, so that if we regard the lateral canal as composed of segments defined by the internal openings of the dermal tubules and the intermediate occurrence of sense organs, then the lateral line ossicles will lie at the anterior extremities of these segments. Each cylinder is imperfect externally, the space being obliterated by the periosteal membrane. The length of one taken from about the region of the pectoral fin was 7 mm. Anteriorly they increase in size, the first, just posterior to the post-temporal, being an irregular imperfect tube 11 mm. long.

#### E. *GADUS MORRHUA* AND *G. VIRENS* COMPARED.

The differences between these two species are few but decisive. The sense and pit organs of both are the same (*roughly* as regards the pit-organs) both in number and position. The only variations I could find were in the dermal tubules. These will be at once noticed if a comparison be made between figs. 1 and 2, Pls. 21 & 22 (representing *G. morrhua* and *G. virens* respectively), and are as follows:—

1. The ninth dermal tubule on the infra-orbital canal of *G. morrhua* is absent in *G. virens*. This, as far as I am aware, is a perfectly constant difference. I have never failed to find it in *G. morrhua*, nor have I ever seen it in *G. virens*.
2. In *G. virens* the hyomandibular canal opens anteriorly on to the surface, but does not do so in *G. morrhua*. This, I believe, is another constant variation.
3. In *G. morrhua* the third dermal tubule of the lateral canal is of variable occurrence. In the fish from which fig. 1 was drawn it was present on the left side, but absent on the right. It will be noted that the nares also were abnormal in that fish on the left side, being fused there, but quite normal on the right side. In *G. virens* the fourth dermal tubule of the lateral canal of *G. morrhua* is, I have found, invariably absent, nor have I ever seen any fusion on the part of the anterior and posterior nares.

#### F. THE SENSE ORGANS ON THE LATERAL LINE CANALS. (Plates 22 & 23.)

These have been carefully worked out, as well as the number and position of the dermal tubules verified, from serial sections of *G. virens*. This is the only method which ensures perfect accuracy in this connection. The sense-organs themselves not being obvious to the naked eye, the dissector has to rely on finding the nerve twigs supplying them. If he should chance to overlook one or more of these twigs, as often happens, the corresponding sense organs are, for the time at least, also overlooked, and this may easily nullify the results of the investigation. I accordingly paid a visit to St. Andrews and collected a large number of young "Green Cod" (*G. virens*), many of which have since been cut into serial sections. The heads of the living animals were cut off behind the pectoral fin and fixed in Hermann's platinum acetic osmic mixture. The sections (10 ticks thick, Cambridge rocking microtome) were stained on the slide with Mann's methyl-blue—eosin\*—a most admirable method, giving perfect pictures even of the brain

\* Journ. Anat. & Phys. vol. xxix. (N. S. vol. ix.), p. 100 (1894).

and nerve tracts. The sense organs were then systematically mapped out from the sections, so that it is hoped any possible chance of error has been removed.

*Supra-orbital Canal.*—There are five sense organs on the supra-orbital canal as against four dermal tubules. As a rule, one sense organ is placed midway between the internal openings of two dermal tubules, so that there is usually a rough correspondence between the number of sense organs and that of the tubules. The first sense organ on the supra-orbital canal is placed between the openings of the first and second dermal tubules, but nearer the second; the second between the second and third tubules, but nearer the third (just over the anterior extremity of the nasal sac); the third and fourth anterior and slightly posterior to the supra-orbital commissure respectively; and the fifth near the posterior extremity of the canal, and in the young forms\* exactly dorsal to the optic chiasma.

*Infra-orbital Canal.*—This canal has eleven sense organs and ten dermal tubules. The first two sense organs are situated between the first and second tubules, and just under the first sense organ of the supra-orbital canal. There is a slight overlapping on the part of the first two sense organs, the posterior extremity of the first being above the anterior extremity of the second, and the two together extending practically from the opening of the first dermal tubule to the second. The next six sense organs, the third to the eighth, lie between their respective tubules as shown in the figure; the ninth and the tenth, however, are not separated by a tubule, and this seems to imply that the ninth dermal tubule has degenerated. This tubule is indeed present in *G. morrhua*, and in such a position as would separate the ninth and tenth sense organs of *G. virens*. It is therefore possible that in the latter species the tubule has existed and disappeared. The eleventh sense organ lies between the ninth and tenth tubules, but somewhat nearer the former.

*Hyomandibular Canal.*—Twelve sense organs and thirteen dermal tubules were found in connection with this canal. The first sense organ is slightly anterior to the opening of the second tubule, and the second has the same relations with the succeeding tubule. The remaining ten sense organs are situated between the openings of the tubules as indicated in Plate 22 the last being placed on the narrow portion of the canal at its posterior extremity.

*Lateral Canal.*—The supra-temporal segment of the lateral canal has two sense organs and two dermal tubules, the first sense organ being placed slightly posterior to the opening of the first tubule, and the second lying between the opening of the second tubule and the junction of the supra-temporal portion of the canal with the lateral portion. The third sense-organ is found just anterior to the junction of the two canals mentioned above, whilst the fourth is placed between the third and fourth dermal tubules. The remainder of the sense organs of the lateral canal are situated as usual between the openings of the dermal tubules. The condition of the lateral canal in young Cod behind the operculum will be described and discussed elsewhere.

\* See note on p. 156.

## G. OTHER SENSE ORGANS BELONGING TO THE LATERAL LINE SYSTEM. (Plate 21.)

Belonging undoubtedly to the lateral line system, since they are innervated by the same nerves, are the pit organs or sensory follicles, described by Merkel, Fritsch, Allis, and Ewart & Mitchell\*. These in the Cod are somewhat numerous, and do not occur in the well-defined series that they do in the Elasmobranchs and Ganoids. Their structure has already been fully discussed by the authors above mentioned, so that only a few words are necessary as to their distribution. As will be seen by reference to the figure of *G. morrhua*, the pit organs cannot be separated into groups, being too irregularly scattered. It is equally obvious, however, that most of them occur in connection with the sensory canals, and this is most marked in the case of the hyomandibular canal. In spite of their apparent irregularity and number, they are very constant both in number and position, as will be ascertained by a careful examination of an adult *G. morrhua* and a comparison with the figure. The pit organs are usually conspicuous on account of their pigmented lips, and even where this is slight or absent a contrast in colour usually betrays their existence. As is well known, the pit organs are excavated papillæ formed by an invagination of the skin, and lodging a sense-organ innervated by a twig from one of the lateral line nerves. My figure (Pl. 21) of these organs is the result of a minute examination of the heads of several large specimens of *G. morrhua*.

Contrasting with the numerous pit organs is the complete absence of any traces of Lorenzini's ampullæ and the associated ampullary canals. This fact is duly commented on elsewhere.

## H. RELATION OF THE SENSORY CANALS TO THE SKULL.

That the lateral line system has no definite relations with the primitive skull is quite evident even on *à priori* grounds. An epiblastic structure, necessarily connected with the skin, and actually found on the surface in *Chimæra*, or associated with it in many forms, can only be secondarily connected with the skull. Except in the Elasmobranch fishes, where the lateral canals are firmly embedded in the extensive subdermal tissue, there is a tendency, almost in all fishes, to protect the sensory canals with some form of calcified or rigid support. In *Chimæra* this takes the form of imperfect limy rings, whilst in the majority of bony fishes the support ranges from a partial to an absolutely perfect bony tube. There is, in fact, a strong tendency to surround the sensory canals with a complete extensive osseous deposit.

Such being the case, it becomes necessary to distinguish between lateral line bones and the cranial bones *sensu stricto*, and to enquire into the connection between the two series where such must obviously exist. We may therefore divide the bones supporting the lateral line into two series:—(a) ossicles developed purely for the support of the sensory canals; (b) cranial bones with which the lateral line ossicles have become secondarily connected. The excellent work which has been done by McMurrieh on the osteology of *Amiurus catus* (1883-4, 136) has made perfectly clear the bearings of the lateral line

\* See full discussion below.

system on the morphology of the skull\*. This author discovered the important fact that the frontal bone, for example, consisted of two parts — the frontal properly so-called + a fused lateral line ossicle. The supra-orbital canal in the region of the frontal first acquired its bony support corresponding to a true lateral line ossicle, and the latter, as development proceeded, became fused on to the frontal. The same process was observed in the case of the sphenotic, pterotic, dentary, and articular. In the Cod this process may be easily deduced from the structure of the articular portion of the hyomandibular canal. We may therefore classify the osseous support of the lateral line in the Cod and perhaps other forms as follows:—

<i>Lateral line Ossicles.</i>	<i>True Cranial Bones + fused Lateral line Ossicles.</i>
Nasal.	
Lachrymal or adnasal.	Frontal.
Supra- or infra- (with post-) orbitals.	Sphenotic (most forms).
Dermal Sphenotic ( <i>Amia</i> ) = the Post-frontal.	Pterotic (most forms).
Dermal Pterotic ( <i>Gadus</i> ) = the Squamosal.	Dentary.
Supra-temporals.	Articular.
Pre-operculum.	

Two things must be pointed out with reference to this table: first, I fully agree with McMurrich that the nasal and pre-operculum are true lateral line ossicles; second, there is some doubt in the Cod as to the nature of the pterotic. In *Amiurus* there is no doubt that it is a cranial bone bearing a fused lateral line ossicle. In *Gadus*, however, the bone usually termed the pterotic has no connection with the ear, and may be easily detached from the underlying ear bones. It seems probable, therefore, that the Cod's "pterotic" is a lateral line ossicle which has not become fused on to the adjacent true pterotic (cp. particularly p. 181) †.

Whilst it is obvious from these facts that the lateral line system has no connection whatever with the primitive cartilaginous and membrane skull, such is by no means the case with regard to the later development of the latter. Whilst, further, above the Amphibia, the lateral canal system and its nerves completely disappear, leaving no traces behind (omitting the auditory organ), we cannot say the same in the matter of the bony supports of the canals. The nasal, for example, performs a double function—on the one hand supporting a portion of the supra-orbital canal, for which purpose it was primarily developed; on the other hand, having relations with the nasal capsule, which represents a secondary modification. When, therefore, the supra-orbital canal disappeared, the nasal would remain behind, to perform its accessory nasal function. It therefore seems to me certain that the higher vertebrate skull bears very considerable traces of the lateral line system of Fishes and Amphibians and it would be a very interesting study to determine what these relations are. For example, admitting the homology between the ear and the lateral line system, to what extent are the bones of the auditory capsule profoundly modified lateral line ossicles?

\* McMurrich, by the way, also considers the lachrymal to be the modified first sub-orbital. So also does Pollard, 1892 (160, p. 410).

† See Postscript, p. 205.

The first author to recognise the important bearings which the lateral line system might possibly have on the morphology of the skull was, I believe, Dr. Traquair (1865, 207), who, as I have previously pointed out, made considerable and skilful use of the relation of the two structures in solving the problem of the asymmetrical skull. Sagemehl (1883, 170), writing independently of McMurrich, says\* :—" I desire to mention, at this point, that hitherto the relations of the mucous canals to the bones of the cranium have hardly been given a thought, and yet they deserve a closer study, as these relations are very constant, and in questionable cases they can be used to determine doubtful homologies." Allis (1889, 4) points out (p. 461) that "it is only within the last five or six years that the constant relations of the cranial canals to the dermal bones of the head, and their importance in determining these bones in doubtful cases, have been recognised. Both Sagemehl and Van Wijhe have called special attention to this. . . . ." Since 1883, Sagemehl, Bridge, and numerous other authors have, when dealing with the skull of bony fishes, also described the cranial sensory canals, with the result that the relations of the lateral canals with the skull have been shown to be remarkably constant. Hence the table given above may be said to represent the facts in most bony fishes.

#### 1. THE TRIGEMINO-FACIAL GANGLIONIC COMPLEX.

*General Statement.*—As it is impossible to arrive at an accurate appreciation of this complex by observations on the adult, the following description has been based upon a study of sections of young forms. The trigemino-facial ganglion in these sections is seen to consist essentially of three portions arising by two roots, which are from above downwards :—

- (1) A Lateral line ganglion. Consists of two parts united in front, one being situated ventral to the other. The dorsal part gives rise to the superficial ophthalmic and buccal lateral line nerves, which arise as a single trunk and separate into superficial ophthalmic and buccal trunks as a passage is made through the second portion of the trigemino-facial ganglion. The ventral portion is doubtless connected with the external mandibular lateral line nerve.
- (2) A "Trigeminal" or "Gasserian" ganglion †. This is situated internal and largely anterior to the second or ventral portion of (1). From this portion of the complex the superficial ophthalmic of the trigeminus, the maxillo-mandibular trunk, and, probably, the post-branchial division of the facial arise. If the latter statement be correct, as seems certain, this ganglion should be called the "trigemino-facial."
- (3) A "Facial" ganglion. This is a long and perfectly distinct ganglion which lies ventral to (2). It is connected with the palatine nerves and also with the

\* English translation by Shufeldt, p. 752 (1885, 187).

† I have called this ganglion the "trigeminal" or "Gasserian" in order to distinguish it from the "facial" ganglion. The question of the latter is discussed below. It is sufficient to remark here that were it more distinctively a ganglion of a cranial nerve, and less a sympathetic ganglion, the morphology of the "trigeminal" ganglion would doubtless be less difficult to decide.

pre-spiracular or chorda tympani divisions of the facial. It also communicates (*a*) directly with the sympathetic trunk; (*b*) by means of Jacobson's anastomosis (see below) with the glossopharyngeus.

In the adult Cod (see Pl. 22. fig. 2) there are two roots to the trigemino-facial complex, but these fuse in such a way that it is impossible to follow the nerves through the point of fusion. Nor is there any obvious ganglion beyond the lateral line ganglion (fig. 2, *L.G.*). It seems to me to be probable that there are lateral line fibres in each root. The roots are separated by the orbital vein.

*Special Description.*—The posterior or dorsal root of the trigemino-facial complex, as seen in the sections, arises from the side of the medulla on a level with the dorsal border of the horizontal semicircular canal and the posterior portion of the infra-orbital sensory canal. Its posterior edge overlaps the anterior edge of the first acoustic root, and it leaves the medulla at a level just dorsal to this auditory root. There is a slight mingling of fibres between the two roots at the point where they emerge from the medulla, but as both roots belong strictly to the lateral line system, this, happily, does not introduce any complication.

On emerging from the brain the dorsal root swells into an external knob containing ganglion cells (=dorsal portion of (1) above), and then, internal to this knob, passes straight downwards internal to the vestibule of the ear and alongside and in front of the first auditory nerve. No ganglion cells were seen on this descending part of the root. As the dorsal root passes downwards ventral to the ganglionic projection just described, another root is received which arises anterior and slightly ventral to the first, and passes backwards to join it. At the point where the two roots join is another mass of ganglion cells (=ventral portion of (1) above), and this second ganglionic enlargement itself becomes augmented by a further collection of cells (= (2) above) which lies internal and largely anterior to it. In front the three ganglionic masses become closely opposed, but the boundaries of all three can be easily distinguished.

That the trigemino-facial complex is in a somewhat specialised condition may be inferred from the fact that the two roots just described are the only roots for the whole complex—that is to say, they stand for the three anterior lateral line nerves as well as for the trigeminal and facial cranial nerves. The precise course of the fibres of these two roots through the ventral portion of the lateral line ganglion and the trigeminal ganglion my sections failed to demonstrate, but the following facts were made out with tolerable certainty. Setting aside the palatine nerves, which will be found described below, the first nerve to issue from the trigemino-facial ganglion posteriorly is the hyomandibular trunk. The most ventral fibres of this trunk go to form a portion of the facial proper, which is also described in connection with the facial ganglion. The passage of the orbital vein splits the hyomandibular trunk into two parts—a postero-dorsal and an antero-ventral. Along the former portion the cells of the second or “trigeminal” portion of the compound ganglion, which have hitherto been entirely intra-cranial, pass outside the pro-otic notch and are spread over the dorsal portion of the hyomandibular trunk outside the cranium and slightly external to the orbital vein. Distal to the vein

the two parts above unite and the fibres are almost immediately shuffled into two bundles—a posterior and an anterior—described with the buccal trunk. The origin of the facial proper fibres is mentioned in the description of the facial ganglion. The lateral line fibres of the hyomandibular trunk seem to be derived from the ventral portion of the lateral line ganglion.

In front of the hyomandibular the trigeminal ganglion lies partly within the cranium and partly outside it, the orbital vein separating the dorsal trigeminal from the ventral facial ganglion. The maxillo-mandibular + buccal trunks issue together from the trigeminal ganglion. The former is connected with the trigeminal ganglion, and there cannot be the least doubt that the latter passes upwards and backwards through the same ganglion, and arises, in common with the superficial ophthalmic lateral line nerve, from the dorsal portion of the lateral line ganglion. Some of the trigeminal ganglion cells extend along the dorsal border of the maxillo-mandibular trunk. In front of the exit of the maxillo-mandibular + buccal trunk, the trigeminal ganglion tapers down and gives off the superficial ophthalmic division of the trigeminus which accompanies the lateral line nerve of the same name as described below.

The facial ganglion is perfectly distinct from any other part of the complex and lies entirely outside the skull. It commences anteriorly above the orbital vein, and immediately ventral to the trigeminal ophthalmic, passing downwards and backwards, and increasing in size so as to lie external to the orbital vein, and ventral and external to the anterior extremity of the trigeminal ganglion. At this region a thin strand passes downwards externally and connects the dorsal with a ventral portion, which lies immediately under the orbital vein. The ventral portion, therefore, does not extend as far forwards as the dorsal portion, whilst the latter only extends as far back as the maxillo-mandibular + buccal trunk—at which point it ceases to exist. The ventral portion, however, passes backwards under the orbital vein and internal to the above trunk. Internal to this ventral portion the most ventral fibres of the hyomandibular trunk pass downwards and outwards under the orbital vein and enter into relations with the facial ganglion. The first branch to be given off from these fibres passes through the inner region of the facial ganglion, turning inwards, downwards, and forwards, and passing among the muscles of the alimentary canal. The next branch passes almost through the middle of the ganglion and courses forwards external to the previous branch. The third and largest branch passes obliquely through the centre of the ganglion, turns inwards, and then divides to form two large nerves—one of which passes forwards and the other backwards. The forward division again divides, and represents the true palatine branch of the facial nerve and its two divisions, the anterior and posterior palatine nerves described by Allis in *Amia*. The posterior division passes backwards and slightly outwards and accompanies the cephalic sympathetic trunk, but has otherwise no connection with it. It finally takes an upward and outward turn and passes into the ganglion of the glossopharyngeus. It thus represents the nerve known as Jacobson's anastomosis, connecting the facialis with the glossopharyngeus. The remainder of the ventral fibres of the hyomandibular pass outwards with the latter trunk and the facial ganglion, but apparently have no connection with it, and are

continued as the pre-spiracular or chorda tympani division of the facial. The precise origin of the post-branchial or hyoidean branch of the facial has already been described as doubtful from the "trigeminal" ganglion, but there could be no doubt as to the association of the palatine and chorda tympani fibres with the ganglion now described.

Behind the hyomandibular trunk the facial ganglion thins down considerably, and is seen to be perfectly spherical in transverse section. It is still visible, however, as a thin cord containing ganglion cells as far back as the dorsal portion of the lateral line ganglion. Behind this region it imperceptibly merges into the cephalic sympathetic trunk which passes straight backwards and accompanies Jacobson's anastomosis, but, as before stated, does not mingle with it. Opposite the glossopharyngeal ganglion the sympathetic swells into a ganglion from which are given off some fibres which accompany Jacobson's anastomosis to the glossopharyngeal ganglion. Behind the latter nerve the connections between the sympathetic ganglia were very difficult to see\*, although the ganglia themselves were obvious at intervals as far back as my sections went.

#### J. MORPHOLOGY OF THE FACIAL GANGLION.

I have hesitated considerably before committing myself to any opinion as to the nature of this interesting but most puzzling ganglion. When I first recognised it in my sections, and saw that its cells were small and corresponded precisely to the cells in the ciliary ganglion, with which I compared it, I concluded at once that it must be the anterior sympathetic ganglion of the cephalic system described by the older anatomists. When, however, subsequent investigation showed me its undoubted connection with some of the fibres of the facial nerve, I was compelled to admit that it might also belong to the trigemino-facial complex, and indeed represent a portion of that complex which was in the act of migrating from its original position and becoming converted into a typical sympathetic ganglion. In order to avoid "settling" the matter with an offhand suggestion, I delayed its further consideration until an opportunity was afforded me of carefully working out the literature, a discussion of which I now append.

Omitting the work of Cuvier (56, t. ii. pp. 512-515, 1799), the first authors to describe the sympathetic of Fishes were Desmoulins and Magendie (1825, 60), who traced the cephalic sympathetic as far forwards as the "trigeminal" nerve, and were probably the first to do this. Giltay followed in 1832 with a description of the sympathetic of *Esox* (87), which he found communicating with the vagus as well as with the "trigeminus," and in 1834, in a general treatise on the structure and physiology of the sympathetic of Fishes (88), describes the cephalic sympathetic of *Gadus aeglefinus*. He says (pp. 54-55): "Pars cephalica, continuatio trunci, eodem modo sese ab utroque latere habet. Curvaturam sequitur partis basilaris ossis occipitis et ad vagum pervenit. Nexus inter nervum sympathicum et nervum vagum mihi non lucide apparuit; hoc certum est, non cum ganglio vagi directe conjungi; sed contra nullum vidi ramum, cui conjunctio tribui possit, quæ tela cellulosa absolvi videtur. In multis speciminibus etiam

\* Possibly non-existent at the stage of my sections.

*frustra conubium cum glossopharyngeo quesivi, quamquam semper usque ad par quintum persequi potui n. symp., in cujus ganglio finem habet.*" (Italics mine.) The statement above *re* the vagus is of course erroneous, but it is interesting to note that Giltay did not regard the facial (= a portion of his trigeminal) ganglion as belonging to the sympathetic system. This, however, was done by Büchner (1835, 36) in "*Cyprinus barbns*" (= *Barbus vulgaris*), who describes as the first sympathetic ganglion what is undoubtedly my facial ganglion. Stannius (1842, 198) does the same for "*Gadus callarias*," and also describes a sympathetic anastomosis with the glossopharyngeus, whilst Bonsdorff (1846, 30) goes still further, and not only considers the facial ganglion to belong to the sympathetic system, but compares it with the otic ganglion of mammals—a clever suggestion which should by no means be summarily rejected.

In his general work (1849, 199), Stannius largely recapitulates the results of his former paper, but adds very considerably to the information there given. He adheres to his first interpretation, and further describes the anterior palatine as arising from the facial ganglion, but failed to determine the relations of the posterior palatine and the cephalic sympathetic. He was thus largely in agreement with his predecessors. Swan (1864, 205) states that the cephalic sympathetic of the Cod is connected with the vagus, glossopharyngeal, and "trigeminal" nerves, and figures these connections; and Owen (1866, 149, pp. 320-321), treating of the sympathetic of Fishes, says: "The first or anterior communication of this nerve, in the Cod, is with a branch of the fifth, and a filament is sent forward to the ciliary ganglion . . . Ganglions [*i. e.* sympathetic] are sometimes found at the junction of the sympathetic with the fifth, as well as at that with the glossopharyngeal and with the vagus, before the great splanchnic is formed: small ganglions are more rarely discernible at the junction of the sympathetic with the spinal nerves." (Italics mine.) Baudelot (1883, 16) describes the first sympathetic ganglion of the Perch as "*appliqué au-dessous de la branche antérieure du trijumeau*," and says that the cephalic sympathetic communicates behind with the glossopharyngeus and vagus.

The two papers published by Gaskell in 1886 and 1889 (82 & 83) have great theoretical importance, and I quite agree with Strong (204, p. 209) that "it is upon lines of work approaching those of Gaskell that, in my opinion, the most fruitful results will be obtained." Gaskell's studies were unfortunately confined principally to Mammals, which has necessarily caused him to overlook several points and to make some errors. His methods have already to a certain extent been applied to the lower Vertebrates by Strong and other American zoologists, and many important results have been obtained. In his first work Gaskell emphasized the fact that besides the dorsal and ventral roots of a metameric nerve there was also a morphological third root—the visceral, sympathetic, or lateral root. The visceral sensory fibres have a different origin from the motor fibres, the former probably arising in the case of the posterior cranial nerves largely from the funiculus solitarius. Referring to the distribution of the visceral nerves, Gaskell says (82, p. 11): "From the upper cervical region they pass out [*i. e.* from the central nervous system] in a single stream to the ganglia on the main stems of the vagus and glossopharyngeal nerves." Again, in the section<sup>3</sup>, "On the relation of the posterior root ganglia to the visceral nerves," he

remarks, p. 61: "The ganglia of the main sympathetic chain must, according to Onodi, be considered as offshoots (*Abkömmlinge*) of the posterior root ganglia. If this is so, we may conceive that the posterior root ganglion in the thoracic region may be double, part belonging to the somatic, part to the splanchnic root. Remak described the origin of non-medullated fibres from the posterior root ganglion as well as from the sympathetic ganglia . . . . The connection of the fibres of the ramus visceralis with the cells of the ganglion on the posterior roots of the thoracic nerves is most clearly visible in the case of the tortoise. In this animal the ramus visceralis does not spring from the ventral branch of the spinal nerve as in Mammalia, but arises directly from the ganglion on the posterior root." I extract the following from the section in Gaskell's second paper (p. 162), containing a definition of a complete segmental nerve: "Turning our attention now to the arrangement of the fibres composing a complete segmental spinal nerve, the results arrived at in my previous paper show that we must look upon both afferent and efferent roots as ganglionated, for the whole argument in my former paper as to the meaning of the sympathetic system was to prove *that the sympathetic ganglia are the ganglia belonging mainly to the fine medullated fibres of the anterior roots*, so that we must look upon a spinal nerve as possessing efferent or motor ganglia as well as afferent or sensory ganglia. These efferent ganglia have, according to the observations of Onodi, *travelled away from the original ganglionic mass situated on the roots of the spinal nerve*, so that we may term these motor ganglia 'vagrant' in contradistinction to the 'stationary' sensory ganglia on the posterior root; it follows then that a spinal nerve must be defined as formed by (1) A posterior root composed of afferent fibres, both somatic and splanchnic, the ganglion of which root is *stationary in position and is always situated near the entrance of the fibres into the central nervous system. . . .*" (Italics mine.) On p. 174 Gaskell states his belief that the facial nerve of mammals "has lost its primitive stationary ganglion and the afferent fibres in connection with that ganglion; I would therefore look upon the existing sensory distribution of the nerve [cp. particularly p. 173] as belonging to the same system as that of the Vth: *i. e.*, as already mentioned, a system of sensory nerves which has taken the place of the lost sensory elements of the primitive group of segmental nerves." I shall give, further on, reasons for doubting Gaskell's latter statements.

In 1890 an important work was published by Chevrel (1887-90, 41) on the sympathetic nervous system of Fishes. This author states that in the bony fishes the first sympathetic ganglion is *always associated with the "trigeminus" and lies under the Gasserian ganglion*. The second sympathetic ganglion is described as follows (p. 179):— "*Le 2<sup>e</sup> ganglion céphalique est placé sous le facial ou en arrière de ce nerf qui lui envoie ses racines. Il émet un ou deux filets pour le facial et ses ramifications; il en émet toujours un autre pour le rameau antérieur du glossopharyngien.*" (Italics author's.) It seems from these quotations that the facial ganglion of the Cod may represent Chevrel's first and second ganglia fused. In the Physostomi Chevrel makes the remarkable and interesting statement that the visceral branches of the vagus are all connected with the first sympathetic ganglion, which in the case of these fishes is attached to the vagus and not to the trigeminus.

Shore, in 1889, applying Gaskell's methods to the fishes, arrives at some noteworthy results. He states that the vagus is mostly composed of the visceral elements of the anterior spinal nerves rather than a compound of several complete metameric nerves, as Gegenbaur maintained in his memorable *Hexanchus*\* paper. Shore discovered on the dorsal branch of the vagus a small ganglion which he homologises with a dorsal root or "somatic sensory" ganglion †. At the most, however, it can only represent a portion of this ganglion. The branchial (= post-branchial) ganglia are considered to represent the vertebral or vagrant ganglia of the sympathetic trunk, and the præ-branchial ganglia (first described by Shore) the præ-vertebral or collateral ganglia of the sympathetic system. The latter statement will be discussed later on, but I may mention now that Shore admits the fibres which join the præ-branchial ganglia should be non-medullate, which the præ-branchial fibres are not. Omitting the dorsal branch and its ganglion, the vagus, according to Shore, contains the sympathetic elements only of a spinal nerve, and not its somatic elements. He further states that the post-branchial nerve contains some splanchnic sensory fibres, and believes finally with Hubrecht that the lateralis lateral line nerve is equivalent to the lateral strands of the Nemertea—a conclusion which our knowledge of the lateralis nerve enables us absolutely to disprove.

Ayers (1892, 7), referring to the chorda tympani of Mammals, a subject which we shall see later on interests us in this connection, says (pp. 312-313):—"As is well known, the sensory fibres subserving the sense of taste in the anterior two-thirds of the tongue run through the chorda tympani, and the recent investigations of Sapolini make it fairly certain that the chorda tympani is a continuation of at least a portion of the fibres of the portio intermedia Wrisbergi, which pass through the ganglion geniculi to the chorda tympani."

Ewart (1893, 70), after referring to the small size of the cells in the ciliary ganglion (see, *re* size of cells in facial ganglion, below), says, in describing the palatinus facialis of Elasmobranchs, that it "dips downwards and breaks up into numerous branches, which end in the mucous membrane of the roof of the mouth. At the root of this trunk there are always numerous ganglion cells. Sometimes these cells are continuous with the cells at the root of the facial trunk; but in others they extend a short distance into the root of the palatine, and are completely, or all but completely, separated from the ganglion of the facial trunk. I have no hesitation in saying that the palatine nerve of the skate corresponds, as has been suggested by Gegenbaur and others, to the great superficial petrosal of the mammal, and that further enquiries are likely to show that the ganglion at the root or in the trunk of the palatine nerve corresponds to the spheno-palatine (Meekel's) ganglion of the mammal. Or, to put it another way, were a spheno-palatine ganglion developed in the skate, it would be derived from the cells (or some of

\* Cp. Minot (140, pp. 650-651). Whether formed of *complete* metameric nerves or not I do not propose to discuss, but that the vagus *is* a compound nerve is not a "bold hypothesis" but an anatomical *fact*, lack of embryological evidence notwithstanding.

† An omission in my *Chimara* paper (46) may be corrected here. On p. 671, line 15, for "*is in connection*," read "*is also in connection*."

them) lying in the root of the palatine trunk." In my *Chimera* paper I was inclined to doubt the separate existence of the palatine cells described by Ewart, and considered them part of the geniculate ganglion—in which is seen the evil of basing general conclusions on a special study. It is now obvious to me that these cells form a perfectly distinct pre-branchial ganglion, comparable to the facial ganglion of the Codfish. We have seen that Bonsdorff compared the latter to the otic ganglion, and Ewart now compares it to the sphenopalatine ganglion. Both conclusions are erroneous, although both come somewhat near the truth. There is less objection to the sphenopalatine than to the otic ganglion, since the former is apparently more distinctively connected with the facial nerve than the latter. Both ganglia are essentially vagrant and largely motor, and hence cannot correspond either to the facial ganglion of the Cod or Ewart's palatine cells in Elasmobranchs. But Dixon's work (61) conclusively settles the matter. He shows that both ganglia are developed in connection with branches of the trigeminal nerve, and only become secondarily connected late in development with the facial. They cannot therefore correspond to a ganglion belonging essentially to the facialis. Before leaving Ewart's work I should like to quote a passage on p. 3 which has some bearings on the present issue. He says:—"In the skate there is but a single ganglionic swelling on the root of the glossopharyngeal, but this swelling contains two kinds of cells. The dorsal part from which the dorsal branch springs consists of large cells, *while the deeper part, from which the fibres of the pharyngeal branch proceed, consists of small cells.*" (Italics mine.)

The important work published by Strong (1895, 204) helps us very considerably in clearing up the morphology of the facial ganglion of the Cod. In all Fishes and Amphibians there is an important system of fibres entering into the composition of the VIIth, IXth, and Xth cranial nerves, to which Osborn (147) devoted considerable attention, and which was called by him the *fasciculus communis* system. These fibres were carefully investigated and grouped by Strong, who showed (1) that they had a distinctive origin in the brain; (2) *that they formed the palatine or visceral and pre-branchial (=chorda tympani in case of facial) divisions of the branchial nerves*; and (3) that they were ganglionated. It hence follows (1) that the pre-branchial ganglia described by Shore and Ewart are simply the ganglia on the fasciculus communis fibres; and (2) *that the pre-branchial fibres have a different internal origin in the brain than the post-branchial fibres.* As to the nature of the fasciculus communis tract, Strong says (p. 182) that it is "composed *exclusively, or almost exclusively, of visceral (splanchnic) fibres innervating the alimentary canal and its appendages*" (italics mine), and considers that it is "mainly sensory" in function. Other important conclusions arrived at by Strong, after careful investigation and consideration of the literature, are (1) *that the fasciculus communis corresponds with the mammalian fasciculus solitarius in every detail*; (2) that "as the fasciculus solitarius is continued cephalad into the portio intermedia, it is evident that the *portio intermedia* is represented in the tadpole by the fasciculus communis root of the VIIth, the *ganglion geniculi* by the ganglion of this root, fused in the tadpole with the ganglion Gasseri, but separate in *Amblystoma*, and the *chorda tympani* by the portion of the fasciculus

communis which, on emerging from its ganglion, unites with hyomandibularis VII., separates as the R. mandibularis internus\*, and innervates portions of the floor of the pharynx, especially the part in the tadpole near the site of the future tongue" (p. 186); and (3) that the R. palatinus facialis corresponds to the great superficial petrosal †, *the latter being a visceral sensory and not a visceral motor nerve* (cp. Turner, Journ. Anat. & Phys. vol. xxiii. p. 523, 1889).

Kingsbury (1895, 113, and 1897, 114) states that the fasciculus communis system arises from the dorsal columns of the medulla and that it is largely sensory in function, whilst Allis (1897, 6) must be held to have completely established that the palatine and præ-branchial fibres of the branchial nerves are composed of visceral sensory fibres and the post-branchial nerves of visceral motor fibres. This is also borne out by his dissections and descriptions of the facial, glossopharyngeal, and vagus nerves, where the fasciculus communis fibres were traced on to the mucous membrane ‡ and the post-branchial fibres into the branchial muscles. On p. 611, after a lengthy discussion of the fasciculus communis system, he says:—"The fibres of the fasciculus communis tract thus seem destined to form in part or in whole the præ-trematic and pharyngeal branches of the nerves with which they are associated, and it is always in the regions which, whether on the outside or the inside of the body, are, from their relation to these nerves, presumably innervated by them, that terminal buds are found. *The fibres of the tract that join and form part of the facialis enter into, or form entirely, the inferior and superior branches of the palatinus facialis, and those two branches are respectively the pretrematic and pharyngeal branches of the nervus.*" (Italics mine.) On p. 612, after stating that he considers it probable *the terminal buds arise in connection with the pretrematic ganglia and ectodermal thickenings*, he concludes, "in short, the nerve fibres arising from the fasciculus communis tract seem destined in large part, if not in whole, to the supply of terminal buds, as Strong has suggested might be the case. The fibres so arising may issue from the brain as a separate and distinct root, on which a separate and distinct ganglion is found; they may issue in part as components of certain nerves with the roots of those nerves, and in part as a separate root which becomes immediately more or less fused, it and its ganglion, with other roots and ganglia; or they may apparently, issue entirely as components of certain nerves. To the first category belongs, apparently *Protopterus*; to the second, *Amia*, *Rana*, and many other fishes and amphibia; to the third, birds, judging from Brandis' descriptions, *for he finds the fibres of the funiculus solitarius issuing from the facialis and glossopharyngeus, and possibly also with the vagus, and the funiculus solitarius of higher vertebrates corresponds, according to Strong, in every detail with the fasciculus communis of fishes and amphibia.*" (Italics mine.) Two points I must emphasize in connection with Allis's conclusions. First, he

\* I have already shown (46, pp. 658 & 673-4) that this is a misnomer. See also later, p. 200.

† Cp. 46, p. 660. See also later, p. 144.

‡ In his general summary he says (p. 747):—"The ramus pharyngeus and ramus prætrematicus traverse regions *where terminal buds are found.*" (Italics mine.)

appears to consider that the fasciculus communis system is in part somatic as well as splanchnic, which is inadmissible in the present state of our knowledge\* (but see p. 175); second, as Kingsbury (1897, 114) has pointed out (p. 29), the system is not entirely confined to the innervation of terminal buds. With regard to the first objection, it is of course difficult, if not impossible, in the region of the visceral clefts, to determine where the somatic region ends and the splanchnic begins. As Allis apparently considers that the terminal buds of the mouth were originally on the surface (and therefore somatic sensory), and have since wandered on to the gill arches and visceral surfaces, he must hold the visceral character of this portion of the fasciculus communis system to have been secondarily acquired.

Max Fürbringer (1897, 79) †, in commenting on the connections between the occipital nerves and the true cranial nerves, says (p. 568):—"Die Anastomosen mit dem *Sympathicus* dagegen repräsentiren zu einem grossen Theile wirkliche Wurzeln desselben (*Rr. viscerales*) und sind insofern von Interesse, als sie den Beweis für die immer noch von Einzelnen bezweifelte Thatsache erbringen, dass sympathische Fasern und Ganglien auch den ventralen Spinalnervenzwurzeln entstammen." In a footnote Fürbringer draws attention to a statement by Van Wijhe of the existence of sympathetic ganglia on the ventral roots of the posterior cranial nerves of *Scyllium* embryos. Finally, Herrick (1897, 98) states that the fasciculus communis system innervates taste buds and other specialised sense organs (other than the lateral sense organs) and the visceral surfaces in general, and on p. 428 says that the palatinus facialis consists of "fasciculus communis fibres from the geniculate ganglion distributed exclusively to the taste buds of the mouth."

The above consideration of the literature makes the solution of the problem a somewhat easy matter, and we may at once draw up the following general conclusions:—

- (1) The facial ganglion of the Cod is precisely comparable in every respect to a præ-branchial or præ-trematic ganglion, since it is the ganglion of the palatine and chorda tympani nerves which consist of fibres belonging to the fasciculus communis system.
- (2) It is hence physiologically and morphologically comparable to a sympathetic ganglion, since the fasciculus communis fibres belong essentially to the sympathetic system and innervate the visceral surfaces.
- (3) The ganglion has been well known to anatomists for a long time, and was considered by most of the older zoologists to be the most anterior sympathetic ganglion, and to exist only in the osseous fishes. It was rediscovered in Elasmobranchs by Shore and Ewart, and further described by Allis and Strong (Amphibia); but these authors failed to homologise it with the ganglion in the osseous fishes, and refer

\* I am aware of certain statements of Ramsay, Wright, Kingsbury, and Herrick to the contrary, but think the bulk of the evidence goes to show that the fasciculus communis fibres belong to the visceral system. In any case, however, my argument is unaffected, since the fasciculus communis fibres in the palatine and præ-branchial nerves are admittedly visceral sensory.

† I am indebted to the generosity of the author for a copy of this fine work.

to it variously as the præ-branchial, præ-trematic, palatine, or fasciculus communis ganglion (in part). Some of the older anatomists regarded it as belonging to the trigemino-facial complex, and others described more than one ganglion in this region in Teleosts.

- (4) We have seen that the facial ganglion is a ganglion placed on fibres that undoubtedly belong to the seventh or facial cranial nerve. It seems therefore to belong to the trigemino-facial complex, and cannot, in face of this fact, be considered a purely sympathetic ganglion. But we have further seen that it has many sympathetic characters, for in the first place it is connected with the fibres of the fasciculus communis system which we know to be essentially sympathetic in character; in the second, its cells are small and correspond to the cells found in the ciliary and true sympathetic ganglia; and in the third, it gives origin to the cephalic sympathetic trunk. It cannot, by the very nature of its structure and connections, correspond to a pre-vertebral ganglion, as Shore has suggested (and, indeed, Shore himself advances a very good reason against this), nor can it represent a typical vagrant ganglion, since these are connected with visceral *motor* fibres. The only alternative left is that it represents the visceral portion of a dorsal root ganglion, since the latter is partly in connection with visceral sensory fibres. And this I believe to be the case. How, then, is its isolated position to be explained? We know from Gaskell's classic researches on the sympathetic nervous system, for which every vertebrate morphologist is grateful to him, that the splanchnic ganglia on the main trunk of the sympathetic system, or "vagrant" ganglia as he calls them, are in reality ganglia belonging to the roots of the metameric nerves which have wandered from their original position. May not the facial ganglion of the Cod be in an intermediate condition? Here we have a ganglion of which the structural relations are such that it defies classification—it can neither be classified as a cranial nerve ganglion nor as a typical sympathetic ganglion, unless indeed we disassociate the fasciculus communis system from the cranial nerves altogether and add it to the sympathetic. In the Elasmobranch fishes, which we know from palæontology represent a more primitive condition than the Teleosts, the pre-spiracular ganglion (=facial of Cod) is still in very close association with the main facial ganglion. In the specialised Teleosts, on the other hand, the ganglion is found to be completely separate from the trigemino-facial complex. We are therefore forced to the conclusion that the facial ganglion of Teleosts is in the act of doing what we know the visceral motor ganglion to have done, *i. e.* is migrating from its original position, and will perhaps become in the course of time a typical sympathetic ganglion. In short the facial ganglion of the Cod is an exemplification of the principle of evolution, and shows us a stationary ganglion becoming converted into a vagrant or true sympathetic ganglion.
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We may hence classify a typical branchial nerve as follows:—

Component.	Name.	Central Origin.	Ganglion.	Distribution.
A. Somatic sensory.	Dorsal branch.	Spinal Vth tract.	Stationary or dorsal root ganglion (in part).	General cutaneous.
B. Visceral sensory.	Palatine and præ-branchial (latter = chorda tympani in case of facialis).	Fasciculus communis.	Remainder of dorsal root or stationary ganglion (= facial ganglion in case of VIIth.)	Terminal buds and visceral surfaces of pharynx.
C. Visceral motor.	Post-branchial.	Motor nucleus.	Vagrant (corresponds to ganglion on sympathetic trunk).	Muscles of its visceral arch.

I have already here and there referred to the facial nerve of man and mammals, the morphology of which may be treated of here. In my *Chimæra* paper I pointed out (46, p. 660) that the general anatomy of the facial nerve in man was in close agreement with the same nerve in the lower vertebrates. A more careful enquiry into the facts confirms this somewhat remarkable conclusion even in many of the details.

The facial nerve of man and mammals may be divided into two parts, which may be held to correspond to the same parts in the branchial facial nerve of fishes. These parts are (1) a pre-branchial part, largely or in part visceral sensory, = the nervus intermedius or pars or portio intermedia of Wrisberg, comprising the geniculate ganglion, great superficial petrosal (palatine), and chorda tympani (præ-branchial); and (2) a post-branchial part, comprising the main trunk of the facial, and being at least partly a visceral motor nerve\*. The points of agreement between the facial nerve of the fish and mammal are as follows:—

- (1) In central origin. It is probable that the fibres of the nervus intermedius arise from the funiculus solitarius, which is a centre of visceral sensory fibres, and which, as Strong has shown, corresponds precisely to the origin of the fasciculus communis of fishes and amphibia.
- (2) In the nature of the fibres. The fibres of the nervus intermedius are "very small," and hence correspond to the fasciculus communis fibres. Further, they are mainly visceral sensory in function, and are certainly continued in part into the chorda tympani, and perhaps also into the great superficial petrosal. The visceral motor fibres of the facial trunk are represented at least by the fibres supplying the stapedius muscle and those muscles of the "hyoid" developed in connection with the second visceral arch.
- (3) The geniculate ganglion is a stationary ganglion mainly in connection with visceral sensory fibres of the nervus intermedius. It hence corresponds to the facial ganglion of the Cod and to the pre-spiracular or palatine ganglion of Elasmobranch fishes.

\* See Wiedersheim (1897, 221), where the relations of these nerves are well shown (p. 183).

Now to endeavour to show that the facial nerves of fishes and mammals resemble each other in every minute detail would be to prove far too much. Differences are to be expected, and they certainly exist. The most striking difference is in the existence of a large somatic motor component in the mammalian facial. Assuming that the facial muscles of mammals cannot be derived from visceral arch muscles, upon which I am not competent to offer an opinion, we must regard this component as a special development and characteristic of the higher vertebrates. The difficulty *re* the motor character of the great superficial petrosal has already been alluded to, and a still further difficulty with regard to this nerve lies in Lenhossék's contention that its fibres are not connected with the cells of the geniculate ganglion. The chorda tympani too, and with it necessarily the nervus intermedius, is supposed to be partly motor. The absence of a visceral motor ganglion corresponding to the post-branchial ganglion of the fish is noteworthy, but it is perhaps represented by the degenerate ganglion described by Gaskell. This is indeed what we should expect, in view of the reduced condition of the hyoid arch and its muscles.

We thus see that even if the facial nerve of mammals does not correspond detail for detail with the same nerve in lower vertebrates, which is indeed not to be expected or desired, there is yet a sufficient general resemblance between the two to show that they are genetically related. The mammalian facial, in short, bears in its present-day structure undoubted evidence of its descent from the branchial facial nerve of a fish.

#### K. MORPHOLOGY OF JACOBSON'S ANASTOMOSIS.

The morphology of Jacobson's anastomosis, of which I have a new explanation to offer, may be treated of here in connection with the trigemino-facial ganglionic complex, with which I have described it. This anastomosis is essentially a connection between the facial and glossopharyngeal nerves, and, as I shall show, is perfectly homologous in the highest as well as in the lowest vertebrates, and is further a branch of the glossopharyngeus which accompanies a branch of the facial.

Jacobson's anastomosis was first identified in the lower vertebrates by Stannius\* in 1842 (198). He found it in "*Gadus callarias*" (= *G. morrhua*) and described it under the name of the "*R. anterior s. gustatorius*." The correct explanation of the nerve, that it is in the first place a branch of the XIth and not of the VIIth nerve, and in the second the palatine or visceral branch of the IXth, may be deduced even from Stannius's description and figures. Bonsdorff (1846, 30) confuses Jacobson's anastomosis with the sympathetic, but Jackson and Clarke (1876, 106) correctly consider it to be the pharyngeal division of the glossopharyngeus. Van Wijhe (1882, 222) describes it in *Acipenser* (p. 237) in almost the same condition as it is in the Cod and *Amia*, *i. e.* as connecting the glossopharyngeus with the palatine division of the facial. An important and interesting difference, however, is that it passes further forwards still and becomes

\* In his later work (1849, 199) he describes the palatinus facialis as being occasionally reinforced by the palatinus glossopharyngei.

connected with the "palatine" division of the trigeminus. Goronowitsch (1888, 89) largely confirms Van Wijhe. He mentions a lateral line anastomosis between the vagal and facial groups, as in *Protopterus*, and also a true Jacobson's anastomosis between the palatine divisions of the VIIth and IXth, as in *Amia* and *Gadus*.

Pollard (1892, 160) correctly homologises Jacobson's anastomosis in a table printed on p. 398, and shows in Taf. xxvii., fig. 7, a somewhat similar condition to that described in *Amia* by Allis. The anastomosis is, however, continued forwards and unites also with the trigeminus. There is no description or mention of the nerve in the text. The anastomosis therefore in *Polypterus* agrees with the condition found in *Acipenser* by Van Wijhe. In the fine work by Pinkus (1894, 157) on *Protopterus annectens* a lateral line anastomosis is described (outside the auditory capsule) connecting the root and ganglion of the lateralis lateral line nerve with the common root of the superficial ophthalmic and buccal lateral line nerves (cp. Goronowitsch). Jacobson's anastomosis is in much the same condition as in *Gadus* and *Amia*. The palatine branch of the IXth as it passes forwards sends an anastomosing branch to the visceral or palatine branch of the facial. There is no connection with the trigeminus.

The anastomosis in *Rana* between the VIIth and the IXth is apparently of a different nature, though it also properly belongs to the IXth. Strong (1895, 204) says (p. 146):—"The other inner division of mixed fibres is the *R. communicans ad facialem* to the *R. hyomandibularis*. Its final distribution is described in connection with the latter, and it has there been found to be a general cutaneous nerve." (Italics mine.) The fact that the nerve in *Rana* consists of somatic sensory fibres makes it impossible to homologise it with a true Jacobson's anastomosis. Strong, however, seems to have had an inkling of the truth, for he remarks (p. 207): "Furthermore, among the Fishes, the palatine nerve would appear to be formed by a union of post- and pre-auditory nerves (Goronowitsch, Pollard). The development of the auditory organ has probably caused a separation of nerves formerly more closely connected."

In man the tympanic branch of the glossopharyngeal, or nerve of Jacobson, undoubtedly corresponds to the nerve called after it in the lower vertebrates. Its origin from the petrosal ganglion, which seems to me to be morphologically comparable to the "facial" or geniculate ganglion—that is, in connection with splanchnic sensory fibres—at once suggests this. Unfortunately the composition of the tympanic nerve is, I believe, not known in man. Its connection with the facial is partly by means of a small branch which passes into the geniculate ganglion. This branch at least must be splanchnic sensory, and is thus of the same constitution as Jacobson's anastomosis of the fish. Its continuation, however, the small superficial petrosal nerve, is usually regarded as a splanchnic motor nerve. Jacobson's anastomosis in man, therefore, seems to resemble the same nerve of the fish in every essential detail. The exception, that it does not *directly* anastomose with the great superficial petrosal (=the palatinus facialis), is of course of no morphological importance\*. Dixon (1896, 61) has conclusively proved, if such proof were wanting, that the nerve of Jacobson belongs to the glossopharyngeal.

\* Apparently it does so in the embryo. Cp. Dixon, p. 63.<sup>9</sup>

He says (p. 58): "The nerve of Jacobson is present in this embryo, as an outgrowth from the petrous ganglion of the glossopharyngeal, but is very short. This nerve passes vertically upwards, and ends a considerable distance below the level of the inferior maxillary nerve." Dixon also states (p. 66) that the nerve of Jacobson grows out from the petrous ganglion in the rat.

Jacobson's anastomosis is described in *Amia* by Allis as follows (6, pp. 685-686):—"In the palatine canal the ramus pharyngeus lies on the median side of the ramus palatinus facialis, and at the point where that nerve separates into its anterior and posterior branches the pharyngeus, in one dissection, separated also into two portions, *one of which accompanied each of the two branches of the palatinus* [facialis]. In other dissections this separation was not evident, the pharyngeus glossopharyngei *accompanying the anterior branch of the facialis* and issuing on the ventral surface of the vomer to be distributed to dermal tissues there." (Italics mine.) This description hardly tallies with plate xxxviii., where a complete anastomosis with the palatinus facialis is figured. Allis does not homologise it with Jacobson's anastomosis, but it is obvious that this is what it is, seeing that it is formed by the visceral branch of the IXth accompanying the corresponding division of the facial.

Ruge (1897, 169), after referring to anastomoses described by Stannius (*Aeipenser*, *Perca*, *Tinea*), Johannes Müller (*Polypterus*, *Lepidosteus*), and Fischer (*Menobranchus*, *Siren*), concludes with reference to the mammalian tympanic nerve:—"Es besteht aber ausserdem die Möglichkeit, dass in der Fortsetzung des N. tympanicus das Homologon des Ramus pharyngeus (IX.) enthalten sei. Ist dies der Fall, so entspricht der N. petrosus superficialis minor sowohl dem N. palatinus als auch einem der Rr. branchiales n. vagi der Fische. Die Anastomose, welche zwischen Facialis und Gl.-phar. ganz ausserhalb des Schädels besteht, darf mit der erwähnten nicht verwechselt werden. Sie ist sehr wahrscheinlich durch die Verschmelzung der motorischen Endgebiete beider Nerven entstanden" (p. 213). Finally, fig. 148, p. 182, in the new English edition of Wiedersheim's 'Comparative Anatomy' (1897, 221), for the accuracy of which I am partly responsible, should be corrected in two respects: (1) the dotted pharyngeal branch should be deleted, and so also should the nerve labelled *Jak.* (Jacobson's anastomosis). The latter, we have seen, is represented by the palatinus glossopharyngei.

It is hence clear that three nerves have been described connecting the vagal and facial groups of cranial nerves, each of which has a distinctive composition. These are:—

(1) *A somatic sensory anastomosis.* Described by Strong in *Amphibia*. This is the only instance known, I believe, of an anastomosis of this nature. It is possible that Strong may have been mistaken as to its character, especially as it, too, is distinctively a branch of the glossopharyngeal; but however that may be it cannot be considered comparable to a true Jacobson's anastomosis.

(2) *A lateral line anastomosis.* This more usually connects the facial with the vagus, but where a portion of the lateralis lateral line nerve accompanies the glossopharyngeus, it may connect that nerve with the facial. The character of this nerve cannot be mistaken, since it usually exists side by side with Jacobson's anastomosis.

(3) *A visceral sensory or true Jacobson's anastomosis.* That the nerve which usually

connects the VIIth and IXth nerves is homologous throughout the different classes of vertebrates there can be little doubt. It is further certain that this nerve is a branch of the glossopharyngeal, is primarily quite distinct from the facial, and in the adult only accompanies a branch of the latter nerve. It is the main body of the first, visceral, palatine, or pharyngeal branch of the IXth, and as such, in the lower vertebrates at any rate, belongs to the fasciculus communis system, and consists very largely, if not entirely, of visceral sensory fibres. It passes forwards, and, as a general rule, becomes related to the palatinus facialis, and either accompanies the main trunk of the latter or some of its branches, or it may completely fuse with it. It is hence usually not an anastomosis at all, in the sense that an anastomosis should be a perfect mingling of two nerves. Its forward continuation to the trigeminus, described by Van Wijhe and Pollard, I am inclined to view with some doubt, and await further details on the point. The difficulty in the case of the trigeminus is that the visceral sensory branch is typically unrepresented in this nerve (cp. Goronowitsch, 1888, 89), and the anastomosis could not, therefore, as Van Wijhe describes, be connected with its "palatine" branch. The explanation of an anastomosis at all is to be sought for in the fact that both nerves concerned have a similar peripheral distribution, and may hence fitly accompany one another. The interpolation of the auditory organ has doubtless assisted in further separating the nerves, and thus converting a simple fact into a phenomenon.

#### L. THE METAMERISM OF THE LATERAL LINE SYSTEM.

A description of the nerves supplying the lateral sense organs would naturally follow the description and discussion of the trigemino-facial ganglion and Jacobson's anastomosis, but it is obvious, however, that before this can be attempted it is expedient to enquire into the morphological value of these nerves, to determine to which of the cranial nerves, if any, they belong, and in fact to consider the whole question of the metamerism of the lateral sense organs. The structure and development of the lateral sense organs show conclusively that they were originally confined to the head, and have only secondarily been continued on to the trunk. How did they arise? Are they segmental at all, and if so is the segmentation primitive or acquired? It is perhaps unnecessary for me to point out that these questions can only be solved satisfactorily by determining the morphology of the nerves supplying them. It is indeed true that the position of the organs themselves and the relation they have to the dermal bones of the skull may in some way help us, but their position and structural relations are too variable, and their significance too equivocal, to have anything more than confirmatory importance attached to them. We thus have to review the facts of development and adult structure and to ascertain in what direction modern research is leading us.

Eisig (1887, 65), whose work will also be discussed elsewhere, naturally considers the lateral line organs metameric, and in fact goes so far as to consider the probability of their being once connected with spinal nerves. This he endeavours to establish by referring to the work of Julin and Ransom and Thompson on the Lamprey. These authors, however, were dealing with the so-called lateralis nerve of *Petromyzon*, and as I shall shew later on that this is *not a lateral line nerve at all*, Eisig's contentions must

consequently fall to the ground. Van Wijhe (1882, 222) was perhaps the first to draw attention to the undoubted metamerism of the lateral line organs *on the body* in some forms, and points out that each lateral line scale in *Amia* corresponds to a segment of the body. He is inclined to think that some such relation may be found to exist between the lateral line ossicles and the segments of the head. Beard (1884, 17), as the title of his paper implies, advocates the metamerism of the lateral sense organs, whilst Ramsay Wright (1884, 227) finds that in *Amiurus* the sense organs *of the body* are metameric, and correspond exactly to the number of spinal nerves.

The papers of Froriep and Beard (1885, 19) are of considerable importance, since it is upon the evidence of these authors and others following them that the plea for the metamerism of the lateral sense organs is very largely based. It must be pointed out at the outset that the "branchial" or "epibranchial" sense organs are only doubtfully metameric, and several authors have commented on Beard's significant alteration of the name from "segmental" to "branchial." The whole question depends on the metameric value of the visceral clefts, but at any rate the bulk of the evidence goes to show, and for the purposes of the present discussion we may admit, that if the branchial sense organs are not now metameric there is strong reason for believing that they were so in past time. The innervation of these very interesting sense-organs is, according to Beard, from seven dorsal branches or supra-branchial nerves. These are:—(1) Ophthalmicus profundus; (2) superficial ophthalmic of the Vth; (3) superficial ophthalmic "of the VIIth"; (4) the buccal division "of the VIIth"; (5) the dorsal or supra-temporal branch of the IXth; (6) the dorsal or supra-temporal branch of the first division of the Xth; (7) the lateralis nerve of the remainder of the Xth. There can be no doubt that, should this evidence prove trustworthy, we have very strong reasons for regarding the lateral sense organs as metameric structures, since the latter are supposed to be formed by the growth and extension of the branchial sense organs.

Allis (1889, 4), without definitely committing himself to an opinion, is undoubtedly favourable to the metamerism of the lateral organs, even if we only call to mind his statement that they are innervated by the dorsal branches of two cranial nerves—the facial and the vagus. On pp. 517–518 he destroys one of Beard's supra-branchial nerves, and points out that the supra-branchial nerve from the first vagus ganglion is in *Amia* "the first dorsal or supra-temporal branch of the lateral nerve," and hence has no metameric significance. On p. 523, referring to Van Wijhe's views above, he remarks:—"The arrangement of the sense organs and nerves of the lateral system, the regular occurrence of primary tubes between consecutive dermal bones of the head, as well as between consecutive scales of the lateral line, and the singular correspondence between the infra-orbital and opercular canals is further evidence in this same direction" [*i. e.* of metamerism]. I am not inclined, however, to attach much weight to these considerations. In the first place, there are too many exceptions to the regular occurrence of the primary pores between consecutive dermal bones for this consideration to have much value\*, and in the second place, although in the case of the Cod there is a

\* Allis says (p. 537):—"Although some of the primary tubes issue through the bone, one always issues between every two consecutive bones along each line."

certain correspondence between the infra-orbital and hyomandibular lateral canals, it does not occur, as far as I am aware, in any other fish. And surely, in any case, the correspondence has absolutely no significance. The hyomandibular canal is situated on a region *morphologically posterior to the infra-orbital canal*, and cannot belong to the same segments or segment of the head. If the correspondence had been between the supra- and infra-orbital canals (and these do not correspond either in *Amia*, *Gadus*, or any other fish that I know of), it might have had some significance, although, I am inclined to think, very little.

An interesting addition to the developmental literature was made in 1891 by Wilson (225), who was the first, I believe, to discover that the lateral line organs and auditory organ *may arise from a common sensory anlage*. This seems to be opposed to the metamerie view, but Wilson himself believes it to be a physiological adaptation and to have no phylogenetic significance. He favours Beard's views with regard to the head, but does not think the lateral organs of the body were primitively segmental. Cunningham (1890, 55) draws attention to the fact (p. 75) that in the Sole, "corresponding to each scale of the lateral line, there is a pore in the skin which leads into the dermal tube of the lateral line." On p. 81, however, he says:—"There is not a sense organ to every scale of the lateral line; in the middle of the body there is a sense organ on every third scale: that is to say, there are two scales bearing no sense organs between two scales which bear them. The position of the sense organ in relation to the scale on which it is situated is always the same." Fig. 6, pl. xiv., shows this somewhat anomalous condition. Without impugning the accuracy of Cunningham's statement, I may point out that it is a remarkable exception to the almost universal law that there should always be at least one sense organ between the openings of two dermal tubules\*.

Mitrophanow (1890, 141) confirms Wilson's statement *re* the common anlage of the lateral line and auditory systems, and in 1892 (142) disagrees with Wilson and states his belief that the lateral organs are not metamerie. In a full paper published in 1893 (143) Mitrophanow repeats his former statements, but adds that the common anlage gives rise to the auditory organ, the lateral line organs, and *Beard's branchial sense organs*. He considers this sufficient ground for maintaining that the lateral organs were not primitively metamerie, and says this conclusion is based on the study of all the Ichthyopsid types he has investigated. Houssay (1891, 103), in an interesting review of Mitrophanow's second work above, is inclined to accept Eisig's invertebrate origin of the lateral organs, and combats Mitrophanow's statement that they are not metamerie.

Ayers (1892, 7) endeavours to show that the auditory organ is not supplied by a discrete cranial nerve but by the branches of two cranial nerves, *i. e.* the facial and the glossopharyngeal (=the vagus: he considers the lateralis lateral line nerve to be a branch of the IXth). He thus favours the metamerie view of the lateral organs. On p. 314 he says:—"As Froiep has shown, the ectodermal thickenings which Beard described as giving rise to the lateral line organs have in fact another fate. The genuine lateral line organs escaped Beard's observation, and in consequence Beard's conclusions

\* Sense organs may exist without dermal tubules (cp. Ewart & Mitchell, p. 100), but not *vice versa*.

as to the homology of the vertebrate auditory organ are incorrect"\* . Although Ayers' views as to the innervation of the auditory organ cannot any longer be maintained, it is possible that his latter statement is to some extent sufficiently near the truth to require a reopening of the whole question of the "branchial" or "epibranchial" sense organs.

In his *Lacmargus* paper (1892, 68), Ewart supports the view of the innervation of the lateral sense organs taken by Friant and Allis. He does not consider that Beard's scheme applies to the adult Elasmobranch, nor does he consider the lateral canal as composed of ontogenetic metameric sense organs (p. 79). In his paper with Mitchell we find (69, p. 100):—"But while the sense organs and tubules *have a metameric arrangement in the trunk, there is no relation between the sense organs and segments in the head region*; and, as already pointed out, some portions of the cranial canals, though possessing numerous sense organs, have no tubules connecting them with the exterior. In all the cranial canals, both dorsal and ventral, there are far more sense organs than segments; *e. g.* in the supra-orbital canal there are nearly ninety sense organs, and in the infra-orbital there are over ninety." Pollard (1892, 161), referring to the relation between the lateral canals and the dermal bones, in which connection we should remember Allis's statements above, says (p. 527):—"In *Clarias* it is by no means a rule that pores should open at sutures"; but on p. 539 we find the absolutely contradictory statement that "as the dermal bones are much reduced in *Auchenaspis* the close relationship of pores to sutures, which exists in *Clarias*, is not seen." Willey (1894, 223) makes a somewhat remarkable statement. He says (pp. 44-45): "It seems certain that at first the sense organs of the lateral line must have been innervated by spinal nerves. This follows both from *à priori* considerations and also from the condition in *Amphioxus*, where the ectoderm of the metapleural folds is innervated by the *Rami cutanei ventrales* of the dorsal spinal nerves. Under these circumstances it is necessary to suppose with Eisig that the lateral line nerve (*Ramus lateralis rami*) arose as a *collector*." I am unacquainted with any evidence in support of this statement. Eisig's views on the subject I have already dealt with, but I may mention that his explanation of the lateralis nerve has never been accepted by vertebrate morphologists.

Bashford Dean (1895, 58) evidently considers the metamorphism of the lateral canal a secondary modification. He says (p. 51), after considering the probable phylogeny of the system:—"The sensory cells are no longer scattered evenly along the floor of the canal; they now occur in metameral masses supplied with a distinct nerve branch, located in the region immediately below the external tubules." Again on p. 52 he remarks:—"The original significance of the lateral line system as yet remains undetermined. As far as can be judged from its development, it appears intimately, if not genetically, related to the sense organs of the head and gill region of the ancestral fish: in response to special aquatic needs, it may thence have extended further and further backward along the median line of the trunk, *and in its later differentiation acquired its metameral characters*." Loey (1895, 130) agrees with other observers that the branchial sense organs of Beard and Frierie are *not* the lateral sense organs, but may perhaps correspond

\* When Ayers wrote this he must have forgotten what he had previously written on p. 213!

to the segmental sensory papillæ of Annelids. On p. 577 *et seq.* he confirms for *Squalus* the observations of Wilson on *Serranus* and Mitrophanow on *Acanthias* and other Elasmobranchs as to the common anlage of the lateral sense organs and auditory organ, and states:—"Mitrophanow departs from the usual point of view that the organs of the lateral line are metameric, and in that particular, I think, I should be inclined to follow him." Strong (1895, 204) is more emphatic on the point. He says (p. 197): "It is also evident that the lateral line system has no specially segmental character, and that it cannot properly be used in the manner in which it has been attempted to use it, as a general guide in determining the segmentation of the head."

Miss Julia Platt (1896, 158) argues from the opposite point of view\*. She states (pp. 502-503):—"Since Mitrophanow claims as the result of his study that the segmentation of the lateral-line system is entirely secondary, I shall be interested to discover when I again have my *Acanthias* material with me whether traces of primitive segmentation so evident in *Necturus* cannot also there be found, for it is difficult to believe that the great similarity which exists in the position and direction of the main lines of sense organs in *Necturus* and *Acanthias* should not be the result of a similar course of development." Miss Platt also describes four of the sense organs of the infra-orbital line as being partly innervated by the ophthalmicus profundus, and concludes (pp. 530-531):—"I do not, for this reason, include the trigeminus among the lateral line nerves, but should nevertheless hesitate to say that the 'trigeminus proper does not participate in the innervation of the lateral line system.'" With regard to the ultimate fate of Beard's branchial sense organs, Minot (1897, 140) says (pp. 706 & 709):—"We have further to emphasize those traces which have been discovered of long series of sense organs, of which the nose, eye, and ear are probably derivatives, in the ancestors of the vertebrates, although in all known vertebrates most of these series have become rudimentary or lost. The serial sense organs I designate under the comprehensive name of ganglionic sense organs. There are probably two, and only two, series along each side of the body: one series, the upper, corresponds to the lateral line of comparative anatomy, the other to the epibranchial line." After pointing out the differences between the two series, he concludes:—"The sense organ above the gill cleft [*i. e.* branchial or epibranchial sense organ], though differentiated, is a larval structure only, and disappears in the adult." Finally Wilson and Mattocks (1897, 226) confirm for *Salmo* the discovery already made by the former author in *Serranus* of a common anlage of the lateral and auditory sense organs, and state further that the portion in front of the auditory saucer gives rise by bifurcation to the supra- and infra-orbital canals, whilst the portion posterior to the saucer grows backwards and forms the lateral canal.

We thus see that the metamerism of the lateral line nerves and their associated sense organs has for a long time been a problem, the solution of which has been attended with considerable difficulties. The older anatomists considered the nerves to be branches of the trigeminus, facialis, and vagus, until it was shown by Friant in 1879 that the

\* But cp. pp. 492 and 501, which go to show that Beard's branchial sense organs do not belong to the lateral line system.

nerves usually considered to be branches of the trigeminus really belonged to the facial. To Friant, therefore, belongs the credit of being the first author to arrive (approximately) at the truth with regard to the innervation of the lateral sense organs. His work was confirmed by Marshall and Spencer in 1881 and by Allis in 1889, and it was thus established that the superficial ophthalmic and buccal lateral line nerves belonged to the facial, rather than to the trigeminal, nerve. The work of Beard and Froriep in 1885, important as it is, has added considerably to the confusion which exists on the subject. There can be no doubt that if the branchial or epibranchial sense organs ultimately develop into the lateral sense organs of the adult, then the latter must have been (primitively) segmental structures. But we have seen there is good evidence against the identity of the two series of sense organs, and even before this evidence transpired it is significant that the innervation of the adult lateral sense-organs could not be harmonised with the supposed embryonic conditions (cp. especially Allis and Ewart). And added to this the fact that the lateral organs and the auditory organ have been found to develop from a common sensory anlage, which discovery has been extended to several forms *and has been found to apply to Elasmobranchs as well as to specialised Teleosts*, we have an opposing view of the development of the lateral organs which has the advantage of being easily reconcilable with the facts of adult structure. This leads us to the latter view of the question.

In his 1889 paper, Allis, independently following Friant, and working on the lines laid down by Marshall and Spencer, described the lateral line nerves as branches of the facial, glossopharyngeal, and vagus nerves. In this he was largely followed by Ewart (1892) and Pinkus (1894), until it was considered completely established that the lateral nerves were undoubtedly branches of the facial and vagus, and perhaps also of the glossopharyngeus. In the meantime Mayser (1882), Pollard (1892), and Strong (1895) had been working out a totally different hypothesis, the tendency of which was in the first place to regard all the lateral line nerves as morphologically branches of one trunk, and in the second to associate that trunk with the auditory nerve and system. This view was developed by me in my *Chimæra* paper, in which I endeavoured to show that the lateral line system was an independent system of sense organs innervated by a distinctive and independent series of nerves of characteristic size of fibre, and further that the whole was the morphological equivalent of the auditory organ, with which it should therefore be associated. I further stated the belief that the branch of the glossopharyngeus innervating sense organs of the lateral line would be found on investigation to be a branch of one of the lateral line nerves, and finally, pending further investigation, provisionally associated the lateral line nerves with the facialis. These views have been entirely confirmed by recent investigations, such as those in 1897 by Kingsbury, Herrick, and Allis, so that the present position, from the point of view of the comparative anatomist, and setting aside for the moment purely developmental evidence, may be summarised as follows:—

(1) The lateral line system is an independent series of sense organs, differing histologically from any other cutaneous sensory system, such as the terminal buds described by Merkel and other authors, and not innervated by the same nerves.

(2) That this system is innervated by a series of lateral line nerves which are undoubtedly independent of *any* of the recognised cranial nerves, and are in fact morphologically branches of one trunk.

(3) That the lateral line branch of the glossopharyngeal belongs to the lateralis lateral line nerve.

(4) That the lateral sense-organs and nerves are precisely comparable to the auditory organ, with which they should be associated—the lateral and auditory nerves arising from a common centre in the brain which is further peculiar to this system of nerves. It is also possible that the lateral sense organs, together with the auditory organ, in most forms arise from a common sensory anlage from the skin.

We have seen that the developmental evidence in favour of the metamerism of the lateral line system is too conflicting to be made the basis of any discussion, but there is no room for doubt that the sense organs of the body canal are often metameric in the adult, as has been described above. It is hence necessary to enquire into the nature of this regular occurrence of the body sense organs. I have previously pointed out that the lateral sense organs primitively belong to the head, and have only secondarily extended on to the trunk. This can be proved both by the development and adult structure of the lateralis canal. Even in young adults of *Gadus* the body canal posterior to the shoulder girdle is still very imperfectly formed, and in fact is somewhat difficult to detect in sections. In all known cases of development the body canal grows from before backwards, and its most posterior part is the last to be formed of any of the sensory canals. When the sensory canals are quite perfect in the head and have fully reached their adult condition, the posterior section of the body canal is still nothing more than a mere rudiment or anlage. It is hence impossible to regard any condition of the body canal as representing a primitive condition, since it is itself only a secondary structure. The innervation of this canal, however, settles the point. The nerve which supplies it is in all fishes the lateralis lateral line nerve, which, as it is not a collector, and is absolutely independent of the metameric nerves, must be held to disprove the essential metamerism of the body canal, and indeed shows that such a condition of this canal is purely superficial.

Now it is obvious that the independent character of the lateral line system, which is such a characteristic feature of the post-embryonic condition of existing fishes and amphibians, may be either primitive or acquired. It may be, either that the lateral nerves were originally branches of the various cranial nerves, and that the present apparent relations with the latter are the vestiges of that connection, or that the lateral nerves were primitively independent and have already commenced to fuse with, and to form an essential part of, the true cranial nerves. It seems to me that the latter conclusion, although it was advocated by myself, is being hastily and injudiciously adopted, and that further embryological investigations will have to be concluded before we have sufficient data to arrive at an accurate appreciation of the subject. The question may be viewed from the three standpoints of Embryology, Comparative Anatomy, and Palæontology. With regard to the former, in spite of the numerous and bulky memoirs that have been written on the subject by such naturalists as Dohrn, Goette, Balfour,

Van Wijhe, and Beard, much has yet to be done. From an embryological standpoint, the first alternative above is still a *possible*, if not a probable, explanation of the facts, and unless the evidence from Embryology is to be rejected altogether, which is out of the question, it is necessary to wait until further investigation from this standpoint definitely upholds one view or the other. Whatever result is finally arrived at, it should be one in which both embryologists and anatomists concur, and it seems to me that this result will most probably be one that is adverse to the metamerism of the lateral organs.

Comparative anatomy helps us but little. It is true that in *Chimera*, which shows us the innervation of the lateral sense organs in its simplest known condition, all the lateral nerves, except the external mandibular, arise separately from the brain, and are not in any way connected with the true cranial nerves. It is also true that as we go higher in the vertebrate scale we get every possible gradation between this comparatively independent condition and the very complex one found in the highly specialised recent Teleosteans—where the mingling between the lateral and cranial nerves is at its maximum. It is now a question of whether it is permissible to argue from this that the primitive condition must have been that in which the nerves were concentrated and independent, and therefore not metameric, since the cartilaginous fishes are simpler than the Teleostean forms, and fossil Ichthyology tells us that they have departed less from the primitive type. Such a contention of course accepts as granted that the soft parts have advanced *pari passu* with the specialisation of the skeleton. It is evidence of perhaps little or doubtful value, but it may, I think, be used to confirm a view already resting on a more solid basis of fact.

From Palaeontology we learn still less, and it is most valuable when it is able to throw light on the ancestry of a type that we have other reasons to believe is primitive. It shows us also that the lateral line system is an extremely archaic structure, and further that as regards the geography of the sensory canals it has remained in a largely unmodified condition for untold ages. What bearing this has on the innervation of the system it would be hazardous to conjecture.

Briefly, the question at issue between embryologists and anatomists is whether the lateral line system is metameric or not. The most valuable evidence that has been advanced from the latter point of view is that in which the lateral nerves have been microscopically traced both to their central origin and peripheral distribution. Considering this evidence, and pending agreement among embryologists, I take up the provisional position (which, however, I believe to be a very strong one) that it is not. I shall therefore in the present communication describe the lateral nerves as purely independent structures having no connection, other than purely secondary, with the true cranial nerves.

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The following description of the innervation of the lateral canals of *Gadus* is based partly on dissections and partly on an examination of serial transverse sections of young adult *Gadus virens* (= "*G. carbonarius*").

M. INNERVATION OF THE SENSORY CANALS IN *GADUS*. (Plate 22.)(1) *Supra-orbital Canal.*

*Superficial Ophthalmic Trunk.*—This consists of two portions, which are (*a*) the superficial ophthalmic of the trigeminus, and (*b*) the superficial ophthalmic lateral line nerve. The latter arises from the posterior dorsal edge of the proximal portion of the lateral line ganglion, and at its origin lies between the ventral edge of the cerebellum and the anterior extremity of the auditory capsule. Owing to a certain amount of overlapping on the part of the facial and auditory nerves, the origin of the lateral ophthalmic nerve is somewhat difficult to determine, owing to the close apposition of its root to the anterior edge of the auditory ganglion. It would in fact be difficult to say whether some auditory fibres did not mingle with the lateral ophthalmic. There are a few ganglion cells at its base, but otherwise no cells whatever in the course of the nerve, and the few above belong, strictly speaking, to the lateral ganglion.

The lateral ophthalmic now passes horizontally forwards over the trigemino-facial ganglion and soon commences to pass upwards. As, however, it leaves the ganglion, it receives a conspicuous root containing a few ganglion cells from the anterior dorsal edge of the ganglion, and this is the root of the trigeminal ophthalmic, since it is from the direct continuation of this portion of the trunk that the general sensory fibres arise. The root of the trigeminal ophthalmic is at first very flat, and closely opposed to the ventral surface of the lateral ophthalmic root, but no mingling of the fibres could be detected either at this region or any other.

As the trunk passes gradually upwards towards the posterior portion of the infra-orbital canal, the trigeminal portion becomes narrower and is almost completely separated from the lateral portion by a small blood sinus or vessel. Further forwards, however, the two nerves become approximated by passing under this vessel. By this time the nerve has entered what appears to be a rudimentary eye muscle canal, and lies opposite the ventral edge of the alisphenoid over the posterior portion of the eye, and (in the young forms but not in the adult \*) somewhat close to the brain opposite the dorsal border of the optic thalami and the origin of the optic nerves. The twig to the fifth sense organ of the supra-orbital line is given off from the dorsal or lateral portion of the trunk at this region. It perforates the wall of the eye muscle canal, passes upwards and forwards to the outside of the alisphenoid, finally piercing the frontal to reach its distribution.

Continuing its course, the ophthalmic trunk passes obliquely upwards and assumes a position between the dorsal border of the eye and the supra-orbital canal. Soon after supplying the twig to sense organ 5, the lateral ophthalmic gives off a somewhat large branch (*S.O.*<sup>3</sup>) which, after coursing parallel with the main trunk for a short distance,

\* The relations are by no means the same. For example, a transverse section may pass through both the optic lobes and a portion of the eye in the young forms, whereas in the adult no such section could pass through *any* part of the brain and eye at the same time.

divides into three twigs whilst still lying near the brain in the eye muscle canal and opposite the edge of the inner ventral process of the frontal. The inner of the three twigs passes inwards and upwards, perforates the frontal, and lies between the frontal and the sensory canal. In this position it passes forwards for some little distance and innervates sense organ 4 of the supra-orbital line. The remaining two twigs doubtless innervate pit organs in this region.

Opposite the point where the twig to sense organ 4 perforates the frontal, the ophthalmic trunk divides into two conspicuous nerves, a larger dorsal lateral portion, and a small ventral trigeminal portion—as is shown by the nerves arising from them, the lateral-line twigs arising from the dorsal nerve and the general cutaneous fibres from the ventral nerve. As the trunk passes forwards the division becomes more marked, until two rounded nerves are distinctly differentiated. The lateral portion soon gives off a twig which passes upwards and enters the frontal slightly anterior to the supra-orbital commissure. It passes obliquely through the substance of the bone inwards and forwards, perforates it dorsally, lying between it and the supra-orbital canal, and finally innervates sense organ 3 of the supra-orbital line. Anterior to the region where this twig enters the frontal, the two divisions of the ophthalmic trunk begin to approximate and once more continue their course together. At this region too, a small blind sac is seen in the sections to open into the supra-orbital canal external and opposite to the supra-orbital commissure and partly opposite the fourth sense-organ. It contains no sense organs and no lateral line twigs could be traced to it, and seems to me to correspond precisely to a much larger but otherwise similar structure in the same position described by Hyrtl in *Lota*. It therefore possibly represents a degenerate or modified dermal tubule.

In the region of sense organ 3 the supra-orbital trunk shows a tendency to split up again, and can clearly be resolved into its two constituents with the higher power of the microscope. This tendency, however, is soon lost and the nerves become inseparable as before. It is here, moreover, that the ophthalmic trunk leaves what I take to be the eye muscle canal, and becomes for the first time perfectly round in transverse section. It immediately enters the frontal at the junction of the frontal and pre-frontal (=lateral ethmoid or parethmoid), and courses obliquely inwards and forwards in the spongy substance of the frontal. After leaving the latter bone it enters a large space bounded above and internally by the frontal and below by the pre-frontal. Anterior to this space the trunk begins to pass upwards and inwards towards the ligamentous portion of the supra-orbital canal, which it accompanies, and an examination of it with the high power at once reveals the distinctiveness of its lateral and trigeminal portions. These again separate, and the ventral portion or trigeminal ophthalmic gives off a large nerve, which could not be satisfactorily traced in the sections, but seemed to be a cutaneous sensory nerve\*. In front the two ophthalmics again more or less approximate.

Before leaving the space in the frontal mentioned above, the lateral ophthalmic gives off dorsally a twig (*S.O.*<sup>4</sup>) which passes inwards and forwards, curves upwards round the

\* The fibres of this nerve undoubtedly came from the trigeminal ophthalmic.

anterior edge of the frontal, between the latter and the ligamentous portion of the supra-orbital canal near the mid-dorsal line, to the inner side of the sensory canal, and was traced almost on to the skin and then lost. It most probably supplied the pit organs in that region.

Coincident with the ligamentous portion of the supra-orbital canal, the ophthalmic trunk separates into its two components, quite obvious with the low power, the lateral constituent being dorsal and the larger of the two. The latter soon afterwards gives off a twig which perforates the posterior edge of the nasal, lies between the latter bone and the supra-orbital canal, and finally passes obliquely inwards and forwards to supply sense organ 2.

The ophthalmic trunk has now completely split up, both components at first lying close together at the posterior extremity of the nasal, ventral to the latter bone and just below the supra-orbital canal. Opposite the second sense organ the two components commence to run alongside again, but do not mingle. Anteriorly the lateral, together with the greater portion of the trigeminal, ophthalmic pass inwards and upwards along the inner face of the nasal, and whilst there a trigeminal twig is given off (*S.O.*<sup>5</sup>) which, passing outwards and upwards along the outside face of the nasal, is distributed to the skin in that region.

Whilst the ophthalmic nerves are passing along the inner face of the nasal the relation between them is for the first time changed, the smaller trigeminal curling round the larger lateral ophthalmic and assuming the dorsal position. Opposite the anterior extremity of sense organ 2 the two components finally separate out and do not for the remainder of their course come into contact again\*. The smaller dorsal trigeminal ophthalmic (*S.O.*<sup>6</sup>) passes rapidly upwards, dividing into two, is distributed to the skin of the dorsal region of the snout, and, although coursing with the lateral line nerve described in the footnote, is not in any way connected with it. The large ventral lateral ophthalmic, on the other hand, passes forwards, perforates the nasal opposite the opening of the second dermal tubule, and terminates in sense organ 1.

## (2) *Infra-orbital Canal.*

### *Buccal Trunk.*

The buccal trunk, leaving the ophthalmic and buccal ganglion, passes downwards and outwards through the "trigeminal" portion of the trigemino-facial complex, and whilst passing through this ganglion divides into the nerves (1 and 2 below) which issue from the ganglion at different levels.

(1) *Outer buccal branch.*—Issues from the trigeminal portion of the V-VIIIth ganglion dorsal and posterior to the second branch. It is smaller than the latter, and gives off,

\* Just at this region a long nerve from the upper ramus of the inner buccal lateral line nerve passed straight up, crossed the two ophthalmic nerves internally, but was not connected with either, curved outwards and round the dorsal edge of the nasal, and finally passed downwards to innervate a pit organ opposite the anterior extremity of sense organ 1. This curious nerve is not represented in other fishes, and probably consists of lateral superficial ophthalmic fibres following a buccal course.

immediately after leaving the ganglion, the otic nerve, being thereafter continued on to the orbit as the posterior or outer buccal nerve of the buccal trunk. Both these nerves are described below.

Coursing for a time alongside the outer buccal branch and issuing from the "trigeminal" ganglion immediately ventral to it, in fact from the maxillo-mandibular portion of the ganglionic complex, is one of the nerves described by Strong as "accessory branches of the trigeminus," and also mentioned by Allis (6, p. 605, &c.). The nerve now described undoubtedly corresponds to Allis's nerve "c" from the maxillo-mandibular trunk, and is distributed mostly to the tissues behind and below the eye. Also issuing from the ganglion at the same level, but posterior to it, and passing at first outwards and then downwards, is a twig which seems to tally with Allis's branch of the inferior maxillary "*r.lap.do.*" (6, p. 610), since I traced some of its fibres to the dilator-operculi muscle.

(2) *Inner buccal branch.*—Leaves the ganglionic complex ventral and anterior to the first nerve. As it issues from the ganglion and passes into the orbit it is joined and accompanied by the maxillo-mandibular trunk, but lies dorsal and somewhat posterior to it. There is, however, never any connection between them, and sections show the inner buccal branch to be perfectly distinct, from its origin at the ophthalmic and buccal ganglion onwards. The maxillo-mandibular trunk soon begins to separate into maxillary and mandibular nerves respectively, and as it does so the inner buccal branch passes upwards so as to lie dorsal to the superior maxillary, when the separation of the maxillo-mandibular trunk is complete. (I may here remark that the relative positions of the inner buccal and trigeminal nerves in the orbit are subject to some variation. The condition just described is shown in my second figure. In the sections, however, and in other dissections the inner buccal and its two rami were situated below the superior maxillary throughout the whole orbit.) In front the inner buccal crosses over the superior maxillary so as to lie ventral to it. As it crosses the orbit, and just over the division of the maxillo-mandibular trunk into its two derivatives, the inner buccal branch divides into a smaller inner and dorsal portion, and a larger outer and ventral one. These will be described respectively as the upper and lower rami of the inner buccal branch of the buccal trunk.

*Outer buccal branch. Otic nerve.*—This nerve arises from the outer buccal branch immediately the latter emerges through the pro-otic notch, and then passes straight upwards but slightly backwards, accompanied by an arterial twig, over the pro-otic and the external face of the post-frontal, until it reaches a backwardly-directed dorso-ventral canal bored in the substance of the post-frontal. Having passed through this, it emerges on the dorsal surface of the skull between the post-frontal and the anterior overlapping portion of the squamosal. It then passes straight backwards over the squamosal, lying dorsal to the latter bone and ventral to the infra-orbital canal, until it reaches the last or 11th sense organ of the infra-orbital line which it supplies.

*Outer buccal branch. Outer buccal nerve.*—On leaving the ganglion, this nerve passes forwards and downwards. It soon gives off a twig which, travelling upwards and forwards, pierces the sixth suborbital and supplies sense organ 10 of the infra-orbital canal.

Beyond this the outer buccal takes a sharp turn downwards, but before doing so crosses internally the vertical portion of the infra-orbital canal almost at right angles, and takes up a position in front of and above it. Shortly after giving off the twig to the 10th sense organ, and as the outer buccal enters the posterior portion of the orbit, another twig is given off, which, passing downwards and forwards, perforates the fifth sub-orbital and supplies sense organ 9 of the line. In front of this the outer buccal is seen to separate into three nerves. One of these is the main portion of Allis's nerve "c" (described above), which, having hitherto accompanied the outer buccal, now passes upwards to its distribution, whilst of the two ventral twigs the outermost passes outwards and downwards, perforates the fourth sub-orbital, and innervates sense organ 8 of the infra-orbital canal. The remaining one, in front of the twig to sense organ 8, takes a ventral curve, and after giving off a branch ventrally which was traced to a pit organ situated ventral to the canal, pierces the third sub-orbital and supplies sense organ 7 of the line.

*Inner buccal branch.*—This, the larger of the two divisions of the buccal trunk, passes downwards and forwards, as previously described, across the orbit, and consists of two parts. The lower and larger part soon gives off a twig which, after a long course downwards and forwards (lying internal to the sclerotic), perforates the second sub-orbital and supplies sense organ 6 of the infra-orbital canal. Almost opposite this sense organ another twig is separated off from the lower ramus of the inner buccal, and in this region the first and second sub-orbitals are seen in the sections to begin to overlap. The twig above pursues a course somewhat parallel to its predecessor, obliquely perforates the lachrymal, and supplies sense organ 5 of the line. At about the region of this sense organ the two rami of the inner buccal begin to separate, the ventral one passing downwards and approaching the infra-orbital canal, whilst the dorsal ramus passes upwards. The ventral ramus opposite sense organ 5 gives off another twig, and, passing rapidly downwards, lies near the inner face of the lachrymal, slightly dorsal to the upper border of the infra-orbital canal. The twig above perforates the lachrymal at the dorsal border of the canal, and innervates sense organ 4. After supplying this sense organ the ventral ramus comes to lie immediately internal to the inner face of the lachrymal, and exactly opposite the infra-orbital canal. It then gives off a branch which supplies the pit organs ventral to the canal, and immediately afterwards the whole of the nerve perforates the lachrymal and lies between that bone and the upper and lower borders of the canal. There are thus three perforations in the lachrymal for twigs of the ventral ramus of the inner buccal to sense organs of the infra-orbital line. Before reaching the third sense organ the ventral ramus divides into two—the ventral twig supplies sense organ 3, whilst the dorsal passes forwards *and supplies sense organ 2 only*.

To return to the upper ramus of the inner buccal. After separating from the ventral ramus it passes upwards and ventral to the nasal sack, and is joined by a branch of the superior maxillary division of the trigeminus. The two nerves do not, however, mix. The upper ramus then gives off its first branches, which terminate in the numerous pit organs in the region of the snout between the supra- and infra-orbital lines. It now passes downwards and becomes opposed to the inner face of the lachrymal at a spot immediately dorsal to the place where the ventral ramus passes through its most

anterior foramen in the lachrymal. It then courses forwards parallel and dorsal to the ventral ramus, and, after giving off dorsally more twigs to the pit organs of the snout, passes slightly downwards, perforates the lachrymal opposite the dorsal border of the infra-orbital canal and slightly posterior to sense organ 2, and *finally supplies sense organ 1.*

(3) *Hyomandibular or Operculo-mandibular Canal.*

*Hyomandibular Trunk.*

This large nerve (*H*), just at its origin from the trigemino-facial ganglion, is divided by the orbital vein into two portions. The anterior ventral portion consists of two parts representing the morphological palatine and pre- and post-spiracular nerves or the "facial proper," whilst the posterior dorsal portion constitutes the "lateral line root of the facial." These constituents run alongside one another external to the vein, but are soon quite separable by the microscope into an anterior bundle (*H*<sup>1</sup>), composed of the pre-spiracular and main trunk of the external mandibular branch, and a posterior bundle (*H*<sup>2</sup>), which is mostly formed by the post-spiracular nerve, but also includes a branch of the external mandibular. In dissections it was noticed that the pre-spiracular separated off before the hyomandibular trunk divided into the two preceding bundles.

*External mandibular nerve.*—The posterior branch above of this nerve arises as already described, and then passes straight outwards, downwards, and backwards. It is closely applied to the postero-external border of *H*<sup>1</sup>, and receives some lateral line fibres from it ventral to the orbital vein. As the entire hyomandibular trunk passes downwards, on approaching the hyomandibular bone the two bundles *H*<sup>1</sup> and *H*<sup>2</sup> become separated so as to form two distinct nerves. The posterior, or smaller of the two (*H*<sup>2</sup>), which is composed of a branch of the external mandibular + the hyoidean nerve, or post-spiracular division of the facial proper—the latter being the larger bundle, passes through the oblique backwardly-directed facial canal in the hyomandibular bone, whilst the larger bundle (*H*<sup>1</sup>) traverses a foramen in the hyomandibular larger, just ventral, and somewhat anterior and internal to it. Distally the apertures are somewhat widely separated owing to the backward direction of the facial canal.

The hyoidean nerve + the posterior branch of the external mandibular, on emerging from the facial canal, immediately take a sharp turn downwards and slightly backwards, coursing near and parallel to the posterior edge of the anterior downward process of the hyomandibular. On leaving the facial canal the two parts of the nerve are seen to be separated, in the sections the external mandibular being situated externally to the facial proper component. The two nerves pass downwards and slightly backwards together, and pass under the preoperculum at the base of the deep notch at its upper extremity. The external mandibular fibres (*H*<sup>2</sup>) leave the hyoideus near the ventral extremity of the facial canal, and, passing outwards, downwards, and backwards, soon collect into two bundles. The upper passes downwards, perforates the preoperculum, and supplies the 12th sense-organ of the hyomandibular line. The lower, after a somewhat long course downwards, obliquely tunnels the preoperculum some little distance

above sense organ 11 of the line, which it supplies. The motor hyoideus ( $H^4$ ), the post-spiracular nerve, passes downwards and becomes related to the anterior face of the hyoid arch. With the distribution of this nerve we are not concerned.

The anterior or larger division of the hyomandibular trunk ( $H^1$ ) consists, as already described, of two parts: (a) the main trunk of the external mandibular lateral line nerve ( $H^5$ ); and (b) the "internal mandibular" of Allis ( $H^3$ ). I shall show later on that Allis was wrong in his interpretation of this nerve, and that it really corresponds to the modified pre-spiracular nerve, or chorda tympani, of the cartilaginous fishes, and as such cannot be the internal mandibular, which is a post-spiracular nerve. The internal mandibular or post-spiracular nerve is really the hyoideus. Sections show that this trunk consists of two parts, an anterior chorda tympani and a posterior external mandibular. The chorda soon separates off, passes downwards, and becomes related to the posterior face of the lower jaw. On leaving the hyomandibular bone the external mandibular immediately passes straight downwards over the anterior downward process of the hyomandibular, and accompanied by a blood-vessel which in spirit dissections looks astonishingly like a nerve\*. Shortly after emerging from the hyomandibular foramen a long nerve is given off from the external mandibular ( $H^7$ ) which passes forwards through the adductor mandibule to innervate some pit organs in the neighbourhood of the infra-orbital canal. It then courses downwards and forwards to supply certain of the pit organs lying ventral to the hyomandibular canal. Before passing downwards, however, it sends down a long fine nerve which innervates the posterior set of pit organs in connection with the hyomandibular canal. These nerves are mentioned by Allis (1897, p. 632). They also undoubtedly correspond to Allis's nerves *mef.vl.* and *mef.mdl.* innervating the vertical cheek and mandibular lines of pit organs.

Soon after leaving the canal in the hyomandibular a twig is given off, which, passing downwards and backwards over the external face of the anterior process of the hyomandibular, perforates the preoperculum ventral and somewhat internal to its anterior upward process, and just dorsal to the point of the backward process of the quadrate. It supplies sense organ 10 of the hyomandibular canal. After giving off the above twig the external mandibular nerve passes downwards over the outer process of the hyomandibular and begins to take a marked turn forwards. Leaving the hyomandibular it passes over the symplectic, and whilst on this bone gives off the twig to sense organ 9 of the line. This twig passes forwards over the symplectic, perforates the preoperculum internal to the facet for the quadrate and at about the anterior third of the facet, and so reaches its sense organ.

The external mandibular now begins to assume a horizontal position, and arriving at about the middle of the posterior edge of the symplectic, where the body of the quadrate overlaps it, passes almost horizontally, but still somewhat downwards, in a rough canal

\* Several of the more important nerves in the Cod are accompanied by blood-vessels, which often appear, as in the case of the superficial ophthalmic trunk, to arise directly from the nerve. (They really perforate it.) In specimens that have been a long time in spirit these vessels are remarkably like nerves, and have been taken for such by several naturalists!

formed by the superposition of the quadrate on the symplectic. Whilst passing between these two bones it gives off the twig to the 8th sense organ, which, passing downwards on the internal face of the quadrate, perforates the preoperculum near the anterior extremity of its dorsal border (close to the quadrate facet) and thus reaches its destination.

Having passed between the symplectic and the quadrate, the external mandibular courses downwards over the inner face of the latter internal to its head, and then by a downward curve reaches the inner face of the articular, where it lies in a deep horizontal groove situated at a level somewhat dorsal to this section of the hyomandibular canal and opposite the head of the articular. Whilst on the head of the articular the twig to sense organ 7 of the hyomandibular line is given off. This arises somewhat anterior to the sense organ, passes backwards, enters the articular opposite and ventral to the anterior edge of the facet for the quadrate, and passes transversely through it to its sense organ. At this point a branch of the inferior maxillary division of the trigeminus comes down and runs alongside the external mandibular, lying immediately dorsal to it; but although they may be very closely opposed there is no real connection, the ventral branches of trigeminal branch curving round the inner and outer surfaces of the lateral line nerve to reach their destination.

The external mandibular nerve now commences to pass slightly downwards, and first lies internal and somewhat above Meckel's cartilage, and afterwards, in front of the 6th sense organ, is situated directly internal to it. The branch to sense organ 6 is separated off somewhat in front of the twig to the 7th sense organ. It courses forwards and outwards, obliquely perforates the dentary, and after running alongside the sensory canal for some little distance reaches and supplies its sense organ. The mandibularis externus is now opposed to the inner face of Meckel's cartilage, and there gives off the twig to sense organ 5. This proceeds downwards and forwards, and, obliquely piercing the dentary, reaches its respective sense organ. At about this region a nerve is seen to pass downwards under Meckel's cartilage from its outer surface and then turn upwards to become opposed to, but never connected with, the outer face of the external mandibular. It is at first situated between the latter nerve and the cartilage, but finally comes to lie on the top of the lateral line nerve at the place where the twig to the fourth sense organ perforates the dentary. This nerve is undoubtedly Allis's branch "*r.gli.*,"\* springs from the inferior maxillary division of the Vth, and constitutes a part of the innervation of the geniohyoid muscle. Of the twigs to sense organs 3 and 4 nothing need be said further than that they passed through separate perforations in the dentary, and that each gave off a very small bundle of fibres which were traced ventral to the hyomandibular canal and then lost. They doubtless innervated the pit organs of this region. The external mandibular is still situated internal to Meckel's cartilage.

Anterior to sense organ 4 the lateral line nerve commences to pass downwards so as to occupy a position ventral and somewhat internal to Meckel's cartilage. Here also the anterior termination of the main trunk of the inferior maxillary division of the trigeminus

\* Cp. Allis, 6, p. 639.

is seen lying internal to and above Meckel's cartilage\*. In front the external mandibular passes still further downwards, finally taking up a position ventral to Meckel's cartilage and slightly dorsal to the hyomandibular canal. It is still accompanied by trigeminal fibres, which, however, pass to their destination anterior to the termination of the external mandibular. The twigs to sense organs 1 and 2 pass through the same foramen at the anterior extremity of the dentary.

#### (4) *Lateralis Canal.*

The lateral line nerve pursues a course somewhat analogous to that of the buccal. It gives off a supra-temporal branch, which corresponds to the otic, and like it supplies one of the termini of its canal, and then splits into a dorsal and a ventral ramus which may be said to coincide with the two divisions of the buccal trunk. The dorsal ramus innervates the anterior or abdominal half of the lateral line canal with its associated pit organs, and the ventral ramus does the same for the posterior or caudal moiety of the canal. Both rami are of course typical lateral line nerves, and as such are composed of special sensory and not of typical somatic sensory fibres. They may be united by one or more commissures, and together form what are referred to in the text-books as the "cutaneous branches of the vagus."

#### *Lateralis Trunk.*

This large nerve emerges from the medulla at a high level immediately behind the lateral line ganglion of the trigemino-facial complex, in front of the root of the glossopharyngeus and some distance in front of and dorsal to the root of the vagus. The latter nerve arises by a double root from the medulla distinctly ventral and posterior to the lateral line. On leaving the medulla the lateral line passes downwards and backwards, and soon swells into the large lateral line ganglion. It still continues the same course and passes external to the root of the glossopharyngeal, to which, as it passes, it gives a very small twig which accompanies the pre-branchial division of the IXth. The lateral line ultimately joins the vagus, which it accompanies, lying external to it. Hitherto there have been ganglion cells along almost the whole of the length of the lateral line root, but as soon as it reaches the vagus the ganglion cells largely disappear, and only a few are to be seen. Coincident with the disappearance of cells in the lateral line root is their appearance in the root of the vagus, in which they multiply as the nerve recedes from the brain. Both nerves pass through the same canal in the exoccipital, the vagus occupying the anterior and internal position, and the lateral line still possessing a few ganglion cells. No mixing of the two nerves was observed at any part. Outside the exoccipital foramen the vagus root immediately enters the large compound (?) vagus ganglion, and there is also a further collection of ganglion cells on the lateral line in connection with, and at the base of, its supra-temporal branch.

\* Allis (6, p. 610) says that this part of the inferior maxillary accompanies the "r. buccalis facialis," but this is obviously a slip for "r. mandibularis externus facialis."

*Supra-temporal branch.*—This branch arises from a clump of ganglion cells (which also extend into its proximal portion) from the lateralis immediately the latter emerges from the skull. It curves round the auditory capsule, and passes at first in a vertical plane outwards and then upwards. The first branch to be given off is a small posterior one. It arises from the ventro-external portion of the supra-temporal a little distal to the ganglion cells, and passes straight backwards, pierces supra-temporal 4, and supplies the fourth sense organ of the lateral or body canal. It also gives off two branches: first, a somewhat obvious one, which passed forwards and somewhat downwards, bifurcated, and was lost on the skin (this was separated off near the origin of the posterior branch of the supra-temporal); second, a bundle of fibres which was given off as the parent nerve approached the fourth sense organ, and which passed backwards and was also lost on the skin. Neither of these nerves ended in the vicinity of pit organs.

The larger part of the supra-temporal now takes an upward and forward turn, but before reaching the lateral canal divides into two—a dorsal and an anterior division. The former ( $L^3$ ) passes upwards and crosses the lateral canal internally and posterior to the entry of the supra-temporal canal, whilst the latter ( $L^4$ ) passes at first straight forwards just below the lateral canal.  $L^3$  soon divides into two branches. The lower of these perforates the second supra-temporal and innervates sense organ 2 of the supra-temporal canal; the upper courses upwards and forwards, perforates the first supra-temporal, and supplies sense organ 1 of the line.  $L^4$  passes forwards and slightly upwards, passes in between the opposed horizontal edges of supra-temporals 2 and 3, and thus reaches sense organ 3 of the lateral canal. Just as it passes in between these ossicles it gives off a twig which passed forwards and was lost on the skin above the lateral canal. Here also there was an absence of any pit organs. It seems to me probable that this branch, as well as the similar ones first described, are composed of fibres of the vagus which have accompanied the supra-temporal nerve and its branches\*.

The main trunk of the lateralis, after giving off the supra-temporal branch, passes downwards, outwards, and backwards, and in the sections is seen to be situated between the dorsal border of the pseudobranch and the kidney. As it passes backwards it divides to form two conspicuous nerves, one of which is distinctly smaller than the other. The smaller division passes upwards and outwards over the top of the pseudobranch, and then straight backwards, but before doing the latter gives off externally a largish nerve, which itself separated off a very small twig and then passed straight downwards in the inner wall of the branchial chamber. I was unable to trace this branch. The parent nerve, however, then coursed outwards and upwards, pierced the first lateral line ossicle, and innervated sense organ 5 of the lateral or body canal.

After giving rise to the nerve above described the smaller or dorsal ramus of the lateralis trunk continues to pass upwards and backwards approaching the lateralis canal, and as it does so it sends off a branch dorsally which passes first upwards and then forwards for some little distance and markedly dorsal to the lateral canal. It was finally lost on the skin. Almost immediately afterwards another small branch was given off,

\* Cp. particularly description of posterior root of accessory lateral nerve, p. 176.

which coursed backwards for an interval with the parent nerve, and then passed upwards, crossed the lateral canal internally, and innervated a pit organ just dorsal to the canal. By the time the parent nerve has reached the surface tubule 5 it has come to lie immediately ventral to the lateral canal. Beyond this tubule the nerve gave off a dorsal branch which passed upwards, pierced the second lateral line ossicle, and innervated sense organ 6 of the line and its two closely associated pit organs. Posterior to the origin of this twig a smaller one was given off which passed straight up and supplied a pit organ dorsal to the body canal. Behind this again the branch arises which perforates the third lateral line ossicle and is connected with sense-organ 7 of the line and its two neighbouring pit organs.

The ventral or larger ramus of the lateralis trunk coursed backwards and steadily downwards until reaching the pectoral fin, from which point it passed almost straight backwards somewhat dorsal to the fin and following the line separating the dorsal from the ventral musculature. I was unable, however, to detect any branches from its anterior moiety.

#### N. THE STRUCTURE AND MORPHOLOGY OF THE RAMUS LATERALIS ACCESSORIUS.

##### *Synonymy.*

- (1) Nervus lateralis accessorius (Weber, 1820).
- (2) Nerf ptérido-dorsal (Desmoulins & Magendie, 1825).
- (3) Ramus lateralis trigemini (Weber, 1827, and most other authors).
- (4) Ramus quartus s. lateralis nervi trigemini (Bonsdorff, 1846).
- (5) Dorsale Schedelhöhlenast (Stannius, 1849. Cp. also Hoffmann & Pollard).
- (6) Ramus recurrens trigemini et facialis (Stannius, 1849).
- (7) Ramus recurrens facialis (Siluroids. Stannius, 1849. Cp. Pollard).
- (8) Ramus cutaneus quinti (T. J. Parker, 1884).
- (9) Nervus Weberi (Goronowitsch, 1897).
- (10) Nervus accessorius Weberi (in part. Haller, 1897).

Under the name of “ramus lateralis accessorius” (the reasons for retaining which are given below) I propose to describe those curious and interesting nerves familiar to all students who have dissected a Codfish, and which I at first thought were modified lateral line nerves. A minute investigation of the roots, however, and, further, an examination of the literature, convinced me not only that this conclusion was absolutely erroneous, but also pointed to the correct view, as I think, of their morphological value. This small investigation also led to an examination of the essential meaning of the so-called lateralis nerve of the Lamprey, the results of which, however, are given in the succeeding section.

That the so-called “cutaneus quinti” of *Gadus* corresponded to the “recurrent facial” nerve described by Stannius and Pollard, was pointed out independently by Allis and the writer—the former in his second *Amia* paper (6, p. 628), whilst a note to that effect was inserted in the second English edition of Wiedersheim’s “Comparative Anatomy” (221, p. 187) at my suggestion. As, however, we were both anticipated by earlier

writers, the point is of no importance, but may serve to emphasize the correctness of the homology.

The first description of the accessory lateral nerve is to be found in E. H. Weber's famous work on the auditory organ of fishes (1820, 216). He here describes and figures (*i. e.* root only, tab. v. fig. 30) the nerve afterwards called the "recurrent facial" of *Silurus glanis*. He says:—"Ramus primus nervi trigemini, per tectum cranii exiens, (in apicibus processuum spinosorum ad caudam usque progrediens, ibique cum nervis spinalibus ramisque nervi lateralis magni plexum complicatum nervorum componens,) nervi lateralis accessorii nomine appellandus." There can be no doubt as to the homology of this nerve, and it is to be noted that Weber considered it a branch of the trigeminus and not of the facial as his successors did.

Desmoulins & Magendie (1827, 60) refer to the nerve as the "ptérigo-dorsal" (Part II. p. 369), and were the first to recognise the homology between it and the superficial nerve of the higher Teleosts. They give a fairly long description of its peripheral distribution in the latter fishes, which is, however, not as accurate as that published later by Stannius. Weber himself in 1827 (217) devotes further attention to the matter, and successfully homologises his first nerve with the elaborate cutaneous system in "*Gadus lota*" (= *Lota vulgaris*), thus confirming independently the conclusion of Desmoulins & Magendie. He renames the system the "Ramus lateralis trigemini," which is the name by which it has usually been known to anatomists, and describes its anastomoses with the spinal nerves.

In 1830, Cuvier & Valenciennes devote a section of their work on the Natural History of Fishes (57) to a consideration of the accessory lateral nerves. They are both figured and described (t. i. pp. 440-441), and erroneously considered to be largely motor. The anterior and posterior roots are described, and so also are the anastomoses of the dorsal ramus with the spinal nerves. They found the branches to the pectoral and anal fins, but not, however, to the pelvic, and clearly recognised the homology between the recurrent nerve of the Siluroids and the better developed system in the specialised Teleosts, believing that representatives of the system were probably to be found in *all* fishes. Their figure of the nerves of the Perch, showing the accessory lateral nerves, has been copied by Owen (149, vol. i. p. 304), Nuhn (146, p. 558), and into several other text-books. Büchner (1835, 36) states that the accessory lateral is characteristically developed in the Cyprinoids, and describes it in "*Cyprinus barbatus*" (= *Barbus vulgaris*), but fails to distinguish it from the lateralis lateral line nerve. He, however, correctly compares it with its more specialised form in the modern Teleosts. Alecock (1839, 3) says (p. 268): "Lastly, in many [fishes] the nerve [trigeminus] is distributed in a manner and to an extent for which there is no analogy among other animals, the fins being throughout furnished with branches from the fifth. Hence in fish, in which the distribution of the nerve is so much more extended than in other animals, both the size of it is proportionately greater, and it consists of a greater number of divisions; these, which in the three other classes of vertebrate animals are only three, amounting with them to from three to six." A figure of the brain and "fifth" nerve of the Cod is given on p. 276, which shows the anterior root of the accessory lateral nerve

and its double origin. A brief description of it is also to be found in Bonsdorff's work published in 1846 (30), in which the two roots of the accessory lateral and their course through the parietal are described in "*Gadus lota*," but little is said about its peripheral distribution, whilst it is again renamed the "Ramus quartus s. lateralis nervi trigemini."

The description which Stannius gives of the accessory lateral nerves (1849, 199) is concerned rather with their peripheral distribution, which, as far as the description goes, is perfectly accurate. *Gadus* and other Teleosts are carefully described and figured, and one may mention the figure of the former as being particularly admirable, whilst an account is also given of the homologous nerves in the Siluroid Teleosts. In establishing experimentally the somatic sensory nature of the nerves, and confirming the connection which they have in some of the modern Teleosteans with the dorsal, pectoral, pelvic, and anal fins, and also with the dorsal branches of the spinal nerves, Stannius went a long way towards the elucidation of their true morphology, which subsequent observers failed to follow up\*.

Hoffmann (1860, 100) briefly refers to the accessory lateral of *Cyprinus carpio* as the "dorsale Schädelhöhlenast" (one of Stannius's terms), but only devotes a few lines to it. He mentions the connection with the "trigeminus," and figures the posterior root in *Cyprinus*. Swan (1864, 205) also mentions it in a few lines, points out the connection of the dorsal ramus with the dorsal branches of the spinal nerves, and states that the system is not represented in the Skate. He gives two figures which show the origin and distribution of the accessory lateral nerves (which he calls "posterior branches of the fifth"), one of the brain and roots, and another illustrating its peripheral distribution to the dorsal, pectoral, pelvic, and anal fins. I believe this figure, which appeared in the first edition of this work, published in 1835, was the first to accurately show the peripheral distribution of the accessory lateral system. Baudelot (1870, 15) briefly mentions and figures it (figs. 2 and 6) as the recurrent branch of the "trigeminus," whilst Fée, who describes and figures in a number of Teleosts both the true lateral and accessory lateral systems, agrees with the erroneous conclusion of Weber that both these systems are perfectly homologous; although he had noticed that the true lateral nerve was never connected with the spinal nerves. As the result of numerous experiments Fée concluded that neither the true nor the accessory lateral nerves were motor in function. Owen (1866, 149) says (p. 303):—"A branch of the vagus ascends forward to join the fifth in forming the dorsal division of the 'nervus lateralis,' which escapes by a foramen in the parietal bone," by which it will be seen that both the anterior and posterior roots of the accessory lateral were well known at that date. Baudelot (1868, 11) takes a somewhat bold step when he compares a recurrent branch of the pathetic nerve distributed to the pia mater with the ramus lateralis trigemini! In the same volume (12), after an investigation of *Leuciscus rutilus*, he concludes that the true and accessory lateral nerves are perfectly homologous, and after referring to several authors who had

\* As I have been working from the second edition of Swan's Atlas, published in 1864, I am taking it after Stannius's work. The first edition, however, was published before Stannius's, and anticipated it in many important respects, especially as regards the branches to the fins and the connections with the spinal nerves.

discussed the supposed anastomosis of the true lateral nerve with the spinal nerves, he decides in favour of the connection between the two. It seems to the writer, from a careful examination of the various descriptions of this supposed connection, that the writers concerned have been dealing with the lateral ramus of the accessory lateral nerve, and have indeed found the connections they described, but mistake one of the nerves they were dealing with. However this may be, it is certain that the true lateral nerve never anastomoses with the spinal nerves.

The "opercular branch" mentioned by Baudelot (1869, 14) in various Cyprinoids seems to belong to the accessory lateral system, since it arises partly from the vagus and partly from the "trigeminus," and moreover has a cutaneous sensory distribution. Friant (1879, 73) describes the origin of the recurrent facial in Cyprinoids and "*Barbus fluviatilis*" (= *Barbus vulgaris*) in terms that practically amount to a brief anticipation of Pollard's work. He also describes and figures the accessory lateral nerve in many bony fishes, including "*Gadus carbonarius*" (pl. v.) and "*Gadus lota*" (pl. vi.), the latter showing the system and its anastomoses with the spinal nerves especially at the pelvic fin branches.

Emery (1880, 66) describes the accessory lateral nerve in *Fierasfer* as follows (p. 36): "Il ramo laterale del trigemino è ridotto ad un sottilissimo filamento, il quale corre sotto la volta del cranio e fuoriesce dietro il margine posteriore del parietale, per continuarsi, senza ramificazioni, sotto i muscoli della pinna dorsale; non ho veduto anastomosi di questo nervo col vago." The accessory lateral of *Fierasfer* is thus an exceedingly simplified edition of the Cod type. Baudelot, in his posthumous monograph (1883, 16), rediscusses an anastomosis he had previously described (1868, 13) between the vagus and the "trigeminus." He now compares it with the recurrent facial of Cyprinoids, but from his description and figure he must undoubtedly have been dealing with a lateral line anastomosis such as that described by Pinkus in *Protopterus*. This explanation is further suggested by the fact that his anastomosis communicated with the auditory nerve. Pl. iii., figs. 12 & 13, show a curious origin of the accessory lateral nerve in *Lota vulgaris* if correct\*. The posterior root, with its two vagal rootlets, is fairly normal, but the anterior root is formed by the union of a small and large rootlet, both of which arise from the trigemino-facial ganglionic complex. These two rootlets doubtless spring one from the trigeminus and the other from the facial—much as in *Cyprinus carpio* (Haller). Baudelot figures (pl. v. fig. 3) the roots of the system in the latter fish, but I propose to rely on Haller's account of them. Ramsay Wright (1884, 228) states that the "Ramus lateralis trigemini" is connected with the first, second, and third spinal nerves, "and acts as a collector for slenderer branches from all the other rami dorsales" (*Amiurus*), and further that the bulk of its fibres is derived from the fine-fibred root of the facial. Fritsch (1887, 75) very briefly mentions the system as the "nervus lateralis trigemini."

In the Sole, the nerve that seems to me to correspond to the accessory lateral of the symmetrical fishes is, as one would expect, in a very interesting condition. Cunningham (1890, 55) says:—"The right dorsal branch of the fifth, after its upward course on the

\* Not confirmed by Goronowitsch (1897, 90).

internal surface of the skull, emerges by a small foramen in the flat proximal portion of the right frontal bone, and thence passes forwards, at some depth from the surface, between the cephalic portion of the lateral muscle and the membrane which forms the dorsal boundary of the dorsal (left) orbit. It supplies the skin of the extreme anterior end of the dorsal fin on the upper side. It seems at first sight that this nerve has changed its morphological relations; for, since it belongs to the right side of the head, we might expect to find its anterior part on the ventral or right side of the interorbital septum, with the right orbito-nasal; whereas it actually runs on what is morphologically the ventral side of the left eye, crossing in its course the left olfactory and orbito-nasal nerves. But the explanation of this apparent anomaly is not difficult. The dorsal branch of the fifth is a sensory nerve, and was connected in the original symmetrical fish with the skin of the extremity of the dorsal fin, which was originally posterior to the eyes. The fin remained behind the eyes during the rotation of the latter, and after the left eye had travelled round to the right side, the dorsal fin with the neighbouring muscles began to extend forwards. But instead of extending forwards along the now distorted median dorsal line, the fin grew forwards along the edge of the left ectethmoid bone, which supports the left eye in its new position, and which is morphologically ventral to the left eye. The nerve connected with the fin necessarily accompanied the latter in its growth, and thus the nerve comes to be actually dorsal and morphologically ventral to the left eye. The origin of the nerve remains in its original position, posterior to the eyes on the right side of the skull." It seems to me that this nerve fulfils most of the requirements of the definition of an accessory lateral nerve, and it is interesting to note the light that the peripheral distribution of the cranial nerves throws on the asymmetry of the skull—in the above case supporting Traquair's view of the process.

Pollard's description of the "recurrent facial" in Siluroids (1892, 161) is somewhat open to criticism. In *Clarias*, he says (p. 529):—"From a posterior dorsally placed ganglionic extension arises the great Ramus dorsalis recurrens facialis (often wrongly called trigemini) or 'Schädelhöhlenast.' It passes upwards intracranially to the parietal bone in which it lies, taking its course directly backwards near the depression in the centre of the parietal. It supplies the mucous canal at the base of the dorsal fin." Again, on p. 533, in *Auchenaspis*:—"The last nerve to be described is the great recurrent branch of the facialis. This stoutest of all the nerves passes upwards and backwards, inclining medianly. In position it arises *internally to the anterior semicircular canal of the ear*, and a portion of its ganglion occupies the common space enclosed by cartilage. The nerve runs back into the parietal bone, which it leaves before the posterior end of the cranium is reached. It then takes a deeper course among the body muscles and divides, one portion passing on probably to supply a dorsal canal, *though this was not actually observed*, while the other becomes closely applied to the first spinal ganglion. No interchange of fibres could be observed, however, and the nerve penetrates the stout bone which runs out to support the shoulder-girdle in Siluroids, *and follows a direction towards the pectoral fin. In the parietal, as before mentioned, this recurrent nerve receives the supra-temporal branch from the vagus.*" (Italics mine.) In *Trichomycterus*, he remarks (p. 536):—"This latter nerve [the recurrent facial] gives

off remarkably far forward the large nerve *which proceeds to the pectoral fin*, and which in this case has unmistakably no connection with the first spinal ganglion." Finally, in *Chætostomus* we find (p. 539):—"The great recurrent branch of the facial leaves the complex of ganglia belonging to the trigeminus and facial dorsally, and proceeds upwards to the parietal bone, *in which it lies for part of its course, receiving the supra-temporal branch of the first vagus branch*, and giving off more posteriorly the branch which passes by the 1st spinal ganglion on its way probably to the pectoral fin." (Italics mine.)

If the above description by Pollard be compared with the description of the accessory lateral nerve of *Gadus* given below, it will be seen that the two systems of nerves correspond with each other, detail for detail, in a most remarkable way. As, however, I can conclusively prove that the accessory lateral is *not* a lateral line nerve, it follows, either that the comparison does not hold good, or that Pollard's conclusions as to the nature of the recurrent facial are altogether erroneous. The former alternative is put out of the question by the extraordinary resemblance of the one system to the other. It is hence necessary to enquire into the possibility of the latter.

First, according to Pollard's own statement, his work was based entirely upon sections; and although this is a very valuable method of investigation, I fully agree with Allis that unless the results so obtained are as far as possible checked by dissection, the most disastrous errors are often committed. For example, I should most certainly have described the accessory lateral of *Gadus* as belonging to the lateral line system had I not previously ascertained by careful dissections that it did not. The way in which the roots of the nerve are applied to the lateral line ganglia (*i. e.* the external mandibular and lateralis ganglia) would deceive the most careful investigator not working with Weigert sections and not knowing beforehand the macroscopic anatomy of the nerve. It thus seems to me inevitable that Pollard has mistaken, or rather failed to determine, the precise origin of the fibres of his recurrent facial\*. The only factor in the peripheral distribution of the recurrent facial which points to its being a lateral line nerve is the statement that it "supplies the mucous canal at the base of the dorsal fin." What this canal is must remain a mystery until Pollard's work is revised, since he gives absolutely no description of it, nor any figure. In the meantime I agree with the remark made by Allis (6, p. 627) that "the canal may, however, be of the kind described by Emery as the accessory lateral line of *Fierasfer*, and hence not comparable at all with the canals of the lateral line system as found in *Amia* and Teleosts." Allis, unfortunately, is not consistent on the point. He disbelieves in the canal as a lateral line structure in *Polypterus*, but accepts as such exactly the same canal in *Clarias* and *Auchenaspis*, without considering the possibility of the innervation of it in the latter forms having been erroneously described. On the above grounds, therefore, I consider the "recurrent facial" of Siluroids to be a somatic sensory but *not* a lateral line nerve, comparable in every respect to the so-called cutaneous branches of the trigeminus or the accessory lateral nerves in *Gadus* and other Teleosts.

\* I am leaving out of consideration the origin of the facial portion of the nerve, since Pollard does not mention from which portion of the complex it arises—whether from the lateral line ganglion or the facial ganglion *sensu stricto*.

According to Vogt and Yung (215) the accessory lateral nerve must be small in *Percu*, in which they differ from Cuvier and Valenciennes, but their description and figure do not agree, and the anterior root of the system must remain a matter of doubt. It is probable, however, as described by Cuvier and Valenciennes (from whose figure that given in Vogt and Yung seems to have been largely compiled), that this root resembles the anterior root of *Gadus*. Willey (1894, 223) considers the accessory lateral to be comparable to the true lateral system. He says (p. 45):—"It is not impossible that the lateral line nerve (*R. lateralis vagi*) is homodynamous with the remarkable *Ramus cutaneus quinti* (*R. recurrens trigemini et facialis* or *Nervus lateralis trigemini*, Stannius) of Teleosteans, which runs to the base of all the fins, paired as well as unpaired; just as the paired fins themselves are known to be homodynamous with the median fins. In this case the *R. cutaneus quinti* would be of primitive significance, notwithstanding the fact that it is absent in Selachians; and it would be another of those features of organization in the possession of which Teleosteans exhibit more primitive relations than do the existing Selachians." I have already emphasized the fact that the accessory lateral nerves are not in any way comparable to the true lateral system, and hence Willey's argument, based indeed on an assumption that is "not impossible," must fall to the ground.

Turning to Allis's last work on *Amia* (1897, 6), we find the following passage (p. 628):—"The great recurrent branch of the facialis described by Pollard seems to be the ramus lateralis trigemini of other authors. In *Silurus glanis* this nerve is distributed to the dorsal fin, as in *Clarias* and *Auchenaspis*. In *Trichomycterus* and *Chaetostomus* a large branch is sent from it to the pectoral fin, and in *Gadus morrhua* I find this branch distributed to the breast fin also. In Elasmobranchs and Amphibia the nerve is wanting, so far as I can find. Its distribution indicates that it is destined largely or entirely to the supply of terminal buds, for these buds are not found on the body in Elasmobranchs and Amphibia, and are found in great quantity, but with a greatly varied distribution, on the body, but more especially on the fins, in Teleosts. The nerve in *Gadus* lies immediately beneath the skin, but crosses the lateralis vagi internal to the nerve. It arises as two nerves or bundles from the deeper portions of the trigemino-facial ganglion, the two bundles embracing the root of the buccal and ophthalmic branches of the facialis exactly as the first pair of branches of the ophthalmicus superficialis trigemini in *Amia* embrace the ophthalmicus facialis. The nerve in *Gadus* has, contrary to the arrangement of the branches found in *Amia*, an intracranial course, as it has in Siluroids, issuing on the top of the skull near its hind end. As the trigemino-facial ganglionic mass lies, in *Clarias* at least, inside the skull beside the brain, this difference of course is probably of no importance."

This passage is unfortunate in many respects. In the first place, the homology between the Siluroid and the modern Teleostean nerve is, as I have already shown, by no means new, and has been pointed out by many authors. Secondly, the branches in *Gadus* to the breast (=pelvic?) and other fins were described as far back as 1835 by Swan, and are even described in the practical handbooks (*e. g.* Owen's "Vertebrates" and Parker's "Zootomy"). Thirdly, the accessory lateral is, I think, not wanting in

Elasmobranchs, although I made a statement to that effect in my *Chimæra* paper (46, p. 663). I find in my notes on the Skate (*Raia batlis*) that a large nerve arises from the hyomandibular trunk just outside the auditory capsule, which, passing almost straight backwards, gradually acquires a superficial position, courses over the visceral clefts, and ends on the skin of the back in that region\*. It seems to me that this nerve is the representative of the accessory lateral in the Skate. Fourthly, as described and figured by Stannius, the accessory lateral passes *external* to the lateralis lateral line nerve. Finally, and most important, the large posterior or vagal root is completely overlooked, which is the more extraordinary seeing that it also is a text-book fact, and is described and figured by Owen, Parker, and other writers. It must be noted, however, that Allis is perfectly correct in the more essential considerations—first in homologising the Siluroid “recurrent facial” with the accessory lateral system of the modern Teleosts, and second in regarding the latter as a somatic sensory and not a special sensory or lateral line nerve.

Allis (1897, 6, p. 599), after describing two branches of the ophthalmicus trigemini which seem to me to correspond to the anterior or trigemino-facial root of the accessory lateral system of *Gadus*, writes as follows (p. 691):—“Its [the vagus’s] small intracranial branch arises more from the main vagus root than from the dorsal branch itself. It, however, *arises from the fibres that go to form that branch, and hence can be considered as a branch of it.* It runs upward and forward, internal to the root of the lateral nerve, and issues on the top of the chondrocranium by a small foramen lying near the middle line of the head, near its hind end. Its further course could not be traced. From its position, at its exit, it would seem to be the ramus lateralis trigemini, or ramus recurrens facialis, of Teleosts. Its apparent origin is, however, from the vagus, and not from the trigeminus or facialis. If it be the ramus lateralis trigemini, the first pair of dorsal branches of the ophthalmicus superficialis trigemini cannot be that nerve, or can only be a part of it. *Both nerves, and the main supra-temporal as well, are distributed to regions where terminal buds are formed, this being especially true of the posterior branch of the main nerve.*” (Italics mine.) Here it will be seen that Allis contradicts his own statement that the accessory lateral nerve of *Amia* has not an intracranial course (cp. previous quotation). His failure to homologise definitely his two sets of nerves is due, of course, to his oversight *re* the roots of the system in *Gadus*. It is not difficult to recognise his trigeminal branches as corresponding to the anterior root, and his vagal branch to the posterior root of the accessory lateral system, as indeed Allis himself surmised in his summary (p. 747).

There seems to be no homologue of the accessory lateral nerves in *Protopterus*, according to Pinkus (1894, 157), but the system is briefly mentioned as the “nervus Weberi” in *Lota vulgaris* by Goronowitsch (1897, 90), where, as one would expect, and as far as Goronowitsch’s description goes, it closely resembles the same nerves in *Gadus*.

\* In this connection cp. Jackson & Clarke (1876, 106). It is possible that the nerves they describe as anastomosing with the first spinal nerves may also represent a part of the accessory lateral system.

The most complete account of the system to be found in modern literature is that published in the admirable work on the vagus group of Teleosts by B. Haller in the third volume of the "Festschrift für Gegenbaur" (1897, 97). Haller carefully redescribes the origin of Weber's accessorius (=accessory lateral in part) in *Cyprinus carpio*, where the accessorius is found in a very interesting, and perhaps primitive, condition. An anterior root (Taf. ii. figs. 7 & 8 a) is formed by the union of two twigs from the Gasserian ganglion, *one from each side*, and two twigs from the facial ganglion. This root passes backwards and anastomoses with the fused "ventral roots of the vagus" (Gegenbaur), or what is usually identified as the Ichthyopsid "hypoglossal." From the ganglion of the latter close to the entry of the root above, arises one of the roots of the accessory lateral system, which passes upwards, receives a root from the vagus, and then doubtless has the usual peripheral distribution. Before a correct interpretation of these roots and nerves is possible, an investigation will have to be conducted as to the internal origin and peripheral distribution of the fibres of the roots above described, and this has yet to be done. My own provisional interpretation differs from that given by Haller, and is perhaps the more logical one in the present state of our knowledge. We know that a generalised accessory lateral system would consist of the collected dorsal somatic sensory branches, or portions of them, of the Vth, VIIth, IXth, and Xth cranial nerves, and most of the spinal nerves. Haller's nerve *a*, therefore, forms what is doubtless the morphological anterior root of the accessory lateral system. It is anomalous in so far as, instead of anastomosing directly with the posterior or vagal root, it passes first backwards to the hypoglossal ganglion. The dorsal branch that leaves the hypoglossal ganglion, therefore, represents the morphological posterior extremity of the anterior or trigemino-facial root (Haller's nerve *a*) of the accessory lateral system, +doubtless the additional dorsal branch of the hypoglossal. The posterior or vagal root is normal. The peculiarity of the accessory lateral system in *Cyprinus*, therefore, is that the anterior root first "collects" the dorsal branch of the hypoglossal, instead of that branch being collected after the two roots of the system have united and the resulting trunk is passing backwards. This irregularity has necessarily resulted in the morphological anterior root as it passes upwards occupying a position posterior to the posterior root. Should my interpretation of these nerves prove on further investigation to be correct, *Cyprinus* will have provided us with a very interesting and unique chapter in the history of the accessory lateral nerves.

C. J. Herrick \*, in a recent note (1897, 98), describes the accessory lateral nerve of *Menidia notata* as follows (p. 428):—"Ramus recurrens VII. Commonly called ramus recurrens V, but as the fibres are all fasciculus communis, that name is inappropriate. These fibres arise from the geniculate ganglion in several strands, pass dorsal in the meninges and finally emerge on the dorsal surface of the head, and then turn caudad into the trunk. They anastomose with each other, and farther back with the dorsal ramus of each spinal nerve. I have not been able to demonstrate that they supply either

\* This author, by the way, accuses me in my *Ohimara* paper of associating the lateral line system with the facial nerve. He must surely have overlooked paragraph 5 on p. 638, in which I point out that such an association must be considered as purely provisional and not morphological.

canal organs or end buds. They have not, however, been traced caudad more than a few segments into the trunk. They clearly correspond to the superficial, or accessory "lateral line," nerves of the Gadoids." Here the lateral line character of the accessory lateral is out of the question, but I am astonished to find that its fibres all belong to the fasciculus communis system, since this, as we know from Strong (1895, 204, p. 182), consists in Amphibia exclusively or almost exclusively of visceral fibres \*. It is true, as I have previously pointed out, that other recent authors have made similar statements, and Strong himself has been somewhat misrepresented in the matter. The somatic sensory fibres cannot be considered to belong to the fasciculus communis system, unless we are to be guilty of the sophism of extending the definition of this system in order to admit them. The authors in question disassociate visceral sensory from visceral motor fibres, and then unphilosophically proceed to associate somatic with splanchnic fibres and call the result by a name which was originally applied to a system of visceral sensory nerves. The system adopted by Strong and Herrick of ascertaining both the internal origin *and* the peripheral distribution of the cranial nerve components is the only one by which to attain results of any value, and we must accordingly await further investigation on these lines as to the nature of the fasciculus communis system in fishes. In the meantime we may or may not choose to believe in the conversion of splanchnic into somatic fibres.

It is hence perfectly clear that the accessory lateral nerves of fishes consist, as has been proved microscopically, of somatic sensory fibres. And their peripheral distribution has also been clearly described and figured by many authors, such as Swan and Stannius. Their origin, however, excepting the doubtful accessory lateral described by Haller, has hardly been investigated at all, and the utmost we know is that in many fishes it is formed by roots from at least two cranial nerves. I therefore made a careful investigation of the origin of the system in *Gadus virens*, with the results detailed below.

In *Gadus*, as is well known, the accessory lateral nerve arises by two roots—a large stout anterior root, and a much smaller posterior root. An anatomical and microscopical examination of these two roots reveals the following facts:—

*Anterior or Trigemino-facial root (anatomical).*—Arises from the trigemino-facial ganglion by two rootlets—a larger and a smaller. Owing to the fact that these arise from the complex just as the latter is passing through and leaving the skull, and as the nerves are here closely invested by a tough membrane very difficult to dissect off, the origin of the rootlets is difficult to ascertain. The larger one, however, was connected by several bundles with the base of the hyomandibular trunk, and the smaller one with the maxillo-mandibular trunk. The actual origin of the fibres I was unable to determine by dissection. The two rootlets embrace the trigemino-facial ganglion in much the same way as the rootlets of the posterior root embrace the trunk of the vagus.

*Anterior root (microscopical).*—Both the rootlets arise from the trigemino-facial complex intracranially, or rather as the complex is passing through the pro-otic notch. The larger rootlet arises by several bundles from the most ventral fibres of the hyomandibular

\* Cp. also pp. 195-6.

trunk, *i. e.* from the facial proper. It passes upwards and backwards, and is soon joined by the smaller rootlet which arises from the dorsal or external face of the "trigeminal" ganglion. In neither case could I trace any connection with lateral line fibres. By the union of these two rootlets the anterior root is formed, which passes at first backwards and upwards closely wedged in between the pro-otic and the ventral portion of the lateral line ganglion, from which it might easily be thought to arise, but with which it is not connected. Soon after leaving the lateral line ganglion the anterior root passes almost straight upwards over the cerebellum to reach the parietal, which it perforates obliquely, and then passes outwards and backwards. Whilst passing through the parietal canal it receives and fuses with the posterior root from the vagus.

*Posterior or vagal root (anatomical).*—Arises from the vagus by two rootlets—a larger and a smaller, the larger one appearing to arise from the lateralis. Both these rootlets themselves arise from a number of bundles which embrace and arise intracranially from the root of the vagus just as the latter enters the skull. One of these rootlets sent a very small twig which accompanied the lateralis nerve—this being the only connection observed between the posterior root and the lateralis. None of the fibres of the former, therefore, are lateral line fibres, *but in some cases the glossopharyngeus\* contributed a bundle to the root.*

*Posterior root (microscopical).*—This is variable even in the same specimen. It arises by two rootlets, as described above, which embrace the root of the vagus not far from its point of issue from the medulla. These two rootlets join and then pass internal to the lateralis nerve, being very closely opposed to it, but with no exchange of fibres. The root then passes upwards and forwards, and immediately on leaving the lateralis swells into a large ganglion which was not observed in the sections of the anterior root. The posterior root then passes upwards to the parietal, where it fuses with the anterior root as previously described. The posterior root may pass *external* to the lateralis, in which case it begins to swell into its ganglion before leaving the lateralis, so that the ganglion as well as the nerve is closely applied to the lateralis. The connection with the lateralis is very close, and the subsequent central course of the nerve requires very careful tracing.

*Connections with spinal nerves.*—The accessory lateral system is connected with the anterior spinal nerves in Teleosts generally, either directly by means of the spinal ganglia, or the dorsal branches of the spinal nerves, or indirectly by means of the branches of the system to the pectoral and pelvic fins (*Gadus*). As was carefully demonstrated by Swan and Stannius, the branch of the system to the dorsal fin communicates in the region of the trunk in *Gadus* with the dorsal branch of every spinal nerve (Stannius, 1849, 199, Taf. iv. fig. 2)—a significant fact which is very helpful in determining the morphology of the accessory lateral nerves.

\* In many specimens of *G. morhua* that I dissected the glossopharyngeus arose immediately *ventral and anterior* to the root of the lateralis. This it does in some other Teleosts. In the sections of *G. virens*, however, it arose behind the lateralis and between it and the vagus, which is its normal origin.

The above consideration of the literature and description of the facts in *Gadus* enable us to draw up the following general conclusions as to the structure and morphology of the accessory lateral nerves:—

- (1) The accessory lateral system of nerves is essentially compound in nature, the anterior branches as they pass backwards acting as collectors and picking up branches from nerves situated posterior to them.
- (2) The system therefore belongs as distinctively to the spinal as to the cranial nerves. It originates in the latter, passes backwards, and collects branches from the former.
- (3) It is distributed to the fins—typically, as in *Gadus*, to all the fins of the body, but in some fishes it may be distributed to only one or more of the fins.
- (4) In connection with the fins are a number of terminal buds or *Endknospen*, and the fibres of the accessory lateral system are largely, if not entirely, in connection with these sense organs. The system is therefore both essentially somatic and sensory in function.
- (5) Hence we cannot escape the conclusion that it is formed by the dorsal branches of the cranial and spinal nerves which the exigencies of their distribution have caused to more or less fuse together peripherally.
- (6) Further, the ganglion on the posterior or vagal root in *Gadus* is comparable to the somatic sensory portion of the dorsal root ganglion of a spinal nerve. This ganglion (and it is possible there are others) belongs distinctively to the accessory lateral system.
- (7) The system in any one fish may be formed either by the whole or portions of the dorsal somatic sensory branches of the trigeminal, facial, glossopharyngeal, and vagal cranial nerves, together with the whole or portions of the dorsal somatic sensory branches of a variable number of spinal nerves.
- (8) Upon no grounds can it be considered as belonging to the lateral line series of nerves, since it differs from the latter in three essential respects: (*a*) in internal origin; (*b*) in the character of its fibres; and (*c*) in its peripheral distribution. The one system acts as a collector, whilst the other is absolutely independent of any of the cranial or spinal nerves.
- (9) It is hence imperative to sink such terms as “*ramus lateralis trigemini*,” “*ramus cutaneus quinti*,” and “*ramus recurrens facialis*,” since no term can be considered satisfactory, or indeed justifiable, which implies that any one cranial or spinal nerve either invariably takes a part in, or entirely forms, this complicated system of nerves. I have adopted the term “*Ramus lateralis accessorius*” for three reasons: (1) it implies nothing as to the formation and origin of the system; (2) it was the first term to be applied to these nerves; (3) its meaning that it is an accessory lateral nerve is one that may fitly be applied to it, and is not ambiguous, since the term “*lateralis*” has been indifferently applied both to special and general cutaneous nerves\*.

\* Hence my term “*lateralis lateral line nerve*,” which leaves no room for doubt as to its distribution.

O. MORPHOLOGICAL VALUE OF THE LATERALIS NERVE OF *PETROMYZON*

Whilst working at the accessory lateral system of Teleosts, my attention became directed to the "lateralis" nerve of *Petromyzon*, and it occurred to me, whilst reading Ahlborn's second paper on the Lamprey, that this nerve was not, as is usually supposed, a lateral line nerve, but really belonged to the accessory lateral system. The fact that a definite lateral or body canal is unrepresented in *Petromyzon*, or at the best only represented by a few scattered sense organs, shows that the nerve, whatever it may be, is certainly not a lateral line nerve, which confirmed my former impression and necessitated further enquiry into the question.

As far back as 1849, Stannius (199, pp. 95 and 96) had maintained that the lateral nerve of the Lamprey was not a lateral line but a general cutaneous nerve, but did not compare it with his "dorsale Schedelhöhlenast." Ahlborn (1884, 2) described an anastomosis between the "lateralis" and the facial, which has been compared both with the lateral line anastomosis of *Protopterus* and also with Jacobson's anastomosis. From what has preceded it is impossible that it can represent either of these nerves. If, on the other hand, my suggestion be correct, it is easy to see that this anastomosis represents the anterior or trigemino-facial root of the accessory lateral system.

The short but important paper by Ransom & Thompson (1886, 165) conclusively shows (1) that the "lateralis" of *Petromyzon* is a somatic sensory nerve, and (2) that it is connected with the dorsal roots of the spinal nerves. They further state that it has no ganglion, and consider it to represent a commissural system between the dorsal roots of the spinal nerves. Dohrn (1888, 62) has endeavoured to show that there is no connection between the spinal and "lateralis" nerves, and Beard, believing the latter to be a true lateral line nerve, also discredits the assumption. He says (1888, 21, p. 215): "We know nothing of such connection of spinal nerves with the sense organs of the lateral line, either now or in the past, and any opinion one may express in favour of such a view is only an assumption." This is quite true, but does not, as we have seen, apply to *Petromyzon*. Dohrn's denial of Ransom & Thompson's statements has not been confirmed by subsequent investigation, which has indeed completely established the connection between the "lateralis" and spinal nerves of *Petromyzon*.

Eisig (1887, 65), who believed the lateral sense organs to be sometimes innervated by spinal nerves, naturally considered the "lateralis" of *Petromyzon* a lateral line nerve, which conclusion was also taken for granted by Julin (1887, 109). This author, whose conclusions were reprinted in his larger work published in the same year (112), confirms Ransom & Thompson's statements as to the connection of the "lateralis" with the spinal nerves\*, but states further that it is connected with the ventral roots also. His admission at the outset of Langerhans' contention that the Lamprey's "lateralis" is a true lateral line nerve is, omitting that it is a pure assumption, unfortunate, since he is thereby induced to formulate an elaborate theory as to how the connection came about.

\* Julin states in a footnote at the end of his paper that he has discovered connections between the lateral line nerve and the dorsal roots of the spinal nerves in embryos of *Scyllium* and *Spinax*. This connection, to my mind most improbable, has never been confirmed.

This theory, besides being obviously opposed to the facts, is based upon the *probable* mode of development of the "lateralis" nerve of the Lamprey, and assumes that this nerve develops in the Lamprey just as it does in Elasmobranchis.

It seems to me, therefore, that there is room for little doubt as to the morphological value of the "lateralis" nerve of *Petromyzon*, since all the known facts of its anatomy point to the conclusion that it belongs to the accessory lateral series. First, we know that its roots correspond to those of the accessory lateral system in the higher Teleosts, and that besides its posterior or vagal rootlets it has also an anterior or (trigemino-?) facial root; second, its fibres are of the same nature, being somatic sensory in function; and third, it is connected with the spinal nerves in a manner characteristic of the accessory lateral series, and such as to justify Ransom & Thompson's description of it as a commissural nerve. In these three conditions we recognise the most characteristic features of the accessory lateral system of the Teleostean fishes—features which may indeed be described as fully diagnostic of this series of nerves. Finally, the "lateralis" of *Petromyzon* doubtless does include a few lateral line fibres to the scattered sense organs of the body, but these are probably contained in a small accompanying nerve and would of course be morphologically distinct from the main bulk of the "lateralis."

I had written the above before noting that Strong (1895, 204) discusses the same question, and arrives at conclusions precisely identical with mine. He brings out some additional points in favour of the view, which practically establish it as a fact, and which are included in the following quotation (pp. 199-200; see also p. 157):—  
 "Furthermore the N. lateralis [*i. e.* of *Petromyzon*] is formed partly by a recurrent branch from the facialis passing around outside the auditory capsule—a thing which does not occur in the N. lateralis in the higher forms [except in *Protopterus*]. Again, on comparing the course of the N. lateralis with the arrangement of the pits, it is evident that *only a small proportion of them would be innervated by this nerve, which has a position near the mid-dorsal line*. When these facts are considered—*especially the non-derivation of this nerve from the Acusticus centre*, thus differing from the origin so universal for the N. lateralis in all other forms—it must be regarded as very probable that this nerve does not represent the N. lateralis vagi of higher forms . . . . What it does represent is probably the R. lateralis trigemini, so-called, of Teleosts—a nerve which is formed principally, as we have seen, by a recurrent branch of the facialis, derived from the lobus trigemini [?], and which is reinforced by a branch from the vagus. It would then much more probably innervate the papillæ which are so numerous on the dorsal fin, and which probably correspond to the structures innervated by the so-called R. lateralis trigemini." (Italics mine.)

#### P. *GADUS* COMPARED WITH OTHER FORMS.

Hyrŕl (1866, 105) finds the sensory canals of *Lota* in a very curious condition. The lateral or body canals open terminally on to the surface behind, as also do the supra-orbital canals in front, and these are the *only* communications between the sensory canals and the exterior (*i. e.* two on each side)! These openings are situated on fine papillæ.

There are supra-temporal and supra-orbital commissures, and opposite the latter on each side is a large blind caecum, corresponding exactly to the smaller one found by me in young *Gadus vivens*. As three of these caeca are also found on the infra-orbital canal (two posterior and one ventral to eye) in positions occupied in other forms by dermal tubules, they doubtless correspond, as I surmised above in describing the one found in *G. vivens*, to modified dermal tubules. The sensory canals of *Lota* are, further, largely ampulliform. In *Salmo*, W. K. Parker (1873, 152), who regarded the sensory canals as glandular organs, describes the hyomandibular canal as communicating with the lateral or body canal (p. 99), the Salmon in this respect differing from *Gadus*.

From the description given by Emery (1880, 66) it is easy to derive the lateral canals of *Fierasfer acus* from the *Gadus* type. There are, however, some differences, of which the most important are:—(1) there is an anterior infra- and supra-orbital anastomosis, which is an Elasmobranchian rather than a Teleostean character—the anastomosis in *Amia* is between the two infra-orbital canals; (2) the two supra-temporals anastomose across the back to form a supra-temporal commissure, which is situated immediately opposite the operculo-mandibular canal and leaves the body canal on the *squamosal*: the innervation, however, is precisely as in *Gadus*; (3) there is a supra-orbital commissure, but the median unpaired tubule is represented by two posteriorly directed blind sacs; (4) the operculo-mandibular canal does not end blindly behind, but opens into the main canal of the head; (5) the dermal tubules are much reduced in number, and where present are large, blind, and ampulliform as described by Hyrtl in *Lota*. *Fierasfer dentatus* agrees with *F. acus*, but represents a still simpler condition. To put it briefly, *Fierasfer* represents a simplified edition of the Cod type.

Sappey (1880, 175) figures (pl. xi. figs. 1 & 2) and describes (p. 13) a very curious condition of the sensory canals in the “congre commun” (*Conger vulgaris*). The canals are reduced to the two lateral or body canals, and a very short operculo-mandibular canal, which communicates with the body canal on each side and terminates opposite the angle of the jaw in a large ampulla. In *Cottus*, according to Bodenstein (1882, 24), the geography of the sensory canals is much the same as it is in the Cod. There is a supra-orbital commissure giving off a median dermal tubule as in *Gadus*, but the two supra-temporal canals also form a commissure. The operculo-mandibular canal does not anastomose with the body canal. There are fewer dermal tubules, and consequently there must be fewer sense organs. In *Amiurus* Ramsay Wright (1884, 227) describes an occipital commissure, but failed to find one between the supra-orbital canals. The operculo-mandibular canal is separate from the body canal. Fritsch states (1887, 75) that the lateralis lateral line nerve consists of two (upper and lower) rami as in *Gadus*, which he calls respectively the R. superficialis lateralis vagi and the R. profundus lateralis vagi.

An examination of Allis's first *Amia* paper (1889, 4) discloses many points of resemblance between that fish and *Gadus*. We have seen that in the latter fish the sensory canals have a ligamentous support only in two places. In *Amia*, Allis says (p. 469):—“In their passage from one bone to another, where the bones are not naturally connected, the canals lie in a dense connective tissue, which forms the deeper part of the cutis.

This occurs particularly between the frontal and nasal on each side, and between the upper and lower ends of the preoperculum and the squamosal and angular [=articular] respectively." In *Salmo*, according to W. K. Parker, the upper extremity of the operculo-mandibular canal between the preoperculum and the squamosal is supported by a small ossicle, whilst in *Gadus* of course the operculo-mandibular canal ends blindly and is not connected with the main body canal at all. *Amia* agrees with *Salmo* in that the mandibular and body canals are connected near the posterior extremity of the squamosal. There are two commissures between the sensory canals of *Amia*—an infra-orbital commissure at the extremity of the snout, and a supra-temporal commissure on the back. In *Gadus* the supra-temporal canals, which correspond precisely to the commissure in *Amia*, are not united across the back, whilst the infra-orbital commissure is similarly absent, but the supra-orbital commissure, which is very characteristic of the modern Teleostean fishes, is, on the other hand, wanting in *Amia*.

I have previously remarked (p. 132, also p. 205) on the anomalous condition of the so-called squamosal or pterotic of *Gadus* (Pl. 21, fig. 1, *Se.*), and it is very interesting to note that the post-frontal or sphenotic of *Amia* is in a very similar condition. Allis says (pp. 478. 479):—"The dermal portion of the post-frontal is a small bone, somewhat triangular in shape, exactly filling a large notch extending from the middle of the lateral edge of the frontal to the hind edge of the bone. Its small posterior end usually fits into a notch on the anterior end of the squamosal, which overlaps somewhat its lateral edge. It rests directly upon the deeper post-orbital ossification, and is so closely connected with it that in attempting to remove it in fresh specimens one of the bones is usually broken, and a fractured surface obtained; but in skeletons properly prepared—by maceration or boiling—the two bones are easily parted, leaving a clean and perfect surface of separation." These facts open up questions of considerable import, especially one which I have previously mentioned, as to how far we may regard the ear ossicles (sphenotic, pro-otic, epiotic, pterotic, and opisthotic) as modified lateral line ossicles. In any case it seems to me that the dermal portion of the post-frontal or sphenotic of *Amia* should be kept perfectly distinct from that bone, and should rank as a lateral line ossicle since it is developed round a portion of the infra-orbital canal. (But cp. p. 132.) The same remark applies to the separate pterotic or squamosal of *Gadus*. Both bones are precisely comparable to true lateral line ossicles such as the lachrymal or preoperculum.

Before proceeding to compare *Amia* and *Gadus* in detail we may note that the lateral or body canal of the former corresponds to the condition previously described in *Gadus*. Allis states (p. 491):—"Towards the tail there are usually but one or two pores in a scale, and the development here is often so greatly arrested that the lateral canal, through one or more scales, is an open channel." Again, on p. 504:—"On the body, and particularly towards the tail, the organs retain nearly this [superficial] condition even in the adult; but on the head they are later so much withdrawn from the surface that only a series of minute holes indicates their position."

In *Amia* there are 47 \* sense organs on each side of the head, counting as far back as the supra-clavicle, as against 32 in *Gadus*. These have the following distribution:—

\* Allis (p. 499) says "forty," but this is doubtless a miscalculation, since the numbers he gives total 47.

(1) *Supra-orbital canal*.—In *Amia* there are three on the nasal and four in the frontal, of which the first nasal and the last frontal are those perhaps missing in *Gadus*. In both types the sense organs are fewer than in any of the other canals. The second dermal tubule of *Amia* is missing in *Gadus*, the fourth undoubtedly corresponds to the 3rd of *Gadus*, whilst the 6th, 7th, and 8th of *Amia* are again missing. Indeed, the *Gadus* supra-orbital is, for perhaps some functional reason, exceptionally abbreviated.

(2) *Infra-orbital canal*.—I must first protest against Allis's definition of this canal, which is very unphilosophical. He considers rightly the innervation of the lateral canals to be the best criterion of their boundaries, and applies this method to all but the infra-orbital canal, yet offering no justification for the exception. Behind the operculo-mandibular anastomosis the main canal is innervated by the lateralis lateral line nerve (including the lateral line branch of the IXth, which belongs to the lateralis), and this should determine the boundary of the body canal: in fact the operculo-mandibular anastomosis with the main canal is situated between the infra-orbital and lateral canals. Ewart (1892, 68) also criticises Allis's definition of this canal, and considers, with the writer, that its posterior segments belong to the lateral canal, whilst Miss Platt (1896, 158) agrees with Ewart and correctly limits the infra-orbital canal to the buccal nerve. I hence consider Allis's sense organs 17–21 infra-orbital to be situated on the lateral or body canal.

The ethmoid and ant-orbital or pre-orbital ossicles of *Amia* are unrepresented in *Gadus*. Both are probably lateral line ossicles and do not belong to the skull *sensu stricto*—the ant-orbital being doubtless a modified sub-orbital plate. This difference makes it difficult to homologise the sense organs of the two forms, but assuming that the first post-orbital of *Amia* represents two fused ossicles, as seems probable, then sense organs 9 . 10 . 11 . 12 . 13 *Amia* = 6 . 7 . 8 . 9 . 10 *Gadus*. Sense organ 14 of *Amia* in the sphenotic is absent in *Gadus*, but the course of the otic nerve in the latter form is marvellously suggestive either of its having once existed there, or, what is perhaps more probable, that it has shifted backwards and now forms the 11th sense organ on the pterotic. The otic branch of *Amia* innervates two sense organs, both on the pterotic, of which the 16th seems to be the one missing in *Gadus*, since the 16th dermal tubule is absent. Dermal tubules 13 and 14 *Amia* are also wanting in *Gadus virens*, but 13 is present as No. 9 in *G. morrhua*. The absence of 13 in *G. virens* is somewhat remarkable, but I have not seen it in any of the specimens I have examined. The outer buccal nerve is represented in *Amia* by the branches to sense organs 11 . 12 and 13 infra-orbital, with perhaps the branch to sense organ 14.

(3) *Hyomandibular canal*.—The dentary of *Amia* bears 7 sense organs as against 6 in *Gadus*, but it would be impossible to say which was absent in the latter genus. The canal then enters in *Amia* what Allis calls in his first paper the “angular,” but is somewhat doubtful about the point. The bone undoubtedly corresponds to the Teleostean articular, which homology Allis has recognised in his last paper. Bridge's small ossicle and Allis's ossicle  $\alpha$  (1897, 6, figs. 1 & 2) are doubtless comparable to the Teleostean angular. There are three sense organs in the Amian articular as against one in *Gadus*, and six in the preoperculum as against five. In the latter case there can be little doubt

that it is the organ 16 of Allis that is wanting in *Gadus*, and further that dermal tubule 11 *Amia* corresponds to No. 8 *Gadus*.

(4) *Lateralis canal*.—Here it is at once obvious that the first organ of *Amia* situated in the squamosal (=the glossopharyngeal organ No. 17 infra-orbital Allis) is absent in *Gadus*. The next four (*Amia*) are situated in the single supra-temporal or extra-scapula, and these doubtless correspond respectively to the first four sense organs and the four supra-temporals of *Gadus*. It is possible that facts like this (and there are many others) show that each sense organ had originally its own supporting ossicle. The post-temporal or supra-scapula of *Amia* has one sense organ, but none in *Gadus*, whilst a further difference is that the scapula or supra-clavicle of *Amia* supports a portion of the body canal and two sense organs, but takes no part in the support of the canal system of *Gadus*. It is true that some authors consider the supra-clavicle a post-temporal ossicle, but it is impossible to satisfactorily homologise the two bones, and hence the difference between *Amia* and *Gadus* must remain. Behind the region of the skull and shoulder girdle both forms agree in that the lateral line or body canal is supported at intervals by small lateral line ossicles.

We thus see that the two forms agree in a very remarkable manner. This will be seen if a comparison be made between Allis's fig. 49 and fig. 2 of this paper. Except that *Amia* has more sense organs, and omitting differences in detail, the Ganoid form does not differ as much from the Teleostean form as many of the latter do among themselves. In fact the resemblances between the two are much more remarkable than their points of difference. These facts of course strongly support the view originally maintained by fossil Ichthyologists that the Ganoids cannot be ordinarily separated from the Teleosts.

Guitel (1890, 94) describes the lateral line nerve in Cyclopterids exactly as it is in the Cod. There are the dorsal and ventral rami—the dorsal innervating the anterior part of the body canal, and the ventral the posterior moiety. The same author (1891, 95) has given us a somewhat full paper on the lateral line of *Lophius*. He has unfortunately made an insufficient study of the literature, and hence misnames the nerves. He states, for example, that the supra-orbital canal is innervated by the "ophtalmique du trijumeau," and also that a part of the operculo-mandibular line is supplied by "le nerf operculaire superficiel du pneumogastrique qui échange des fibres avec l'operculaire superficiel du facial." Further, the infra-orbital canal is said to be supplied by the "maxillaire supérieur du trijumeau." Guitel mentions Allis's first *Amia* paper, but omits to state on what grounds he rejects the latter's nomenclature and adheres to the old views. His errors are perhaps largely explained by the fact that he did not follow out the components of the nerves with the microscope. A supra-orbital commissure is described as in *Gadus*.

In Elasmobranchs we find the lateral line system in its most complex form. Beyond in a very general way any comparison between the sensory canals of Elasmobranchs and bony fishes is somewhat out of the question. This is very largely due to the absence of dermal bones, which afford a very valuable guide in determining the homologies of the individual sense organs and portions of the canals. Ewart (1892, 68) describes infra-orbital and supra-temporal anastomoses in *Lamargus*, the former lodging two sense organs. The infra-orbital also anastomoses with the supra-orbital and hyo-

mandibular, and the otic nerve innervates the free anterior extremity of the lateralis canal, which extremity must therefore be considered to belong to the infra-orbital line. In the Skate (*Raia batis*) the remarkable reduction of the dermal tubules in several places is a noteworthy feature, and enjoins an investigation into the development of these portions of the canal system (Ewart & Mitchell, 1892, 69).

Pollard (1892, 161) states that the superficial ophthalmic and buccal lateral line nerves arise from a single trunk in *Clarias* (p. 529) and *Auchenaspis* (p. 532). This is interesting when we remember the description of the development of these canals given by Wilson, Mitrophanow, and Loey. In *Callichthys*, however, the otic nerve arises separately from the ganglionic complex and not from the buccal nerve (pp. 534-535). In *Clarias* sense organ 1 of the lateralis canal (= s. o. 7 main canal, Pollard) is stated in the text (p. 529) to be supplied by the glossopharyngeal, whilst the figure of this form shows an innervation from the lateralis lateral line nerve. On p. 534 in *Callichthys* the ampullation of the "main canal" is described as a "remarkable phenomenon hitherto unrecorded in any other animal." It is in fact described by several authors, notably by Traquair (1865, 207), Hyrtl (1866, 105), and Sappey (1880, 175). In *Clarias*, *Auchenaspis*, and *Chatostomus* the operculo-mandibular canal communicates with the body-canal, but in the Siluroids, where the canal system is reduced, it is unconnected with any of the other canals. In comparing the lateral line system of Siluroids with *Coccosteus*, Pollard apparently overlooked until too late the accurate description by Traquair published two years before, and makes use of the somewhat erroneous figure by Pander.

The lateralis lateral line nerve of *Percu*, according to Cuvier and Valenciennes (1830, 57), Vogt and Yung (1894, 215), and other authors, is in much the same condition as in *Gadus*, dividing into an upper ramus to the anterior portion of the body canal, and a lower ramus to the posterior portion of the same canal\*. Herriek (1897, 98) finds in the highly specialised Acanthopteran *Menidia* that although macroscopically the nerves are fused and their relations disguised, yet microscopically the whole of them may be reduced to the common type, of which *Leamargus*, *Raia*, *Chimera*, *Protopterus*, *Amia*, *Gadus*, and the Siluroids are other examples. The vagus ganglion can be broken up into five ganglia—four of which belong to the branchial nerves and one to the visceralis. Herriek finds the body canal of *Menidia* occupying a superficial position posteriorly just as it does in *Gadus*, and further points out that the lateral line branch of the glossopharyngeus is really a branch of the lateralis. The common origin of the lateral line and auditory nerves is confirmed, and the V-VIIth nerves arise by a double root as in *Gadus*, of which the ventral one is the motor root of the facial and is connected with the hyomandibular trunk only. All the lateral line nerves, except the lateralis, arise from the dorsal root of the trigemino-facial complex, but in two bundles—a dorsal bundle for the superficial ophthalmic+buccal, and a ventral bundle for the external mandibular. The otic nerve innervates three sense organs, whilst two apparently derive

\* In *Protopterus* there are four rami to the lateralis, and all distinctively lateral line nerves (Pinkus, 1894, 157), whilst the accessory lateral system is completely absent.

their innervation from the glossopharyngeus. There is thus a general agreement between *Gadus* and *Menidia*, and the differences between them are certainly not greater than between *Gadus* and *Amia*.

#### Q. THE LATERAL SENSE ORGANS OF VERTEBRATES AND INVERTEBRATES.

Before proceeding to discuss the phylogeny of the lateral sense organs, it is first necessary to enquire into the evidence relating to their supposed homology with the lateral organs of Invertebrates, as maintained by Eisig, Whitman, and other authors. The bulk of the evidence is against such an homology, but the position of some morphologists with regard to the question renders its discussion somewhat necessary.

Leydig (1868, 126), who was one of the first authors to conclude that Savi's vesicles, Lorenzini's ampulke, and the sensory canals all belonged to the same system, *i. e.* the lateral line system, was also the first to connect the lateral sense organs with the sense organs of Annelids. This view was, however, first elaborated in detail by Eisig (1879, 64, and 1887, 65), who in his Naples monograph devotes considerable attention to the question (pp. 501-547). He endeavours to show that the two series of organs are homologous in all essential respects, and even goes to the length of comparing a transverse section through the branchial region of a Vertebrate with an inverted transverse section of a Capitellid worm. The resemblances to which he draws attention in this connection are of a very superficial character, and certainly not sufficient to establish the relation of the two sets of sense organs on a reliable foundation. Eisig seems to have been misled by mistaking the lateralis nerve of the Lamprey for a true lateral line nerve, for his theory demands that the lateral organs of Vertebrates should be metameric, and the lateralis nerve of *Petromyzon*, if a lateral line nerve, would strongly support that view. We have already seen, however, that the bulk of the evidence is against the primitive metamerism of the vertebrate lateral line system, and this consideration in itself is sufficient to disprove the theory that Eisig seeks to maintain. Balfour, writing however, before the publication of Eisig's mature views, says (1881, 9, vol. ii. p. 143):—"The organs which resemble those of the lateral line are the remarkable sense organs found by Eisig in the Capitellidæ; but I am not inclined to think that there is a true homology between these organs and the lateral line of Vertebrata."

In his first paper, Whitman (1884, 219) compares the segmental sense organs of the Leech with the vertebrate lateral line, and believes that both may be traced back to a common origin. In his next work (1889, 220) he considerably develops this view, and considers further that the lateral organs have served as a starting point not only for the taste organs, nose, and ear, but also for the eye. He assumes, what is indeed possible, that the vertebrate lateral organs were derived from invertebrate sense organs of some sort, but it is only adding assumption to assumption to further postulate a metameric arrangement for these sense organs. The evidence is in fact wholly insufficient to justify a comparison between the two series of organs, and it is hence to be regretted that Dr. Whitman did not, as far as I am aware, fulfil his expressed intention of publishing more fully on the question.

Beard (1888, 21), who at first combated Eisig's views, finally accepts them in the following words (p. 216):—"Like Dr. Eisig I support, as the result of these researches, Kleinenberg's view of the homology of the spinal ganglia of Vertebrates, and the parapodial ganglia of Annelids. But I go further, and say that what in the sense given above may be called the cranial neural ganglia of Vertebrates, are also morphologically equivalent to the parapodial ganglia of Annelids. I am also fully prepared now to accept with Eisig the homology of the branchial sense organs of Vertebrates with the Seitenorgane of Annelida." That the branchial sense organs, which are doubtless more archaic structures than the lateral sense organs, and were perhaps, if not now, primitively segmental, correspond to the segmental sense organs of Annelids is most probable, but we have already seen that the branchial sense organs are not the lateral line organs, and hence Eisig's comparison must in the meantime lapse.

Further opposition to the Annelidan homology is supplied by Wilson (1891, 225), who opposes Eisig's views, and points out, what we now know to be true, that the Capitellidan lateral sense organs have a totally different development to the lateral organs of Vertebrates. Ayers (1892, 7), after insisting that the "auditory organs of Invertebrates are not the forerunners or the ancestral forms of the vertebrate auditory organs" (p. 317), remarks that "it is of course possible that other sense organs of the invertebrate body have developed in the course of descent into the canal organs from which the vertebrate ear arose." Mitrophanow (1893, 143) is very emphatic on the point. He maintains that the lateral sense organs of Vertebrates have nothing in common with the lateral organs described by Eisig in Capitellids, and states, what I have previously discussed, that the former are not metameric (pp. 211-216)—a vital difference between the two series of organs. Finally, Leydig (1895, 128) and Loey (1895, 130) are somewhat in favour of the comparison, the latter, however, whilst connecting vertebrate with invertebrate sense organs, considering the branchial sense organs, and not the lateral organs, to be the homologues of the sensory papillae of Annelids.

To sum up, there are two, to my mind fatal, objections to Leydig's and Eisig's views that the segmental sense organs of Annelids are the direct homologues of the lateral sense organs of Vertebrates. Before such a comparison can be said to hold good, the most essential feature of the invertebrate organs, *i. e.* their metamerism, must be satisfactorily established in their supposed homologues, the vertebrate lateral sense organs. We have already seen that the latter are metameric only on the body, and that this metamerism is purely secondary, whilst there is practically no evidence to show that the vertebrate organs were primitively segmental. My second objection is based on the palaeontological fact that the vertebrate lateral line system is an extremely archaic structure. It existed in the oldest fossil fishes known, *i. e.* in Silurian times. If, therefore, we accept Dr. Eisig's homology, we must believe that the sense organs of the specialised Annelids have had an ancestral history equally archaic. This of course is possible, but it is to my mind too improbable to base even a speculation upon, and perhaps what shadow of possibility it has is removed by the fact that the Invertebrates possessing lateral sense organs cannot be considered primitive forms.

## R. THE PHYLOGENY OF THE LATERAL OR SENSORY CANALS.

The solution of this problem directly follows on the systematic arrangement of the known facts of the anatomy and development of the lateral line system. The history of our knowledge of the phylogeny of the sensory canals is coincident with three discoveries—the discovery that the “mucous” canals contained sense organs, the discovery of Savi’s vesicles, and the discovery of the ampullæ of Lorenzini. As I propose to view the evidence in a somewhat new light, and hope to indicate the various stages through which the sensory canals have passed before reaching their present condition, I have devoted a section to the consideration of the above question.

Lorenzini’s discovery of the existence of the ampulliform type of “mucous” organ, as apart from the canal type discovered by Steno, was further augmented in 1844 by Savi (178), who described (pp. 332–340) on the ventral surface of *Torpedo* a number of sensory pits which he called the “appareil folliculaire nerveux,” and which he thought were innervated exclusively by the Vth nerve, and failed to find in other forms. He was further unable to determine either their homology or their function. We now know that all three types belong to the lateral line system, and I shall suggest that they represent three stages in the development of a canal—the most superficial condition, represented by the pit organs and Savi’s vesicles; the full development, represented by the canal; and the intermediate type, forming neither a Savi’s vesicle nor yet a canal, represented by the ampullæ of Lorenzini.

In 1852, H. Müller (145) stated his belief that the “mucous” canals were primarily a sensory and only secondarily a mucous apparatus. He and Leydig were the first authors to rank together as sensory structures the pit organs, ampullæ, and “mucous” canals of Savi, Lorenzini, and Steno. McDonnell, however (1860–71, 137), still considered them to be organs for the secretion of mucus, nor did he think that Savi’s vesicles belonged to the lateral system. The latter view is shared by Boll (1875, 27), who believed in the independent nature of Savi’s vesicles, nor did he consider them connected with the electric organs as some authors had done. He states, as Savi did, that they are innervated by the trigeminal nerve. Dercum (1880, 59) goes further, and considers both the vesicles of Savi and the ampullæ of Lorenzini to be independent of the “mucous” canals.

An important contribution to the question is supplied by Emery (1880, 66), who, as far as I am aware, first discovered what undoubtedly correspond to Savi’s vesicles outside *Torpedo* (*i. e.* in *Fierasfer*). These organs are situated at the bottom of epidermal pits—each pit communicating with the surface by a slit like aperture, and containing only one sense organ, which corresponded in structure with the sense organs in the lateral canals. They were found in regular lines on the body, and in some of the lines *the sense organs were connected by shallow longitudinal epidermal depressions*. These organs, besides corresponding to the vesicles of Savi, are further homologous with the pit organs of Allis and the “Spait-papillen” of Fritsch and Ewart & Mitchell. Fritsch’s term was obviously suggested by the nature of the apertures of the sacs. Whilst I do not mean to assert that the vesicles of Savi, the sensory depressions of

Emery, the pit organs of Allis, and the "Spalt-papillen" of Fritsch and Ewart & Mitchell are the same in every structural detail, it cannot be denied (1) that all these organs belong to the lateral line system, and (2) that they are all varieties of one form of sense organ representing the first stage in the phylogeny of a sensory canal.

Merkel's work (1880, 138), published independently of Emery's, places the whole question on a solid basis of fact. He showed that there were several kinds of epidermal pits, all differing but slightly from each other, and yet roughly characteristic of the different groups of fishes. His sharp distinction between the "Endknospen" or terminal buds, which do not belong to the lateral line system at all, and the sensory pits, which do, has been of the utmost service in determining the homology of the latter in the various groups of fishes. He further pointed out that the presence of these pit organs is correlated with the occurrence of other sense organs of the lateral line system, *i. e.* that they were most numerous in those Teleostean fishes where the canal organs were reduced in number, and *practically absent in the Elasmobranch fishes, where they are replaced by the ampullæ of Lorenzini.* The importance of this fact will be emphasized further on. Sappey (1880, 175) makes some curious mistakes. He considers Lorenzini's ampullæ to be "glandes," but distinguishes between the ampullary system and the canal system—the latter having no "glandes" and consisting of canals opening on to the surface by a variable number of tubules (=dermal tubules). Sappey believed the "non-glandular" sensory canals to be probably tactile in function. It is interesting to note that Solger considered a line of pit organs to represent a potential canal, and he describes (1880, 193) the lines of pit organs accompanying the lateral or body canal as accessory lateral lines.

Balfour's views on the question are in many respects prophetic, and of such importance as to be quoted *in extenso*. He says (1881, 9, vol. ii. p. 445): "It is clear that the canal of the lateral line is secondary, as compared with the open groove of *Chimæra* or the segmentally arranged sense bulbs of young Teleostei; and it is also clear that the phylogenetic mode of formation of the canal consisted in the closure of a primitively open groove. The abbreviation of this process in Elasmobranchii was probably acquired after the appearance of the food-yolk in the egg, and the consequent disappearance of a free larval stage. While the above points are fairly obvious, it does not seem easy to decide *à priori* whether a continuous sense groove or isolated sense bulbs were the primitive structures from which the canals of the lateral line took their origin. It is equally easy to picture the evolution of the canal of the lateral line either from (1) a continuous unsegmented sense line, certain points of which became segmentally differentiated into special sense bulbs, while the whole subsequently formed a groove and then a canal; or from (2) a series of isolated sense bulbs, for each of which a protective groove was developed, and from the linear fusion of which a continuous canal became formed\*. From the presence, however, of a linear streak of modified epidermis in larval Teleostei, as well as in Elasmobranchii, it appears to me more probable that a

\* Since this was written, Allis has described the lateral canals of *Amia* as arising in precisely the manner here described (*i. e.* 2).

linear sense streak was the primitive structure from which all the modifications of the lateral line took their origin, and that the segmentally arranged sense bulbs of Teleostei are secondary differentiations of this primitive structure." Wright (1884, 227), who insisted on the histological difference between the terminal buds of Merkel and the lateral sense organs of *Amiurus*, re-discovers the pit organs of Emery and Merkel\*, and calls them the "accessory lateral organs," whilst Eisig considers the mucous sacs of *Myxine* to be very ancient structures and homologises them with the lateral mucous organs of Annelids. He further thinks it probable that the latter have been incorporated or bound up with the vertebrate lateral line organs.

The cousins Sarasin, who believed that all the cells of a lateral line organ were formed by the division of a single cell, announce the interesting discovery of two accessory sense organs in *Ichthyophis* (1887, 177). One of these organs is a flask shaped structure containing a club like "cupola," and which is called the "Nebenohr" or "Becherorgan." An examination of the description of this structure at once suggests the probability that it corresponds to a Lorenzini's ampulla of a cartilaginous fish. The other sense organ is a more superficial structure, and this may be said to represent the fish pit organ as described by Emery, Allis, and Ramsay Wright. The peculiarity about the various species of more or less superficial sense organs found in Fishes and Amphibia is that whilst they are sufficiently similar in structure to denote a genetic affinity, yet the corresponding organs in different types never precisely agree.

Fritsch and Garman were, as far as I am aware, the first authors to state that the pit organ class of sense organ belonged definitely to the lateral line system. Earlier authors, as already stated, had agreed in ranking together the three classes of integumental organs as sensory and not mucus secreting structures, but hitherto no one had recognised that Savi's vesicles, pit organs, &c., Lorenzini's ampullæ, and the lateral canals themselves, all belonged to one and the same system. Fritsch's works (1888, 76, & 1890, 77) contain the first description of the "Spalt-papillen" of *Raia* previously referred to, and which I homologised with the pit organs and Savian vesicles of other forms, whilst Garman not only recognised the connection of the pit organs with the lateral line system, but also rightly saw in them organs in an intermediate or transitory condition. He considers in fact that the pit organs are on their way to becoming canal organs, but his assumption that they are consequently functionless is a physiological anachronism which is somewhat out of the question.

In his first *Amia* paper, Allis (1889, 4) describes the development of the sensory canals as occurring in the manner foreshadowed by Balfour. He says (p. 536): "The canal organs also sink below the surface, but they carry with them the surrounding tissues, and by a process of infolding become enclosed in short canals, each containing a single organ. These short canals then become continuous, a single surface opening being left between every two consecutive organs along each line. These simple openings, or primary pores, may be retained in the adult, but most of them undergo a repeated dichotomous division, thus giving rise to groups of surface pores and to corresponding dendritic systems of

\* Wright, however, was writing without access to Merkel's work.

canals." Before this can take place, however, the anlage of the system must be formed, and Allis finds (p. 535) that "each group [*i. e.* line of sense organs] develops from the cord of cells lying in the deeper layers of the epidermis, and each cord from a special sensory thickening, which when first seen from the surface in specimens hardened in chromic or micro-sulphuric acid, appears as a large, whitish, and slightly raised spot." From this anlage all the canal organs arise, and "in the early stages of their development lie below the surface, but they soon push through the overlying epidermal cells, and their upper central portions become exposed. Each pit organ subsequently sinks slightly below the surface, and a little epidermal pit is formed above its central portion" (p. 536). The canal organs are developed as above described. Combining Allis's results first with the work of Balfour and the earlier embryologists and then with the recent observations of H. V. Wilson, Mitrophanow, and Locy, we are enabled to draw up the following scheme\* of the development of the lateral canal system, which is known to apply to some, if not to all, fishes:—(1) A small sensory anlage arises in the neighbourhood of the ultimate position of the auditory organ, the differentiation of which gives rise both to the auditory organ and the system of sensory canals. (2) This anlage grows forwards and backwards as a *non-segmental* cord of cells. In front this cord bifurcates and forms the anlagen of the supra- and infra-orbital canals. Behind it forms the anlage of the lateral or body canal. (3) Along the non-segmental cord arise series of sense organs, which, in the case of the body canal are segmental, but are not known to be such in the other canals. (4) Each sense organ sinks down, carrying the skin with it, so that it ultimately lies at the bottom of a groove. The lips of the groove fuse—each sense organ therefore lying in a short tube opening at each end on to the surface by a pore (= "half pore," Allis). (5) The short tube extends both ways and fuses with the two adjacent tubes, adjacent half pores fusing to form a single "primary" pore which in most fishes forms the external aperture of a dermal tubule. In the Ganoid fishes the primary pore, by a process of repeated dichotomy, produces what is known as a "dendritic system." A lateral canal is therefore formed by the end-to-end fusion of pieces or segments, and not by the formation of a primitive continuous furrow, and it further follows that there must have been primitively a dermal tubule between every two adjacent sense organs.

Bateson (1889-90, 10) fails to distinguish between terminal buds and pit organs, and although pointing out that these two sets of organs have not the same histological structure, seems to have overlooked the previously described fact that the pit organs belong to the lateral line system. According to Coggi (1891, 42), Savi's vesicles develop in the same way in *Torpedo* as the sense organs of the lateral canals, but his description differs somewhat from Balfour's observations on *Scyllium*. Ayers (1892, 7), who occupies an isolated position on some aspects of the question, believes Savi's vesicles to have been produced retrogressively from canal organs, and considers that they are "without doubt descendants of the canal organs" (p. 161). He bases this opinion on the observations of Fritsch, which he thinks show that the Savian vesicles

\* This scheme ignores the operculo-mandibular canal, of the development of which our knowledge is still very imperfect. I see no reason, however, why it should not develop in just the same way as, for example, the infra-orbital does, *i. e.* by branching from the main trunk.

“are transformed from the canal type during ontogeny,” and concludes that “the Torpedoes possess a system of organs which is lacking in all other Batoids, but which is represented in these forms by the more primitive canal type.” It cannot, I think, be admitted that there is any foundation for the view that Savi’s vesicles are degenerate canal organs. The observations of Allis, Coggi, Boll, Merkel, and numerous other authors, show that the pit organs, Savian vesicles, and other more or less superficial sense organs, develop as the canal organs do up to a certain stage, but that there they stop. There is no evidence of retrogression, and none in fact that any of the lateral line organs ever acquire a more central position than that which they ultimately occupy in the adult. The fact that a sensory canal of one form may be represented by a line of pit organs in another, may be more reasonably explained by precisely the opposite hypothesis, *i. e.* that the one type represents a more advanced condition than the other. This is the view adopted by most morphologists, and the one that has the sanction of the facts\*.

The pit organs of *Amia* are correctly homologised by Ewart & Mitchell (1892, 69) with the sensory follicles they described in the Skate and the “Spalt-papillen” of Fritsch. Bashford Dean (1895, 58), in referring to the phylogeny of the lateral canals, says (p. 49):—“The ancestral condition of the lateral line of Sharks appears to have been represented in an open continuous groove, lined with ciliated sense cells, and protected only by an overlapping margin of shagreen denticles. In this condition it at least exists in the ancient Sharks and in *Chimera*. That the canals of the head region were also primitively of this character appears exceedingly probable; they are thus retained in the adult *Chimera*.” Leydig (1895, 128) gives a brief expression to a very important and significant fact when he states that there are so many varieties of lateral sense organs, from the superficial organs to the canal organs, that it is impossible either to divide them into groups or even to draw sharp lines between individual forms.

A passage in Miss Platt’s work on *Necturus* (1896, 158) is interesting in this connection. She says (p. 526):—“At each side of a mid-dorsal fold in the skin a row of mucous glands is found, composed of a few cells invaginated from the deeper layer of the ectoderm, and now lying below the surface, tiny balls of cells surrounding a central cavity that opens to the surface by a small pore. Similar glands are found on the ventral surface of the body between the fore-limbs, and on the tail. Although these glands are about the size of sense organs, nothing in their structure or in the manner of their development suggests the genetic affinity of sense organ and mucous gland on which Leydig [1895, 128] insists.” Whilst it is true, as Miss Platt maintains, that there is no genetic affinity between the lateral sense organs and mucous glands, it is also true that a lateral sense organ consists of sensory and secretory portions, and it is indeed probable, as Eisig suggests, that certain dermal mucous organs have become incorporated into the lateral line system. In his last *Amia* paper (1897, 6) Allis says (p. 627):—“In early stages of development they [*i. e.* canal organs and pit organs] closely resemble

\* Ayers’ views on the morphology of the semicircular canals compel him to take up the position that he does (see particularly pp. 218-220). Nevertheless I submit that *there is no known fact in the history of the lateral line system tending to show that there is any differentiation in the canals after they are once enclosed.*

each other, but in later stages they differ greatly, the pit organ retaining its embryological form and individuality, while the canal organ first increases greatly in size, and then, by the independent growth of other similar organs immediately adjoining it, gives rise to a large sensory patch, or nerve ridge (Merkel), in which the separate organs lose to a greater or less extent their individuality." Again, on p. 629, he says:—"A line of pit organs represents apparently the possibility of a canal; with the disappearance of the organs the possibility of the canal, even in rudiment, would certainly disappear."

A striking fact in the comparative anatomy of the sensory canals that has hitherto been overlooked is the relative abundance of the mucus secreted. Starting with the Cyclostome fishes, we find most elaborate mucous organs and a very imperfectly developed lateral line system. In *Myxine* the mucous sacs occupy the position of the lateral or body canal in the higher fishes, and I think it must be agreed with Eisig and Dohrn that these sacs represent very archaic structures which must have existed before the lateral canal system itself. In the Elasmobranch fishes we get a condition in which mucous and sensory elements are combined, but in which the sensory elements as it were have developed at the expense of the mucous elements. In other words there is a combination of sensory and secretory cells, but the latter now exercise a subordinate (though prominent) instead of a predominant function. Above the cartilaginous fishes the mucous elements become more and more reduced, until the minimum is reached when they are reduced to a few secretory cells at the base of each sense organ. Further, in the recent Teleosts, the sense organs themselves are unmistakably reduced in number—in some cases very considerably. The lateral sense organs were, as is well known, for a long time regarded as secretory organs. On the discovery, however, of sense organs in the canals, opinion veered round to the other extreme, and completely ignored the undoubted occurrence of glandular structures in the lateral canals and ampullæ. This is the further surprising since the existence of such structures is to be expected. The other sense organs of the head—the nose, the eye, and the ear—have all accessory glands connected with them, and the physiological necessities of the lateral sense organs postulated the existence of glandular cells here also. Now the glandular organs appear to have played at first a predominant, and then an accessory part in the history of the lateral line organs, and it consequently follows that if they were at first predominant they were also pre-existent and independent structures. There is therefore, in my opinion, some justification for the view that the sensory and secretory portions of the lateral line system were at first independent of each other, and that the incorporation of the latter into the former necessarily followed on the adoption of the canal in preference to the superficial type of sense organ. The rapidly evolving lateral line system, as it sank below the surface, seized on the glandular organs and subordinated them to its own use. But what is this use? I think it is sufficiently obvious. From the structure and consistency of the lateral canal mucus, it follows that it has considerably departed from its original function of lubricating the surface of the body, and can no longer perform that function. In the lateral canals it forms a delicate jelly, the "shivering" of which agitates the sensory hairs and thus conveys a message from without. It thus corresponds precisely to the endolymph of the ear, is physiologically unnecessary in a superficial

sense organ, but became an obvious necessity when the superficial organs, increasing in number, size, and sensitiveness, were sinking below the surface. The later process, whilst it afforded the desirable protection to the sense organs, necessarily removed them further from the sphere of their activity and demanded the physiological compensation supplied by the introduction of mucus into the canals.

That the superficial type of sense organ preceded the central canal organ, or, in other words, that the sensory canals arose primitively on the surface and then sank into their usual subdermal position as definite canals, is to my mind amply proved both by fossil Ichthyology and Embryology. The former shows us that in the most ancient fishes known, such as the Ostracoderms, Arthrodira, and the older Sharks (*Cladoselache*, *Cladodus*), the lateral canals existed as superficial grooves, which must therefore be held to be the most primitive known condition. The development of the canals in existing fishes is further evidence in the same direction, and tells us that superficial grooves arise first by a process of decentralisation, whilst the canals themselves are formed in segments afterwards *in situ*. These two considerations enable us to form a general idea as to the lines upon which the lateral canals were laid down. Turning to the comparative anatomy of the system, we can not only confirm the view suggested by the above evidence, but are enabled to follow the process in some detail. Whilst I fully concur in Leydig's contention previously mentioned, we may for the purposes of convenience classify the lateral sense organs under three heads, as follows:—

- |                                |   |   |              |
|--------------------------------|---|---|--------------|
| (1) <i>Superficial type</i>    | } | (a) Pit organs <i>sensu stricto</i> , as in Teleosts. Most superficial.                         |              |
|                                |   | (b) Savian vesicles ( <i>Torpedo</i> ) and nerve-sacks (Ganoids). Intermediate between 1 and 2. | Intermediate |
| (2) <i>Intermediate type</i> . |   | Ampullæ of Lorenzini (Elasmobranchs).   |              |
| (3) <i>Central type</i> .      |   | The canal sense organs (almost all fishes).   |              |

Here we have a continuous series connecting the superficial sense organs on the one hand with the canal organs on the other, and indicating the manner in which the canals and their organs may have been produced. In nearly all fishes the lateral line system is in a very unstable condition. In Elasmobranchs the pit organs have sunk below the surface, and have been converted either into Savian vesicles or ampullæ of Lorenzini, principally the latter, with the result that pit organs *sensu stricto* are largely absent. In Teleosts, where Lorenzian ampullæ are absent, we find, as we should expect, the pit organs on the surface, and existing in large numbers, perhaps as compensation for the more or less reduction of the canal organs themselves. In Ganoids, where the canal system, as far as our limited information goes, still flourishes, the pit organs are comparatively few and have in some cases been converted into what Merkel calls nerve-sacks. In many cases we find undoubted evidence of a canal in one form being represented by a line of pit organs in another, showing that the latter represent the possibility of a canal. Thus there seems to be a constant migration of sense organs from the surface to the interior—a constant stream of superficial organs inwards forming canals and organs in some cases and reinforcing them in others. It is easy to see, for example, from what we know of the development of the canal organs, how a line of ampullæ might form a canal. The insinking would only have to form a furrow

instead of an ampullary tube, and every condition for the development of a canal would be satisfied, since the latter, as we know, is formed in segments. This brings us to the final question as to whether the canals were originally formed as continuous furrows or by the fusion of contiguous pieces. On this point the evidence is unanimous and conclusive. The comparative anatomy of the different classes of sense organs and canals, and especially the development of the latter where known, prove beyond doubt that the lateral canals were formed, not by the closure of continuous furrows, but by the fusion end to end of adjacent tubes. The precise processes, as far as can be judged, would take place in the following order:—(1) Formation of cords of indifferent cells along the lines of the future canals; (2) differentiation of sense organs along these cords; (3) sinking down of each sense organ to form a furrow, and the fusion of the lips of the furrow to form a tube open at each end; (4) fusion end to end of series of these tubes in such a way that continuous canals are formed, and there is an opening on to the surface between each two sense organs. Such, I believe, has been the phylogeny of the sensory canals, and the question must now be left for further investigation either to substantiate or to disprove this view.

#### S. THE LATERAL SENSE ORGANS AND THE AUDITORY ORGAN.

Thomas Willis (1664, 224) may be said to have suggested the morphology of the auditory organ to his better informed successors, when, in the same year that the lateral line system was discovered, he described the auditory nerve as the dorsal branch of the VIIth, and considered both nerves to constitute the seventh pair of cerebral nerves. Leydig, however, was the first to derive the auditory organ from lateral sense organs (1850, 120), but he unhappily recanted in 1868 (126), and described the lateral organs as forming an organ of 6th sense, and having no morphological connection with the auditory organ. In 1870 (182) Schulze, who erroneously thought that water flowed through the sensory canals, regarded the latter as accessory auditory organs; whilst Dercum (1880, 59) went still further, and minutely compared the histology of the lateral sense organs with the macule of the ear, concluding that they resembled each other in every essential respect. Emery (1880, 66), who agrees with Schulze that the lateral organs represent an accessory auditory system, first discovered that the lateral organs possess a well marked cupula, which he believed to be formed of successive cuticles secreted by the peripheral cells of the sense organ, and correctly compared with the cupula terminalis of the ear. This important and interesting discovery has been extended to several other forms besides *Fierasfer*, and I find a very well marked cupula in young *Gadus virens* (see Pl. 23. fig. 4).

The important work by Mayser (1882, 135) is perhaps the first scientific contribution to the question, and formed the basis upon which all further work was conducted. This author discovered in *Cyprinus* that the fibres of the lateral line nerves and also the fibres of the auditory nerve arose from a common centre in the brain—the tuberculum acusticum. He was consequently led to regard the lateral line system as a low form of auditory organ, and indeed describes the lateralis lateral line nerve as the “hintere

Acusticuswurzel," and regards the semicircular canals as modified lateral tubes. I entirely concur with Ayers that "Mayser was much nearer the truth than he ever realised when he arrived at the conclusion above quoted" (7, p. 142). Mayser's discovery of the common origin of the two sets of fibres has been fully confirmed and also extended by many subsequent authors, such as Strong, Kingsbury, and Herrick, so that it must now be considered as an established fact. Bodenstein (1882, 24) briefly discusses (p. 137) Mayser's conclusions, and largely concurs. He compares the semicircular canals with the canals of the lateral line, and considers the endolymph of the ear to correspond to the mucus in the lateral canals, but is somewhat inconsistent in regarding the auditory organ as phylogenetically older than the lateral line system.

Beard (1884, 17) looked at the question from a new aspect when, instead of regarding the lateral system as an accessory auditory organ, and therefore discounting the value of the comparison by implying that the two systems are only homoplastic and not homologous structures, he derived the auditory organ from the lateral line system, and concludes that "the auditory organ of Vertebrates is fundamentally a specialised portion of the system of sense organs of the lateral line." This view, that the ancestral Vertebrate possessed a system of lateral sense organs which gave rise both to the auditory organ and to the modern lateral line system, has been abundantly supported by further evidence, and now stands as one of the most probable views of vertebrate cephalogenesis. Beard subsequently developed his hypothesis (1885, 19), and considered, with Gegenbaur, Marshall, Balfour, and other embryologists, that the auditory nerve was a dorsal branch of the facial.

In 1884, Wright (227) followed Bodenstein in comparing the endolymph of the ear with the mucus in the lateral canals, and in a further publication in the same year (228) independently confirms Mayser by describing a common origin in the brain for the lateral line and auditory nerves of *Amiurus*. He, however, still perpetuated the mistake of his predecessors in classing most of the lateral line nerves with the trigeminus, and further states, what must be regarded as doubtful, that the buccal nerve "contains fibres other than those derived from the *tuberculum acusticum*." Eisig (1887, 65) discusses Beard's derivation of the auditory organ from lateral sense organs, and is favourably disposed towards the view (pp. 711-712); whilst Fritsch (1887, 75), who was unable to find a cupula to the lateral sense organs of *Malapterurus*, advances the extraordinary explanation that it may have been washed away by the passage of sea water through the canals.

The cousins Sarasin (1887, 177), who favour the derivation of the auditory organ from lateral sense organs, and further consider that the latter function as accessory auditory organs, enter into an elaborate comparison between the histology of the auditory and lateral sense organs, and endeavour to establish that both are identical in all essential respects. Cunningham (1890, 55), discussing the cupula of the lateral sense organs, is "inclined to think the cupula is, during life, of a mucous nature, and therefore semi-liquid. It seems certain that the sensory hairs are imbedded in the cupula. It is difficult to understand how such cells as those of the sense organ should secrete mucus or form a cuticle; perhaps the cupula is nothing more than the ordinary mucus of the dermal tube,

which keeps a constant position in preparations because it is retained by the numerous sensory hairs" (p. 81). Here Cunningham has overlooked the gland cells at the base of the sense organ, which are doubtless responsible for the secretion of the cupula. There is therefore no necessity to suppose that it is secreted by sensory cells. Fritsch (1890, 77) was again unable to find a cupula in the Torpedoes, but after careful investigation admitted that the lateral sense organs agreed very closely in their minute histology with those of the auditory organ.

In 1892 Ayers published his elaborate and important memoir on the morphology of the vertebrate ear (7). In this work he endeavours to show that the cupulae terminales of the lateral and auditory sense organs are "artifacts produced in the main from the auditory hairs of the sensory cells" (p. 314). He says (p. 163):—"Now, while there is no question that some mucus is present in all cases (all in which exact analyses have yet been made), there is no evidence to show that in a state of nature it exists as a dome-shaped mass covering the sense organ. On the other hand, it is clearly proven that the most typical cupulae yet studied are products of the action of reagents, and that so far as fibrous structures in the channels occupied by sense organs (whether ear organs or those of the lateral line system) are concerned, they have in every thoroughly studied case shown themselves to be hairs more or less unchanged." I have previously referred to the existence of cupulae over the lateral sense organs as evidence that the latter and the auditory organ are genetically related. Whether the cupulae are artifacts or not is a question that does not affect this argument, since the conditions producing the artifact must be the same in both cases, and the artifact therefore open to be used in argument as denoting equally important and similar conditions in both systems of sense organs. The following quotations from Ayers' valuable monograph briefly summarise his line of argument:—"The whole process of the formation of this [auditory] cup is an exact repetition of the formation of a canal organ and its canal as seen in *Amia*, or the formation of an ampulla and its canal in the Salmon" (p. 175). "There could not be a more complete agreement between two developmental processes, occurring in different animals, than there is between the formation of the canals on the surface of the body in *Amia* and the formation of the canals of the internal ear in the Herring and Salmon, as given by Von Noorden. Of the correctness of the account for the latter I am certain, for I have observed the same process both in the whole embryo and serial sections. From our present knowledge of the development of the labyrinth in the bony fishes we have only agreement with the type of growth of the surface organs" (p. 181). "The so-called semicircular canals develop as more or less curved structures, because they are formed out of a portion of the external surface of the body, which has been enclosed within the head. Since on the surface of the body, in the typical and usual process of development, the canals always open at both ends on the surface, so inside the auditory vesicle they open at both ends" (p. 222). "It is proven that there is no essential difference between the sense organs of the internal ear of the vertebrate group and the superficial sense organs of the Ichthyopsida as they exist in the surface canals of these forms. Both consist of canals containing sense organs lying below the surface of the body, and they may (as in ordinary canals and the ear in some Elasmobranchs) or they may not (as in

Savi's vesicles [!] and the ear in the majority of Vertebrates) communicate with the surface. Both forms may or may not be entirely enclosed in cartilage or in bone. The *semicircular canals* of the ear are simply remnants of the canal system of the surface, and although bent into shapes more or less semicircular, they still retain their communication with the (morphological) exterior by means of their terminal (*i. e.* surface) pores or openings in the walls of the utriculo-sacculus, which in its turn often communicates with the surface of the head by the endolymphatic duct or surface canal . . . . Thus it is true that the development of the semicircular canals in the ear is due to phylogenetic and mechanical causes, and is not in the least a response to physiological necessities or requirements, and conversely the canals have no active part in the auditory function. They serve merely as chambers to hold the liquid necessary to float the auditory sensory hairs" (p. 308).

Ewart & Mitchell (1892, 69) remark (p. 100):—"Resting on the top of the hillock there is often what Solger terms the 'Cupulabildung.' This seems to consist of mucin. In some cases we have seen long threads of mucin extending from the hillock into the cupula or across the canal, the threads having frequently leucocytes entangled between them." A similar condition of the cupula is described by Emery (1880, 66). Willey (1894, 223) and Bashford Dean (1895, 58) agree that the auditory organ represents a specialization of the lateral line system, and belongs to the same category as the sense organs of the remainder of the lateral line. Loey (1895, 130) goes further, and regards the ear, the nose, and probably the eyes as derived from the lateral line system, and states on p. 547 that "there is now general agreement that the ears belong to the lateral line series." Again, on p. 579, he says:—"The history of the auditory vesicle in sharks has been worked out beyond this period by Ayers, and it is very clear from its mode of growth that it is directly related to the canal organs of the lateral line." Finally, Miss Platt (1896, 158) remarks (p. 492):—"The ear has developed from the dorso-lateral thickening in the hyobranchial intersegment, and it will be noticed that although the ear undoubtedly belongs in [? to] the lateral line system, and is in fact the centre of that system, it is not properly a 'branchial sense organ,' as Beard suggests, for this term cannot be accurately applied to sense organs above the epibranchial line."

The general fact that the auditory organ is a modified portion of the lateral line system must hence be considered established on a secure basis of fact, and it accordingly follows that the lateral system of the ancestral Vertebrate must have existed before differentiated sense organs, and then diverged in at least two directions (omitting mention of the nose and eye, the phylogeny of which is doubtful)—one producing the lateral canals of recent fishes and the other the vertebrate auditory organ. The association of the two sets of organs is completely justified on the evidence of the innervation alone, since Mayser and Strong have established (1) that the lateral line and auditory nerve fibres constitute a system by themselves, and are quite independent of the other cranial nerves; (2) that this system arises from a common central origin in the brain, which is further distinct from the fibres of any of the other cranial nerves. The argument from the nerves is well backed up by the argument from the minute structure and development of the two series of organs, and I have already drawn attention to the fact

that in both these respects (*i. e.* histology and embryology) the agreement between the lateral and auditory organs is so remarkable as to admit of only one explanation, and that favourable to the close genetic relationship of the two series. When, however, we descend to details, and enquire into the phylogeny of the semicircular canals, the way is not so clear. Ayers contends that a lateral line canal may differentiate further after being cut off from the surface. I have already joined issue with him on this point, and have urged that there is *no* direct evidence favouring this statement. The lateral canals are primitively laid down in the form they are found in the adult, and the only possibility of such differentiation is perhaps to be found in the blind diverticula of the canals described by Hyrtl, Sappey, Pollard, the writer, and others. Ayers' postulate is by no means impossible, but is at present mere speculation, and not founded on fact. The bearing of this on the question of the semicircular canals is obvious. The latter develop as evaginations of the wall of the auditory sac *after the sac has become cut off from the surface* \*, and is in a condition corresponding to a lateral line canal. It is true that the lumina of the semicircular canals are pieces cut off from the outside world, and one can admire Ayers' comparison of a semicircular canal with a single segment of a lateral canal still opening on to the surface (= cavity of sac) by its two terminal pores. These considerations, and the others advanced by Ayers, do not discount the cardinal fact that the semicircular canals of all Vertebrates develop in a way for which there is no parallel in our knowledge of the anatomy and development of the lateral line system. At one time I thought that the ear with its semicircular canals was formed by a concentration of certain lateral canals, and that the aquæductus vestibuli or ductus endolymphaticus corresponded to a dermal tubule connecting an internal canal with the exterior. Both these contentions are held and ably advocated by Ayers, and the latter undoubtedly holds good. The question that remains is whether the auditory organ has arisen by the differentiation of an organ such as an ampulla of Lorenzini, or whether it was formed by the concentration of certain primitive canals of the ancestral Vertebrate. In spite of the wealth of argument employed by Ayers, I cannot pass over the developmental difference described above, and must therefore hold to the former view, which by the way explains why there should be *only one* aquæductus vestibuli in the history of the auditory organ. I therefore follow Beard in regarding the ancestral auditory organ as represented by the primitive auditory sac of the embryo, and that the semicircular canals arose later in the ancestral history of the organ, and after it had entirely lost connection with the lateral line system. Such a view of course involves the corollary that although the semicircular canals bear many points of resemblance to the sensory canals of the lateral line, yet they must be regarded as only homoplastic and not homologous with them. Ayers' view, on the other hand, implies that the auditory organ was from the first a complicated structure and possessed semicircular canals.

\* In some of the lower Vertebrates, of course, this never *completely* happens.

## T. SPECIAL CONSIDERATIONS.

Schulze (1870, 182) was the first author to state that the lateral canals arose in sections with a sense organ in each section, and that the dorsal tubules were formed by the fusion of the adjacent extremities to form a single peripheral tubule and pore. This was confirmed by Solger (1880, 193), Bodenstern (1882, 24), and Allis (1889, 4)—the latter's work in this connection having been previously referred to. Friant (1879, 73) independently discovered with Schwalbe that *there were two superficial ophthalmic nerves*, and further has the credit of being the first author to approximately arrive at a correct appreciation of the trigeminal and facial nerves of fishes, being the first writer to hold that the superficial ophthalmic and buccal lateral line nerves were not branches of the trigeminus\*. He says (p. 103):—"Le *nerf facial* naît isolément des côtés du bulbe, au-dessus de la racine postérieure du trijumeau, se distribue aux méninges, à la peau et aux canaux muqueux du sommet de la tête et de la région sous-orbitaire, aux téguments d'enveloppe de l'œil et de l'orifice nasal, à la peau et aux téguments fibro-musculaires du museau, aux muscles peauciers de la joue, et chez la Perche, à la peau de la région dorsale et aux muscles des nageoires dorsales." It will be seen that for the time it was written this was a very accurate description, and its historic importance makes it extraordinary that Friant's work should hitherto have been overlooked.

The fishes are classified by Sappey (1880, 175) into four groups according to the development of the lateral line system:—(1) the Plagiostoma, in which it is greatest developed; (2) "L'Ange et les Squales," not so well marked; (3) the majority of the bony fishes, where it is more reduced than in 2; (4) fishes having no lateral line system at all[!]. Such a classification, based on so very variable a structure (even though its general anatomy is identical in nearly all fishes), is necessarily artificial, and has little or no taxonomic value. It would involve, for example, placing *Amia* alongside *Gadus*. Baudelot (1883, 16) states that the facial nerve is absent in many bony fishes (*e. g.* the "Carpe") and that in these forms it is represented by a branch of the trigeminus. Such a statement must be due to imperfect observation, and if by "Carpe" we may understand *Cyprinus*, a true facial nerve was described by several authors in that form long before the time at which Baudelot was writing.

Sagemehl (1884, 172) emphasizes the fact that the two dorsal lateral canal commissures are not homologous, and that a parietal commissure cannot be considered to represent a supra-temporal commissure where in any genus the former is the only one found. Ramsay Wright (1885, 229) considers (p. 491) that in *Lepidosteus* a portion of the R. oticus facialis represents the præ-trematic or præ-spiracular branch of the facial, since it supplies the anterior sense organ of the spiracular cleft, and states that a similar condition is found in *Amia*. It is impossible that the two nerves mentioned can be homologous, since the otic is a true lateral line nerve and cannot, therefore, be compared with a nerve consisting of visceral sensory fibres. Wright, therefore, failed to find a præ-spiracular nerve in *Lepidosteus* and *Amia*.

\* Confirmed independently in 1881 by Marshall and Spencer, and in 1889 by Allis (4, pp. 513, 514).

Whilst on the subject of the facial nerve it is necessary that Allis's views on this nerve in *Amia* should be discussed. He says (1897, 6, pp. 615, 616): "After issuing from that [=facial] canal the truncus facialis continues downward, outward, and backward, lying in the depression on the outer surface of the hyomandibular, and separates almost immediately into its two main portions, the truncus mandibularis facialis and the R. hyoideus facialis. The former lies anterior to the latter, turns downward, and soon separates into its two portions, the R. mandibularis externus facialis and the R. mandibularis internus facialis." On p. 618 the "internal mandibular" is described as entering into relations with the lower jaw. Before going further and discussing the homology of the latter nerve with the chorda tympani, it is necessary to point out that Allis has misnamed his nerves. As I have already pointed out (1896, 46, p. 657 *et seq.*), the terms *internal mandibular* and *hyoideus* as first used by Stannius are not only synonymous but apply to a motor post-spiracular nerve related to the anterior face of the hyoid arch, just as the pre-spiracular nerve should be related to the posterior face of the mandibular arch. On this ground alone (and there are others) Allis's "internal mandibular" must be a morphological pre-spiracular nerve, and as such is wrongly named by him. As the whole question, however, involves also the question of the homology of the chorda tympani, it is first necessary to show what Allis's views are on the latter question. He says (6, pp. 638, 639): "As the nerve [*i. e.* the "internal mandibular"], in *Amia*, lies behind the spiracular canal, it is a post-trematic branch of the facialis, and cannot, therefore, be the chorda tympani, for the course of that nerve in man through the upper portion of the tympanic cavity and then downward anterior to that cavity certainly indicates that it is a pre-spiracular nerve. That this nerve, in *Amia*, is the homologue of the nerve of the same name described by Ewart, Pollard, and Strong, in other Ichthyopsida, and considered by them as the homologue of the chorda tympani, is hardly open to question. The nerve in *Amia* is probably to be compared to the branch which, on each side of the branchial arches, runs downward over the anterior face of the arch on to the inner surface of its ventral portion. Its position in *Amia*, along the inner surface of the mandible, could be easily derived from that in Selachians as given by Vetter. In *Heptanchus* what seems to be the nerve is shown lying along the posterior edge of the mandible; from this position, as the hyoideo-mandibular fold of *Amia* was formed, the nerve could as naturally come to lie along the inner surface of the mandible as along the lateral surface of the hyoid." An examination of this passage reveals several flaws. It is true that the chorda tympani is a pre-spiracular nerve, as I have previously shown (1896, 46), but is Allis's "internal mandibular" a post-spiracular nerve? We have seen that Ramsay Wright failed to identify the homologue of the pre-spiracular in *Lepidosteus* and *Amia*, and Allis himself (1889, 4, pp. 501 *et seq.*) says nothing about it. The fact is, nothing is known of the relation of the "internal mandibular" nerve of *Amia* to the spiracular cleft, since the embryonic condition has not yet been worked out, and the cleft itself degenerates in the adult. We are, therefore, not in a position to say whether this nerve is pre- or post-spiracular. Further, what is the definition of a pre-spiracular nerve? It should fulfil three conditions: (1) it should run in front of the spiracle: (2) it should pass along the posterior face of the mandibular arch; and (3) it should consist of visceral sensory fibres. With regard to the first

condition, there are several cases on record where on the disappearance of the spiracle the pre-spiracular accompanies for a time the post-spiracular nerve and thus becomes a topographical, but not a morphological, post-spiracular nerve. It seems to me that when the early development of the nerves of *Amia* has been investigated it will be found that the "internal mandibular" nerve is morphologically pre-spiracular, though occupying a post-spiracular position in the adult. This is what we know has happened in *Rana* (cp. Strong's "internal mandibular"), and what has doubtless also happened in *Chimera* and *Gadus*. The degeneration of the spiracular cleft naturally leaves the nerves unaffected, since they are concerned rather with the sensory and motor supply of the arches, and the latter are untouched by the disappearance of the spiracle. With regard to the second condition above, that is practically fulfilled, and so doubtless also is the third. The "internal mandibular" nerve is certainly not a motor nerve in *Amia*, in which case it must be a visceral sensory nerve, and indeed Allis says that it "is distributed to the inner surface of the hyoid and mandibular arches" (6, p. 745). The "internal mandibular" nerve of *Amia* therefore is, as far as our knowledge of it goes, a morphological pre-spiracular nerve, and in any case is excluded from being the true internal mandibular nerve, since this should be distributed to the muscles of the hyoid arch, and is undoubtedly represented in *Amia* by the Rr. hyoideus and opercularis. In further criticism of the passage quoted above I may remark that it is very much "open to question" that the internal mandibular of *Amia* corresponds to the nerve of the same name described by Ewart. The nerve of the latter author is a motor nerve partly to the muscles of the hyoid arch, and as such differs essentially from the nerve in *Amia*. The nerves described by Pollard\*, Gaupp (1893, 84), and Strong, are correctly homologised, but should not have been named "internal mandibular," as Miss Platt (1896, 158, p. 534) and the writer have pointed out. Finally, an anterior branchial ramus is related to the posterior and not to the anterior face of its arch, as Allis himself mentions is the case with the "internal mandibular" of *Heptanchus*. Pinkus (1894, 157) introduces further confusion into the synonymy of the facial nerve of fishes. He correctly homologises his "inferior palatine VII" with the chorda tympani (but did not recognize that this nerve represented the pre-spiracular nerve of other fishes), and divides the morphological post-spiracular nerve (=, + the lateral line element, the hyomandibular trunk) into three parts—(1) internal mandibular; (2) hyoideus †; and (3) motor VIIth. Pinkus is of course wrong in using two synonyms (*i. e.* internal mandibular and hyoideus) to describe two different branches, and it seems to me that 1 and 3 together represent the internal mandibular of other fishes. The motor VIIth branches correspond undoubtedly to the ramus opercularis facialis of the bony fishes.

There is hence some confusion in the terminology of the facial nerve of fishes, which it is desirable should be removed. I have therefore drawn up a scheme of the constitution of the facial or VIIth cranial nerve in a typical fish, with the synonyms of the three cardinal branches. It is to be hoped that future authors will, before naming a nerve, first ascertain whether it is somatic or splanchnic, and then whether it is sensory or

\* See 1892, 160, pp. 397 and 398 (table). It will be seen that Pollard's nerve is the one I have identified as the chorda tympani in *Gadus*.

† As this is a *sensory* nerve it must be unrepresented in other fishes.

motor. I may mention here that there is a nerve in *Gadus* exactly corresponding to the "internal mandibular" of Allis in *Amia*. I have for the above reasons described it as the pre-spiracular or chorda tympani division of the facial. The following scheme of the constitution of the facial nerve in a typical fish takes no account of the lateral line constituent, which only accompanies the facial and is not a branch of it:—

Facial nerve *sensu stricto* (minus external mandibular lateral line nerve). Forks over spiracular cleft into—

- (1) *Palatinus* or *visceralis facialis*. Is joined by Jacobson's anastomosis (=palatinus or visceralis glossopharyngei), and is a visceral sensory nerve distributed to the mucous membrane of the roof of the mouth in front of the spiracle.
- (2) A visceral sensory nerve arising from the base of (1) and forming part of the same bundle of fibres. *Præ-spiracular, præ-branchial, præ-trematic, or chorda tympani division of facial*. May be continued ventrally on to pharynx, in which case it should become related to the posterior face of the mandibular arch, and be distributed to the mucous membrane of this arch.
- (3) A visceral motor nerve=main trunk of facial. Forms external to spiracle a portion of the nerve known as the truncus hyomandibularis facialis, of which the remainder and larger part here=the external mandibular lateral line nerve. *Post-spiracular, post-branchial, post-trematic, internal mandibular, or hyoidean branch of the facial*. Continued ventrally on to pharynx, where it becomes related to the anterior face of the hyoid arch, the muscles of which absorb most of its fibres (Allis, 6, p. 745). Gives off posteriorly the nerve known as the *Ramus opercularis facialis* to the muscles of the hyoid arch (Allis, *loc. cit.*).

Allis (4, p. 472), in seeking to prove the independence of the supra-orbital canal (which is of course independent as far as innervation proves anything), goes somewhat too far in advancing the developmental independence of the supra-orbital canal from the infra-orbital as proving this point. As the lateral canals, according to his own description, develop in independent segments, each containing a sense organ, his argument proves nothing, especially as there is a dermal tubule at the point of anastomosis between the two canals which involves their independence as a developmental necessity. It will have been noticed that I have not described an ophthalmicus profundus nerve in *Gadus*. The question of the existence of this nerve in Teleosts is fully discussed by Allis (1897, 6, pp. 538 *et seq.*), and he concludes: "In no Teleost, with the single recorded exception, so far as I can find, of *Trigla*, is there a separate profundus ganglion and root. Both ganglion and root are apparently always completely fused with the ganglion and root of the trigeminus." He further points out that the nerve identified by Pollard as the profundus in certain Siluroids is really the ophthalmicus superficialis VII, and, I think, rightly doubts any fusion between the profundus and superficialis as explaining the apparent absence of the former, believing it to be "more probable that the ophthalmicus profundus of Elasmobranchs is entirely wanting in Teleosts." Goronowitseh's and other authors' nerves, therefore, named the ophthalmicus profundus, represent the ophthalmicus superficialis V, and his ophthalmicus superficialis is the lateral line nerve of that name

(1897, 90)\*. In his later work (1897, 6, p. 625) Allis states, what I had previously suggested, that the so-called lateral line branch of the IXth of *Amia* is really a branch of the lateralis lateral line nerve.

A rather curious mistake is made by Ayers (1892, 7), who describes the lateralis lateral line nerve as the "anterior (dorsal) branch of the IXth." Pollard makes a statement which I had overlooked in my previous work, and which is closely paralleled by the condition sometimes found in *Chimara* (46, p. 646). He says (1892, 160, p. 395) "In a young specimen of *Polypterus* about 20 cm. long, which was cut into sections, there appeared to be a commissure from the ganglion of the trigeminus to the ophthalmicus superficialis of the facial. The material was, however, not well preserved, and consequently the existence of this commissure *which would represent the superficial portion of the trigeminus* could not be determined with absolute certainty." The buccal and superficial ophthalmic lateral line nerves of *Polypterus* arise from a common trunk, and the former accompanies the superior maxillary division of the Vth. Miss Platt (1896, 158) describes the IXth nerve of *Necturus* innervating sense organs of the lateral line, and considers the operculo-mandibular line of organs to be composed of two distinct portions. Kingsbury (1897, 114) states that the lobi trigemini of Elasmobranchs and Ganoids are directly homologous and constitute the lateral line centre, but that in Teleosts the lobus trigeminus is another structure and belongs to the fasciculus communis system. I had originally intended writing a section on the function of the lateral line system, but this must be deferred for the present. In the meantime I may refer those interested in the question to the works of Ayers (1892, 7), Dercum (1880, 59), Fritsch (1888, 76, and 1890, 77), Fuchs (1895, 78), de Sède (1885, 129), Richard (1896, 167), Savi (1844, 178), Stahr (1897, 196), (Willey 1894, 223), and Ramsay Wright (1884, 227).

#### SUMMARY.

1. The present communication contains the first description of the lateral sense organs and their nerves in the genus *Gadus*.

2. The sensory canal system of Fishes, both recent and fossil, is resolvable into a common type, to which the lateral canals of all forms can be reduced. This type includes a lateral canal on the body, a canal over the eye, another underneath it, and finally one related to the lower jaw. All these canals may be connected by median commissures with their fellows of the opposite side.

3. The sensory canals of *Gadus* may be described as having diverged but slightly from the typical form. The canal sense organs are somewhat reduced in number, which involves a similar reduction in the dermal tubules. There are no Savian vesicles or Lorenzini's ampullæ, but pit organs of the usual constitution are fairly common.

4. The lateral line systems of *Gadus morrhua* and *Gadus virens* exhibit specific differences.

5. The sensory canals, by their skeletal support, become secondarily related to the

\* He says (p. 30): "Der N. ophth. superf. ist wie bei Knochenfischen ein Ast des Trigemini II. [=lateral line component]. Der N. ophthalmicus profundus von *Aeipenser* ist ausschliesslich ein Ast des Trigemini I. und ist demnach kein vollkommenes Homologon des gleichnamigen Nerven von *Lota*, welcher Elemente des Facialis enthält. Der R. oticus ist bei *Aeipenser* ein Ast des Facialis und des Trigemini II. und kann demnach auch nicht mit dem N. ophthalmicus prof. der Knochenfische direkt verglichen werden."

skeleton of the head, and on their disappearance left a legacy to the skull in the shape of certain of the lateral line ossicles, which either on account of additions to their original function were retained as new elements, or were fused on to, and came to form a part of, bones previously existing.

6. The ganglia of the trigeminal and facial nerves have fused to form an elaborate complex, in which the individuality of the ganglia has been lost, and which arises from the brain by two roots. The ganglion in connection with the lateral line nerve is, however, distinct. The sympathetic trunk is connected with the vagus, glossopharyngeal, and trigemino-facial ganglia.

7. A portion of the trigemino-facial complex which is connected with visceral sensory fibres, and which I have called the facial ganglion, is in such a condition as to strongly suggest the view that it is migrating from the complex and is in process of being converted into a sympathetic ganglion. It is in connection with the sympathetic trunk, and has been described by many authors as a sympathetic ganglion. The condition of this ganglion favours the view that at least the greater part of the facial, glossopharyngeal, and vagus nerves of Fishes belongs to the sympathetic system.

8. A typical branchial nerve has the constitution tabulated on p. 144.

9. The facial nerve of Man and Mammals can be derived from the branchial facial nerve of a fish.

10. The anastomosis of Jacobson is the visceral sensory palatine or visceral branch of the IXth, and connects the glossopharyngeal ganglion with the ramus palatinus facialis (also visceral sensory). It is neither a somatic sensory nor a lateral line anastomosis, and cannot be homologised with either of these.

11. The lateral line system of Fishes is, as far as our present knowledge goes, *not* metameric. This conclusion is supported by the whole of the anatomical and part of the embryological evidence. The observations under the latter head that have hitherto been considered to support the metameric view of the lateral organs are certainly in part, if not entirely, concerned with another series of sense organs, and do not relate to the lateral sense organs at all.

12. The nerves supplying the lateral sense organs (both superficial and canal) form a separate series in themselves, and are not connected with any of the other cranial nerves. They may be named the Superficial Ophthalmic, Buccal, External Mandibular, and Lateralis Lateral line Nerves. The innervation of the lateral sense organs of Fishes and Amphibia is remarkably constant, and should be taken as *the* guide in determining the limits of a canal. The sensory canals and pit organs of *Gadus* are innervated by the branches of these nerves—the glossopharyngeus taking no part in the innervation of the system either in *Gadus* or morphologically in any other form.

13. The system of nerves known as the ramus lateralis trigemini is a ganglionated system of somatic sensory nerves formed typically of the dorsal branches of the Vth, VIIth, IXth, and Xth cranial nerves, with a certain number of the same branches of the spinal nerves, all more or less fused together, and forming the sensory nerve supply of all the fins of the body. Its common name, therefore, should be abandoned in favour of its original name of ramus lateralis accessorius.

14. The so-called lateralis nerve of *Petromyzon* is not a lateral line nerve at all, but its anatomy shows it to belong undoubtedly to the lateralis accessorius system.

15. The lateral line system of *Gadus* is in remarkable agreement with that of *Amia*, except that the latter form exhibits less reduction in the number of its sense organs.

16. The sense organs of the lateral line of Fishes and Amphibia are not homologous with the lateral sense organs of Annelids (*e. g.* Capitellidæ).

17. The sensory canals were probably represented in the ancestral Vertebrate by non-segmental superficial sense organs. These sank below the surface, forming a series of tubes, by the end-to-end fusion of which the sensory canals were formed. As the sense organs sank below the surface, certain lateral glandular organs were also included which secreted the mucus filling the canals. These glands have been subsequently much reduced in importance, and their function now is an accessory one, *i. e.* to secrete a substance corresponding precisely to the endolymph of the ear. Before the sensory canal system extended forwards and backwards it was probably confined to the region now occupied by the auditory organ.

18. There can be little doubt that the primitive lateral line organs gave rise both to the recent lateral system and also to the vertebrate auditory organ. It is doubtful whether the semicircular canals have arisen by a concentration of primitive sensory canals or by the decentral development of a primitive simple sac. The author holds to the latter view, and believes that the semicircular canals are homoplastic and not homologous with the sensory canals.

19. The author's previous view that the chorda tympani nerve of Mammals has been derived from the præ-spiracular division of the facial of the Piscine ancestor of the Vertebrates is confirmed. The nerve referred to as the "internal mandibular" by Allis and some other authors is wrongly identified, and is really the præ-branchial or chorda tympani division of the facial.

20. A typical facial nerve of a fish has the constitution tabulated on p. 202.

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March 2nd, 1898.

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*Postscript.*—Since writing Section H, I have examined a large number of *Gadus* skulls, and have no doubt now that the description does not represent the normal condition, which in the vast majority of the specimens examined was that of complete fusion between the dermal and cartilage pterotic elements, although the point of fusion could always be easily detected. The nomenclature of these two bones is hence in urgent need of revision. The terms post-frontal and squamosal should be reserved for the *separate* dermal lateral line elements, and sphenotic and pterotic for the *separate* cartilage auditory bones. A compound term is also necessary for the condition in which the lateral and cartilage elements have secondarily fused to form one bone. Where the lateral line bones are never known to be separate from the underlying cranial bones *in the adult* there is no pressing need in the meantime for any revision of the nomenclature.—Sept. 27, 1898.

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\* The above list simply contains those papers consulted by the author in writing the present work. A complete Bibliography of the anatomical, embryological, physiological, recent and fossil literature, directly or indirectly treating of the Brain, Cranial Nerves, and Lateral Sense Organs of Fishes and Amphibia, is in active preparation, and will be published separately. Nevertheless, although the present list has already been more than doubled, the author would be extremely grateful for any references not included in it, either to the sender’s own papers, or to any others which should have been recorded. The objects of the forthcoming Bibliography (by no means a mere list) are: (1) to provide an absolutely complete and accurate catalogue of all the works ever published more or less relating to the subject; (2) to be a guide to an author (by means of abstracts, indexing, &c.) newly taking up the subject to the literature immediately affecting his special purpose, and also to those general works it were expedient that he should consult; (3) to supply the pressing need of an *Index Expurgatorius*. With regard to the latter, and perhaps most important, object, it is obvious that an author, however conscientious, cannot be expected (unless, indeed, he is writing an extensive monograph) to wade through at least 700 papers before writing his own. It is equally obvious that many of these papers, either on account of the antiquity of their contents, or other equally potent but less excusable reasons, may very well be consigned to the “silent tomb,” and piously allowed to remain there. The want of such an analytical Bibliography has, even in the confined experience of the author, over and over again impaired an otherwise useful piece of work. It is respectfully hoped, therefore, that a diligent and unprejudiced search through the literature will have the general effect of clearing the air, and thus proving of some service to those subsequently taking up the work.

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## EXPLANATION OF THE PLATES.

The figures illustrating this paper have been carefully drawn, exact size, from nature, and, it is hoped, are something more than mere diagrams. The various structures and bones figured will be found to occupy their natural positions—every care having been taken to ensure this.

## PLATE 21.

Fig. 1. Dissection from the left side of *Gadus morrhua*, showing pit organs, sensory canals, and the skeletal support of the latter. Natural size.

- A.* Articular.  
*Ag.* Angular.  
*D.* Dentary.  
*D.F.* Anterior extremity of dorsal fin.  
*Fr.* Frontal.  
*Fr<sup>1</sup>.* Triangular fossa on frontal lodging the bend of the infra-orbital canal.  
*H.* Hyomandibular canal.  
*I.O.* Infra-orbital canal.  
*L<sup>1</sup>.* Supra-temporal portion of lateralis canal. } = Lateralis canal.  
*L<sup>2</sup>.* Lateral portion of lateralis canal. }  
*Lg.H.* Ligamentous portion of hyomandibular canal.  
*Lg.S.* Ligamentous portion of supra-orbital canal.  
*L.O.* First lateral line ossicle.  
*N.* Anterior and posterior narial openings abnormally fused together (the specimen was normal in this respect on the right side).  
*Na.* Nasal.  
*O.* Opercular fold.  
*Pct.F.* Pectoral fin.  
*P.F.* Post-frontal or sphenotic. † Foramen for otic branch of buccal nerve.  
*Plv.F.* Pelvic fin.  
*P.O.* Pit organs (= sensory follicles).  
*P.Op.* Pre-operculum.  
*P.T.* Post-temporal or supra-scapula.  
*P.T<sup>1</sup>.* Upper or epiotic limb of same.  
*P.T<sup>2</sup>.* Lower or parotic limb of same.  
*Sb.O<sup>1</sup>.* First sub-orbital or lachrymal.  
*Sb.O<sup>2-6</sup>.* Sub-orbitals 2 to 6 (5 and 6 = first and second "post-orbitals").  
*S.O.* Supra-orbital canal.  
*S.O.C.* Supra-orbital commissure.  
*Sq.* Squamosal or pterotic.  
*S.T<sup>1-4</sup>.* Supra-temporals (=extra-scapulae) 1 to 4.

The numbers denote the dermal tubules of the respective sensory canals.

## PLATE 22.

Fig. 2. Dissection from the left side of *Gadus virens*, showing the innervation of the sensory canals. The latter are coloured in segments, to indicate the positions of the skeletal supports. The lateral line nerves are shaded. Natural size.

- A.* Articular portion of hyomandibular canal.  
*B.* Buccal lateral line nerve.  
*B*<sup>1</sup>. Outer buccal nerve.  
*B*<sup>2</sup>. Otic branch of same.  
*B*<sup>3</sup>. Branch of outer buccal to pit organ.  
*B*<sup>4</sup>. Inner buccal nerve.  
*B*<sup>5</sup>. Upper ramus of same.  
*B*<sup>6</sup>. Branches of upper ramus to pit organs of snout.  
*B*<sup>7</sup>. Lower ramus of inner buccal.  
*B*<sup>8</sup>. Branch of above to pit organs below infra-orbital line.  
*C.B.* Cerebellum.  
*C.H.* Cerebral hemisphere.  
*C.N.* Outline of cornea.  
*D.* Dentary portion of hyomandibular canal.  
*D.F.* Anterior extremity of dorsal fin.  
*F.R.* Frontal portion of supra-orbital canal.  
*F.R*<sup>1</sup>. Frontal portion of infra-orbital canal.  
*H.* Hyomandibular nerve trunk.  
*H*<sup>1</sup>. Anterior or larger division of same.  
*H*<sup>2</sup>. Posterior or smaller division of same.  
*H*<sup>3</sup>. Chorda tympani nerve (= præ-branchial or præ-spiracular — facial).  
*H*<sup>4</sup>. Hyoidean nerve (= internal mandibular, or post-branchial, or post-spiracular).  
*H*<sup>5</sup>. External mandibular lateral line nerve.  
*H*<sup>6</sup>. Posterior branch of same to sense organs 11 and 12 of the hyomandibular canal.  
*H*<sup>7</sup>. Anterior branch of same to facial and mandibular pit organs.  
*H.C.* Hyomandibular sensory canal (violet).  
*I.C.* Infra-orbital sensory canal (red).  
*L.* Lateralis lateral line nerve.  
*L*<sup>1</sup>. Supra-temporal branch of above.  
*L*<sup>2</sup>. Posterior division of supra-temporal branch to sense organ 4 of the lateral canal, &c.  
*L*<sup>3</sup>. Dorsal division of supra-temporal branch to sense organs 1 and 2 of the lateral canal, &c.  
*L*<sup>4</sup>. Anterior division of supra-temporal branch to sense organ 3 of the lateral canal, &c.  
*L*<sup>5</sup>. Dorsal ramus of lateralis nerve.  
*L*<sup>6</sup>. Dorsal forward branch of same.  
*L*<sup>7</sup>. Ventral ramus of lateralis.  
*L.C*<sup>1</sup>. Supra-temporal portion of lateralis canal. } = Lateralis sensory canal (brown).  
*L.C*<sup>2</sup>. Lateral portion of lateralis canal. }  
*L.G.* Ganglion of superficial ophthalmic, buccal, and external mandibular lateral line nerves.  
*L.I.* Lobus inferior.  
*L.O*<sup>1-3</sup>. Lateral line ossicles 1 to 3 supporting the lateralis canal.  
*M.D.* Medulla oblongata.  
*M.X.* Third or mandibular or inferior maxillary division of the trigeminus.  
*M.x.* Second or maxillary or superior maxillary division of the trigeminus.

- Mx.Mx.* Maxillo-mandibular trunk (trigeminus).  
*N.* Anterior and posterior narial openings.  
*NA.* Nasal portion of the supra-orbital canal.  
*O.* Opereular fold.  
*O.L.* Optic lobe.  
*OLF.* "Olfactory lobe."  
*PCT.F.* Pectoral fin.  
*P.F.* Post-frontal or sphenotic portion of the infra-orbital canal.  
*PLV.F.* Pelvic fin.  
*P.O.* Pit organs or sensory follicles.  
*P.OP.* Pre-opereular portion of the hyomandibular canal.  
*P.T.* Post-temporal or supra-scapular portion of the lateralis canal.  
*SB.O<sup>1</sup>.* First sub-orbital or lacrymal portion of infra-orbital canal.  
*SB.O<sup>2-6</sup>.* Posterior sub-orbital portions of infra-orbital canal.  
*S.C.* Supra-orbital sensory canal (blue).  
*S.CM.* Commissure between the two supra-orbital sensory canals.  
*S.O.* Superficial ophthalmic nerve trunk (= lateral line and trigeminal portions).  
*S.O<sup>1</sup>.* Superficial ophthalmic lateral line nerve.  
*S.O<sup>2</sup>.* Superficial ophthalmic or first division of the trigeminus.  
*S.O<sup>3</sup>.* Branch of *S.O.<sup>1</sup>* to sense organ 4 of the supra-orbital canal. The two twigs probably supply pit organs.  
*S.O<sup>4</sup>.* Branch of *S.O.<sup>1</sup>* to pit organ (?).  
*S.O<sup>5</sup>.* Branch of *S.O.<sup>2</sup>* to skin.  
*S.O<sup>6</sup>.* Anterior termination of *S.O.<sup>2</sup>* which has become separated from the lateral line nerve.  
*SQ.* Squamosal or pterotic portion of the infra-orbital canal.  
*ST<sup>1-4</sup>.* Supra-temporal or extra-scapular portions of the lateralis canal.  
*V.* Vagus nerve with compound (?) ganglion.  
 I. Olfactory tract, peduncle, or "nerve."  
 II. Optic nerve.  
 V.-VII. Trigemino-facial ganglionic complex (adult condition), with portions of its two roots.  
 The numbers denote the sense organs and dermal tubules of the respective sensory canals.

## PLATE 23.

Fig. 3. Transverse section of the head of a young adult *Gadus virens*, passing through the eye posterior to the lens.  $\times 27$ . Drawn with camera.

- |  |  |
|--|--|
| 1. Supra-orbital sensory canal.  | 9. Inferior maxillary Vth.   |
| 2. External aperture of the 1th dermal (commissural) tubule of supra-orbital canal.  | 10. Allis's nerve "c" (see text). Distributed to tissues behind and below eye. |
| 3. Superficial ophthalmic lateral line nerve.  | 11. Hyomandibular sensory canal, showing sense organ 8 of this line.           |
| 4. Branch of above (= <i>S.O.<sup>3</sup></i> of Fig. 2) to sense organ 4 of supra-orbital canal (note its condition on the other side). | 12. External mandibular lateral line nerve.                                    |
| 5. Ophthalmicus superficialis trigemini.   | 13. Mandibular pit organ.  |
| 6. Infra-orbital sensory canal.  | 14. Optic chiasma.   |
| 7. Upper and lower rami of inner buccal lateral line nerve.  | 15. Posterior extremity of cerebral hemispheres (no lateral ventricles).       |
| 8. Superior maxillary Vth.   | 16. Frontal bone.  |

- |  |   |
|--|---|
| 17. Fifth sub-orbital.                             | 28. Branchiostegal rays.  |
| 18. Anterior extremity of pre-operculum.           | 29. Gill arches, with attached muscles, blood vessels, and gills. |
| 19. } Primordial cranium. 20=the "supra-orbital    | 30. Fragments of thyroid gland.                                   |
| 20. } bands" of Parker (152, p. 129).              | 31. Pharyngeal chamber.   |
| 21. "Great fontanelle" (Parker, <i>loc. cit.</i> ) | 32. Anterior extremity of opercular chamber.                      |
| 22. Fused trabeculae ("inter-trabecula").          | 33. Retina.   |
| 23. Parasphenoid.                                  | 34. Sclerotic.  |
| 24. Metapterygoid.                                 | 35. Superior rectus   |
| 25. Symplectic.                                    | 36. Inferior ,,   |
| 26. Quadrate.                                      | 37. Internal ,,   |
| 27. Cerato-hyal.                                   | } eye muscles.  |

Fig. 4. Transverse section of sense organ 3, supra-orbital canal, from a young *Gadus virens*.  $\times 240$ .  
Details filled in with Zeiss Apochr. Hom. Imm. 2.0 mm., apert. 1.30, oc. compens. 4, 45 mm.

- |   |  |
|---|--|
| 1. Sensory cells of sense organ.  | 4. Nerve of sense organ.   |
| 2. Glandular cells of same (note periphery of organ consisting entirely of gland cells, 2', and centrally the secretion of the latter passing between the sensory cells). | 5. Supra-orbital canal in transverse section.  |
| 3. Cupula terminalis (apparently contracted from its original attachments).   | 6. Blood vessels.  |
|   | 7. Lateral frontal ( <i>i. e.</i> lateral line ossicle secondarily fused on to frontal). |
|   | 8. Frontal.  |







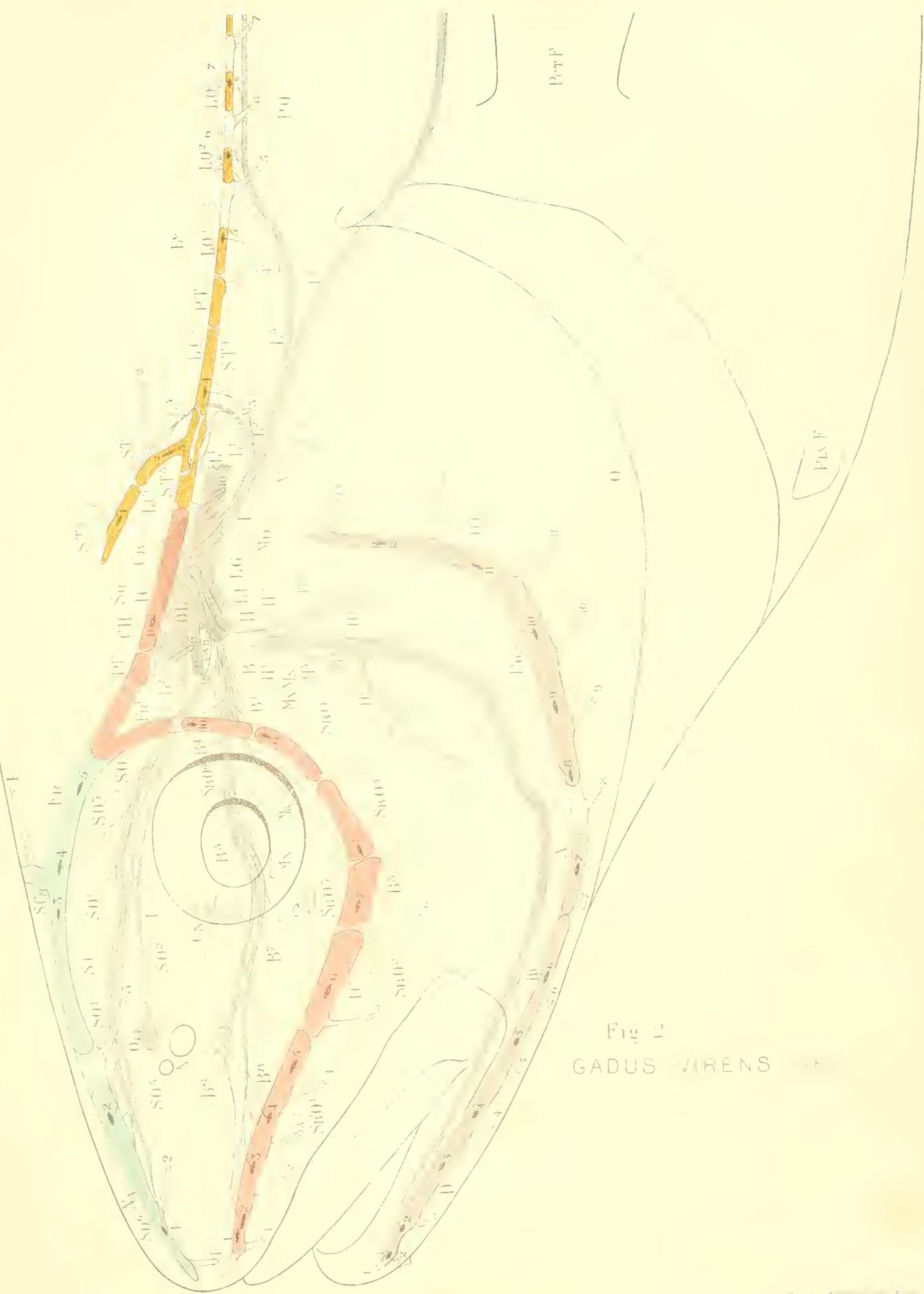


Fig 2  
GADUS VIRENS



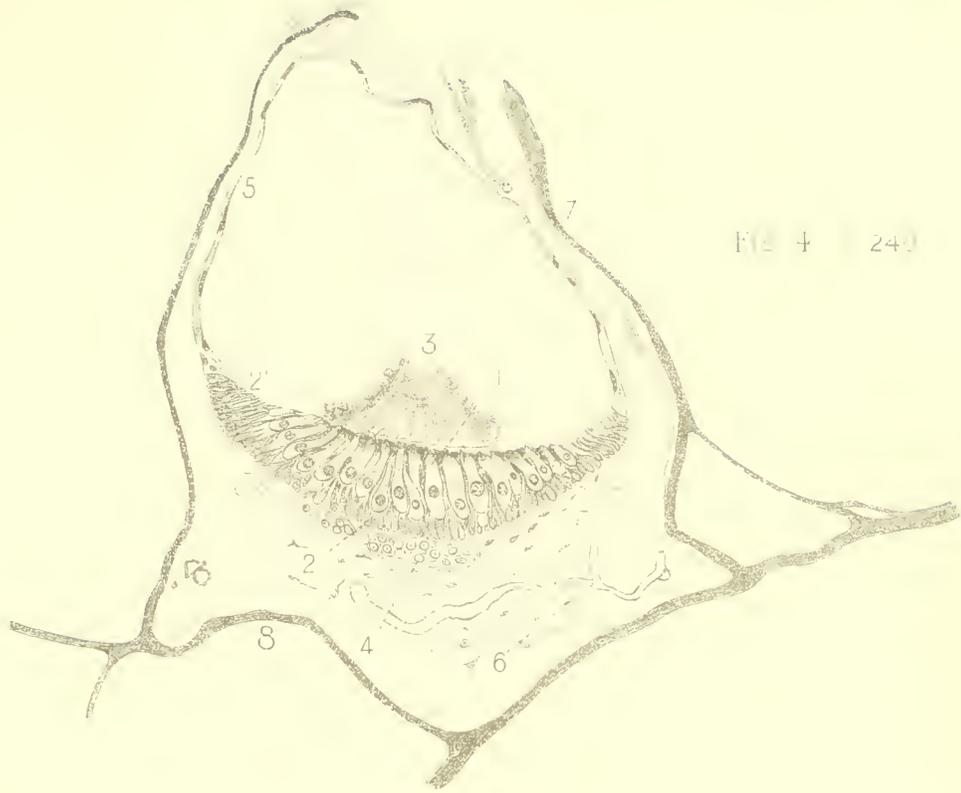


Fig 4 240

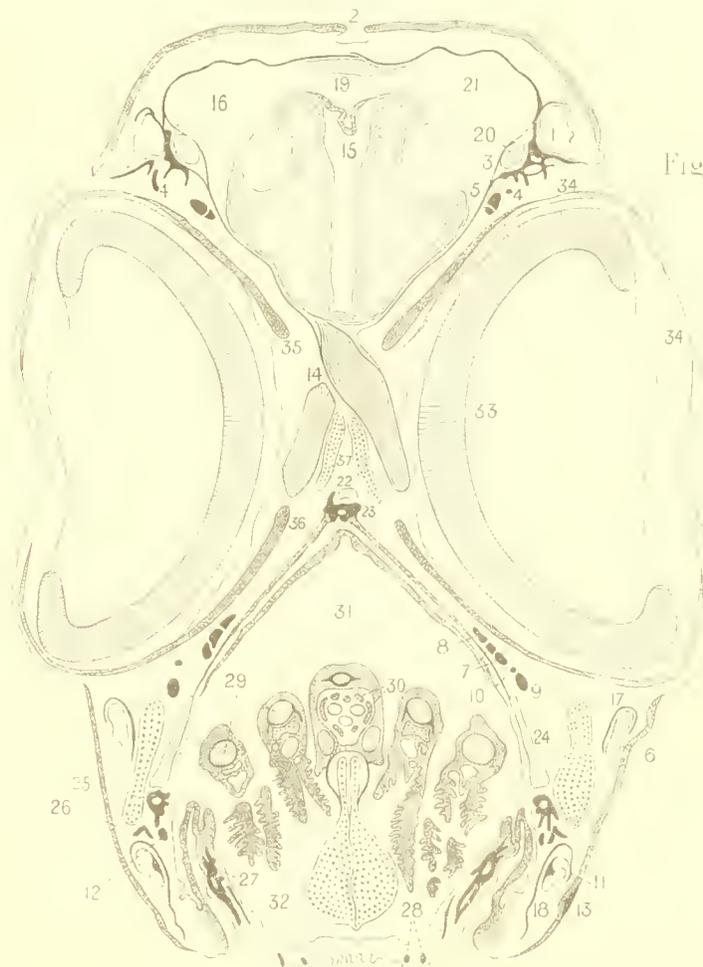


Fig 3 27





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Part	XVIII. 1888. ....	0 2 6	0 2 0		Part	I. 1897. ....	0 12 0	0 9 0
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THE  
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A CONTRIBUTION TOWARDS OUR KNOWLEDGE OF THE  
MORPHOLOGY OF THE OWLS.

BY  
W. P. PYCRAFT, A.L.S., M.B.O.U.



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VI. *A Contribution towards our Knowledge of the Morphology of the Owls.*By W. P. PYCRAFT, *A.L.S., M.B.O.U.*

(Plates 24-29.)

Read 21st April, 1898.

## PART I.—PTERYLOGRAPHY.

## I. INTRODUCTORY.

THE foundation of the present paper was laid by Prof. Newton, when, at the close of the year 1895, he sent me the remains—in the shape of a trunk—of a *Sceloglaux albifacies* which had but recently died, with a request that I would try to “make something of them,” inasmuch as the bird was exceedingly rare and verging on extinction. This trunk was that of a bird which had for some three years been in the possession of Sir Francis Boileau, who had brought it to England from New Zealand. Unfortunately it had been sent immediately after death to a taxidermist, who had, however, been instructed to save the body for Mr. J. H. Gurney, from whom it came, through Prof. Newton, to the Department of Comparative Anatomy of the University Museum of Oxford, where I was then working. Thus it happens that certain points concerning the external anatomy are probably lost for ever. The general pterylosis, and details of the form of the external aperture of the ear, ought to have been carefully examined in comparison with that of other species; but as it is, the only information on the subject we possess we owe to Mr. J. H. Gurney (7) and the kindness of Prof. Newton, who generously lent me a stuffed specimen and gave me permission to relax the skin and make what I could of an examination of its pterylosis. This I have done, and the results will be found embodied in this paper.

It struck me that the best method of learning something about *Sceloglaux* was to be attained by first of all gathering as much information as possible about all the other Owls, as by this means we might hope to gain some insight as to its probable systematic position.

The present paper represents the first fruits of an attempt to realize this end, and deals with the external topography only. Later I propose to describe the Osteology, Myology, Syrinx, Sacral Nervous System, and Visceral Anatomy of all the species whose pterylosis is now described, and of as many additional species as can be obtained.

The pterylosis of *Asio accipitrinus* has been taken as the type of the paper and is described in some detail, while only the salient features of the remaining species have been touched upon.

In this first part the pterylosis of some 20 species is described. I have been liberally supported by friends interested in the subject, and wish here to record my deep sense of indebtedness to those who have contributed material.

First of all my thanks are due to Prof. Newton, who started the work, provided me with a valuable collection of skeletons, and furnished me with an unlooked-for chance of examining the pterylosis of *Sceloglaux*. Moreover, he has helped me throughout the preparation of this essay by kindly sympathy and advice.

To Dr. Slater and Mr. Beddard I owe much; they have furnished me with valuable material from the Zoological Gardens, amongst which I would mention *Bubo lacteus*, *B. virginianus*, *B. torquatus*, *Speotyto*, and the only Barn Owl I have been able to examine.

Mr. Jesse, of La Martinière College, Lucknow, sent me some beautifully preserved embryos of *Athene brama* and other material. Mr. Allan Wilson, of Wadham College, Oxford, procured me the Tawny Owl from which the description which follows was taken, and since then I have had one other from the Zoological Gardens.

Lastly I have to record the share contributed to this paper by one who has since passed away. I allude to the death of one of my kindest and best of friends, Mr. Daniel Meinertzhagen. His loss will be keenly felt, not only by those to whom he had endeared himself in a thousand different ways, but by ornithologists at large. Young, enthusiastic, an exquisite draughtsman, a most careful worker, and imbued with a deep love of Ornithology, he seemed in every way one from whom we might expect great things, and had he lived we should not have been disappointed. He took the keenest interest in the progress of this work, and furnished me with most of the forms herein described from his aviaries at Mottisfont Abbey. Amongst the rarest are the Tengmalm's Owl, Ural Owl, Snowy Owl, *Ninox*, Hawk Owl, and *Scops*. To his pen we owe the very beautiful and accurate figures which form the Plates illustrating this part. These were drawn in Prof. Lankester's Laboratories at Oxford, where we were both working, and they represent the last work he ever did before taking his farewell of the University.

## II. HISTORICAL.

Almost all that we know concerning the pterylography of the Owls we owe to Nitzsch (13). Regarding them as closely allied to the Accipitres, he yet realized that they differed pterylogically from them in many important particulars, such as the absence of an aftershaft to the feathers, the absence of down-feathers on the pterygæ, and the nude oil-gland. In their general pterylosis, as he pointed out, they bear what is certainly a striking resemblance to the Falcons; but, as will be shown later, the points which he selected as distinguishing the Owls from these break down when applied to a large series of examples.

His study of the pterylography induced him to divide the Owls into two sections by cutting off the Barn Owls as a group by themselves apart from the rest. Later researches, taking into account the osteology and myology of the two groups, have confirmed his action.

According to Nitzsch the pterylosis of all the Owls, save *Strix*, was exactly the same as in *Bubo* (*Strix bubo*, L., = *B. ignavus*, Forst., was the type figured), save in one or two minute points, the various species being distinguished one from another by the relative

lengths of the primaries and the amount of the emargination of their inner vanes. In *Speotyto*, save for the spinal tract, he tells us that "the pterylosis differs in no respect from that described for *S. bubo*."

In the Barn Owls the ventral tract is said to "agree precisely with that of *Cathartes*, only differing in that, in *Hybris* (= *Strix flammea*), the contour-feathers are more numerous and stand closer together." He was the first to draw attention to "two minute feathers seated at the apex of the oil-gland."

The form and nature of the facial disc are very carefully described, but he does not seem to fully appreciate the differences in the form of the external aperture of the ear and of the opercular fold in the various Owls.

I have been unable to confirm his description of the disc-feathers of *S. otus* (= *Asio otus*). According to him, "they consist of a large tube perfectly open above, upon which a very small, sparsely-barbed shaft is seated."

As will be seen later, my own investigations bear out the main conclusions of Nitzsch's work most completely. The wonder is that he failed to notice the numerous small but very real differences by which not only genera but even species may be distinguished. It is also a matter for some surprise to find him so closely associating *Syrnium* and *Scops*, the pterylosis of which is said to be "as in *Bubo*." The resemblance between *Bubo* and *Scops* is undoubtedly very great, as he indicates, but *Syrnium* can be very readily distinguished from either.

It is somewhat strange to find that Kaup (8), in his "Monograph of the Strigidæ," published in the Trans. Zool. Soc. 1862, makes no mention of Nitzsch's work. He takes into account only such facts as the presence or absence of "horns," the form of the disc—which he divides into a central "veil" surrounded by a "wreath,"—the length of the primary remiges, and whether or not they are emarginate, and the presence or absence of feathers on the acetarsium and aeropodium. He draws attention to the fact that the feathers seated in the posterior membranous fold surrounding the external aperture of the ear are so arranged as to slope in opposite directions, meeting at an obtuse angle. The feathers in the upper half of the fold are directed downwards, those in the lower half are directed upwards. The feathers in this fold constitute the "wreath."

Besides these, he also employed such external features as the form of the nostrils, the development of the "cere," and the size of the external aperture of the ear. The points noticed in the latter were (1) the size, measured with relation to the long axis of the eyelids, its symmetry or asymmetry, and (2) the presence or absence of an operculum or "anterior ear-lap" and of a posterior or "hinder ear-lap." The somewhat complicated relations which obtain in the asymmetrical ear-apertures of *Asio* are fairly well described.

The systematic arrangement resulting from his labours\*, however, is decidedly inferior to that of Nitzsch. He divided the Owls into two subfamilies, *Syrniinæ* and *Striginæ*.

\* The osteology of the skull also found a place in his diagnoses. He employed such characters as the form of the occipital region and the pneumaticity of the bones. He was, I believe, the first to point out the swollen spongy nature of the interorbital septum of the Barn Owl.

The former contained the genera *Glaucidium*, *Nyctala*, *Athene*, *Syrnia*, and *Ieroglaux*, the latter *Scops*, *Otus*, *Bubo*, and *Strix*.

In the earlier editions of Yarrell's well-known 'History of British Birds,' the scheme of classification which was followed for the Owls was that of dividing the group into "horned" and "hornless." This plan was discarded some six-and-twenty years ago by Prof. Newton when he undertook the task of re-writing this work (12). He adopted in the main that of Messrs. Sclater and Salvin. Internal characters apart, they were divided into two groups, the one, representing the Barn Owl and its allies, characterized by the disposition of the feathers of *pt. ventralis*, the form of the operculum, the straightness of the beak at the base, and a serrated middle claw. The other was further subdivided into "the Owls which possess an operculum to the ear and the Owls which do not;" . . . . "to the first of these belong the Tawny, Tengmalm's, the Long-eared and Short-eared Owls, and to the second the remainder of the species."

Whether the subdivision adopted for this latter group is destined to prove the right one or not I will not venture to say; for my own part I have some doubt as to its power to hold its own. The form of the operculum and cavernum (p. 259) in *Asio* and *Syrnium* have really very little in common, whilst that of *Nyctala* can hardly be called an operculum at all.

The minor characters utilized in the formation of genera were such as the form of the facial disc, length of the remiges, presence or absence of "ear"-tufts, feathering of the legs, and the form of the external aperture of the ear, whether symmetrical or not.

Four years after the publication of Prof. Newton's work Dr. Sharpe brought out his 'Catalogue of the Striges' (16). Measurements, and such points as the size of the external apertures of the ear, measured with relation to the length of the horizontal axis of the eyelid, the presence or absence of an operculum, and the development of the facial disc, are the characters which he adopted for the purpose of breaking up the group into genera and species.

Following Sclater and Salvin, he divided the Owls into two groups—the *Strigidae*, containing the Barn Owl and its allies, and the *Bubonidae*. The only external characters adopted for the purposes of this division were the relative lengths of the middle toe and the presence or absence of a serration along the inner margin of the claw of that digit.

The *Bubonidae* were further subdivided into the *Buboninae*, with the "ear-conch not larger than the eye (? eyelid), without an operculum; facial disc unequal, the portion below the eye being always much greater than the area above the latter;" and the *Syrniinae*, with the "ear-conch much larger than the eye, with very large operculum shutting in the ear; facial disc always distinct, and extending as far above the eye as below it." These two sub-families agree with Prof. Newton's—those which possess an operculum to the ear, and those which do not. In addition, however, to the question of the presence or absence of an operculum, Sharpe takes into account the size of the aperture of the ear; this was a step in the right direction, but it was not enough, since even now Owls are brought together which ought to be placed in separate sub-families.

Thus, *Syrnia*, *Carine*, *Speotyto*\* are placed in the *Buboninae*, to which I do not think they rightly belong, whilst *Asio*, *Syrnium*, and *Nyctala* probably represent as many sub-families.

Dr. Gadow (2-4) accepts Nitzsch's diagnoses of the general pterylography of the Owls. In one point, however, he is confident where Nitzsch wavered, inasmuch as he states that down-feathers occur and are confined to the apteria. Nitzsch was doubtful on this point, but observed that he had never found them when he searched for them. As a matter of fact, they occur only in the *pt. alaris* (Pl. 24, *d.f.*).

In the structure of the neossoptiles Gadow considers the Owls to approach the Goat-suckers. He remarks that they are double as long as the neossoptiles of the Accipitres, and are further characterized by their extreme softness ("weichheit"). As will be pointed out later (p. 253), the "nestling-down" of the Accipitres is of two kinds—one preceding the future definitive contour-feather, and one preceding the future definitive down-feather; and it is probably with this last that the "nestling-down" feather of the Owl has been compared, instead of with the former, with which it really corresponds.

Moulting takes place once annually, in July and August.

Although the curious separation of the external aperture of the asymmetrical ears of *Asio* into two chambers (p. 259) is briefly described, no mention is made of the "operculum" or of the posterior membranous fold fencing in this aperture from behind.

Meijere, in his papers on the distribution of the hair in the Mammalia (9) and of the feathers amongst Birds (10), has brought to light some most interesting and valuable facts. In his first paper he sets himself the task of proving that there is considerable evidence to show that the arrangement of the Mammalian hair indicates the presence of an earlier clothing of scales †. On the loss of the scales the hairs remain, and thus is explained their peculiar distribution in groups of three or more, as the case may be.

The author, in his second paper (10), points out the close similarity in the arrangement between hairs and feathers, and remarks that, though he does not wish to imply an homology between these structures, yet their close resemblance in this particular would be a not unimportant argument in favour of such homology if it were supported by other evidence. But our knowledge on this point is as yet very meagre.

According to Meijere, at a certain stage in the development of the Avian type the body-clothing consisted of alternating groups of similar feathers, whose long shaft bore a biserial system of branches—Rami. These, in their turn, supported a biserial system of smaller branches—Radii. The latter consisted of a row of cells, provided distally with a pair of fila ("wimperchen"), which probably here and there took the form of hooklets. Later, the middle feather of each group developed at the expense of the rest, which now assumed the form of the diminutive feathers which we know as Filoplumes. The middle

\* I am only taking into account such genera as I have had the opportunity of studying; *Heteroglaux* and *Gymnasio* have not yet come under my ken.

† The nature of the combined covering of scales and hairs can be studied on the scaly tails of such animals as *Mus decumanus*. Here they arise in groups of three from behind each scale, the middle one being the strongest. In some cases the number of hairs associated with each scale is greater than three. In *Castor fiber*, for instance, there are eight such hairs. In cases of this kind the hairs seem all to be of equal calibre.

feather became either a true contour-feather, in which the Fila became more and more perfectly specialized to form "Hooklets," at the same time as the shaft, rami, and radii increased in strength, or it became a true down-feather. In the latter case the change might be brought about in two ways:—(1) the radii became relatively weaker and more numerous, and the fila of the radii became metamorphosed in various ways, or (2) the shaft became very considerably shorter and weaker. Umbelliform ("doldenförmige") down-feathers represent reduced long-shafted feathers. The same, he thinks, may be said of umbelliform neossoptiles. As to which is the older of these two primitive types of long-shafted feathers we know at this time nothing for certain.

In the course of his paper on the distribution of feathers Meijere briefly discusses the arrangement of the feathers covering the tarso-metatarsus of a young Barn Owl. These he describes as seated in groups of three, a median and two lateral, under the anterior margin of the scales of the podotheca. Such an arrangement recalls, he reminds us, that which obtained on the scaly tail of *Mus decumanus*. The median feather was much the largest; the two lateral represented degenerate contour-feathers sunk to the level of filoplumes. On the tibio-tarsus the feathers are also described as arising in groups of three, but the median feather is here much more developed, possessing a distinct though semiplumous vane. In an adult Barn Owl the lateral feathers of the scales of the podotheca were wanting or occurred sparingly. Down-feathers and degenerate filoplumes are described as occurring on the dorsal apterium. On the breast filoplumes are stated to occur sparingly.

I find myself unable to confirm one or two small points in this paper, inasmuch as after careful search I failed to find more than a single filoplume to each feather on the tibio-tarsus, nor could I succeed in finding any filoplumes associated with the down-feathers of the Owls examined by me.

As touching matters of identification, it seems to me that Meijere has failed to distinguish between true down-feathers and semiplumes. The latter occupy the position of and represent contour-feathers which are in process of degeneration and final disappearance—the *modus operandi* of the formation of pteryæ. Down-feathers occupy the spaces between contour-feathers. This makes it rather difficult to accept the hypothesis that they are degenerate contour-feathers.

### III. PTEROLYSIS OF THE ADULT.

ASIO ACCIPITRINUS, Pall. (Pl. 25. figs. 1-3.)

*Pteryæ*:—

*Pteryæ capitis*.—For the purposes of convenience in description this tract will be described throughout under the following subdivisions:—

**FRONTO-PARIETAL AREA**.—This extends from the base of the beak to the crown of the head. It is clothed by a narrow median band of feathers, expanding later to cover the occipital area. On either side of this median band, in the region corresponding with the level of the superior limb of the crescentic membranous folds surrounding the

external aperture of the ear, lies a single longitudinal row of some 6-7 feathers distinctly longer than those in the neighbourhood, whose shafts are directed outwards and backwards; they form the "ear"-tufts or "horns." Running along the outside of the bases of these "ear"-tufts is an oblong apterium.

**Occipital area.**—This is a backward continuation of the parietal area, terminating at the occiput. The feathers radiate from the middle line outwards and somewhat upwards. As they approach the free edges of the post-aural fold they gradually decrease in size, and become at the same time more thickly planted.

**Loreal area** (Pl. 25. fig. 2).—This is occupied by a somewhat crescentic and densely-packed group of stiff-shafted feathers (p. 256). Its upper limb runs backwards to terminate in the region above the middle of the eye. The lower limb runs downwards and backwards behind the gape to join the feathers of the operculum.

**Ocular area.**—In consequence of the fact that the eyes, instead of being sunk entirely within the orbit, are directed outwards and forwards, a considerable portion of the sclerotic ring is brought into close relation with the outer world. This portion is protected by the eyelid, which is on this account of greater relative size than in other birds. It is clothed by a more or less regular series of semicircular rows of feathers, decreasing in size as they approach its free edge.

**Circumaural area.**—As its name implies, this area concerns the region around the external aperture of the ear. In the present species, and in some other Owls, this region is characterized by the considerable development of membranous folds of skin—the pre- and postaural folds. When the former is largely developed, it is known as the "operculum."

**Operculum.**—The feathers seated along the free edge of the operculum (Pl. 25. fig. 2) are all elongated, with narrow vanes; they form a series of from 3 to 4 rows having an outward and upward direction. Running parallel with the feathers on the free edge, but separated by a considerable apterium, is a single row of feathers, differing only from those of the free edge in that they are of a more slender character.

**Postaural fold.**—The feathers seated along the free edge of this fold form the periphery of the disc (Pl. 25. fig. 2). They belong respectively to the fronto-parietal, occipital, and ramal areas, and are continued downwards and forwards to unite in the middle line near the symphysis of the mandible. They are comparatively short, slender, and narrow-vaned, so densely packed that their embedded bases form a thickened rim to the fold. The feathers occupying the lower segment of this "rim" are directed upwards, and those in the lower segment downwards; as a consequence, where the two series meet a notch is formed (Pl. 27. fig. 3). This point was apparently first noticed by Kaup (p. 225).

**Ramal area** (Pl. 25. fig. 2).—This may be divided into two sections—an anterior, extending from the gape on each side of the ramus to the junction of the pre- and postaural folds, and a posterior strongly-marked triangular section, the base of which merges with the feathers of the postaural fold.

**Interramal area.**—The space from the symphysis of the mandible backwards to the point where the inferior limb of the crescentic peripheral disc-feathers converges is occupied by a broad truncated-conical patch of elongated, slender, forwardly-directed

feathers. It is bounded on either side and in front by an apterium. The remainder of the interramal area lies behind the convergent ends of the peripheral disc-feathers, but is almost directly lost in the *pteryta colli ventralis* (Pl. 25. fig. 2). It forms a narrow tract of some two feathers in width. In one case, however, this expanded to merge on either side with the mandibular area.

The facial disc is formed by the feathers of the opercular and loreal areas and those of the postaural fold. These last form the periphery of the disc.

*Pt. colli dorsalis* (Pl. 25. fig. 3).—A densely-feathered tract, not closely investing the neck, but seated upon extensive lateral folds of skin, forming the T-shaped expansion of a vertical median membrane. The tract is widest a little below its origin at the occiput, then suddenly contracting, so that, at the point where it emerges with the *pt. spinalis*, it is reduced to an obliquely-transverse row of some 5 feathers. A membranous fold investing a retractor muscle runs from the underside of the lateral neck-membrane at a point a little below its greatest width, in an obliquely-downward direction, to the *pt. colli ventralis*, and thence to the shoulder (Pl. 25. fig. 2).

*Pt. spinalis* (Pl. 25. fig. 1).—It is not possible to draw a hard-and-fast line separating this at its upper end from the *pt. colli dorsalis*. It is divided into an upper A-shaped and a lower Y-shaped portion. The former will henceforth be called the *interseapular fork*, and the latter the *lumbar fork*. The arms of the interseapular fork arise in the upper third of the interseapular region—in one specimen at the root of the neck, where it took origin from the *pt. colli dorsalis*, there being no stem—and terminate on a level with the free end of the scapula. The feathers are seated in obliquely-transverse rows of not more than 4 feathers in each row. The branches of the lumbar fork are wide apart and continued upwards on to that portion of the axillary membrane lying between the humeral tract and the arms of the interseapular fork. A double row of semiplumous feathers enters into the formation of each branch, and these converge into the common stem some distance in front of a line drawn through the acetabular region. The stem is made up of transverse rows of feathers arranged in triplets (thus—, .). It is bifurcated posteriorly, terminating just in front of the oil-gland, after somewhat increasing in width.

*Pt. caudæ*.—There are 12 rectrices.

*Pt. colli ventralis*.—This comes into existence in the form of a backward continuation of the interramal tract. At first made up of a treble (transverse) row of feathers, it gradually increases in width to the middle of the neck, where it forks, each branch running to join the *pt. centralis* at the shoulder.

*Pt. ventralis* (Pl. 25. fig. 3).—Three branches must be recognized in this tract—an outer, a median, and an inner. The outer is very distinct and runs backwards from the shoulder across the pectoral muscles to the preaxial border of the patagium. The median and widest of the three arises at the shoulder and runs backwards to within a short distance of the level of the posterior border of the sternum; here it turns abruptly upwards and forwards to join the hypopteron. This upward limb is the “hook” of Nitzsch. The area between the hook and its main stem is more or less thickly

besprinkled with feathers. The inner branch arises from the inner border of the median at a point rather in front of the level of the anterior end of the carina sterni, and runs backwards and inwards to join its fellow of the opposite side in front of the cloacal aperture. It is widest on the breast, and contracts suddenly on the abdomen, to form a narrow band at some distance from the middle line. Its anterior end is obliquely truncated; the lower and outer angle receives the feathers forming the preaxial border of the *pt. marginalis*; the upper and inner angle is formed by a single row of feathers of the *pt. ventralis* at the shoulder.

*Pt. femoralis* (Pl. 25. fig. 2).—The limits of this tract are not sharply defined. It is continued forwards to form a *pt. lumbalis*. Along the posterior border of the thigh there runs a strongly-marked band of stout feathers, which is continued forwards to terminate below the knee-joint. This band I shall call the *femoro-crural* band.

*Pt. cruralis* (Pl. 25. fig. 2).—The feathers of this tract are slender and do not invest the leg completely, but leave the inner surface bare. This tract is continued downwards over the acetarsium and acropodium, to terminate over the penultimate phalanx of each digit. The planta is bare.

*Pl. alaris* (Pl. 24):—

Metacarpo-digitals (primaries) 11; 9th longest (reckoning from within outwards); outer vane of the 10th serrated, with the tip of the inner vane emarginate; distal end of the 9th with the outer vane serrated; 11th reduced to the condition of a remicle. Cubitals (secondaries) 14, the innermost small, not easily distinguished from their major coverts. The wing is aquitocubital.

*Tectrices*:—

*T. majores*.—The major coverts of the dorsal surface of the manus large; the 11th much longer than its remex (the remicle), but least of all the coverts of the hand belonging to this row. Carpal covert and remex large, closely attached by their base one to another and to the base of the 1st metacarpo-digital. The covert is larger than the remex.

The dorsal major coverts of the cubital remiges are of uniform length throughout; sometimes, however, there is a distinct break in the continuity of the line formed by the distal ends of these coverts. In such cases the break is found to be due to the fact that the coverts 1-5 are slightly longer than the rest of the row, whilst no. 6 is slightly shorter\*. The row terminates at the elbow-joint, and is not carried inwards on to the humerus. The overlap is distal.

On the ventral surface the feathers of the manus, with those of the cubital remiges, gradually increase in length from without inwards. Overlap distal.

*T. mediæ*.—On the dorsal surface of the manus this row commences at the 3rd meta-

\* As will be shown later, in the Owls the cubital major coverts of the dorsal surface are usually of uniform length throughout. Inequality in the length of the major coverts is never found except in aquitocubital wings. The 5th major covert is distinctly longer than the 6th in *Leptoptilus javanicus*, *Grus australiensis*, *G. cinerea*, *Ardea cinerea*, *Palamedea cornuta*, *Ceryle torquata*, and *Conurus*.

The 5th major covert is shorter than either the 4th or 6th in *Megapodius nicobariensis*.

carpal remex. The overlap is distal. On the forearm the coverts 1-5 are very considerably the longest in the row, gradually increasing in length from without inwards. The series terminates at the elbow and is not continued inwards on to the arm. The overlap is proximal.

On the ventral surface of the manus this row terminates at the base of the 6th remex. The feathers of the cubital series are fairly long and uniform in length, but concealed by the 1st row of the *t. minores*, which are slightly longer and closely approximated at their bases.

*T. minores*.—On the dorsal surface these coverts are wanting on the manus. There are about 3 cubital rows, all with a proximal overlap. With the 1st row, as with the median series, coverts 1-5 are considerably the longest in the row. The same is true of the two succeeding rows, preaxially, but in the case of each row the differences of length decrease rapidly.

On the ventral surface of the manus they are moderately long, replacing the *t. mediae* after the 6th metacarpal remex. Those of the cubital remiges are slightly longer, and therefore conceal the *t. mediae*. The 2nd row is made up of much smaller feathers than the 1st. It is only represented on the manus by 3 feathers lying at the bases of the metacarpal remiges 1-3. The 3rd row is not represented on the manus. On the forearm it follows the course of the ulna. In texture the feathers of this row are small and semiplumous. The patagial membrane is clothed with 2 rows of degenerate semiplumous contour-feathers.

*T. marginales*.—On the dorsal surface there are 2 rows running along the preaxial border of the manus. The greater part of the surface of the patagium is clothed by some 4-5 rows, which are continued inwards along its margin as a closely-set triple row of feathers, which ultimately join the *pt. humeralis*.

On the ventral surface there are from 2 to 3 rows. The coverts of this series are seated in closely-packed obliquely transverse rows. The postaxial row, seated on the patagium, are very long, and overlap the semiplumous *t. minores*.

*Parapteron*.—This is made up of some 8 obliquely-transverse rows of 3 feathers in each row. Of these, the middle feather is the longest. The most preaxial feathers at the distal end of the arm rest on the humerus, the remainder on the muscles of the arm. Viewed as a whole, the parapteron is of a rounded conical form. It is connected by a double row of small feathers with the tectrices on the forearm. Whether these feathers can be brought into serial relation with the *tectrices majores* and *mediae* of the forearm is a point not easy to determine.

*Hypopteron*.—Elongated, delicate, semiplumous feathers, running along the under surface of the arm in some 6 transverse rows of 3 feathers in each row, make up the *Hypopteron*. Proximally they merge with the recurved end of the median branch of the *pt. ventralis*.

*Ala spuria*.—Four strong feathers take part in the formation of the *ala spuria*.

It is a point worthy of remark that the feathers of the dorsal surface of the *pt. ataris*, instead of being set in quincunx, form obliquely-transverse rows sloping from without

nwards. The only other birds that I can recall in which a similar arrangement obtains are *Caprimulgus* and *Rhea*.

*Semiplumæ* :—

Semiplumes\* occur in the interseapular fork of the *pt. spinalis*, and compose the branches of the lower Y-shaped portion of this tract. The femoral tract is largely made up of semiplumes. The inner border of the *pt. humeralis* is bounded by semiplumes, so also is the *pt. colli ventralis*; they also cover the axillary patagial fold. If the wing of a freshly-killed Owl be raised, a large bare space will be seen entirely bounded by semiplumes. They run along the recurved limb of the median branch of ventral tract, downwards, or, rather, backwards, from the origin of this to the *pt. femoralis*, the anterior border of which forms its posterior boundary, and hem in the space dorsally through the branches of the lumbar fork of the *pt. spinalis*, finally joining the posterior end of the *pt. humeralis*. Thus, this portion of the *apt. trunc. laterale* (p. 234) is entirely shut off from that lying between the *pt. humeralis* and *pt. spinalis*, and that between the inner and median branches of the *pt. ventralis* and the inner branch of the *pt. ventralis* and the thigh.

*Plumulæ* :—

Plumule or down-feathers are entirely absent on the trunk; they occur *only* on the wing, and are distributed as follows:—On the dorsal surface they are absent along the preaxial border of the wing; behind this they occur singly between the contour-feathers in such a way as to form a quincunx with them (thus— $\cdot \begin{matrix} \cdot \\ \cdot \end{matrix} \cdot$ ), the down-feather occupying the centre. Two are found at the base of every major covert, and two at the base of every remex (Pl. 27). On the manus there is but one down-feather to each major covert. Their distribution on the under surface of the wing is much as on the upper.

*Filoplumæ* :—

The filoplumes are very slender and not easy to find. One or more occur at the base of every contour-feather on the body.

*Rhamphotheca*.—The reniform external nares pierced through the anterior margin of a soft slightly tumid membrane at the base of the beak, resembling the cere of the Accipitres. For convenience' sake this will in future be called the cere.

*Podotheca*.—Clothed with feathers save the base of the terminal phalanx, which is covered by 3 scales.

*Claws*.—There are no claws on the wing; those of the foot not much curved, rounded, the inner border of the middle claw forming a sharp edge, decreasing in size from the base downwards.

*Uropygium* napiform. It is not tufted.

*Moulling*.—Moulling takes place once a year, in July and August. (*Gadow*.)

\* It must be remembered that Semiplumæ are nothing more than degenerate contour-feathers, and can always be distinguished from down-feathers in consequence of their position on the body, which is, necessarily, serial with the contour-feathers. Down-feathers are always placed between contour-feathers when they occur on pterylae. Semiplumes always occur along the margins of pterylae—if the whole pteryla is not made up of semiplumes—and indicate a further restriction of a once wider tract.

*Apteria*:—

*Aptorium capitis*.—The apteria of the head are represented by the bare spaces surrounding the eyelids, the spaces on the operculum, and the space on the outer side of the feathers forming the “ear”-tufts (Pl. 25).

*Apt. colli laterale* (Pl. 25. fig. 2).—Extends from the base of the neck, as a continuation of the *apt. trunci lat.*, forwards to the base of the head, where it branches into an upper limb, running to the postaural fold, but terminating some distance from its free edge (Pl. 25. fig. 3), and a lower, which serves to separate the ramal from the interramal areas of the *pt. capitis*.

*Apt. trunci laterale* (Pl. 25. fig. 2).—Arising at the shoulder, it serves to divide the humeral from the spinal tract, and is continued backwards to the tail, and thus separates the spinal from the femoral tracts. At the free edge of the axillary fold it runs downwards to embrace the whole side of the body. Its extreme ventral limit is bounded by the inner border of the *pt. ventralis*.

*Apt. spinale* (Pl. 25. fig. 1).—This is the space enclosed by the branching arms of the upper and lower portions of the *pt. spinalis*.

*Apt. mesogastræi* (Pl. 25. fig. 3).—The dimensions of this space can be seen at a glance in the figure.

*Apt. crurale*.—This is the space at the back of the leg (p. 231), and is continued downwards on the tarso-metatarsus.

*Apt. alæ superioris*.—The space dividing the humeral from the wing-tract.

*Apt. alæ inferioris*.—Embraces the bare region of the arm and patagium.

## ASIO ORUS, Linn.

*Pt. capitis*:—

FRONTO-PARIETAL AREA.—The feathers forming the “ear”-tufts are distinct from the general plumage of the head, and consist of a longitudinal row of some 7–8 feathers, bounded on either side by an apterion.

LOREAL AREA.—Sharply defined; upper limb free, more slender than in *A. accipitrinus*.

INTERRAMAL AREA.—The anterior symphysial portion shorter antero-posteriorly than in *A. accipitrinus*; the posterior portion joining the feathers of the ramal area on either side.

*Pt. colli dorsalis*.—The lateral neck-folds gradually tapering backwards, and not suddenly expanded just behind the head. With a retractor muscle.

*Pt. spinalis*.—Interseapular fork commencing at the confluence of the *pt. colli dorsalis* and *pt. spinalis*. The free ends of the interseapular fork are received into the arms of the lumbar fork, which are continued outwards on the posterior patagial membrane as in *A. accipitrinus*. The tract bifurcates posteriorly, embracing, but not surrounding, the oil-gland.

*Pt. colli ventralis*.—Very broad at the point of bifurcation.

*Pt. femoralis*.—Femoro-crural band terminating at the base of the patella.

*Pt. ventralis*.—Inner branch somewhat nearer the middle line than in *A. accipitrinus*.

*Pt. alaris*.—

*Tectrices*:—

*T. majores*.—The dorsal major coverts show an interesting departure from the general rule, in that, instead of the break in the uniformity of the length of these coverts occurring after the 5th covert, it occurs after the 4th, the 5th being slightly shorter than the 4th, but, as usual, longer than the 6th.

*T. mediae*.—The break in the uniformity of the length of the coverts is here very marked, the 6th covert being much shorter than the 5th.

*T. minores*.—The remarks apply to the first two rows of these coverts as to *T. mediae*; in the 3rd row the difference is not so marked.

Such other points as are unnoticed are indistinguishable from *A. accipitrinus*.

BUBO IGNAVUS, Forst.

*Pt. capitis*:—

Fronto-parietal area.—The two areas included under the name can here be readily distinguished. The frontal area is represented by a broad median band of feathers running from the base of the beak to a point corresponding with a line drawn across the head behind the eyes, where the tract rapidly expands to form the parietal area. This distinction is not so readily seen in the case of *B. maculosus* on account of the smaller size of the feathers.

The feathers forming the ear-tufts, in a single row, bounded posteriorly by an apterium, the anterior extremity of the *apt. colli laterale*.

Circumaural area:—

Preaural fold.—This is but slightly developed; there is a double row of feathers along its free edge, the bases of which form a "rim."

Postaural fold.—The upward and downwardly directed feathers along its free edge converging at about the middle of the fold, the bases of which form a "rim." The peripheral disc-feathers terminating on the mandible, just in front of the gape.

Ocular area.—The rows of feathers encircling the region of the outer wall of the eye can be well studied in this species.

Loreal area not sharply defined, the lower limb continued backwards to join the feathers at the confluence of the opercular and circumaural folds.

Ramal area not extending to the proximal end of the jaw, but turning inwards in the form of a narrow band on the throat.

Interramal area.—In the form of a broad tract, bounded on either side by a wide apterium.

*Apt. colli laterale*.—Continued upwards from the neck on to the proximal end of the mandible; from thence it can be traced upwards and forwards on to the crown, where it serves to isolate the row of feathers forming the "ears." The continuity of the space is interrupted, however, by two tracts of feathers, one running from about the middle of the postaural fold, the other from the region immediately above the fold, to the feathers of the occipital area.

*Pt. colli dorsalis*.—Vertical and lateral neck-folds moderately well developed. No retractor muscle.

*Pt. spinalis*.—Branches of the interscapular fork arising at the commencement of the interscapular region; arms long, but not extending to the end of the scapula.

Branches of the lumbar fork arising about midway between the anterior end of the ilium and the region over the acetabulum, running forwards to embrace the ends of the interscapular fork, and terminate over the proximal  $\frac{1}{3}$  of the free end of the scapular. Stem forked posteriorly, branches widely divergent, terminating some distance to the outer side of the oil-gland.

*Pt. ventralis*.—Outer branch strongly developed, arising at the summit of the shoulder. Median branch broad, very strong, with an upward trend at its free end, where it gives off the "hook." Inner branch wide, not sharply defined at its upper end; the breast between the median branch and the carina being almost continuously feathered.

*Pt. humeralis* not continued forwards to join the *Pt. ventralis*.

*Pt. femoralis*.—The femoro-crural band terminating on the crus some distance below the knee.

*Pt. cruralis*.—Continued downwards on the acrotarsium and terminating on the acropodium. The base of the ungual phalanx clothed with scales. Proximal end of the planta bare.

#### BUBO VIRGINIANUS, Sw. & Rich.

##### *Pt. capitis*:—

Parietal area.—"Ear"-tufts very distinct, the stumps of the feathers appreciably larger than those of the neighbouring feathers. They are seven in number, arranged to form a longitudinal row, the inner border of which is bounded by a large lenticular apterium.

Loreal area.—Upper limb not continued upwards beyond the level of the anterior corner of the eyelid.

Circumaural area.—Preaural fold feebly developed, a double row of feathers along its free edges; a broad apterium separating these from the ocular area.

Postaural fold.—The convergent feathers along the free edge of the postaural fold meeting near its middle. The feathers behind the free edge arranged in the form of a triangular patch. Peripheral disc-feathers arising on the crown of the head just behind the eye, terminating on the mandibular area.

Mandibular area.—Extending beyond the articular end of the mandible, very broad, at the level of the gape turning sharply inwards to merge with the feathers of the interramal area.

Interramal area.—Very broad, at the level of the gape merging with the ramal area.

*Apterium colli laterale*.—Extending on to the postaural fold and skirting the articular area of the lower jaw. Passing behind the triangular patch of the postaural fold upwards, it attains the level of its superior angle, but is cut off by a broad band of feathers from the lenticular apteria to the inner side of the "ear"-tufts.

*Pt. colli dorsalis*.—Lateral neck-folds considerable; with a retractor muscle as in *Asio*.

*Pt. spinalis*.—Arms of the interscapular fork arising about the middle of the interscapular region; branches short, running almost parallel, not widely divergent, extending to the end of the scapula.

Lumbar fork.—Arising behind the middle of the preacetabular region of the ilium; well developed, extending forwards on to the axillary membrane. Stem cleft posteriorly into two long arms, not extending to the oil-gland.

*Pt. colli ventralis*.—As in the other species of *Bubo*, branching about the middle of the neck to join the *Pt. ventralis* at the shoulder.

*Pt. ventralis*.—Outer branch strong, arising low down from the outer border of the median branch. Median extending backwards as far as the posterior  $\frac{1}{3}$  of the carina sterni. Inner branch broad, but more sharply defined than in *B. maximus* or *B. lacteus*.

*Pt. alaris*:—

*Remiges*.—Metacarpo-digital 11; cubitals 19; the innermost 2-3 cubital remiges scarcely differing in size from their coverts.

*Tectrices*:—

*T. majores*.—The major coverts of the dorsal surface uniform in length.

*T. mediae*.—With a distinct break in the uniformity of the length of the series, the 6th being much shorter than the 5th.

*T. minores*.—With a break in each row, similar to that seen in the *T. mediae*.

*Parapteron*.—Made up of some 10 obliquely-transverse rows sloping from without inwards. Each row composed of 4 feathers, the most postaxial a semiplume, and overlapping the next, a true contour-feather, and much longer; this in turn overlaps the one next above and longest of the series, which is overlapped by the most preaxial feather. Proximally these humeral feathers rest upon the muscles of the arm; distally, upon the humerus; running along the upper surface of the humerus is a row of semiplumes, all with the tips directed towards the tip of the wing.

Between each of the transverse rows just described, and on the extreme postaxial border of the humerus, are two semiplumes, one lying a little above the other. The uppermost one runs parallel with the larger feathers of the parapteron; the lower is pressed close to the arm, with its tip directed towards the end of the wing. Whether these feathers are really serially homologous with the dorsal and ventral major coverts and the dorsal row of median coverts, and a ventral row of minor coverts, as represented by the semiplume, or not, remains to be proved. It will be noted that in this case the remiges are wanting.

The coloration of the feathers of the parapteron is not to be distinguished, save in minute points of detail, from those of the fore arm.

*Hypopteron*.—Three parallel rows along the arms, somewhat semiplumous in texture.

*Pt. femoralis*.—Femoro-crural band terminating considerably below the knee.

*Pt. cruralis*.—Toes thickly feathered. Terminal phalanx covered by 3 broad scutes.

## BUBO MACULOSUS, Bp.

*Pt. capilis*:—

Fronto-parietal area.—The feathers forming the “ear”-tufts in a single longitudinal row on the crown of the head, with a well-marked apterium on either side.

Loreal area.—Not sharply defined; upper limb scarcely extending beyond the anterior corner of the eyelid.

Circumaural area.—The preaural fold is but feebly developed, and does not form an operculum. It bears but a double row of feathers along its free margin, the bases of which form a “rim” to the margin.

The feathers of the postaural fold seated along the free edge of the upper part are, as usual, all directed downwards, those of the lower part upwards, the two series meeting in the middle of the fold. There is no “rim” to this fold.

The peripheral disc-feathers apparently terminating below on the mandible, near the base of the rhamphotheca.

Ramal area.—Truncated posteriorly, not extending backwards to the proximal end of the jaw.

Interramal area.—Wide anteriorly, gently tapering posteriorly to join the *pt. coll. ventralis*.

*Apl. colli laterale*.—Occupying the lower portion of the circumaural fold, and running upwards and forwards behind a triangular patch of feathers clothing the upper part of the fold, to cut off the row of feathers forming the “ear”-tufts from the rest of the parietal area.

*Pt. colli dorsalis*.—Vertical and lateral neck-folds of slight extent; the posterior end of the tract where it joins the *pt. spinalis* 4 feathers in width.

*Pt. spinalis*.—Branches of the interseapular fork arising in the middle of the interseapular region; arms not extending to the free end of the scapula.

Branches of the lumbar fork arising about midway between the anterior end of the ilium and the acetabular. Strongly developed, embracing the ends of the interseapular fork, crossing the free end of the scapula, and terminating on the axillary membrane. Stem strong, broad, bifurcated posteriorly, but not reaching the oil-gland.

*Pt. ventralis*.—Outer branch broad, arising at the summit of the shoulder.

Median branch not extending backwards beyond the level of the upper  $\frac{1}{3}$  of the carina sterni. It is very sharply defined, with an upper trend at its free end. Its great distinctness seems to cut it off from the recurved branch or “hook” characteristic of this portion of the tract.

Inner branch arises rather above the middle region of the clavicle, and follows the course of that bone up to the carina sterni; running along the upper end of this for a short distance, it turns rapidly outwards and backwards to the region over the posterior lateral process of the sternum; from this point it runs backwards to join its fellow in the middle line a short distance in front of the cloacal aperture.

*Pt. humeralis* not running forwards to join the *pt. ventralis*.

*Pt. alaris*.—Remiges too abraded and broken to be of use for comparison as to length, &c.

*Tectrices*:—

*T. majores*.—Dorsal major coverts of the cubital remiges unfortunately moulting. The 6th covert not fully developed in one wing and absent in the other. In both wings, however, the old 5th and 7th coverts remain, and furnish a point of interest in that the 5th is considerably shorter than the 7th. The coverts from the 7th inwards gently decreasing in length.

*T. mediæ*.—The dorsal median coverts increase rapidly in length from 1-5, and are the longest in the row. The 5th is considerably longer than the 6th.

*T. minores*.—The dorsal minor coverts resemble the median in that 1-5 in each row are longer than the feathers lying proximally; the difference is less marked in each row from behind forwards.

*Parapteron* and *Hypopteron*, see *Bubo virginianus* (p. 236). The description is from a fresh specimen from the Zoological Gardens, and therefore better for study than in the present species—a spirit specimen.

*Pt. femoralis*.—Femoro-crural band terminating some distance below the knee.

*Pt. cruralis*.—Continued downwards on to the acetarsium and aeropodium. In the latter region the feathers are not sufficiently large to conceal the skin. Base of the terminal phalanx clothed with scales.

*Rhamphotheca*.—The cere having the anterior margin sharply defined against the culmen, much as in Accipitres, slightly swollen immediately around the external aperture of the nostrils.

*Uropygium*.—In form of an elongated cone, bearing 3 apertures at the tip.

## BUBO LACTEUS, Steph.

*Pteryla capitis*:—

Fronto-parietal area.—Resembles in general conformation that of *B. ignavus*, but not so sharply defined. The cut bases of the “ear”-tufts not easily distinguishable from the rest of the feathers of the head.

Ramal area.—Very broad posteriorly, encroaching upon the throat; not continued backwards so far as the proximal end of the mandible.

Interramal area.—Connected with the ramal by two separate lateral branches, one some distance behind the region of the gape, the other near the articulation of the jaw.

Rest of the feathering of the head almost identical with that of *B. ignavus*.

*Apl. colli laterale*.—Extending upwards and forwards in the form of a long narrow space behind the postaural fold, terminating about its middle. It is cut off by a broad band of feathers from the small apertures lying to the inner side of the bases of the ear-tufts.

*Pt. colli dorsalis*.—With vertical and lateral neck-folds slightly developed, less than in *B. maximus*.

*Pt. spinalis*.—Interseapular fork arising in the upper fourth of the interseapular region; the arms extend to the end of the seapula.

Lumbar fork arising rather below the middle of the preacetabular part of the ilium; SECOND SERIES.—ZOOLOGY, VOL. VII. 33

its arms extend outwards on to the axillary membrane, between the *pt. humeralis* and the scapula. Stem forked posteriorly, so as to embrace but not surround the oil-gland.

*Pt. ventralis*.—Outer branch very strong, arising low down, over the dorsal third of the furculum.

Median branch narrower and more sharply defined than in *B. maximus*, extending backwards to the level of the posterior third of the carina sterni. Not recurved at its posterior end, where it passes into the "hook."

Inner branch arising from the median rather about its middle; more sharply defined than in *B. maximus*.

*Pt. alaris*:—

*Remiges*.—Metacarpo-digitals 11; cubitals 19.

*Tectrices*:—

*T. majores*.—The dorsal major coverts of the cubital remiges having the 5th slightly shorter than 4th, but longer than the 6th. 5th and 7th equal.

*T. mediæ*.—1-5 longest in the row; 6 abruptly shorter than 5; from 6 inwards gradually increasing in length.

*T. minores*.—The same remarks apply to these feathers as to the *t. mediæ*. There are three rows of minor coverts.

*Pt. femoralis*.—Femoro-crural band terminating below the knee.

*Pt. cruralis*.—Toes bare, but beset with stumps of old feathers worn down to surface of skin. Terminal phalanx having the base covered with scales.

BUBO TORQUATUS, Daud. (*Syrnium perspicillatum*, Lath., of Sharpe's Catalogue, p. 277.)

*Pt. capitis*:—

FRONTO-PARIETAL AREA.—Frontal area in the form of a broad well-defined band, rapidly expanding above and rather behind the eyes to merge with the parietal area.

LOREAL AREA.—Ill-defined.

INTERRAMAL AREA expanding in the region of the gape to join the ramal area, which does not extend backwards to the end of the jaw.

Periphery of the disc ill-defined.

*Pt. colli laterale*.—As in *Bubo*.

*Pt. colli dorsalis*.—Lateral neck-folds very slight, tract narrow.

*Pt. colli ventralis*.—Divides about halfway down the neck.

*Pt. spinalis*.—Interseapular fork arising in the upper third of the interseapular region; arms narrow, extending to the level of the end of the scapula. Branches of the lumbar fork arising near the anterior border of the ilium; short, running out on to the axillary membrane.

*Pt. ventralis*.—Outer branch well defined, arising at the summit of the shoulders; median long, narrow, not curved terminally (as in *Syrnium*); inner branch broad, sharply defined from the median, and, rising near the summit of the shoulder, joins its fellow of the other side just in front of the cloacal aperture.

*Pt. femoralis*.—Femoro-crural tract terminating at the knee-joint.

*Rhamphotheca*.—Cere of considerable size, slightly inflated at the base; aperture of the nostrils circular, looking slightly downwards.

*Podotheca*.—Acrotarsium feathered. Acropodium covered with warty protuberances. Terminal phalanx with the base sheathed by three scales.

*Uropygium*.—The oil-gland is conical, as in *Bubo*.

The pterylosis closely resembles that of *Bubo maculosus*, but the vertical and lateral neck-folds are much less in extent than in this species. *Bubo torquatus* \* and *Syrnium aluco* compared together prove conclusively the affinities of the former with *Bubo* rather than with *Syrnium*, with which it appears to have been generally associated.

BUBO NYCTERUS, L. (*Nyctea scandiaca*, Pl. 26.)

*Pteryla capitis*:—

Frontal area shorter and wider than in *Bubo*; it is also much arched.

Parietal area.—Feathers of the "ear"-tufts in a single longitudinal row, some 6 in number; their bases conspicuously larger than those of the surrounding feathers, and bounded on the inside by an elongated lenticular apterium.

Loreal area merging above with the frontal area.

Circumaural area.—Preaural fold feebly developed, with a double row of feathers along its free edge. Postaural fold as in *Bubo*, e. g. *B. ignavus*. The periphery of the disc, as demarcated by the cut bases of the feathers, arising just above the postaural fold, rather below the level of the top of the eye, runs downwards and forwards along the postaural fold on to the mandible, terminating midway between the gape and the rhamphotheca.

Ramal area extending backwards to the articular end of the jaw; broad posteriorly, extending downwards to join the interramal area.

Interramal area.—The anterior end giving off a narrow lateral branch on each side, at right angles to the main axis of the tract, from the region rather in front of the angle of the gape; behind this the tract is constricted, expanding again immediately after to join the hinder end of the ramal area.

*Apt. colli laterale* extending forward on to the base of the postaural fold, but entirely cut off from the apterium at the base of the feathers of the "ear"-tufts.

*Pt. colli dorsalis* very broad anteriorly. Vertical and lateral neck-folds considerable.

*Pt. spinalis*.—Interscapular fork arising in the upper fifth of the interscapular region. Arms long, wide apart, extending to the end of the scapula, and almost joining the arms of the lumbar fork, so as to enclose a space.

Lumbar fork.—Arms sharply defined (Pl. 26), arising in about the middle of the preacetabular region of the ilium; they extend forwards on to the axillary membrane, meanwhile expanding so as to assume a conical form. Stem sharply defined, broad posteriorly, forked, the arms wider apart than the width of the oil-gland and terminating in front of this.

\* Cf. footnote at bottom of p. 270.

*Pt. ventralis*.—Outer branch distinct, arising rather below the summit of the shoulder. Median broad, terminating at a point corresponding with a line drawn through the carina sterni at its middle. Inner branch broad, arising about halfway down the inner side of the median branch. Nowhere sharply defined on the breast, but very distinct on the abdomen.

*Pl. alavis*:—

*Remiges*.—Metacarpo-digitals 11. Cubitals 18.

*Tectrices*:—

*T. majores*.—Coverts 1-5 of the dorsal surface longest, 6 slightly shorter than 5, 7 equal in length to 5.

*T. medie*.—Damaged.

*T. minores*.—Three rows. All showing an abrupt break in the length of the feathers in each row. 1-5 always considerably the longest.

*Pt. femoralis*.—Femoro-crural band terminating some distance below the knee.

*Pt. cruralis*.—Continued downwards over the acrotarsium on to the acropodium, terminating behind the unguis phalanx, the base of which is clothed by scutes. The feathers on the acrotarsium and acropodium very long, half concealing the claws. Planta bare in region of tarsal joint only.

*Uropygium*.—In the form of an elongated cone, slightly swollen at the base.

All the tracts are very narrow, but the feathers are of great length; a humeral feather measured 8 in. from lower umbilicus to tip, and one from the median branch of the *pt. ventralis* 7 in.

#### C OPS LEUCOTIS, Temm.

*Pt. capilis*:—

Fronto-parietal area.—Feathers of the “ear”-tufts or “horns” in 2 longitudinal rows of about 5 feathers in each. Their massed bases are surrounded by an apterium, except anteriorly, where they merge with the broad band of feathers occupying the median line of the head, thus tending to form short branches to this band.

Loreal area.—Moderately well defined, crescentic in form, the upper limb longest and terminating above the region of the middle of the eye. Feathers of great length.

Circumaural area.—The preaural fold feebly developed, not forming an operculum. A double row of feathers runs along its free edge, the bases of which form a “rim”; in front of this is a single row set in an apterium, as in *Asio accipitrinus* (p. 229).

The bases of the feathers along the free edge of the postaural fold also form a “rim,” as in *Asio* &c.

Interramal area.—Very wide posteriorly, merging with the mandibular area from the gape backwards, rapidly contracting on the upper part of the neck, where it becomes the *pt. colli ventralis*.

Ramal area.—Broad, extending backwards beyond the end of the mandible.

*Lateral cervical apterium* terminating at the base of the lower half of the circumaural fold (Pl. 26).

*Pt. colli dorsalis*.—With a slight lateral skin-fold : no retractor muscle.

*Pt. spinalis*.—Arms of interscapular fork arising rather above the middle of the interscapular region, not widely divergent, but running almost parallel, terminating at the end of the scapula. Branches of the lumbar fork arising midway between the anterior end of the ilium and the acetabulum ; widely divergent ; base of the stem forked posteriorly, so as to embrace the oil-gland.

*Pt. ventralis*.—Outer branch feeble ; median strong, recurved ; inner relatively broad and strong, arising just in front of the region of the anterior end of the carina of the sternum, terminating in front of the cloacal aperture.

*Pt. humeralis* continued forwards to form the *pt. ventralis* at the summit of the shoulder.

*Pt. alaris* :—

*Tectrices majores*.—The 5th cubital covert of the dorsal surface slightly shorter than the 4th, but equal in length to the 6th.

*T. mediae*.—The 5th cubital covert of the dorsal surface much the longest in the series, the feathers rapidly lengthening from 1-5 ; 6th much shorter than 5, slightly shorter than remaining proximal coverts. The proportions of the rest of the coverts much as in *A. accipitrinus*.

*Pt. femoralis*.—Femoro-crural band terminating over the distal end of the femur above the knee-joint.

*Pt. cruralis*.—Acrotarsium covered with relatively short feathers. Feathers on the acropodium scanty, degenerated, confined strictly to the upper surface ; sides of toes bare, covered with granulated skin ; base of unguis phalanx covered by three scales.

*Rhamphotheca*.—Cere very short, much inflated. Nostrils pierced in its anterior border ; aperture circular, looking directly forwards, and not laterally, as in other Owls.

*Uropygium* napiform, with a tendency to a conical form, as in *Bubo*.

#### SCOPS GIU, Scop.

*Pteryla capitis* :—

LOREAL area not quite so well defined as in *S. leucotis*, and the feathers not elongated as in that species.

INTERRAMAL area with a narrow branch running obliquely backwards to join the ramal area behind level of the gape.

RAMAL area narrow, not extending backwards beyond the end of the mandible.

*Pt. colli dorsalis* with a lateral skin-fold and a short retractor muscle crossing the neck obliquely.

*Pt. spinalis*.—Interscapular fork as in *S. leucotis*. Lumbar fork with the branches rising near the anterior border of the ilium and dividing at the base into two rows of semiplumes, one of which runs out on to the axillary membrane, and one is continued upwards to join the free ends of the interscapular fork, enclosing an oval apterium.

*Pt. alaris* :—

*Tectrices majores*.—The 5th cubital covert slightly shorter than the 4th, but longer than the 6th.

*Pt. femoralis*.—Femoro-crural band terminating below the knee-joint.

*Rhamphotheca*.—Cere somewhat longer antero-posteriorly than in *S. leucotis*, and with a slight lateral swelling.

*Podotheca*.—Aeropodium covered with small round scales.

*Uropygium* napiform, with a long tubular extremity resembling that of *Carine*.

#### NINOX NOVÆ-ZEALANDIÆ, Gm.\*

*Pteryla capitis* :—

Loreal area ill defined.

Circumaural area :—

Postaural fold.—The feathers along the free edges of this fold seated in a double row, the massed bases of which form a “rim.”

Interramal area suddenly contracting in the region of the gape, to pass backwards into the *pt. coll. ventralis*.

*Apt. colli laterale* terminating at the base of the postaural fold.

*Pt. colli dorsalis* with a distinct vertical membranous fold; lateral folds very small.

*Pt. spinalis*.—Branches of the interseapular fork arising in the middle of the interseapular region, short, terminating at the end of the scapula.

Branches of the lumbar fork arising over the anterior ends of the ilium, not widely divergent, but received between the branches of the interseapular fork. The stem is forked posteriorly, but the branches are not sufficiently wide apart to embrace the oil-gland.

*Pt. femoralis*.—Femoro-crural band extending on to the ceres and turning upward to terminate at the femoro-tibial articulation.

*Pt. cruralis*.—Acrotarsium thickly feathered; aeropodium covered with warty protuberances bearing degenerate feathers, the shafts only of which remain. Filoplumes absent. Base of the unguis clothed with three scales.

*Rhamphotheca*.—Cere laterally inflated, resembling that of *Scops*.

*Podotheca*.—Claws short and blunt. Tylari of Digit II. large.

*Uropygium* napiform, with conical tendency.

#### SCELOGLAUX ALBIFACIES, Gray †.

*Pt. capitis* :—

Loreal area not extending upwards above the eye.

Interramal area broad, expanding to merge with the ramal area at the gape.

Circumaural area.—Preaural and postaural folds with a rim; no “notch” in the rim of the postaural fold.

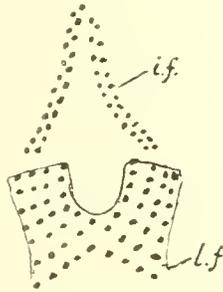
*Apt. colli laterale* terminating on circumaural fold, not extending on to the head. ? No parietal apterium. A large apterium above upper eyelid, as in other Owls.

\* This description is taken from a plucked specimen.

† Examined from a skin kindly lent by Prof. A. Newton, from the Cambridge University Museum.

*Pt. spinalis*.—Arms of interscapular fork long, arising higher up, not widely divergent. Stem of lumbar fork *very* wide. Seven feathers, forked posteriorly. Arms short,

Fig. 1.



Portion of the upper end of the lumbar fork of *Sceloglaux albifacies*, to show the extreme breadth of the stem and short arms. *i.f.* Interscapular fork. *l.f.* Lumbar fork.

closely approximated, running almost parallel, at their distal ends expanding, so as to clothe the axillary membrane.

*Pt. ventralis*.—Inner branch not sharply differentiated from median, distinguishable by reason of their more sparse distribution and semiplumous character. They form a narrow band on the abdomen.

Apteria generally thickly sprinkled with semiplumes.

Perhaps the most characteristic feature of the pterylosis of *Sceloglaux* is the great width of the stem of the lumbar fork.

*Rhamphotheca*.—Cere slightly swollen; nostril pierced in its anterior margin.

*Podotheca*.—Feathers on the acropodium reduced to bristles. Scales on the acropodium more distinct than on the acrotarsium. *Claws*.—The inner side of the claw of the middle toe with a flange.

#### SYRNIUM ALUCO, L. (Pl. 26.)

##### *Pteryla capitis*:—

**Loreal area**.—Upper limb continued backwards to join the confluent feathers of the pre- and postaural tracts.

**Circumaural area**.—The preaural fold is well developed and forms an operculum (see p. 229 and Pl. 28. figs. 1-2). It supports numerous strong, well-developed feathers, arranged in 4 parallel semicircular rows; rows 1 and 2 are bound closely together, their bases forming a rim to the free edge of the fold; rows 3 and 4 are placed further forwards. At some distance from the most anterior row, and separated by an apterium, is a single row running from the gape, backwards and upwards, to the anterior corner of the base of the operculum. This row is with difficulty distinguished anteriorly from the feathers of the ocular area.

**Postaural fold** almost as extensive as in *A. accipitrinus*. Likewise the feathers seated along its free edge are densely packed, and their bases form a rim to the free edge of

the fold. These feathers help to form the periphery of the disc, which is continued downward and forward to join its fellow of the opposite side beneath the jaw (Pl. 26).

Ramal area extends from the rhamphotheca of the lower jaw backwards to the level of the region where the opercular and postaural folds coalesce. The peripheral disc-feathers divide it into an upper and a lower portion (Pl. 26).

Interramal area broad, sending off on either side a single row of feathers to join the Ramal area in the region where it merges with the *pt. colli ventralis*.

*Apt. colli laterale* extending on to the circumaural fold as far as the peripheral disc-feathers; from its upper border, bounding the *pt. colli dorsalis*, it is continued as a very slender space on to the *pteryla capitis*, terminating at a point somewhat behind the level of the region where the anterior ends of the pre- and postaural folds coalesce.

*Pt. colli dorsalis* tapering from the head backwards. Lateral neck-folds of slight extent; without retractor-muscles.

*Pt. spinalis*.—Branches of the interseapular fork arising about halfway down interseapular region; arms short, 3 feathers in width, not extending to the end of the scapula.

Branches of the lumbar fork represented by a single row of feathers arising far forward on a level with the ends of the scapula; they embrace the arms of the interseapular fork. The stem of the fork bifurcated posteriorly, but terminating short of the oil-gland.

*Pt. ventralis*.—Outer branch joined to the median by a single row of feathers, abruptly expanded near its middle to 3 feathers in width. Median branch broad, with a strong recurved limb springing from its free end—the “hook.” Inner branch broad, arising from the median at the point where the latter passes over the acrocoracoid region from the neck; it follows the course of the furculum for some distance, then runs backwards to join its fellow of the opposite side in front of the cloacal aperture.

*Pt. humeralis*.—Not connected anteriorly with the *pt. ventralis*.

*Pt. alaris*:—

Metacarpo-digital remiges 11; the 11th a remicle, very small, little more than half as large as its dorsal major covert; the 6th remex the longest, giving the wing a short, rounded appearance: the 5th to the 9th remex having the distal end of the outer vane more or less emarginate; outer vane of 10th serrate.

Cubital remiges 15.

*Tectrices*:—

*T. majores*.—Those attached to the dorsal surface of the cubital remiges of uniform length, save the 6th, which is distinctly shorter than the 5th or 7th.

*T. mediae*.—1–5 of the cubital remiges of the dorsal surface gradually increasing in length, and distinctly the longest in the row.

*T. minores*.—1–5 of each row of the dorsal minor coverts markedly longer than the remainder of the coverts of their respective rows.

*Pt. femoralis*.—Well developed; femoro-crural band strong, terminating on the crus, a short distance below the knee.

*Pt. cruralis*.—Continued downwards over the acetarsium and aeropodium; feathers long and thickly placed. Planta having the proximal end bare. Penultimate phalanx of toes scale-covered.

*Rhamphotheca*.—Cere of considerable extent, very slightly inflated.

*Podotheca*.—Claws rounded, not much curved.

*Uropygium*.—Napiform, with a very marked tendency towards the elongate-conical form of the Buboninae.

#### SYRNIUM URALENSE, Pall.

The pterylosis of this species differs only in the following details from *S. aluco*.

*Pteryla capitis*:—

**Interramal area.**—With a lateral branch running at a right angle to join the ramal area in the region of the gape, as in *S. aluco*. A short distance behind this lateral branch it forms a broad expansion merging with the ramal area.

*Apt. colli laterale*.—Extends upwards and forwards to the level of the angle of the exoccipital wing of the tympanic.

*Pt. spinalis*.—Branches of the lumbar fork rising near the anterior border of the ilium, not widely divergent, running up to, but not quite joining, the free ends of the branches of the interseapular fork, thus enclosing a median space. The stem not extending backwards so far as in *S. aluco*, but terminating some distance in front of the uropygium.

*Pt. alaris*.—The 6th major covert of the cubital series shorter than the 5th; the remainder of the other coverts moulting. “Carpal remex” pennaceous, as large as its covert, thus differing from that of *S. aluco*, in which this feather is semiphumous and markedly smaller than its covert.

External aperture of the ear symmetrical, its vertical axis slightly longer than the longitudinal axis of the closed eyelid.

*Uropygium*.—Napiform, with a long terminal tube.

#### NYCTALA TENGMALMI, Gm.

*Pteryla capitis*:—

**Loreal area.**—Not sharply defined, with an apterium at its base, almost dividing the area into two portions, an interior and a posterior, the former including the greater part of the area. The apterium, which is very narrow, arises in the region in front of the eye, on a level with its anterior corner, and runs downward and then upward so as to partly encircle the eye, terminating rather above the level of its posterior corner. This apterium differs from that of *Speotyto* in that it fails to divide this area into two, in that it is less wide, and in that the posterior semi-detached patch is much less in size.

**Circumaural area.**—The bases of the feathers seated along the free edge of the preaural fold form a rim; lying in front of, and parallel with the rim, is a single row of feathers—as in *Asio*—banded on either side of the apterium.

The feathers running along the free edge of the postaural fold are densely packed, their bases of insertion forming a “rim” to the fold. From the base to within a short distance of the superior limb of the fold the feathers seated on this free edge are directed

obliquely upwards; the rest are directed downwards; hence the notch in the rim of the fold (Pl. 27. figs. 5-6).

The peripheral disc-feathers (p. 236) are continued downwards and inwards to meet in the middle line a short distance behind the symphysis of the mandible.

*Inter-ramal area*.—Cut into two by the meeting of the peripheral disc-feathers; the posterior portion somewhat triangular in form, its base planted against the confluent peripheral disc-feathers, its tapering apex merging with the *pt. colli ventralis*.

*Apt. colli laterale* terminating at the base of the circumaural fold.

*Pt. colli dorsalis* with considerable vertical and lateral neck-folds. The tract decreasing rapidly in width from before backwards.

*Pt. spinalis*.—Interscapular fork barely perceptible (Pl. 26).

The lumbar fork, so far as my specimens are concerned, has the branches very feebly developed and disconnected at their bases from the main stem. This last is continued forwards so as nearly to join the interscapular fork (Pl. 26).

*Pt. colli ventralis*.—Very narrow at its upper end, where it joins the interramal area; sends off two branches at the middle of the neck to join the *pt. ventralis* at the shoulder.

*Pt. ventralis*.—Outer branch well developed; median strong, recurved; inner strong, not meeting its fellow in the middle line in front of the cloaca, but terminating over the free end of the pubis.

*Pt. humeralis*.—Not continued forwards to join the *pt. ventralis*.

*Pt. alaris*:—

*Tectrices*:—

*T. majores*.—The dorsal coverts of the cubital remiges of uniform length, save the 6th, which is much shorter than the coverts on either side. The same proportions appear to obtain in the *t. mediae* and *t. minores*.

*Pt. femoralis*.—Femoro-crural band turning sharply upwards to terminate over the distal end of the femur.

*Pt. cruralis*.—Acrotarsium and acropodium densely and thickly feathered; penultimate phalanx clothed with 3 scales.

*Rhamphotheca*.—Cere short, inflated, closely resembles that of *Speotyto*.

*Uropygium*.—Small, napiform, but the pointed extremity very short, making the gland almost triangular in form.

#### SURNIA ULULA, Linn.

*Pteryla capitis*:—

*Interramal area*.—Expanding at the gape to join the ramal area.

*Apt. colli laterale*.—Terminating on the postaural membrane.

*Pt. colli dorsalis*.—With an oblique membranous fold, from the *pt. colli dorsalis* to the *ventralis*, similar to that of *Asio*, but more feebly developed.

*Pt. spinalis*.—Interscapular fork barely perceptible; the tract, which is broad, terminating midway down the interscapular region. The posterior moiety of this tract has a very broad anterior end, not differentiated into branches.

*Pt. ventralis*.—The median branch is very broad posteriorly.

*Pt. alaris* :—

*Tectrices*.—The major coverts were moulting.

*T. mediæ*.—The 6th median cubital covert was much shorter than the 5th, as usual.

*T. minores*.—The same remarks apply to this series as to the *t. mediæ*.

*Pt. femoralis*.—Femoro-crural band terminating at the knee-joint.

*Rhampholhecu*.—Cere short, slightly inflated.

*Podotheca*.—Densely feathered.

*Uropygium*.—Napiform.

#### SPEOTYTO CUNICULARIA, Molina.

*Pteryla capitis* :—

**Loreal area**.—Divided by an apterium into two portions: an anterior, running round the base of the bill, and a posterior, encircling the anterior region of the eye. This latter is continuous at its lower posterior angle, immediately above the gape, with a single row of feathers running round the base of the lower eyelid and upwards to its posterior corner. The loreal apterium separates this row from the feathers of the ramal area.

**Ocular area**.—The single row of feathers above described as forming a continuation of the lower limb of the loreal area forms the lowermost boundary of this area. Above it, separated by a broad apterium, is another single row of feathers; above this are two other rows, each separated by an apterium. The upper eyelid is clothed with numerous rows of small, downy feathers. A very considerable crescentic apterium separates the uppermost rows from the feathers of the fronto-parietal area. The rims of the eyelids are fringed with some 3 rows of feathers, decreasing rapidly in size as they approach the free edge. The hindmost are characterized by the production of the shaft outwards beyond the vane. In the outermost, nothing but the shafts remains, and these form "eyelashes."

**Circumaural fold** :—

**Preaural fold** (Pl. 28. fig. 5).—This fold is very feebly developed. Along its free edge is a single row of elongated narrow-vaned feathers. They are somewhat curved, the concavity being turned towards the head so as to form a feathery operculum.

**Postaural fold**.—Of greater extent than the preaural. It supports, along its free edge, a row of feathers precisely similar to those on the opercular fold. They are overlapped by the feathers of the preaural fold. (Pl. 28. fig. 5.)

**Ramal area** not extending backwards as far as the angle of the jaw.

**Interramal area**.—Anteriorly, from the region at the level of the gape to the symphysis of the mandibles, surrounded by an apterium, the posterior portion expanded so as to merge with the ramal area.

*Apt. colli laterale* terminating at the base of the lower half of the circumaural fold, and embracing the region of the angle of the mandible.

*Pt. colli dorsalis*.—Borne upon lateral folds, not closely investing the neck.

*Pt. spinalis* (Pl. 26).—The arms of the interseapular fork, arising in the middle of

the interseapular region, very short, terminating a short distance from the free end of the scapula.

The arms of the lumbar fork represented by a single row of feathers arising over the anterior end of the ilium and which, crossing over the free end of the scapula, terminate on the axillary membrane. The stem of this portion very distinct; its free end is bifid, and terminates some distance from the oil-gland.

*Pt. ventralis*.—Outer branch feebly developed, represented by a single row of feathers; median branch broad, short, not extending beyond the middle of the sternum, the recurved branch or "hook" very slender; inner branch, arising in the middle region of the furculum, follows the course of the clavicle and the carina, then turns inwards and upwards to the thigh, whence it takes an almost straight course backwards to join its fellow of the opposite side in front of the cloacal aperture.

*Pt. femoralis*.—Femoro-crural band terminating at the knee-joint.

*Pt. cruratis*.—Feathers on the acetarsium short. Planta bare. Acropodium covered by numerous warty protuberances, each of which bears a degenerate feather; little more than the shaft, with perhaps—here and there—one or two rami, remaining; radii absent. Filoplumes absent. The base of the ungual phalanx clothed with scales.

*Pt. alaris*:—

*Remiges*.—No carpal diastema, the space between the metacarpal and cubital remiges being very much less than that separating the individual cubital remiges.

*Tectrices*:—

*T. majores*.—The major coverts on the dorsal surface gradually increasing in length from 1-5. This last the longest; 6th shorter than 5th.

*T. mediae*.—1-5 gradually increasing in length, but the 5th abruptly longer than 1-4. 6th about as long as 4th. The 5th feather more closely bound to its covert—5th major covert—than the remaining feathers to their respective coverts.

*T. minores* (row no. 1).—Covert 5 abruptly longer than 1-4, but of the same length as 6. Disproportion in the length of the coverts of this group, above the 1st row, less marked.

*Rhamphotheca*.—Cere very short antero-posteriorly, much inflated, forming two pisiform swellings on each side of the culmen. Aperture of the external nares circular, directed more forwards than outwards. Rhamphotheca compressed.

*Podotheca*.—Claws short, very little curved.

*Uropygium*.—Napiform.

#### CARINE NOCTUA, Scop.

*Pt. capitis*.—Fronto-parietal and occipital areas densely feathered.

Loreal area indistinct.

Interramal area expanded to join the ramal area on either side, from the level of the gape backwards.

*Apt. colli laterale* terminating at the level of the posterior limb of the external aperture of the ear.

*Pt. colli dorsalis* borne on a deep vertical fold; no lateral folds.

*Pt. spinalis* with a short interscapular fork, the branches arising below the middle of the interscapular region, short, widely divergent, tapering, terminating rather below the free end of the scapula\*. The stem of the posterior portion *not* forked, but running straight up to the convergent bases of the arms of the interscapular fork. Widest posteriorly, forked terminally; the branches short, not wide enough apart to embrace the oil-gland.

*Pt. colli ventralis*.—Forks almost immediately after its origin.

*Pt. ventralis*.—Outer branch very narrow; median broad and strong, terminating in the middle region of the sternum. The recurved branch ("hook") very feeble. Inner branch arises in the region of the middle of the furculum and runs in the direction of the carina of the sternum; over the middle of the sternum it trends outwards and upwards, again converging on the abdomen, each branch terminating separately some distance in front of the free end of the pubis and *not* meeting its fellow in the middle line in front of the cloacal aperture.

*Pt. humeralis*.—Connected with the *pt. ventralis* by a single row of feathers.

*Pt. femoralis*.—Femoro-crural band terminating over the proximal third of the crus, not running upwards to the femoro-tibial articulation.

*Pt. cruralis*.—Feathers of acetarsium barely concealing the skin; on acetopodium degenerate, shafts only remain. No filoplumes. Planta feathered; the base of the terminal phalanx of the toes covered by 3 scales.

*Rhamphotheca*.—Cere short, inflated, forming two pisiform swellings on either side of the culmen as in *Speotyto*.

*Uropygium*.—Napiform, the tubular extremity relatively long.

#### STRIX FLAMMEA, Linn.

##### *Pteryla capitis*:

Fronto-parietal area.—In the form of a narrow, median tract of feathers, bounded on either side by an apterium.

Occipital area.—Occupies the whole width of the skull, extending outwards on to the postaural fold.

Loreal area.—The base almost obliterated by a semioval apterium lying along the margin of the tomium from the region of the nostril backwards to the gape. The inner boundary of the apterium is formed by a single row of feathers running from the loreal area backwards below the eye to join the feathers of the operculum.

Circumaural area (Pl. 28. fig. 4, p. 229).—The preaural fold is well developed and forms an operculum. It is clothed by some 4 rows of delicate, elongated feathers, having narrow, discontinuous vanes.

Postaural fold.—Its upper portion may be considered to merge into the upper limb of the loreal area above the region of the middle of the eye; below it passes insensibly into the ramal area (see "Periphery of the Disc," p. 252).

\* In a young individual the interscapular termination of this tract was very narrow—but little wider than the stem. The branches were very short, and parallel, not divergent.

*Interramal area.*—The only specimen of a Barn Owl which I have been able to procure I owe to the kindness of Dr. Selater. Unfortunately it is so damaged in this region that Mr. Meinertzbagen and I have been obliged to fall back upon Nitzsch's interpretation and restore the figure after that given by him.

*Periphery of the Disc.*—This is more sharply demarcated than in any other Owl so far examined. The feathers taking part in its formation are seated in a deep fold of skin which stands out abruptly from the general contour of the head in the form of a sharp ridge. Its anterior portion is contributed by the superior border of the loreal area; running backwards into the postaural fold, and downwards along the interior border of the mandible, it finally dies out in the region corresponding to the level of the gape. The feathers in the immediate region of the external aperture of the ear are very long, with narrow, discontinuous vanes, and all much curved forwards, so as to form a hollow around the ear, and a very considerable lateral extension of the postaural fold.

*Apt. colli laterale.*—Terminating at the base of the postaural fold, some distance below the level of the external aperture of the ear.

*Pt. colli dorsalis.*—Not borne upon lateral neck-folds, but closely investing the neck, therein differing from all other Owls so far examined. It forms a diamond-shaped expansion in the middle of the neck.

*Pt. spinalis.*—Interseapular fork arising within the interseapular region. Arms narrow, 3 rows of closely-packed feathers, not extending as far as the free end of the scapula.

The arms of the lumbar fork arise over the anterior end of the ilium, cross the free end of the scapular, and terminate on the axillary membrane. The stem is truncated posteriorly, terminating some distance in front of the oil-gland.

*Pt. colli ventralis.*—Bifurcating on the lower  $\frac{1}{3}$  of the neck, branches very narrow; feathers set in oblique rows of 4 feathers in each row.

*Pt. ventralis.*—Outer branch moderately broad. Median branch narrow, not free posteriorly, but continued backwards to join the inner branch over the region of the posterior lateral process of the sternum. The "hook" is given off just before this junction takes place. Inner branch very distinct; coming off from the median opposite a point corresponding with the region of the ventral  $\frac{1}{3}$  of the furculum, it is continued backwards to join its fellow of the opposite side over the free ends of the pubes.

*Pt. alaris* :—

*Remiges.*—Metacarpo-digitals 11, cubitals 15, the innermost not readily distinguished from their coverts.

*Tectrices.*—For the most part missing in this specimen.

*Pt. femoralis.*—Femoro-crural band terminating below the knee.

*Pt. cruralis.*—Feathers on the acrotarsium degenerate, the shaft only remaining. They occur in groups of 3, of which the centre one, as described by Meijere, is much the longest; the two lateral shafts being in most cases minute, and sometimes absent. Each group of 3 is seated under the anterior border of a soft, swollen scale. On the acropodium the scales become firmer and the feather-remnants fewer.

*Rhamphotheca.*—Cere closely investing the base of the beak, nostrils pierced in its lower anterior border.

*Podotheca*.—Planta feathered, save the proximal end. The feathers on the posterior border of the acrotarsium directed upwards. Scales on the toes more distinct than on the acrotarsium. Pectination of the claw of the middle toe very slightly developed.

#### IV. THE DISTRIBUTION OF THE NEOSSOPTILES OR NESTLING-DOWN.

I hoped to have been enabled to describe the nestling-down of *Asio*, but after all failed to procure a specimen of this genus. By the kindness, however, of my friend Mr. Meinertzhagen, a substitute has been provided in a nestling *Speotyto cunicularia*, which was one of a clutch of 5 bred in the Mottisfont aviaries this spring (1897).

There are two kinds of nestling-down to be distinguished: (1) the down-feathers which precede the future definitive contour-feathers, and (2) those which precede the future definitive down-feathers. This is a point not to be overlooked, inasmuch as the latter, as I have already shown in the case of *Opisthocomus* (14 A), may, from the greater length and number of the rami, bear the greater share in clothing the young bird.

Just as in *Opisthocomus*, the nestling-plumage of the Common Kestrel, *Falco tinnunculus*, is mainly contributed by the down-feathers belonging to the second kind, the down-tufts preceding the contour-feathers being relatively insignificant in size.

One might naturally expect to find that this two-fold down-clothing would obtain wherever contour- and down-feathers were to be found associated together in the adult. This does not, however, appear to be the case, inasmuch as I find that the nestling-down of the Common Duck, for instance, is entirely composed of the down-feathers of the first order—those preceding the contour-feathers.

I would now suggest that these two kinds of nestling-down should in future be carefully distinguished when describing the plumage of nestling-birds. The feathers preceding the contour-feathers might be called *pre-pennæ*, whilst those preceding the future definitive down-feathers might be called *pre-plumulæ*.

In the nestling of *Speotyto* the feathers investing the trunk are pre-pennæ; pre-plumulæ are absent. As is shown elsewhere, the corresponding plumulæ are absent on the trunk of the adult also. The clothing of the wing differs from that of the trunk in that pre-plumulæ occur amongst the pre-pennæ, but they are very small and contribute no great part towards the general covering. Whether these last are really pre-plumulæ or the actual definitive down-feathers I am unable to decide. The question can be settled only by the examination of younger specimens, the one under consideration being half-fledged.

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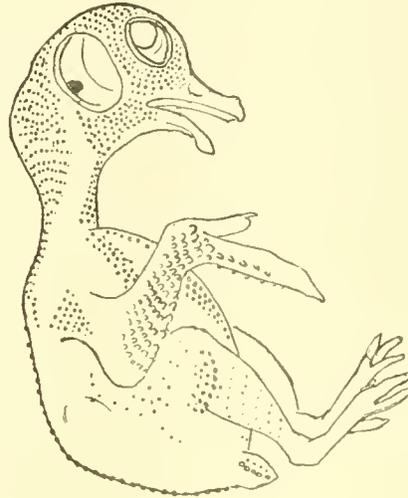
Save the remiges and their dorsal major coverts, and the rectrices, the true contour-feathers of the adult do not seem to be developed till after the first moult. All the nestlings which I have been enabled to examine—ranging up to birds nearly full-grown—have been clothed with a peculiar loose semiplumous covering, sprinkled here and there, in some cases, with typical adult contour-feathers.

## V. PTERYLOSIS OF THE EMBRYO.

*ASIO OTUS*, Linn.

My embryos of this species may be divided into 3 stages, the last corresponding to that of a 10-day chick. In this, only the rudiments of the contour-feathers have made their appearance in the form of the characteristic bead-like papillæ.

Fig. 2.



Right side view of an embryo of *Asio otus*, showing the form of the pterylae. At this stage the pteryla colli dorsalis closely invests the neck as in *Strix flammea*. The external aperture of the ear has not yet reached its full size, and there are no pre- and postaural folds. The beak has not yet assumed its characteristic curved shape.

### STAGE III.

*Pterylae* :—

*Pt. capitis*.—The feathering of the upper part of the head, as indicated by the feather-rudiments, is very uniform, giving no sign of the differentiation into areas—loreal, fronto-parietal, &c.—which appear in the adult.

Interramal area as in the adult.

*Pt. colli dorsalis*.—There are no lateral folds, the skin closely investing the neck, as in *Strix flammea*.

*Pt. spinalis* as in adult.

*Pt. ventralis*.—No outer branch is yet visible.

*Pt. femoralis*.—As in adult, femoro-crural band strongly marked.

*Pt. cruralis*.—No feather-rudiments have yet made their appearance on the podotheca.

*Pt. alaris*.—The position of the future remiges, and nearly all the tectrices, are now indicated, and the wing is seen to be aquitocubital.

The external aperture of the ear has not yet reached its full development. There are no opercular or postaural folds.

*Rhamphotheca*.—Note the straight form of the beak and the absence of any indication of a “cere.”

*Claws*.—There is a small claw on the pollex; there is also an indication of a claw in Digit II.

## STAGE II.

*Pt. capitis*.—Only the feathers of the loreal area and the region about the eye yet indicated. The position of the trunk-feathers is almost as plainly indicated as in Stage III. In the pteryla alaris, however, only the remiges and dorsal major coverts are yet suggested.

## STAGE I.

The skin as yet perfectly smooth.

## CARINE BRAMA, Temm.\*

This embryo almost exactly corresponds to Stage III. of *Asio accipitrinus*.

*Pteryla*:—

*Pt. capitis*.—The feathering of the upper part of the head not differentiated into distinct areas.

Interramal area.—Expanding at the level of the gape to join the ramal area.

*Pt. spinalis*.—The interseapular fork differs markedly from that of *C. noctua* (p. 250), in that there are well-marked interseapular branches present as in *Asio*, *Scops*, &c.; they terminate over the region of the free end of the scapula. In the adult mentioned the interseapular fork is barely perceptible.

There is a well-marked lumbar fork, the branches of which arise near the anterior border of the ilium, are widely divergent, and extend on to the axillary membrane. In this also this species differs from the adult *C. noctua*, in which there is no lumbar fork.

*Pt. femoralis*.—Femoro-crural band terminates at knee-joint.

Both digits, I. and II., of the wing are furnished with claws.

## NYCTALA TENGMALMI, Gm.

STAGE IV.—Areas of feather-distribution as in the adult. There is a claw on both pollex and index digits. The external aperture of the ear is oval in form; its vertical axis is nearly twice that of the longitudinal axis of the closed eyelid; it is entirely closed by the sclerotic ring, which comes quite to the surface.

STAGE III.—The form of the interramal tract can be well studied here. It is very broad on the throat, and narrows suddenly on the upper part of the neck.

*Pt. spinalis*.—The lumbar stem appears to be continued forwards, in the form of two single parallel rows of feathers, to join the free ends of the interseapular branches. It is cleft in front of the oil-gland.

STAGE II.—The papillæ are just appearing; their distribution appears to be the same as in Stage III.

## STRIX FLAMMEA, Linn.

The embryos of this species represent Stages III. to V. That corresponding to Stage III. is most instructive, and best preserved; and from this the following description is taken, the remaining stages being compared with this.

\* For this most beautifully-preserved specimen I have to thank my friend Mr. Jesse of Lucknow.

*Pteryla*:—

*Pt. capitis*.—The papillæ which will give rise to the peripheral disc-feathers are fairly sharply defined from the rest of those covering the head, as a narrow band of closely-set raised points. The aperture of the ear is nearly circular; its vertical axis is less than that of the longitudinal axis of the closed eyelid. There is no trace of an operculum.

*Pt. spinalis*.—Interseapular fork with the branches very long, and joining those of the lumbar fork so as to enclose a space. At the junction of the free ends of the lumbar fork with those of the interseapular fork, a side branch is given off from each to the posterior end of the *Pt. humeralis*.

Stages IV. and V. agree, so far as the distribution of the feathers is concerned, with Stage III. In Stage V. the first trace of the operculum appears.

## VI. STRUCTURE OF THE FEATHERS.

*Contour-feathers*.—These, in the Owls, are of considerable length, and soft and somewhat loose in texture. There is no aftershaft. The remiges in many, e. g. *Asio*, *Bubo*, present on the upper surface of the vexillum a very characteristic velvety pile, due to the enormous elongation of the free ends of the distal radii, which extend forwards over as many as three rami, not including the ramus from which they arise.

The feathers composing the facial disc present a few points worthy of notice. Round the free edge of the operculum they have an elongated and rigid shaft, bearing numerous moderately long rami, which form a discontinuous vexillum. The most distal rami break up into about three short branches, all of which bear fila, thus giving the tips—under the microscope—a curiously frayed appearance. The radii are very short, set almost parallel with the ramus, and showing no more than traces of fila. They also occur on the shaft in the internodes between the bases of the rami.

A feather from the lower limb of the postaural fold shows the following points:—The shaft is bent upon the calamus at a considerable angle in an upward and lateral direction. The calamus is abruptly distinguishable from the scapus by its greater thickness. The inner vexillum is roughly triangular in form, the base extending from the superior umbilicus to the top of the stem; the outer vexillum is much smaller and also triangular, its base running from the upper umbilicus to the middle of the stem. The rami are entirely disconnected and widely separated. The radii are very short; those of the proximal series lie parallel with the ramus; the distal radii are longer. Fila are absent. Short radii run along the scapus in the interval between the rami.

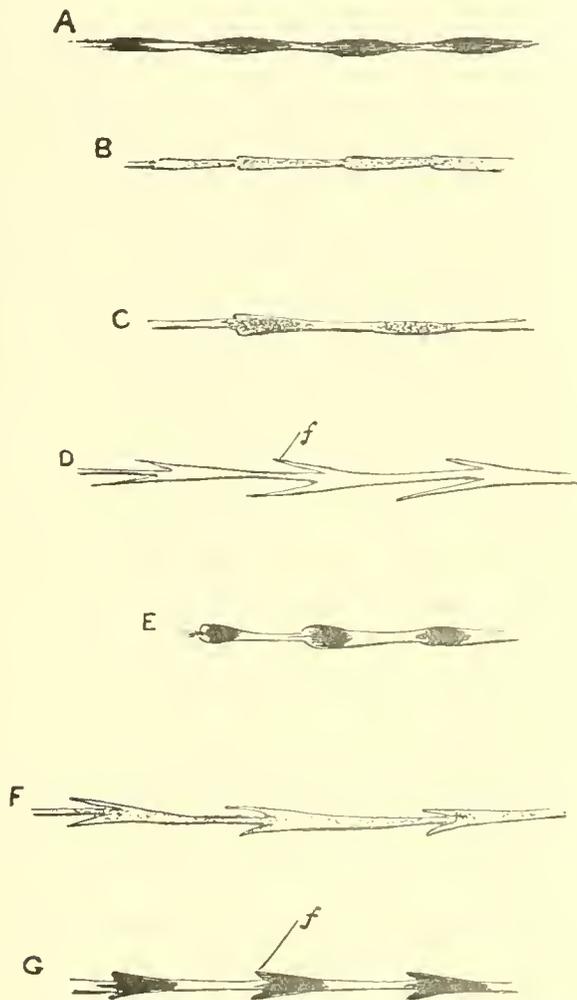
The feathers of the Loreal area are long, with fairly stiff, rigid axes. Rami very short, degenerate, showing neither fila nor hooklets, and decreasing in length on each side of the ramus from the base upwards, finally disappearing. They also run along the internodes on each side of the shaft from the base of one ramus to that of the next in front.

*Plumula*.—In these the rachis is relatively short as compared with the rami, which are of great length. The radii are long, transparent, and divisible into segments—nodes and internodes—by the deposition of pigment in the region of the fila. The fila

occur in pairs (fig. 3, G) at the proximal nodes; beyond this they suddenly disappear, but the corresponding region is marked by a gentle swelling containing a dark pigment, which in masses appears black.

The adult down-feathers of *Asio*, *Speotyto*, and other Owls closely resemble those of the Kestrel (*Falco tinnunculus*, fig. 3, E); but they may be distinguished by the following points:—In the latter the nodal areas of the radii are more numerous, the

Fig. 3.



A, portion of a radius from a definitive down-feather of *Caprimulgus europaeus*. The swelling of the nodes is somewhat exaggerated in the figure. B, portion of a radius of a pre-penna of *C. europaeus*. C, portion of a radius from a pre-plumula of *Falco tinnunculus*. D, portion of a radius from a pre-penna, and E, portion of a radius from a definitive plumule of *F. tinnunculus*. F, portion of a radius from a pre-penna, and G, portion of a radius from a definitive plumule of *Speotyto cunicularia*. *f*, filum.

rhachis is much longer, and there is a vestigial aftershaft. They may be very readily distinguished from those of *Caprimulgus* (fig. 3, A) by the greater length of the radii in the latter, the long black nodes—longer than the internodes and very little thicker,—and the absence of fila. Like the Kestrel, the down-feathers of *Caprimulgus* possess a long rhachis and a vestigial aftershaft.

*Filoplumes*.—In the adult these present no special features of interest. The rhachis is long, bearing from two to three rami (fig. 4). The radii are of moderate length, and bear, here and there, a few fila. The only case in which I failed to find filoplumes in the adult was that of *Speotyto cunicularia*.

In the nestling, however, they were readily visible in the form of somewhat conspicuous packets, one at the base of every contour-feather. Their examination under the microscope revealed some very interesting facts concerning the nature and history of these curiously modified feathers. As will be seen in fig. 5, each at this stage consists of a sheath investing a number of rami, and a rhachis, clustered around a column of "pith-" cells. Before the full growth of the feather is attained everything save the

Fig. 4.



Fig. 5.

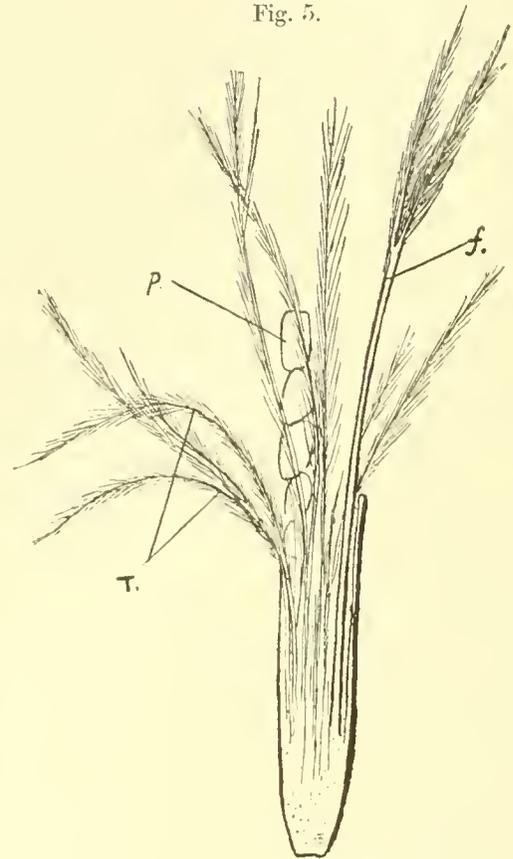


Fig. 4.—The distal end of a filoplume of *Scops leucotis*.

Fig. 5.—Filoplume of a nestling *Spotyto cucularia*. The part marked *f* is all that remains in the adult, and forms the filoplume; *T*, the transitory radii; *p*, pith-cells.

main axis is thrown off. This remains as the typical filoplume of the adult. Dr. Gadow (4) remarks, "their development shows them to be degenerate, and not primitive feathers."

*Neossoptiles*.—As is pointed out in another part of this paper (p. 253), two kinds of neossoptiles must be distinguished—(1) pre-pennæ and (2) pre-plumukæ.

Pre-pennæ\* can be readily distinguished from pre-plumukæ only under the microscope. The component rami of these umbelliform down-tufts, being continuous with those of the definitive contour-feathers, are broken up and spread out horizontally as soon as the tips of these latter have burst through the sheath by which they were enclosed.

\* The pre-pennæ described are those of *Spotyto cucularia*.

The radii—like the rami—are transparent. Fila are generally but not always present. The rami are laterally compressed. Structurally they can scarcely be distinguished from those of *Falco tinnunculus*; but in this latter the fila are longest and regularly arranged along the radius (fig. 3, D).

The pre-pennæ of *Caprimulgus* can readily be distinguished from either *Speotyto* or *Falco tinnunculus*. As in these, they are umbelliform, but the rami are produced considerably beyond the most distal radii into long filamentous processes, and the radii bear minute fila at regular intervals (fig. 3, B).

The pre-plumulæ differ from the pre-pennæ, both in *Speotyto* and the Kestrel, in that the radii are divided up into segments by the collection of pigment in the region from which the fila arise. In this respect they resemble the definitive down-feathers, but can always be distinguished from them. At least this is true of the Kestrel. Thus, in this species, the pigment, though in the form of a dense black deposit in the region of the fila, shows a tendency to be distributed all along the radius (fig. 3, C). Further, the pre-plumulæ are umbelliform, whilst the definitive plumulæ have a rhachis and after-shaft. From the fact that the feathers which I have doubtfully described as pre-plumulæ in *Speotyto* have a distinct rhachis, and the radii are indistinguishable from those of the adult, it is more than probable that these feathers are really definitive down-feathers.

Both the pre-plumulæ and the definitive down-feathers of *Speotyto*—if these, in this case, are not one and the same—can be distinguished from the plumulæ of the Kestrel in that, in the latter, the segments of the radius are more numerous (fig. 3, E) and the rhachis is longer and supports an after-shaft.

#### VII. THE EXTERNAL EAR. (Plates 27–28).

The external aperture of the ear of birds is usually concealed by feathers. If these be raised, a small round or oval opening will be seen leading into a more or less spacious chamber—the outer portion of the auditory meatus. This chamber is continued inwards in the form of a tunnel to the tympanum—the boundary-wall between it and the middle ear. It will be helpful, for clearness' sake, in the present paper to call the cavern-like chamber communicating directly with the outer world the Cavernum, and the tubular inner continuation the Cavernulum.

In *Athene noctua* we have apparently one of the least specialized meatuses of all the Owls. The external opening is almost circular in form and very small, its vertical axis being about half the height of the horizontal axis of the closed eyelid. The cavernum is spacious, and leads backwards and downwards to pass by insensible gradations to the cavernulum. In other words, it represents the typical unspecialized form of the external ear in birds. From this we can pass by a series of slight gradations to forms of considerable relative complexity, as will presently be shown.

What has been described for *Athene* will answer almost equally well for *Speotyto*.

*Bubo lacteus* leads us a step further; at the same time it represents the simplest form of the external ear to be found in the whole genus save that of *B. nycteus*. The

aperture is almost circular; its vertical axis is rather less than the horizontal axis of the eyelid. The cavernum gradually deepens from above downwards and backwards. Its floor is divided into two deep pits by a vertical fold of skin investing the second portion of the temporalis muscle which runs from the postorbital process to the coronoid region of the lower jaw.

In *Bubo nycteus* the external aperture is pyriform in shape, the base being directed upwards and sloping obliquely backwards; its vertical axis is equal to the horizontal axis of the eyelid. The cavernum is spacious, and closely resembles that of *B. maculosus*. It differs, however, in this respect, that the eye projects more laterally, and has given rise to a shallow depression immediately behind it, at the bottom of which lies the mouth of the cavernulum.

In *Bubo ignavus* the aperture is oval, its vertical axis equal to the horizontal axis of the eyelid. The depression behind the eye just described is here much more marked, so that the cavernum is divisible into an anterior and a posterior portion. It is furthermore continued upwards between the skin and the skull to the crown of the head, and backwards between the postaural fold and the skull: thus it has gained a considerable increase in size.

*B. virginianus* differs from *B. ignavus* in that the aperture is somewhat smaller, and the anterior and posterior divisions of the cavernum still more sharply marked.

*B. maculosus* agrees with *B. ignavus* in the size of the aperture, but differs from this species and agrees with *B. virginianus* in that the cavernum is divisible into two portions, the posterior division being even deeper than in this species.

*Bubo torquatus* agrees with *B. virginianus* in the size of the aperture, but more nearly approaches *B. maculosus* in the form and size of the cavernum.

*Scops* and *Bubo* appear to closely resemble one another in the form of the external ear, so far as can be judged from an examination of two species of the former genus. The posterior division differs from that of *Bubo* in that it extends the whole vertical height of the cavernum instead of being confined to its lower third.

In *S. leucotis* the aperture is semilunar, and its vertical axis is equal to the horizontal axis of the eyelid. There is a considerable extension of the cavernum upwards to the crown of the head, between the skull and the skin, and between the postaural fold and the skull.

In *S. giu* the vertical axis of the aperture is only half the horizontal axis of the eyelid. The anterior portion of the cavernum is very shallow, being almost filled by the eye. The transition between the anterior and posterior portions is sudden, and the latter very deep. The floor is spacious.

*Ninox novæ-zealandiæ* has an almost circular aperture, the vertical axis of which is nearly equal to the horizontal axis of the eyelid. The cavernum closely resembles that of *Scops*.

In *Sceloglaux albifacies*, so far as I could make out from a relaxed skin (p. 244), the aperture of the ear was semilunar, equal to, and probably greater than, the horizontal axis of the eyelid. Hazarding a guess, I should say that the cavernum probably most closely resembled that of *Bubo*. Mr. J. H. Gurney (7), after the examination of a

specimen soon after death, gives the measurements of the external aperture as  $\frac{8}{12}$  inch, and describes it as of an elongated shape. "The ears," he writes, "are very low in the head, in fact placed beneath the eyes, and appear, from external examination, to be quite symmetrical; but after the bird was skinned I could see, by looking at the skull from the back, that the hind angle of the inferior mandible was lower on one side than the other."

*Syrnium ulula* has a nearly circular aperture, the vertical axis of which is equal to the horizontal axis of the eyelid. The cavernum is spacious, divisible into anterior and posterior portions, sharply defined; the latter very deep, and passing insensibly into the cavernulum. There is a considerable upward extension of the cavernum between the skin and skull as far as the crown of the head.

So far we have been discussing forms of the external ear which are perfectly symmetrical on the two sides of the head. In the forms presently to be described there is a marked asymmetry, with exceptions, however, which will be noticed in their place.

The first and most remarkable of these is that of *Nyctala Tengmalmi*. The membranous aperture is oval in form; its vertical axis is twice the length of the longitudinal axis of the eyelid. The preaural fold—the loose flap of membrane forming the anterior border of the aperture—forms an imperfect operculum (Pl. 27. figs. 5-6). The cavernum, as in the forms just described, is divisible into an anterior and a posterior portion, the latter being in this case by far the larger. By a considerable development of the lateral wing of the squamosal and exoccipital bones, the form of the meatus has been considerably modified, and is, as just hinted, asymmetrical on the two sides of the head.

On the left side this wing takes the form of a thin bony plate jutting out from the wall of the cranium from behind, outwards, downwards, and forwards to the level of the post-orbital process, so as to form a complete bony outer wall to the posterior portion of the cavernum. It is continued downwards and forwards to overlap the articulation of the lower jaw.

The bony floor of the cavernum is incomplete, being hollowed out or "cut away" to expose the quadrate from behind. Thus the posterior portion is converted into a deep recess roofed over by bone, and looking outwards and forwards on the anterior portion.

On the right side the squamosal wing does not extend along the cranium as far forwards as the base of the postorbital process, but trends outwards and forwards to join the outer border of its lower end, instead of being continued downwards to overhang the articulation of the jaw as on the left side.

Thus the posterior division of the cavernum is converted into a deep recess, differing from that of the left side in that it is open above and that it is shut off below from the outer world and from a portion of itself by the junction of the squamosal wing with the postorbital process. The portion cut off, just referred to, is represented by the deep hollow over the superior border of the articular end of the jaw, and is well shown in fig. 6, Pl. 27.

In *Asio* the asymmetry does not extend to the bones of the skull, but is confined to certain membranes within the cavernum.

In *A. accipitrinus* (Pl. 27. figs. 3-4) the membranous aperture is crescentic in form and of great size, extending from the middle of the lower jaw, from a point corresponding to a line drawn from the base of the cere downwards, backwards, and upwards to a point over the region of the middle of the eye. Thus the cavernum has gained an enormous superficial area, such as has been hinted at in other Owls, in the extension of the cavernum over the skull, and backwards round to the occiput. The pre- and postaural folds are very voluminous, the former being known as the operculum.

That portion of the cavernum which lodges the eye, and the cavity behind, corresponds to the anterior and posterior divisions of the cavernum in other species. The latter division is here much increased, and, by reason of the disposition of certain membranes, has come to be asymmetrical as regards the two sides of the head.

On the right side this will be seen to be divided into an upper and a lower chamber by means of a membranous horizontal partition running from the squamosal wing to the eye, and forward to the operculum. The upper chamber is blind, and may therefore be called the diverticulum. It is possible that it may act as a sort of resonator. The lower, which should, I would suggest, be called the *via recta*, is very spacious and leads to the cavernulum. It is bounded above by the floor of the diverticulum; behind by the squamosal wing; below by a thin membrane from the postaural fold to the operculum, running immediately above the superior border of the lower jaw; and in front by a thin membrane from the lower jaw to a bony tubercle on the postorbital process.

On the left the diverticulum lies below the *via recta*. The membrane dividing the two is placed nearer the lower jaw, and slopes obliquely downwards and inwards. It is also partly attached to the tubercle of the postorbital process just referred to—which tubercle, by the way, occurs *only* in this species.

The ear of *A. otus* differs from the species just described in that there is no postorbital tubercle, that the *via recta* of the left side is without the anterior boundary-membrane, and in that the diverticulum of the cavernum is narrow and deep instead of broad and shallow.

*Syrnium* furnishes us with a third type of modification of the external ear.

In *S. aluco* it is asymmetrical, but the asymmetry is confined to the membranous aperture, which is semilunar in form. The vertical axis of the aperture of the right side is equal to the horizontal axis of the eyelid; that of the left aperture is less.

The cavernum is divisible into anterior and posterior portions, the former larger and shallower, the latter deep, but confined to the lower half of the posterior corner of the cavernum, the floor of which is fairly spacious. The upward continuation of the cavernum over the skull is but slight. The pre- and postaural folds are large, the former, constituting the operculum, overlapping the free edge of the postaural fold when the ear is closed.

*S. uralense* is generally believed to be asymmetrical as regards the form of the external ear, and, moreover, the asymmetry is further supposed to extend to the bones of the skull. A specimen in the flesh from my late friend Mr. Meinertzhagen's aviaries

certainly does not confirm these beliefs—at least so far as the soft parts are concerned; which differed from those of *S. aluco* only in that the vertical axis of the aperture was slightly *greater* than the longitudinal axis of the eye, and that there was no asymmetry, the size of the aperture being the same on each side of the head.

*Strix flammea* concludes the list of those which I have been enabled to examine. The aperture of the ear is almost square; its vertical axis is equal to half the longitudinal axis of the eyelid. The preaural fold constitutes an operculum.

The cavernum is not divisible into anterior and posterior divisions, but forms a deep cavity leading almost directly into the cavernulum.

The operculum, arising a short distance behind the gape as a low ridge, rapidly expands into a square flap terminating some distance above the free edge of the aperture on a level with the top of the eye. The base of the operculum measures about twice the length of the aperture of the ear.

The loose membranous postaural fold supporting the peripheral disc-feathers of *Asio otus* is here represented by a low dermal ridge standing up distinctly from the surface of the head. It arises on the inferior border of the lower jaw, and running backwards, upwards, and forwards, terminates at the base of the beak. This ridge, as previously intimated, serves to support the peripheral disc-feathers. These are much elongated, and narrow-vented, standing out at right angles to the head, and curved so as to present a deeply concave surface forwards, and a corresponding convex surface looking backwards. From their shape and disposition these feathers afford an admirable apparatus for the collection of sound.

It is not surprising to find that the operculum varies slightly in form. In one specimen (of two examined) the lateral border was shorter than that described above; and in consequence the superior border slopes gently upwards, giving the operculum a truncated-conical rather than a square outline.

It would seem, from these facts, that the form of the external ear was at some time subject to considerable variations, the most successful of which have become more or less fixed by selection.

#### RESULTS.

That a detailed study of the Pterylography of the Owls would lead to any very startling results was hardly to be expected, and, as the "Keys" at the end of this paper show, it does little more than confirm what has already been done. It must not be forgotten, however, that these results have been obtained by a deliberate desertion of the beaten track into the neglected highways and byways opened up by Nitzsch, but since allowed to sink almost into oblivion.

I have been enabled to push Nitzsch's methods somewhat further than he himself attempted, for it will be remembered that he founded his genera rather upon the data obtainable by the time-honoured methods of measurements and the relative proportions in the length of the remiges, their number and general outline, and so on, rather than upon pterylogical characters, which seemed to him to differ little, if at all, from his type *Bubo*.

That the common resemblances which pervade the whole group are many, no one will deny, but that nevertheless every species possesses some slight departure of its own from the main type, which, judiciously combined with other external characters, such as the form of the external ear and of the cere, will absolutely distinguish it from every other, is a fact which I believe I have been the first to point out; it now awaits the test of criticism from other quarters.

On the strength of the evidence brought to light during the course of the present investigation, I have felt justified in removing certain genera from their moss-grown pedestals and placing them elsewhere, or even suppressing their claims to generic rank altogether. Sometimes this has been but an act of restoration, sometimes of innovation. This spiriting away of genera has led to the complete isolation of forms generally closely associated: thus, *Asio*, *Syrnium*, and *Nyctala* have been regarded as closely allied by such authorities as Prof. Newton, Dr. Sharpe, and Mr. Ridgway for instance, on the strength of the possession of an operculum and the size of the external aperture of the ear; nevertheless, I venture to think that this relationship is only apparent.

The genus *Syrnium* of Dr. Sharpe's Catalogue, again, probably includes several species which will have to be similarly separated. I infer this from the fact that his *Syrnium perspicillatum*—the *Bubo torquatus* of the present paper—belongs undoubtedly to the genus *Bubo*, since, apart from the absence of an operculum and the small size of the external aperture of the ear, its pterylosis alone shows it to be much more closely allied to this genus than to *Syrnium*.

The real position of *Sceloglaux* and *Ninox* has proved a hard nut to crack, the former especially so. In its general pterolysis it closely resembles *Bubo*, in the form of the cere and external aperture of the ear it resembles *Scops*, while it differs from both these genera in the great width of the lumbar division of the spinal tract; but whether on this account it is entitled to generic rank is open to question. Certain points in the osteology of the skull—to be discussed in my next paper—would have inclined me to place it in the *Nyctalina*; and it remains to be seen whether, when the rest of its anatomy has been worked out, these suspicions will be confirmed.

*Bubo nycteus*, again, has proved rather a stumbling-block. Is this, or is it not, worthy of generic rank?

To place *Carine* and *Speotyto* in the same genus would, I fear, rouse some adverse criticism. I am sorry, but at present this seems necessary. After I have completed my study of the two forms it is possible that I shall find that, after all, they are worthy of separate generic rank.

The skull and the aperture of the ear of *Syrnium uratense* and *S. lapponicum* are generally described as asymmetrical. Whatever may be the case in the latter species, in the former this region is most certainly *symmetrical*, as is proved by a specimen in the flesh generously furnished me by my much-lamented friend Mr. Meinertzhagen. I have besides a skull of this species kindly lent to me by Prof. Newton, which is also quite symmetrical.

That the nestling-down of ptilopædic birds may consist of two distinct kinds of feathers is a point of some interest, and which may yield some useful facts if carefully

studied. It is probable, as I have pointed out in an earlier part of this paper, that "pre-pennæ" only are present in the young Owl, and that the "pre-plumule" are not represented in the very young nestling. When one reflects on the great range of gradation in complexity of structure that obtains in the pre-pennæ of different groups, from the highly complex feathers of the Tinamou, through the less complex feathers of the *Galliformes* and *Anseriformes* to the exceedingly simple hair-like structures of the *Columbæ*, it is pretty obvious that a great deal of work yet remains to be done before this study is exhausted.

Nitzsch was apparently the first to notice the twofold nature of the neossoptiles. He wrote concerning the "nest-plumage of Diurnal Raptorial Birds" that it "consists as usual of downy barbs which are attached to the first perfect barbs of *all the contour-feathers*, even the remiges and rectrices, and disappear as the bird becomes fledged. Moreover, the whole body, with the exception of the axillary cavity and lateral neck-spaces, is covered with true permanent down-feathers, which bear no evanescent tips.' In this last point, that the absence of "evanescent tips" to the feathers in question proved them to be permanent down-feathers, he is evidently mistaken, inasmuch as they are quite distinguishable from the definitive down-feathers, as was pointed out in the earlier part of this paper.

Dr. Gadow has stated that down-feathers occur on the nestling wherever they are found on the adult. This is certainly not the case in the Common Duck, and there are probably many other exceptions.

The position of the femoro-crural band, which is peculiarly well developed in the Owls, if it is not confined to this group, was a point upon which I was for a time inclined to place considerable hope, and even yet it may prove of no little value to the often hard-pressed taxonomist. For the moment, however, with me its trustworthiness is under a cloud. The point, it must be remarked, is to note whether its outer end terminates above or below the knee. After examining a considerable number of spirit-specimens with regard to this point, an uncomfortable suspicion crossed me that this might depend upon the position of the legs when finally fixed by the hardening influence of the spirit: that is to say, it may depend upon the amount of rotation of the femur towards the spine, since the skin in this region seems to have a certain amount of "play," in which case, of course, this band might appear to terminate a little above or a little below the knee, just as this was near to or far from the vertebral column. Certainly the rather large series of *Asio accipitrinus* all agree in having this band terminate at the knee-joint; in *Bubo* it appears to terminate below the knee, and in *Carine* very much below this region. It was over this very species, however, that my faith received its first shock, inasmuch as in a second example of *C. noctua*, which I examined before placing it in spirit, I was able to move the distal end of this tract slightly up or down at will. The amount was slight, but still appreciable; of course my test may be at fault, as I pushed the leg upwards and the skin downwards at the same time. Now this particular specimen had been dead some days, so that the delicate attachments may a'l have broken away directly my somewhat rough experiment was begun; it is to be hoped that someone will try to settle this point soon.

A comparison between the pterylosis of the adult and the embryo could not be expected to lead to any very startling contrasts; nor does it. It is interesting to notice, however, that in none of the embryos of *Asio* which I have examined is there any trace of the voluminous neck-folds of the adult, but the feather-rudiments are seen to closely invest the neck, as in *Strix flammea*. Again, the external aperture of the ear in this species is marked by a shallow depression whose long axis is not more than twice that of the longitudinal axis of the eyelid; the opercular and postaural folds are not even hinted at. In *Strix flammea* the operculum, as in *Asio*, does not appear till later in development; its peculiar four-sided form seems not to be assumed until after the development of this fold.

The branches of the interscapular fork in the embryo of *Strix* appear to be longer than in the adult; but since I have only had the opportunity of examining a single adult specimen, little importance can be attached to this. Similarly the interscapular fork of *Carine brama* differed, and this time markedly, from what one would have expected, inasmuch as its branches were of considerable length, and not, as in the adult of *C. noctua*, short and barely perceptible. This may mean one of three things: (1) the embryo is *not* that of *C. brama*; (2) that *C. brama* may not belong to the genus *Carine*, but some other genus of the *Bubonidae*; or (3) that this may represent an earlier stage in the history of the development of this region of the tract.

In all the embryos there was a distinct claw both on the pollex and index digits. The form of the beak in all the embryos agreed with that of the embryo and adult of *Strix* in being relatively long and straight, and contrasted with the short curved beak of the embryo of *Falco* or of the adult Owls of the Asionid group.

We come now to a question of wider and therefore of more general interest—the nature of the evidence that a study of the Pterylography of the Owls affords as to their systematic position.

Nitzsch (13) years ago, approaching the subject from this point of view, came to the conclusion that they were most nearly related to the Accipitres. They formed his *Accipitrinae nocturnae*. He tells us that “there are two points which essentially distinguish this group pterylographically from the preceding (*Accipitres diurnae*), namely, the constant absence of the aftershaft and the want of the circlet of feathers at the apex of the oil-gland.” And, further, “In their form the tracts agree in general with those of the Falcons, although they present noticeable differences. Among these the chief is that in the Owls the region of the throat between the rami of the lower mandible is never continuously feathered, but the inferior tract issues from the angle of the gonys in the form of a narrow band, and divides on the middle of the neck or close to the front of the furcula. . . .” The *pteryla ventralis* agreed, he found, very closely with that of *Circus*. The *pt. spinalis*, “although arranged in accordance with the principal type of the Falcons, presents this difference—the two arms of the dorsal portion which run to the fork of the scapular portion consist, probably always, of two rows of feathers.”

As the present paper shows, his description of the interramal area must be taken as the exception, not the rule. For the rest, one may adopt the auditor's formula, save in one or two minor details—“examined and found correct.”

Garrod (5) tackled this question after an examination of the pterylosis of *Steatornis*, which he compares with the Owls on the one hand and the *Caprimulgidae* on the other. Judging from internal evidence, I should say that it is probable that his information concerning the two latter groups was gleaned from Nitzsch rather than at first hand. This latter author, by the way, it will be remembered, noticed that in his *Caprimulgi* "the forms of the tracts, singularly enough, have a remarkable resemblance to the type of several Rapacious Birds, but differs in the various genera. Among these analogies I reckon the forking and interruption of the spinal tract between the shoulder-blades in *Caprimulgus*, the emission of an interior branch from the end of the gular portion of the inferior tract in *Nyetornis*, and the division of the dorsal and rump portions of the spinal tract in the same genus." And in describing the *pteryla ventralis* of *Nyetornis* he writes:—"Inferior tract divided from the throat, emitting a narrow curved inner branch which extends upon the breast at the lower extremity of the neck. Behind this branch it is so diminished that it becomes nearly interrupted, as in *Gypaëtos*, to the inferior tract of which it has a great resemblance. . . . In this bird also a hook originates from the end of the pectoral band and runs to the hypopteron."

Thus it is evident that Nitzsch regarded the similarity in the disposition of the tracts in certain *Caprimulgi* and certain "Rapacious Birds" as an interesting coincidence rather than proof of affinity. Moreover, he dwells rather upon the similarity between this group and the Accipitres proper than between this group and the Owls.

To resume: Garrod, after describing the pterylosis of *Steatornis*—which, except for the spinal tract, agrees apparently pretty much with *Caprimulgus*—concludes that "the above-described pterylosis clearly indicates that in the arrangement of its feathers *Steatornis* more closely resembles the *Strigidae* than the *Caprimulgidae*, though it differs considerably from both. It resembles the *Strigidae* and differs from the *Caprimulgidae* in having no aftershaft to the contour-feathers\*, in not having the occipital tract divided up into narrow longitudinal rows, in having spaces on each side of the submaxillary tract, in having the pectoral portion of the inferior tract in two parts, of which the inner approaches the carina sterni above and separates from it as it descends, in having the upper wing-surface uniformly feathered, and in having a large infundibuliform oil-gland. In none of the *Caprimulgidae* does the inferior tract continue simple down the neck, whilst in *Strix flammea*, as in *Steatornis*, it does not bifurcate till in the region of the furcula. But *Steatornis* resembles the *Caprimulgidae* and differs from the *Strigidae* in having ten rectrices; it differs from both, however, in that the inferior portion of the dorsal tract does not unite at all with the scapular fork of the superior portion, in having the outer branch of the pectoral tract diffused and descending far over the abdomen, and in the general tendency to the scattering of the feathers."

Of the points in which *Steatornis* is supposed to resemble the Owls the most important are the second and fourth, but in this last the resemblance is not very close. As Garrod points out, *Steatornis* differs considerably from both *Striges* and *Caprimulgi*. Further evidence on the question has yet to be taken, which is that of the microscopical

\* Dr. Gadow has pointed out (3) that in this Garrod was mistaken: the aftershaft is of considerable size.

structure of the nestling-down and definitive down-feathers, and to my mind this will have greater weight than such points as the absence of an aftershaft or in the occipital tract not being divided up into "narrow longitudinal rows." And it will further outweigh the very slight resemblance which may be traced in the *pt. ventralis*. and overcome what is at present a bar, serving to isolate it from either of the two groups in question—the peculiar form of the lumbar region of the *pt. spinalis*. Garrod's verdict, that "In its pterylosis . . . . *Steatornis* resembles the Strigidae *much* \* more than any of the allied families," is, I think, rather an over-estimation of the facts at present at our disposal.

With Dr. Gadow's evidence (3) the case for the systematic position of the Owls from the standpoint of pterylosis is closed for the present.

Only a very little can be gathered on this point, but that little is almost as much as we can expect or hope for. This is set down under three heads:—

I. The points which the *Striges* share in common with the Accipitres and the *Caprimulgi*. These are:—The thick woolly covering of the nestling; the cervical, dorsal, and ventral apteria; aquitocubital wing; nude oil-gland, agreeing in this point, however, with the *Cathartæ* and *Caprimulgi*, but not with the Accipitres; and the rudimentary (*Caprimulgi*) or even absent (*Cathartæ* and *Pandion*) aftershaft.

II. Characters in which the *Striges* agree with the *Falconiformes*, but differ from the *Caprimulgi*:—such as the presence of a cere in which the nostrils are placed; the arrangement of the dorsal wing-coverts, which resembles that of the *Falconidæ*; the presence of 12 rectrices and 11 remiges, though in the last particular they resemble also the *Coraciidæ*.

III. Points wherein the *Striges* differ from the *Falconiformes* but agree with the *Caprimulgi* or *Coraciidæ*:—They are furnished by the soft dark plumage; the restriction of the adult down to the apteria; and the covering of the podotheca.

The characters reckoned under the first section he regards as of little worth, belonging as much to one group as the other; whilst those of the second must certainly be allowed to be of more importance than those of the third section; though it is obvious that both need further combination with other anatomical data, and this is done in Dr. Gadow's work. The result is that he came to the conclusion that the nearest relations of the *Striges* are the *Caprimulgi*, and especially *Podargus* and *Steatornis*; then follow the *Coraciæ*, and finally the *Cuculi*.

I find myself unable to support Dr. Gadow on two points. The first is that in which he states that the neossoptiles of the *Striges* more closely resemble those of the *Caprimulgi*, structurally, than those of the *Accipitres*; and the second, wherein he states that the down-feathers of both *Caprimulgi* and *Striges* are confined to the apteria. As is elsewhere pointed out (p. 257), the down-feathers of the Owls are structurally much more nearly allied to those of the *Accipitres* than to the *Caprimulgi*; and, lastly, the down-feathers of both Owls and *Caprimulgi* are confined to the *pteryta ataris* and are absent entirely from the apteria. The downy covering of the nestling Owl, however, resembles

\* Italics are mine.

that of the *Caprimulgi* and differs from the *Accipitres* in that it is apparently composed entirely of *pre-pennæ*, whilst that of the *Accipitres* is a mixture of *pre-pennæ* and *pre-plumulæ*. As a piece of additional evidence in favour of Dr. Gadow's position, I would draw attention to the linear, transversely oblique, arrangement of the dorsal tectrices of the wing, which in this particular agree with the *Caprimulgi*.

It seems evident that, in endeavouring to trace out the origin and lines of descent of any given group of birds, we can no more trust the evidence of pterylosis alone than that of any of the other systems or organs that have from time to time been pressed into service to this end, but that, judiciously combined with other characters, it will afford help of some value. As an instrument for defining species it is possible that it may prove a more reliable weapon, but this yet remains to be seen. It would be interesting to apply this test to the examination of some of the reputed species and subspecies, or, as some would have it, varieties of the Barn Owl, and see whether or not the superficial differences were accompanied by corresponding differences in the distribution of the feathers.

*Key to the Families, Sub-families, and Genera.*

- A. The median branch of the ventral tract free posteriorly; the feathers of the hinder border of the acetarsium directed downwards; no filoplumes at the end of the oil-gland . . . . . I. *ASIONIDÆ*.
- a. Interscapular region of the *pt. spinalis* with a long bifurcation . . . Sub-fam. 1. *Asioninæ*.
- a'. Height of vertical axis of the external aperture of the ear three times that of the horizontal axis of the eyelid.
- a''. Preaural and postaural folds voluminous, the former constituting an operculum, which is provided with a valve; oil-gland napiform . . . . . 1. *Asio*.
- b'. Height of the vertical axis of the external aperture of the ear never exceeding that of the horizontal axis of the eyelid; preaural fold not forming an operculum.
- b''. Oil-gland conical; cere not inflated, but closely investing the base of the beak; posterior division of the cavernum confined to its lower half . . . . . 2. *Bubo*.
- c''. Cere laterally inflated, posterior division of the cavernum extending its whole vertical height . . . . . 

3. <i>Scops</i> .
4. <i>Ninox</i> .
5. <i>Sceloglaux</i> .
- c'. Vertical axis of the external aperture of the ear not exceeding that of the horizontal axis of the eyelid; preaural fold forming an operculum, the free edge of which overlaps that of the postaural fold.
- d''. Posterior division of the cavernum confined to its lower third; peripheral disc-feathers meeting in the middle line near the symphysis of the mandible; inner branch of the *pt. ventralis* arising over the region of the head of the coracoid . . . . . 6. *Syrnium*.
- b. Interscapular region of the *pt. spinalis* with a short bifurcation . . . . Sub-fam. 2. *Nyctalinæ*.
- d'. Vertical axis of the external aperture of the ear twice that of the horizontal axis of the eyelid; pre- and postaural folds moderately well developed.
- d''. Cere short; nostrils seated in pisiform inflations . . . . . 7. *Nyctala*.
- e'. Vertical axis of the external aperture of the ear equal to that of the horizontal axis of the eyelid; no operculum; cavernum divisible into anterior and posterior portions.
- f''. Tail long and pointed; oil-gland napiform . . . . . 8. *Surnia*.

- f'*. Vertical axis of the external aperture of the ear half that of the horizontal axis of the eyelid; no opereulum; cavernum not divisible into anterior and posterior portions.
- g''*. Lumbar stem of *pt. spinalis* feebly developed or absent; cere short, much inflated, forming two pisiform swellings on either side of the culmen . . . . . { 9. <sup>♂</sup> *Carine*.  
10. *Speotyto*.

*Key to the Species of the Family Asionidæ.*

Genus 1. ASIO.

- a*. Lateral neck-folds voluminous, with an oblique retractor ensheathed in a prominent membranous fold.
- a'*. Upper end of the dorsal lateral neck-fold lobate; diverticulum of the cavernum broad and shallow, the membrane shutting off the *via recta* passing over a bony tubercle of the postorbital process . . . . . 1. *A. accipitrinus*.
- b'*. Upper end of dorsal lateral neck-fold not lobate; diverticulum of the cavernum narrow and deep; no postorbital tubercle . . . . . 2. *A. otus*.

Genus 2. BUBO.

- a*. Vertical axis of the external aperture of the ear equal to the horizontal axis of the eyelid.
- a'*. Interramal not connected with the ramal area; interseapular fork with very long branches . . . . . 1. *B. ignavus*.
- b'*. Interramal fused from gape backwards with the ramal area, which extends beyond the articular region of the jaw; interseapular fork with very short branches; lateral neck-folds with an oblique retractor as in *Asio* . . . . . 2. *B. virginianus*.
- c'*. Interramal area contracting suddenly behind the region of the gape to form a narrow band; median and inner ventral tract sharply defined; *apt. colli lateralis* continued upwards on to the crown of the head . . . . . 3. *B. maculosus*.
- b*. Vertical axis of the external aperture of the ear less than the horizontal axis of the eye.
- d'*. Interramal joining the mandibular area at the gape; interseapular fork with very short branches; lateral neck-folds without a retractor. 4. *B. torquatus* \*.
- e'*. Interramal area joined, by two separate single rows of feathers behind the gape, with the ramal area; interseapular fork with very long branches; cavernum not divisible into anterior and posterior portions . . . . . 5. *B. lacteus*.
- c*. Aperture of the external ear pyriform. Interramal joined to the mandibular area in front of gape by a single row of feathers, behind it by a very broad band; interseapular fork with very long branches . . 6. *B. nycteus*.

\* This = the *Pulsatrix torquatus* (Daud.) and the *Syrnium perspicillatum* of Latham.

Genus { 3. SCOPS.  
4. NINOX.  
5. SCELOGLAUX.

- a. Vertical axis of the external ear equal to the horizontal axis of the eyelid; interramal joined to ramal area by a broad expansion from the gape backwards; mandibular area extending backwards behind the jaw . . . . . 1. *Scops leucotis*.
- b. Vertical axis of the external aperture of the ear half the horizontal axis of the eyelid; interramal joined to ramal area behind the level of the gape by a narrow branch running obliquely backwards; ramal area narrow, not extending backwards beyond the level of the jaw; lateral neck-folds and oblique retractor; eyelids with a pectinated edge. . . . . 2. *Scops giu*.
- c. Vertical axis of the external aperture of the ear nearly equal to the horizontal axis of the eyelid. . . . . 3. *Ninox nova-zealandiae*.
- d. Vertical axis of the external aperture of the ear equal to the horizontal axis of the eyelid; interramal area broad, expanding to merge with the mandibular area at the gape; arms of the interseapular fork long, arising high up; stem of lumbar fork very wide, arms short, closely approximated, expanding distally; inner and median branches of the *pt. ventralis* imperfectly defined . . . . . 4. *Sceloglaur albifacies*.

Genus 6. SYRNIUM.

- a. Vertical axis of the external aperture of the ear of the left side less than the horizontal axis of the eye; that of the right side greater than this axis; interramal area tapering gently backwards . . . . . 1. *S. aluco*.
- b. Vertical axis of the right and left external apertures of the ear equal, and greater than the horizontal axis of the eyelid; interramal fused with the mandibular area from the gape backwards . . . . . 2. *S. uralense*.

Genus 7. NYCTALA.

- Vertical axis of the external aperture of the ear twice the horizontal axis of the eyelid; loreal area nearly divided into two parts by an apterium; interseapular portion of the *pt. spinalis* with a barely perceptible fork . . . . . 1. *N. Tengmalmi*.

Genus 8. SURNIA.

- Vertical axis of the external aperture of the ear equal to the horizontal axis of the eyelid; interramal merging with the ramal area from the gape backwards; lateral neck-folds with an oblique retractor . . . . . 1. *S. ulula*.

Genus { 9. CARINE.  
10. SPEOTYTO.

- a. Vertical axis of the external aperture of the ear equal to the horizontal axis of the eyelid.
- a'. Loreal area not divided by an apterium; interramal joining the ramal area at the gape, and contracting suddenly immediately after to become the *pt. colli ventralis*; lateral neck-folds with an oblique retractor . . . . . 1. *Carine noctua*.

- b*. Loreal area completely divided into two parts by a broad apterium; interramal area joining the ramal area at the gape, and continued backwards as a broad band to the articular end of the jaw; interscapular fork in the form of two short arms . . . . . 2. *Speotyto cunicularia*.
- B. The median branch of the ventral tract joining the inner branch posteriorly; the feathers along the hinder border of the acrotarsium directed upwards; the oil-gland bearing two or three filoplumous feathers at its tip . . . . . II. STRIGIDÆ.
- External aperture of the ear quadrangular; the vertical axis half the horizontal axis of the eyelid; preaural fold forming a large operculum; interramal area unconnected with the ramal area . . . . . 1. *Strix flammaea*.

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## EXPLANATION OF THE PLATES.

(All the figures are original.)

## PLATE 24.

Fig. 1. Dorsal aspect of the left wing of an adult *Asio accipitrinus*, showing the disposition of the remiges and tectrices. The latter are remarkable for the fact that on the fore-arm they are arranged not in quincunx, but set in obliquely transverse rows, running from without inwards as in *Caprimulgus* and *Rhea*.—Note the position of the plumulæ (d. f.).

d.f. . . . .	Down-feather.
1st—6th cub. rem. . . . .	1st—6th cubital remex, or secondary.
1st—5th maj. cov. . . . .	1st—5th major covert.
P. . . . .	Parapteron.
3. 2. 1. . . . .	Metacarpal remiges, or 1st 3 primaries, numbered from the wrist outwards.
1. 2. 3. . . . .	Cubital remiges or secondaries, numbered from the wrist inwards.

## PLATE 25.

Fig. 1. Dorsal aspect of an adult *Asio accipitrinus*, showing the arrangement of the pteryllæ. The dotted areas represent the pteryllæ; the relative sizes of the feathers are indicated by large and small dots.

Apt. coll. d. . . . .	Aptorium colli dorsale.
Apt. coll. lat. . . . .	„ colli laterale.
Apt. sp. . . . .	„ spinale.
E. . . . .	Eye.
H. . . . .	Feather “horn” or “ears.”
Pt. al. . . . .	Pterylla alaris.
Pt. cap. . . . .	„ capitis.
Pt. caud. . . . .	„ caudalis.
Pt. coll. d. . . . .	„ colli dorsalis.
Pt. cr. . . . .	„ cruralis.
Pt. f. . . . .	„ femoralis.
Pt. hum. . . . .	„ humeralis.
Pt. sp. . . . .	„ spinalis.

Fig. 2. Left side view of the same. The dotted parts as before.

Apt. m. . . . .	Aptorium mesogastræi.
Apt. t. l. . . . .	„ trunci laterale.
L. a. . . . .	Loreal area.
m. f. . . . .	Muscular fold.
Op. . . . .	Operculum.
Postaur. f. . . . .	Postaural fold.
Pt. coll. vent. . . . .	Pterylla colli ventralis.
Pt. v. . . . .	„ ventralis.
R. a. . . . .	Ramal area.

Note the oblique muscular fold (m. f.) running down the neck.

Fig. 3. Ventral aspect of the same. The dotted parts as before.

Pt. cl. . . . .	Pterylla ani s. cloaci.
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## PLATE 26.

Figs. 1, 2, 3, 4, 5. Dorsal views of *Nyctala Tengmalmi*, *Speotyto cunicularia*, *Scops leucotis*, *Bubo nycteus*, and *Bubo maculosus*, to show the form of the spinal tract.—Note the upward extension of the apt. coll. lat. in *B. maculosus*.

Fig. 6. Ventral view of *Syrnium aluco* to show the form of *interramal area* and the *pt. ventralis*.  
Letters as before.

## PLATE 27.

Fig. 1. Left side view of the head of an adult *Asio otus*, to show the form and great size of the external aperture of the ear. This should be compared with fig. 2—the right side of the same head—to show the asymmetrical development of the two sides, and with fig. 3 opposite, to compare the differences between *A. otus* and *A. accipitrinus*.

d. . . . .	Diverticulum.
M. . . . .	Mandible.
M. e. . . . .	Meatus externus, s. <i>via recta</i> , p. 262.
Op. . . . .	Operculum s. preaural fold.
P. f. . . . .	Postaural fold.
R. . . . .	Rim.
S. . . . .	Skull.

The cavernum (p. 259) includes the whole space surrounded by the pre- and postaural folds; the portions M.e. and d. separated one from the other by the valve represent the posterior division of the cavernum of *Bubo* and *Scops*.

Fig. 2. Right side view of the same head. Letters as before.

Fig. 3. Left side view of the head of an adult *Asio accipitrinus*, to show the form of the external ear. Compare with fig. 1 to make out the differences between this and *A. otus*, and with fig. 4 to make out the asymmetrical development of the two sides.—Note the presence of a postorbital tubercle, affording support to the valve. This is wanting in *A. otus*.

* . . . . .	Postorbital tubercle.
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Fig. 4. Right side of same head. Letters as before.

Fig. 5. Left side view of the head of an adult *Nyctala Tengmalmi*, to show the form of the external aperture of the ear. This should be compared with fig. 6, the right side view of the same head, to note the very asymmetrical development of the skull-bones on the two sides of the head.

t. w. sq. . . . .	Tympanic wing of the squamosal.
q. j. . . . .	Quadrato-jugal.

Fig. 6. Right side view of same head. Letters as before.

Fig. 7. Anterior view of the skull of *Nyctala Tengmalmi*, from a specimen in the Cambridge Museum of Zoology, to show the asymmetrical arrangement of the skull-bones.

P. o. p. . . . .	Postorbital process.
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## PLATE 28.

Fig. 1. Left side view of the head of an adult *Syrnium aluco*, to show the form of the external aperture of the ear. Compare with fig. 2—the right side view of the same head—to show the asymmetry in the size of the two apertures; and with fig. 4 to show the difference between the ears of *S. aluco* and *Strix flammea*.

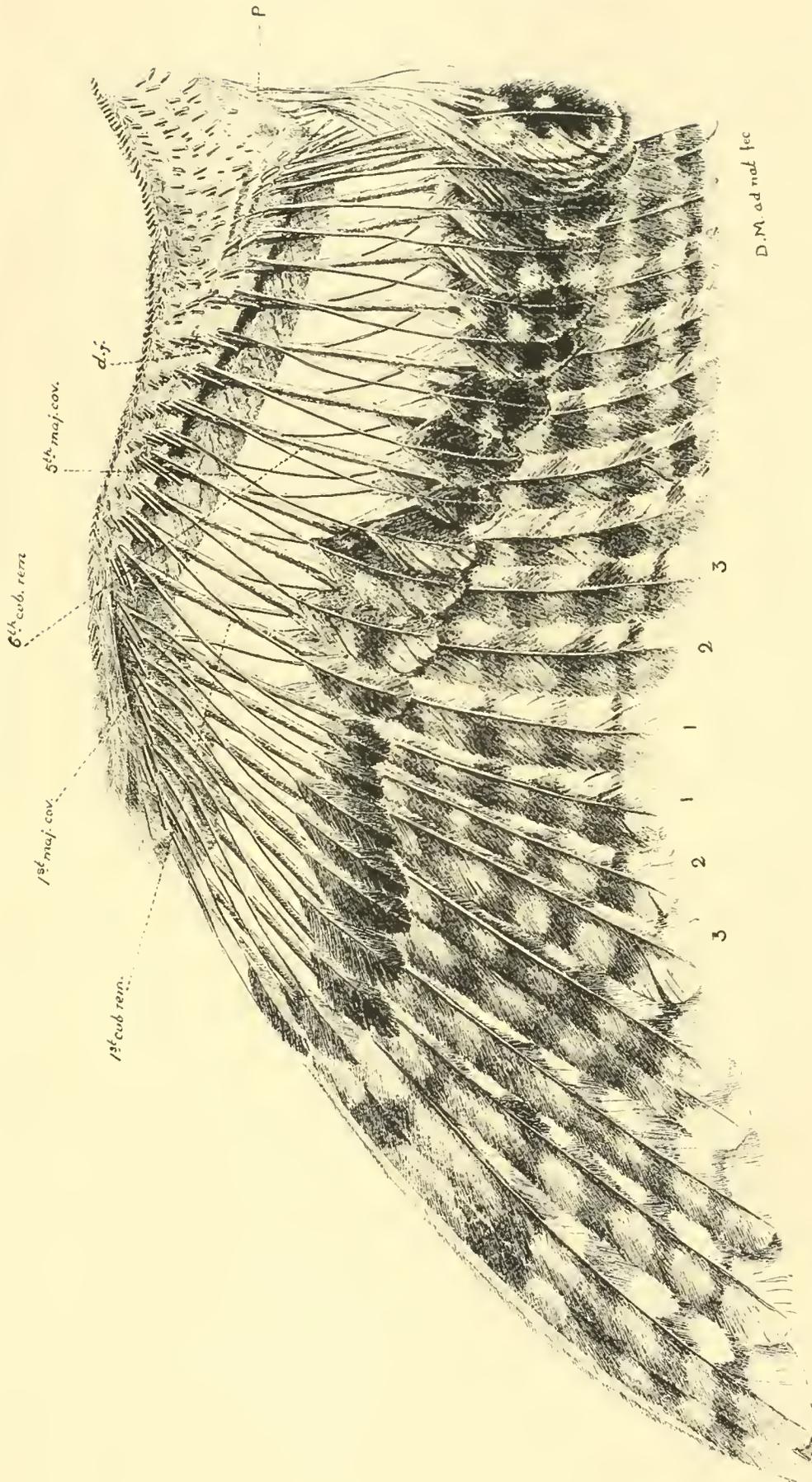
D. . . . .	Peripheral disc-feathers.
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- Fig. 2. Right side view of the same head. Letters as before.
- Fig. 3. Left side view of the head of an adult *Scops leucotis*, to show the form of the external aperture of the ear.—Note the anterior and posterior divisions of the cavernum, described on p. 259. Letters as before.
- Fig. 4. Left side view of the head of an adult *Strix flammea*, to show the form of the external aperture of the ear (see p. 263). Letters as before.
- Fig. 5. Right side view of the head of an adult *Speotyto cunicularia*, to show the form of the external aperture of the ear.—Note the small size of the aperture, and the spiral arrangement of the feathers seated in the pre- and postaural folds. Letters as before.
- Fig. 6. Left side view of the head of an adult *Ninox nova-zealandiæ*, to show the form of the external aperture of the ear. Letters as before.

## PLATE 29.

- Fig. 1. Dorsal aspect of an adult *Strix flammea*, showing the arrangement of the pteryllæ. The dotted parts as before. Letters as before.
- Fig. 2. Left side view of the same.—Note the absence of lateral neck-folds and the outward turning of the inner branch of the pt. ventralis. Letters as before.
- Fig. 3. Ventral view of the same. In this figure the characteristic outward direction of the caudal end of the inner branch of the pt. ventralis is well seen. Letters as before.





Metzger's Gen. del.

West Newman Colotyp

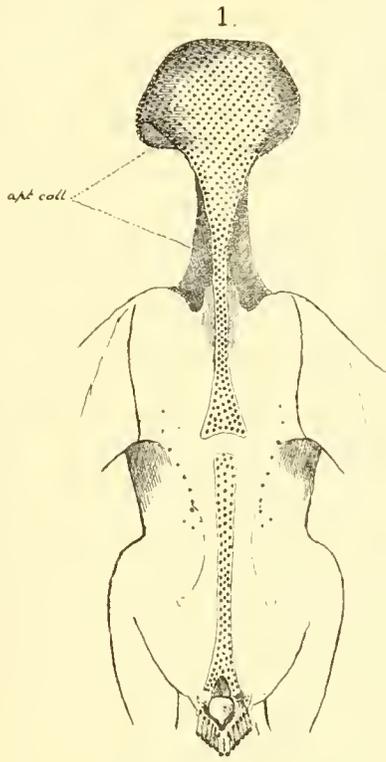
WING OF ASIO ACCIPITRINUS.

MORPHOLOGY OF THE OWLS.

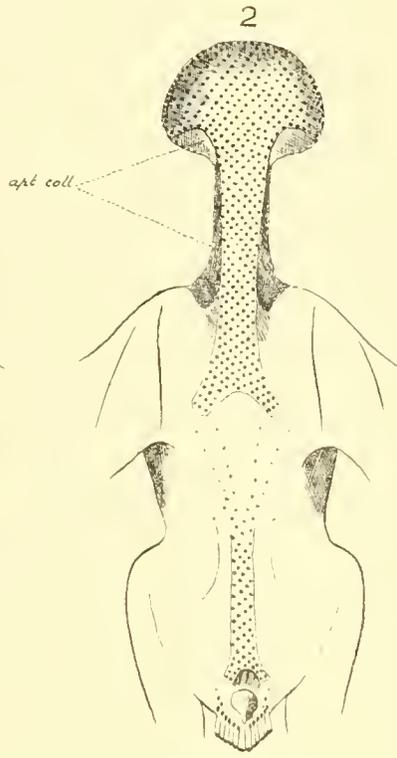




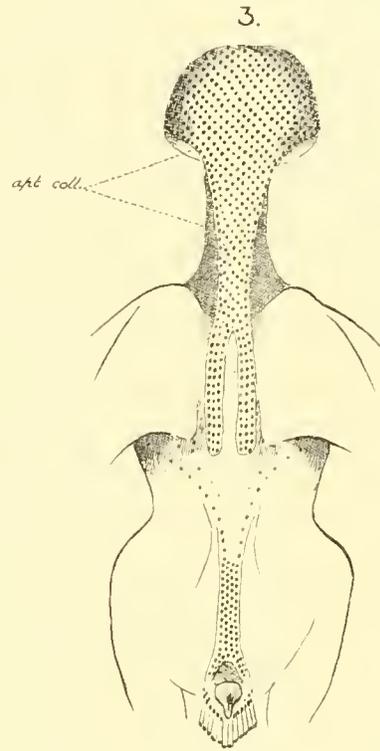




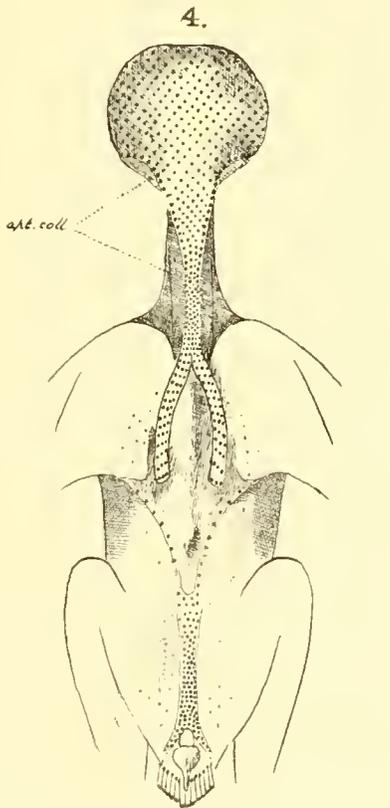
Dorsal view  
NYCTALA TENGMALMI.



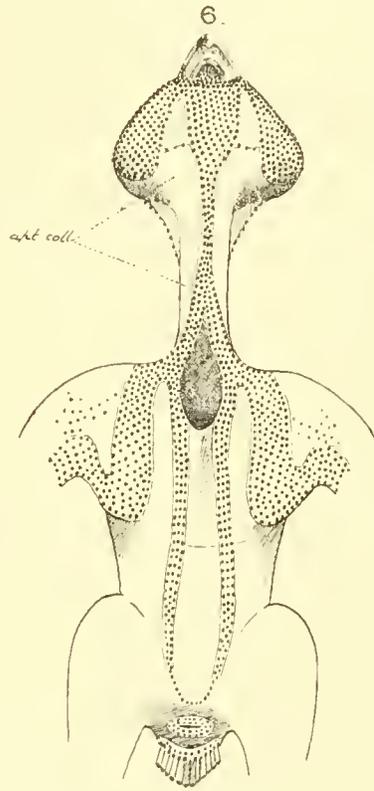
Dorsal view.  
SPEOTYTO CUNICULARIA.



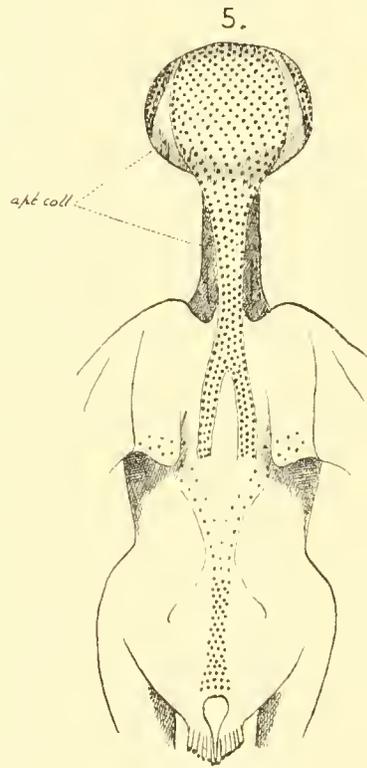
Dorsal view  
SCOPS LEUCOTIS.



Dorsal view  
BUBO NYCTEUS.  
D.M. ad. nat. fec.

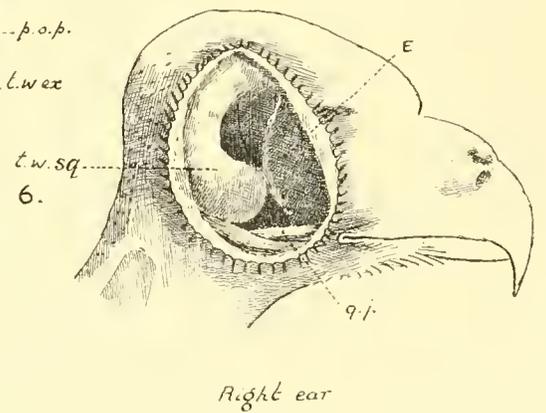
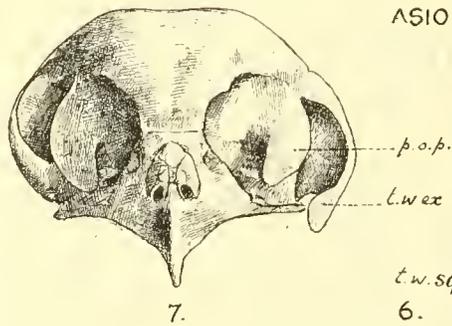
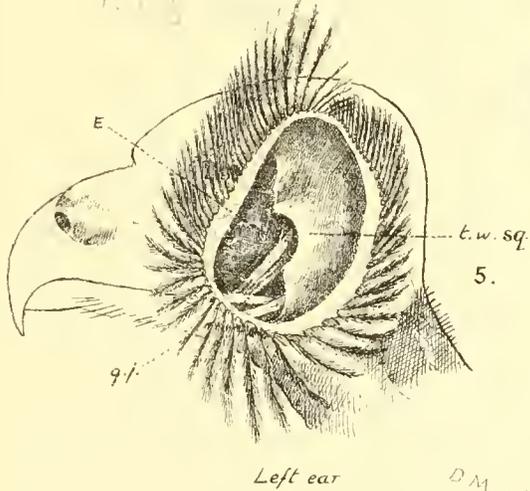
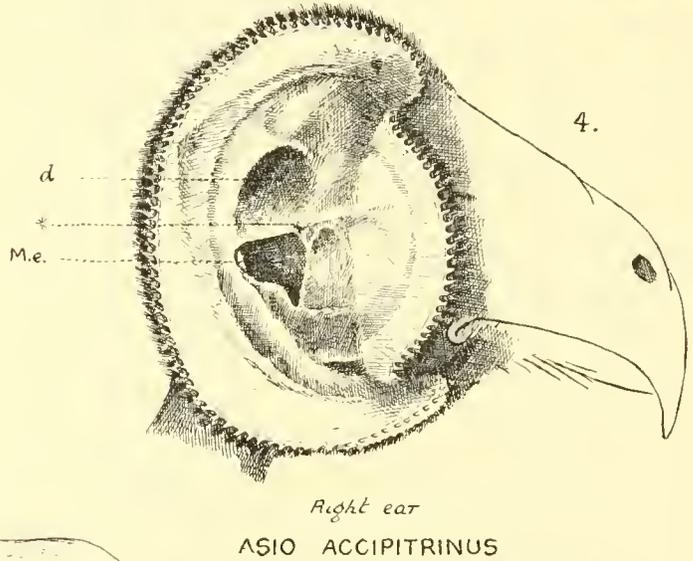
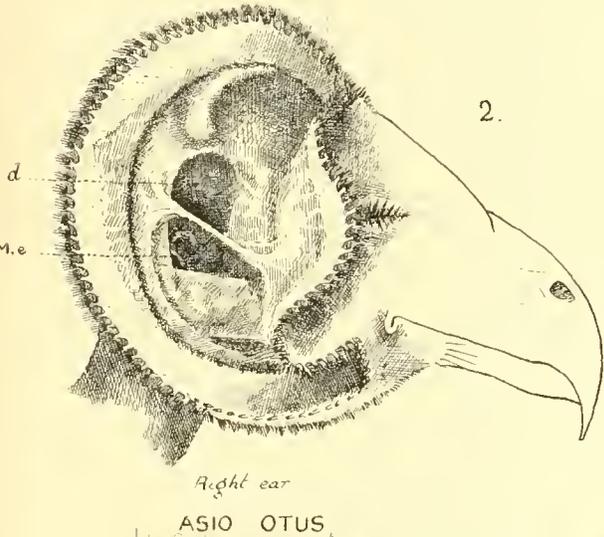
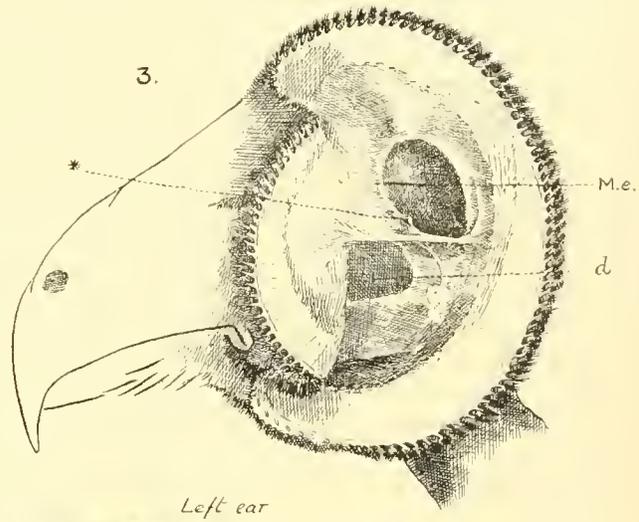
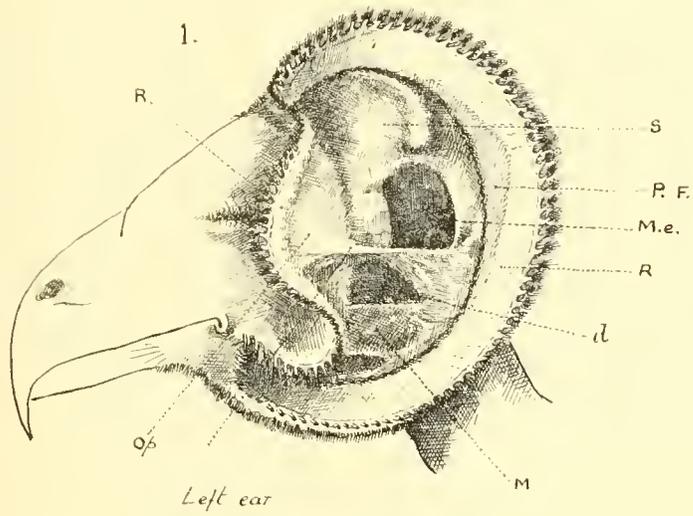


Ventral view  
SYRNIUM ALUCO.



Dorsal view.  
BUBO MACULOSA.

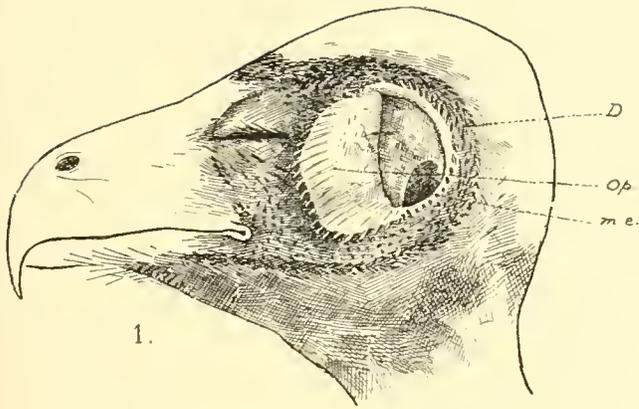




NYCTALA TENGMALMI

D.M. and not fec

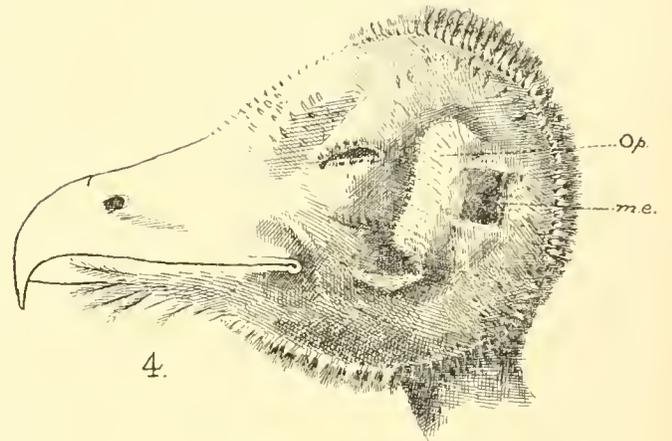




1.

Left ear

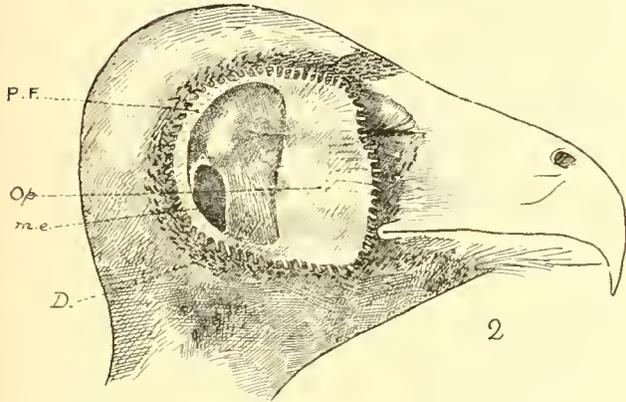
SYRNIUM ALUCO



4.

Left ear.

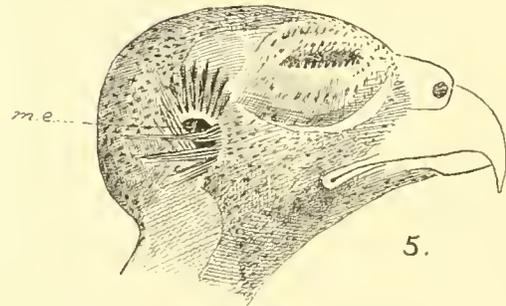
STRIX FLAMMEA



2.

Right ear

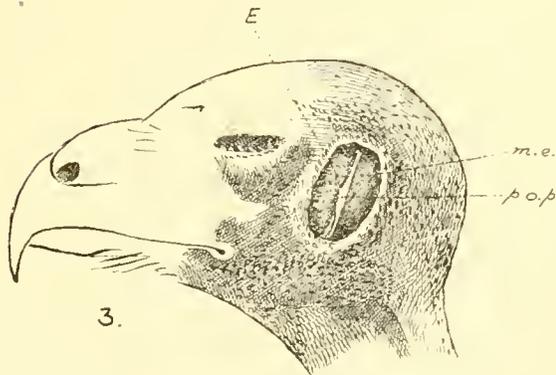
SYRNIUM ALUCO.



5.

Right ear.

SPEOTYTO CUNICULARIA.

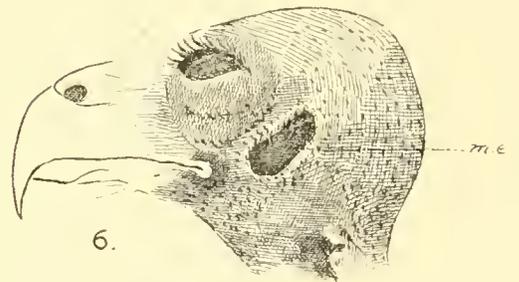


3.

Left ear

SCOPS LEUCOTIS

J M ad nat. sc.

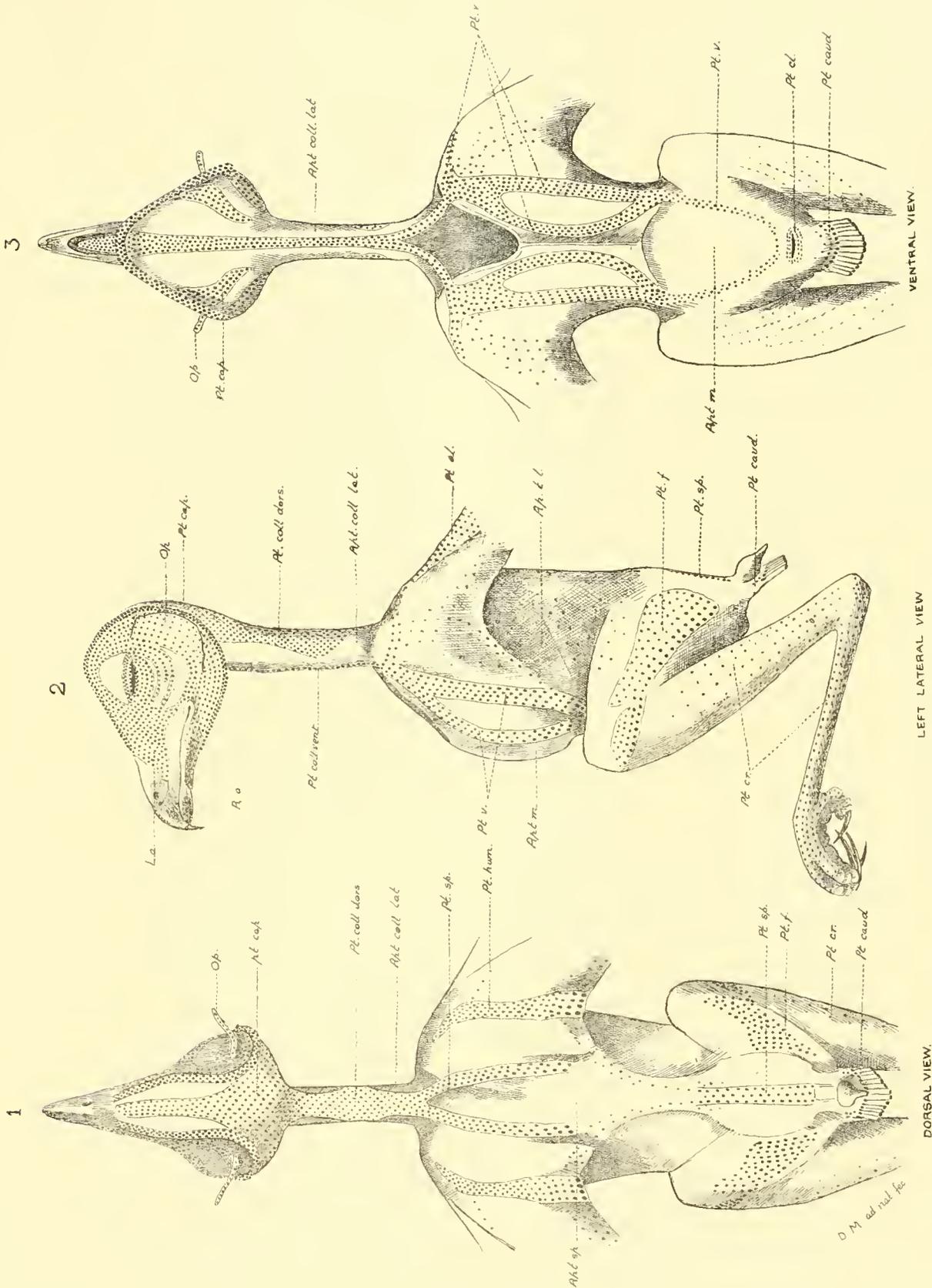


6.

Left ear

NINOX NOVÆ-ZEALANDIÆ





LEFT LATERAL VIEW

STRIX FLAMMEA.

DORSAL VIEW.

VENTRAL VIEW.

D Meinertzhagen del

West Newman Photo lith





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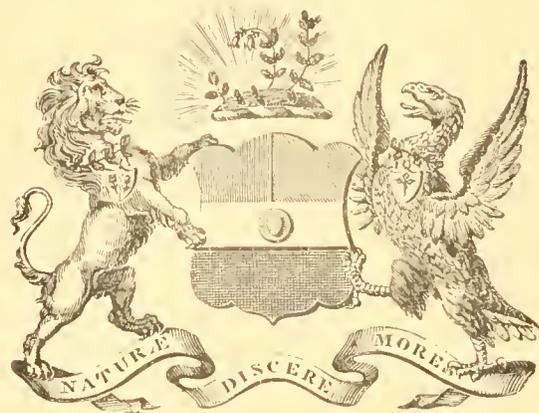
THE BRAIN IN THE EDENTATA.

BY

G. ELLIOT SMITH, M.D. (SYDNEY),

ST. JOHN'S COLLEGE, CAMBRIDGE.

(Communicated by Prof. G. B. HOWES, Sec. Linn. Soc.)



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January 1899.



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(With 36 Illustrations in the Text.)

AUG 25 1899

Read 7th April, 1898.

#### INTRODUCTION.

THE interest which attaches to the study of the brain in any large group of animals is considerably accentuated in the case of such an enigmatical order of mammals as that discussed in this communication. Two aspects of this many-sided interest must appeal to us very forcibly during the investigation of the strange assemblage of mammals which have been gathered into one group under the name Edentata. For we may not unreasonably hope that the obscure problems of the interrelationships of the heterogeneous families which compose this so-called "order," and the even more perplexing question of the wider affinities to other groups of animals, may be elucidated by the evidence afforded by the brain, which, as the master-organ of the body, must be allowed distinctive importance.

Then, again, the study of so many modifications of the mammalian type of brain as we find within the limits of this group must exercise a considerable influence upon the more strictly morphological problem of the "search after the fundamental lines in the structure of the brain," which, as Edinger has well said, is the most important task of the brain-anatomist of the present day. This aspect of the problem becomes all the more interesting in the case of a group of mammals like the Edentata, which it is customary to regard as of lowly organization, when we remember that changes of great significance, which must appeal equally to the systematist and the morphologist, have taken place in the structure of the brain within the Mammalia. For we find certain features in the cerebrum of the Monotremata and Marsupialia which distinguish these groups clearly the one from the other and each from all the Eutheria\*. If the Edentata are as lowly organized as they are generally represented, we might reasonably expect to find some definite evidence of this fact in those regions of the brain which we know to have been so transformed at the birth of the Placentalia. On the contrary, should the results of an examination prove that these recently modified parts of the brain show the typical features as fully developed as they are in such Eutheria as the Ungulata or Carnivora, we might be justified in adopting this as strong corroborative evidence in favour of the view that there is a much closer affinity between the ordinary Eutheria and the Edentata than is usually supposed.

\* These features I have already discussed before this Society ('The Origin of the *Corpus Callosum*, &c.,' Trans. Linnean Society, 2nd series, Zoology, vol. vii, part 3, 1897), and elsewhere; cf. 'Journal of Anatomy and Physiology,' vol. xxxii, pp. 23-58, 1897.

In this investigation our first aim must be the determination of the extent to which the brain in the Edentata conforms to the architectural plans which prevail elsewhere in the Mammalia. Then we shall be able to appreciate the modifications of the prevalent type or types and study the factors which produce these variations, either to meet direct physiological needs which the mode of life of the individual imposes, or to conform to some definite morphological plan which is not so directly the expression of functional modification, and therefore is likely to have some definite taxonomic value.

Before entering into the discussion of these problems, it will be well to review as briefly as possible the state of our knowledge concerning the relationships of the Edentata at the present time.

It would perhaps be difficult to discover elsewhere among the Mammalia five natural groups of mammals which present such striking contrasts in appearance and habits of life as we find in the five families which include all the existing Edentata. Striking as these contrasts are, they are probably equalled by the marked differences in the anatomical features of the animals. The only reason for uniting these heterogeneous families in one group is the fact that they possess in common certain negative characters which distinguish them from all other mammals. The most important of these negative features is the reduction of the teeth, but even the characters of this reduction, the features of the few teeth that remain in certain families, and the little we know of their development present most manifest distinctions.

In spite of the absence of any very decided anatomical links between the different recent families, the evidence of paleontology many years ago showed that both the Sloths and Ant-eaters, although markedly dissimilar in themselves, exhibit signs of close kinship to the extinct Ground-Sloths. Moreover, it is now very generally admitted that the Armadillos also branched off at an early period from a stock common to the ancestors of the Ant-eaters, Sloths, and Ground-Sloths. Hence Gill\* has suggested the separation of these three New-World families as a suborder from the Old-World families. To this suborder he gives the name *Xenarthra*, because in these American families the zygapophyses of the vertebrae possess additional articular facets.

The huge collections of extinct Tertiary mammals which have been unearthed within recent years have thrown a considerable amount of light upon the vexed problems of the kinship of the Edentata.

If we admit that the group of extinct mammals which Wortman has called *Ganodonta* † represents the ancestors of the American Edentata, we must be prepared to recognize in the latter the degenerate representatives of a group of animals which are united by the closest ties of kinship to the ancestors of the Rodentia, Carnivora, and Ungulata. It is not necessary to do more than mention in passing how vastly this suggestion is at variance with the older and as yet more generally accepted view that the Edentata are a very primitive group, which is so distantly related to the ordinary Eutheria that some

\* Gill, 'Standard Natural History,' 1884.

† S. L. Wortman, 'Psittacotherium, a Member of a New and Primitive Suborder of the Edentata,' Author's edition, copied from the Bull. Amer. Mus. Nat. Hist. vol. viii. article xvi. p. 259 (1896).

writers even suggest their separation as "Paratheria." Wortman's hypothesis brings the Edentata into intimate relationship with the ordinary Eutheria, and is quite fatal to the Paratherian idea.

The anatomical features of the two Old-World families, the scaly Pangolins (the habitat of which fringes the Asiatic continent from the Ethiopian region in the west to the islands at the extreme south-east) and the Ethiopian *Orycteropus* (the pig-like appearance of which suggested the name Aard-vark, which the Dutchmen of the Cape apply to it), probably differ the one from the other and each from the American forms as widely as their geographical distribution, and concerning their ancestry palæontology has not revealed much. The present state of our knowledge, or lack of knowledge, of the affinities of the Pangolins and the Aard-varks has been aptly and forcibly expressed by Oldfield Thomas. Writing of *Orycteropus* he says\* :—

"Although called an Edentate, it has always been recognized as possessing many characters exceedingly different from those of the typical American members of the order. It has been placed with them rather on account of the inconvenience of forming a special order for its reception than because of its real relationship to them. Now, as they are altogether toothless or else homodont and monophyodont (apart from the remarkable exception of *Tatusia*), it seems more than ever incorrect to unite with them the solitary member of the *Tubulidentata*, toothed, heterodont, and diphyodont, and differing from them in addition by its placentation, the anatomy of its reproductive organs, the minute structure of its teeth, and the general characters of its skeleton.

"But if *Orycteropus* is not genetically a near relation of the Edentates, we are wholly in the dark as to what other mammals it is allied to, and I think it would be premature to hazard a guess on the subject. Whether even it has any special connection with *Manis* is a point about which there is the greatest doubt, and unfortunately we are as yet absolutely without any palæontological knowledge of the extinct allies of either. *Macrotherium* even, usually supposed from the structure of its phalangeal bones to be related to *Manis*, has been lately proved to have the teeth and vertebræ of a Perisso-dactyle Ungulate, and one would not dare to suggest that the ancestors of *Manis* or *Orycteropus* were to be sought in that direction. Lastly, as the numerous fossil American Edentates do not show the slightest tendency to an approximation towards the Old-World forms, we are furnished with an additional reason for insisting on the radical distinctness of the latter, whose phylogeny must therefore remain for the present one of the many unsolved zoological problems."

I have quoted these conclusions at some length because they summarize so admirably our present state of ignorance of the interrelationships of the Edentata as a group. Nor is our knowledge of the relationship of the group to the other Mammalia on a more satisfactory basis. It is, therefore, strange that so little has hitherto been done to call in the evidence which the nervous system, and especially the brain, affords to help to unravel this perplexing tangle of relationships. For it is hardly conceivable that the master-organ which presides over the activities of the whole body, and is responsive to

\* Oldfield Thomas. 'A Milk Dentition in *Orycteropus*,' Proceedings of the Royal Society, vol. xlvii. (1890) p. 248.

every change of bodily conformation and every variation in the physiological activity of the organism—which, in a word, is the only part of the body which can be said to represent within itself all parts of the organism—could be other than an index of undoubted taxonomic value. But at the present time there is an unfortunate tendency among systematists to lightly esteem the value of the brain in this connection, and either to ignore cerebral features altogether or pay them such scant attention as practically amounts to the same thing. Such loose and utterly erroneous statements as those of Cope, who laconically sums up the characters of the Edentate brain in the words “hemispheres small, smooth”\*, are unfortunately only too often found in the writings of comparative anatomists of the present day.

In considering the peculiarities of the brain in any group of mammals it is necessary to distinguish those features which are dependent upon mere functional modification from those which, though not altogether independent of function, are yet the expression of a definite morphological type. For example, we find that the mesencephalon in almost all mammals conforms to a definite unchangeable morphological type, although the proportions of its various parts undergo the most notable variations as the functional importance of the visual and auditory activities varies. On the other hand, in the cerebral hemisphere we also find evident changes which can be directly traced to functional modification in association with the varying acuteness of the sense organs, while beyond these modifications we find other changes which cannot be explained as purely functional variations, but which are beyond question the expression, as aforesaid, of a definite morphological type.

In seeking for evidence to aid in the interpretation of such problems as these I have not hesitated to cull data from examination of widely differing types. My studies of the Edentata were preceded by an examination of the brain in the Monotremata and Marsupialia, and during the course of this examination I have constantly compared the features of the brains under consideration with those of such representatives of the Insectivora, Rodentia, Cheiroptera, Ungulata, and Carnivora (among other groups) as were available for the purpose.

The results of the only attempt which has hitherto been made to discuss the anatomy of the brain in the Edentata in a systematic manner are embodied in a memoir by Georges Pouchet, which was published thirty years ago †. But many other anatomists, both before and since the time of Pouchet, have given us brief descriptions of the brain in individual members of this group. The extreme variations in external configuration which the brain presents in different members of the so-called order have been made the subject of an admirably illustrated memoir by Paul Gervais, which made its appearance contemporaneously with Pouchet's contribution ‡. Even to this day Pouchet's work is

\* Cope, 'Origin of the Fittest,' 1878, p. 342.

† G. Pouchet, 'Mémoire sur l'Encéphale des Édentés,' *Journal de l'Anatomie et de la Physiologie*, tome v. 1868 no. 6, and tome vi. 1869, nos. 1, 2, 3, & 4.

‡ Paul Gervais, 'Mémoires sur les Formes cérébrales propres aux Édentés vivants et fossiles,' *Nouvelle Archives du Muséum d'Histoire naturelle de Paris*, tome v. (1869).

the only attempt to treat in a comprehensive manner the anatomy of the brain in the whole group. But Pouchet's memoir is altogether inadequate to our present needs. During the thirty years that have elapsed since this work was published the outlook of the student of brain anatomy has been immeasurably widened, his methods of investigation have been utterly changed, and his whole science has been revolutionized. The investigator of to-day approaches the study of a new type of brain with a much better equipment and a considerably clearer appreciation of the significance and relative importance of anatomical features than was possible before Weigert, Golgi, and Marchi introduced methods of research which have enabled us to understand the fundamental plan of the organ with which we have to deal. Instead of describing in a more or less casual manner the general features of a brain as Pouchet did, and thereby accumulating a mass of evidence which is valueless to a succeeding generation, we can, in the light of our present-day knowledge, directly examine with a clearly defined purpose those parts of the brain which we know are undergoing change in the Mammalia. Of all parts of the brain the most recently differentiated portion, the cerebral cortex, is naturally that which is the most changeable, and to which most of our attention must necessarily be devoted. In studying this more than any other part it is necessary to institute comparisons with as wide a series of mammals as possible, in order to gain an insight into the significance of such modifications as we find.

In the light of our knowledge of the important differences which exist between the hippocampal formation and the cerebral commissures in the Monotremata and Marsupialia, and between each of these orders and the so-called Placentalia, I have entered into the consideration of this aspect of the problem in some detail. The regions of the brain-stem, the optic thalamus, the mesencephalon and hind-brain, have been described as briefly as is consistent with clearness, because these stable regions of the brain are subject to very slight variations as compared with the great modifications which affect other regions.

In considering the cerebellum I have entered into the descriptions in considerable detail because, unfortunately, the subject of cerebellar morphology is almost a *terra incognita*. For the purposes of this paper I have found it necessary to examine the cerebellum in as many mammalian brains as were obtainable, in order to arrive at some idea of the fundamental plan according to which this complex organ was built up. As the result of this extensive examination I have elaborated a tentative scheme for describing the cerebellum, the chief merit of which is its extreme simplicity, and the fact that it is applicable to the cerebellum in any member of the Metatheria or Eutheria. This can hardly be said of the method of description which is employed in human anatomy, and which is practically the only system of nomenclature thus far adopted in discussing the cerebellum.

In certain of the better known regions of the brain I have found it necessary to enter into much longer explanations than might otherwise have been needed if the nomenclature had not been so confused. As an example I may refer to the region of the pyriform lobe. So far as was possible with the material at my disposal I have investigated the histology of the brains considered in this contribution, and in the case of *Chlamydomorphus*

a series of coronal sections was carefully examined. But in none of these brains was it possible to detect any histological features which could not be demonstrated much more clearly and to much better purpose in the fresh brains of such Insectivores and Rodents as are always available. For this reason I have not felt justified in giving illustrations to represent histological facts, although my descriptions, and to some extent the figures which accompany these descriptions, are largely based upon the results of histological examination.

When Professor Howes kindly suggested that I should undertake this investigation, he very generously placed at my disposal all the Edentate brain-material which his teaching-collection contained. This nucleus of material, upon which most of the investigation was carried out, consisted of a very well preserved specimen of the brain of an adult *Orycteropus*, as well as representatives of *Tamandua tetradactyla*, *Choloepus didactylus*, and *Chlamyphorus truncatus*, in a somewhat less satisfactory state of preservation. All these brains had been preserved in alcohol.

Professor Max Weber, of Amsterdam, very generously gave me, on the suggestion of Professor Howes, the brain of a young *Bradypus tridactylus*, which had been carefully preserved in a chromic solution, so that it was available for histological work\*.

The magnificent collection of brains in the galleries of the Museum of the Royal College of Surgeons in London includes a valuable series of fifteen Edentate brains, and to these Professor Stewart kindly gave me free access. In this collection are to be found representatives of the genera *Orycteropus*, *Myrmecophaga*, *Tamandua*, *Bradypus*, *Choloepus*, *Dasypus*, *Xenurus*, *Tatusia*, *Tolypeutes*, and *Manis*. The Museum also contains cranial casts of *Choloepus* and the extinct forms *Mcgatherium* and *Glyptodon*.

In addition to this, Professor Stewart very kindly placed the resources of his stock at my disposal, and from this collection I obtained representatives of *Dasypus villosus*, *Bradypus tridactylus*, a small *Manis* of unknown species, and a number of partially dissected brains, more especially of *Myrmecophaga* and *Choloepus*.

From this it will appear that representatives of every genus except *Cycloturus* and *Priodon* have been available for examination; but, as the subsequent account will show, we have imperfect data which, by comparison with other representatives of the same families, will enable us to form a tolerably approximate estimate of the configuration of the brain in the Little Ant-eater and the Great Armadillo.

Among the beautiful series of drawings which the late Professor Huxley bequeathed to the Royal College of Science, there are sketches of the brains of *Orycteropus*, *Tamandua*, and *Dasypus sevcinctus*, none of which have been published. Professor Howes has kindly allowed me to make use of these, and, as two of the sketches represent the appearance in the fresh state of the actual brains of *Orycteropus* and *Tamandua* which were used in this investigation, they proved of service in preparing figures 3 and 25.

\* This brain is apparently the second brain of *Bradypus* which is referred to in Professor Max Weber's memoir, "Vorstudien über das Hirngewicht der Säugethiere," Separat-Abdruck aus Festschrift für Carl Gegenbaur, Leipzig, 1896, p. 109.

To Professor Max Weber and Professor Stewart I must here express my deep sense of gratitude for their generosity in placing such valuable material at my disposal, and in addition I must thank the latter gentleman for granting me for some weeks all the facilities which his laboratory offers.

My indebtedness for so much material for this research and the opportunities for making use of his laboratory is among the least of my many obligations to Professor Howes, who has constantly guided me in the search for literature, and has ever been ready to give me the benefit of his valuable advice. It is with the greatest pleasure that I take this opportunity of acknowledging all this kindly consideration.

## LITERATURE.

Reckoned by the number of memoirs which have appeared upon the anatomy of the brain in the Edentata, it must be confessed that the literature is by no means inconsiderable; but when we proceed to sum up the positive additions to exact knowledge, we are bound to confess that an acquaintance with the Edentate brain derived from this bulky mass cannot be otherwise than very hazy.

In the following table these contributions to our knowledge of this subject are arranged in chronological order:—

**F. TIEDEMANN.**—‘*Icones Cerebri Simiarum et quorundam Mammalium rariorum.*’ Heidelberg, 1821.

Contains figures representing the dorsal and mesial surfaces of the brain of *Cholopus didactylus* and the dorsal surface of the brain of *Cycloturus didactylus*.

**F. LEURET et P. GRATIOLET.**—‘*Anatomie comparée du Système nerveux.*’ Paris, 1839–59.

Contains the figure of the dorsal surface of the brain of *Bradypus tridactylus*, and in the text numerous references to the brains of other Edentates.

**WILHELM VON RAPP.**—‘*Anatomische Untersuchungen über die Edentaten.*’ Geneva, 1843 and 1852.

The dorsal surfaces of the brains of *Cholopus* and *Tatusia* are represented.

**J. HYRTL.**—“*Chlamydochori truncati cum Dasypode gymnuo comparati examen anatomicum.*” Denkschr. d. k. Akad. d. Wiss., Vienna, 1855.

Contains a few brief notes on the brain of *Chlamydochorus*, unaccompanied by any figures.

**ALESSANDRINI.**—“*Cenni sull’ Anatomia del Dasipo minimo, Desm.*” Mem. R. Accad. delle Sc. dell’ Ist. di Bologna, t. vii. 1856.

Contains very brief and unimportant notes on *Tatusia*.

**W. H. FLOWER.**—“*On the Commissures of the Cerebral Hemispheres of the Marsupialia and Monotremata.*” Philosophical Transactions, 1865.

In this classical memoir the mesial surface and a coronal section through the cerebrum of *Cholopus didactylus* have been represented in figures with an exactness which is lacking in the earlier memoirs.

**W. TURNER.**—“*On the Anatomy of the Brain of Dasypus seveinctus.*” Journal of Anatomy and Physiology, vol. i. 1867.

The most complete account we possess of the brain of *Dasypus seveinctus*, illustrated by three figures.

GEORGES POUCHET.—“Mémoire sur l'Encéphale des Edentés.” *Journal de l'Anatomie et de la Physiologie*, tome v. 1868 and tome vi. 1869.

In this important work figures of the actual brain in the genera *Tamandua*, *Cycloturus*, *Chlamydochorus*, *Dasyppus*, *Manis*, and foetal specimens of *Bradypus*, *Choloepus*, *Tatusia*, and *Orycteropus*, have been given in addition to cranial casts of *Choloepus*, *Orycteropus*, *Mylodon*, and *Glyptodon*.

I have been unable to consult Pouchet's earlier “Mémoires sur le grand Fourmilier.”

PAUL GERVAIS.—“Mémoire sur les Formes cérébrales propres aux Édentés vivants et fossiles.” *Nouvelles Archives du Muséum d'Histoire naturelle de Paris*, tome v. 1869.

Contains an excellent series of figures of cranial casts of all the representative existing genera of Edentates as well as most of the extinct forms. In addition there are figures of the actual brain of *Myrmecophaga*, *Manis*, *Dasyppus seveinctus*, and a young *Orycteropus*.

A. H. GARROD.—“Notes upon the Anatomy of *Tolypeutes tricinctus*, with remarks upon other Armadillos.” *Proceedings of the Zoological Society of London*, 1878, pp. 222–230.

The earliest description of the brain of *Tolypeutes*: in addition the author describes, with an excellent illustration, the brain of *Xenurus*.

W. A. FORBES.—“On some Points in the Anatomy of the Great Ant-eater (*Myrmecophaga jubata*).” *Proceedings of the Zoological Society of London*, 1882.

The best account of the brain of *Myrmecophaga* yet published.

W. TURNER.—“The Convolution of the Brain.” *Journal of Anatomy and Physiology*, vol. xxv. 1890.

Professor Turner adds brief notes and two figures of *Choloepus Hoffmanni* to his previous contribution dealing with *Dasyppus*.

H. RABL-RÜCKHARD.—“Einiges über das Gehirn der Edentata.” *Archiv für mikroskopische Anatomie*, Bd. xxxv. 1890.

This brief memoir represents all that has hitherto been accomplished towards the elucidation of the histology of the brain in Edentata, and concerns itself merely with the anterior commissure and the presence of a longitudinal ependymal fold in the roof of the *aqueductus Sylvii* of a foetal *Xenurus*. The most valuable feature of this memoir is the excellent series of figures of sections stained by the method of Weigert.

MAX WEBER.—“Beiträge zur Anatomie und Entwicklung des Genus *Manis*.” *Zoologische Ergebnisse einer Reise in Niederländisch Ost-Indien II.*, Leyden, 1892.

Contains the best description of the brain of *Manis* hitherto published, with illustrations.

At the time when this investigation was undertaken the literature included in the above list represented all that had hitherto been published (so far as the writer is aware) concerning the anatomy of the brain in the Edentata. But since the present memoir was announced, Professor Howes has kindly called my attention to a brief note concerning a monograph upon this subject, which unfortunately has not been published\*.

Quite recently Ziehen has published some comparative notes upon the brain of *Manis* in the first part of a large monograph upon the brain in Monotremata and Marsupialia †.

\* GEORGE HUNTINGTON.—“Contributions to the Visceral Anatomy of *Myrmecophaga jubata*, *Tamandua bivitata*, *Areopithecus didactylus*, *Dasyppus seveinctus*, *Tatusia novemcincta*, and *Manis longicaudata*.” [Abstract.] *Transactions of the New York Academy of Sciences*, vol. xv., January 1896, p. 98.

† THEODOR ZIEHEN.—“Das Centralnervensystem der Monotremen und Marsupialier.” 1 Theil. *Semou's Zoologische Forschungsreisen in Australien und dem Malayischen Archipel*, 1897.

There is much in this important memoir which calls for criticism, but at present I will merely take cognizance of the references to *Manis*. In a future memoir I shall discuss some of the statements in reference to the Monotremata and Marsupialia, as well as some of the more general questions, the consideration of which is precluded here by limitations of space.

Several investigators have recorded the weight of the brain in various Edentates, the most noteworthy contribution to this subject being Max Weber's monograph (*jam. cit.* p. 282).

If we sum up this literature we find that, apart from observations upon the general form and size of the brain, it contains little information of sufficient exactness to be of value to the comparative anatomist. Almost the whole of the data collected in the memoirs concern the cerebral cortex, and even with regard to this important region of the brain we are provided with only the most meagre information, often very vaguely expressed. Almost all writers are silent concerning the basal regions of the brain, which are of especial interest in the lowlier mammals.

Reviewing the literature of the different families, we find that nothing is known of the adult brain of *Orycteropus*, except such information as the examination of cranial casts has provided. The brief notes of Pouchet and Gervais upon the brain of a fetal *Orycteropus* add little, if anything, to our knowledge.

Concerning the *Myrmecophagide*, we have, in the recent memoir of Forbes and the earlier contribution of Gervais, a very good account of the cerebral hemisphere of *Myrmecophaga*, although the base of the hemisphere and the rest of the brain receive very scanty treatment.

Practically nothing beyond the brief and imperfect notes and unsatisfactory figures of Pouchet has hitherto been made known of the brain of *Tamandua*.

For our knowledge of *Cycloturus* we are indebted mainly to Pouchet and the early memoir of Tiedemann.

The knowledge of the brain in the Sloths is even more unsatisfactory, as no minute description has yet been given of the brain in either *Bradypus* or *Choloepus*.

Gervais' beautiful figures of cranial casts in these two orders have made us familiar with the exact shape and size of the brain, and the series of figures of Pouchet and the more recent contribution of Turner have given us a much fuller view of the brain in this order than the earlier works of Tiedemann and Rapp conveyed. But even now our knowledge of the brain in this family is very deficient, and I am able to supply the required information only very imperfectly.

I have endeavoured to supplement and discuss as a whole the data concerning the Armadillos, for which we are mainly indebted to the memoirs of Turner, Pouchet, and Garrod, and which relate to all the genera except *Priodon*, our only knowledge of which is derived from the figure of a cranial cast, which Gervais has contributed.

The interesting brain of *Chlamdyophorus*, concerning which Hyrtl published a few notes, which were supplemented by a fuller description by Pouchet, has been carefully studied in a series of sections stained with carmine. This has enabled me to give

a much fuller and more accurate account of this peculiar brain than Pouchet has provided.

Max Weber has recently contributed an admirably illustrated account of the brain in *Manis*, which is a most valuable supplement to Pouchet's imperfect work. I have been able to add slightly to Weber's account, and upon comparative grounds have interpreted certain features in a somewhat different manner.

#### THE VENTRAL SURFACE OF THE CEREBRUM.

The most convenient landmark with which to begin the description of a brain for the purposes of accurate comparison is probably the optic chiasma. The optic nerve, taking its origin from the eye lying in the orbit, enters the cranium and extends toward the base of the brain at the situation where the brain-stem joins the cerebral hemispheres. In *Orycteropus*\* this point is situated about midway between the cephalic and caudal extremities of the brain, or, to be exact, 52 mm. behind the apex of the hemisphere (which is formed by the olfactory bulb), and 56 mm. in front of the place where the medulla oblongata merges into the spinal cord. (These measurements, as all the figures given in this memoir, refer to material which had been kept in alcohol for prolonged periods.) The optic nerves enter into relationship with the base of the brain at this mid-point, and effect an intercrossing of fibres, the *optic chiasma*, from each side of which a rounded bundle of fibres, the *optic tract*, arches laterally, and with a slight inclination backward, to disappear (at a distance of 6.5 mm. from the mesial plane) under an overlapping fold of cerebral cortex, which we shall subsequently recognize as part of the *pyriform lobe*.

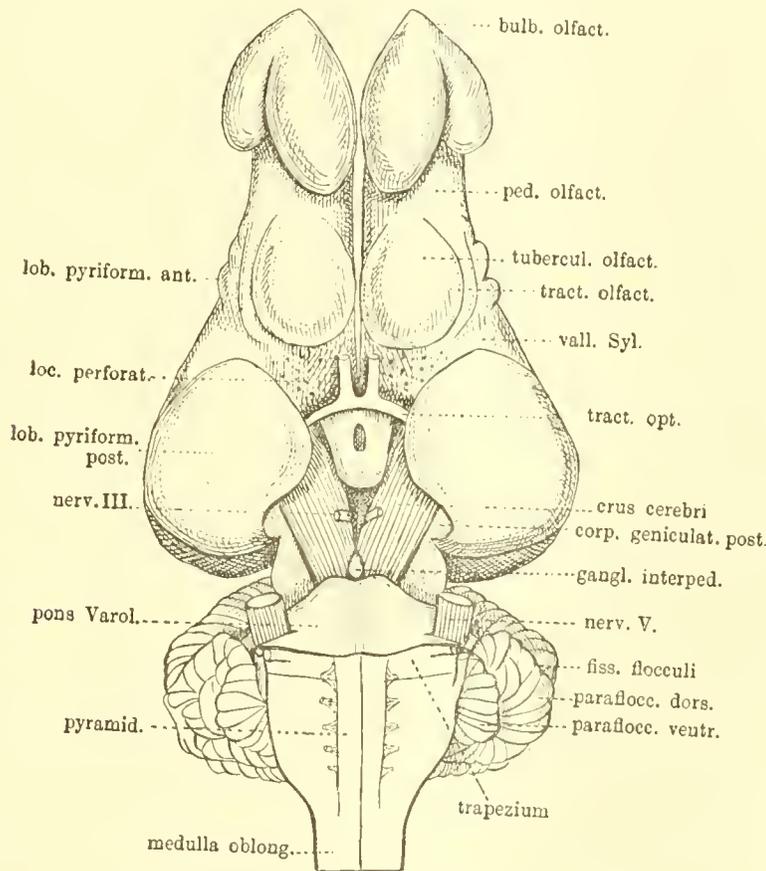
For convenience of description we may regard the areas in front of the optic chiasma as part of the cerebral hemisphere, and the parts behind it as the brain-stem.

Immediately in front of the optic chiasma, on each side of the mesial plane, we find a flat depressed quadrilateral area of about 8 mm. diameter. This is called by different writers a variety of names, of which *locus perforatus (anticus)* is as convenient as any. As I shall not refer to any other *perforated space*, I may omit the qualifying adjective. In front of the perforated space we find a large oval area of grey substance, which is slightly raised above the surrounding regions. This is the *tuberculum olfactorium*. Its major axis, which is sagittal, measures 18 mm., and its maximum breadth 13 mm. It is not confined to the ventral surface, but also extends on to the mesial surface of the hemisphere, and there presents a fusiform outline below the *precommissural area*. The lateral border of the *tuberculum olfactorium* is clearly defined by a furrow in which a very compact strand of nerve-fibres, which constitutes the *olfactory tract*, is found. In a fresh brain the pure white colour of the latter would present a marked contrast to the brownish-grey colour of the olfactory tubercle. The *tractus olfactorius* is situated upon the surface of a cortical area, which we shall call the anterior part of the *pyriform lobe*. This part of the pyriform lobe is visible along the lateral

\* As practically nothing is known of the brain of *Orycteropus*, I describe it in some detail and point out the features in other forms by contrast.

margin of the olfactory tract as a narrow band of grey substance with an irregular tuberculated margin. The pyriform lobe, the anterior part of which is formed by this tuberculated worm-like process, will be found to expand posteriorly and form a large rounded prominence, which is often known as the *natiform eminence*. This expanded portion of the pyriform lobe we may distinguish as the *lobus pyriformis posticus*, to distinguish it from the *lobus pyriformis anticus*, which is merely the tapering cephalic extremity of the same histological formation. These two parts of the pyriform lobe are separated the one from the other by a depression, the *vallecula Sylvii*, which extends obliquely in a mesial direction toward the perforated space.

Fig. 1.

Ventral surface of brain of *Orycteropus*. Nat. size.

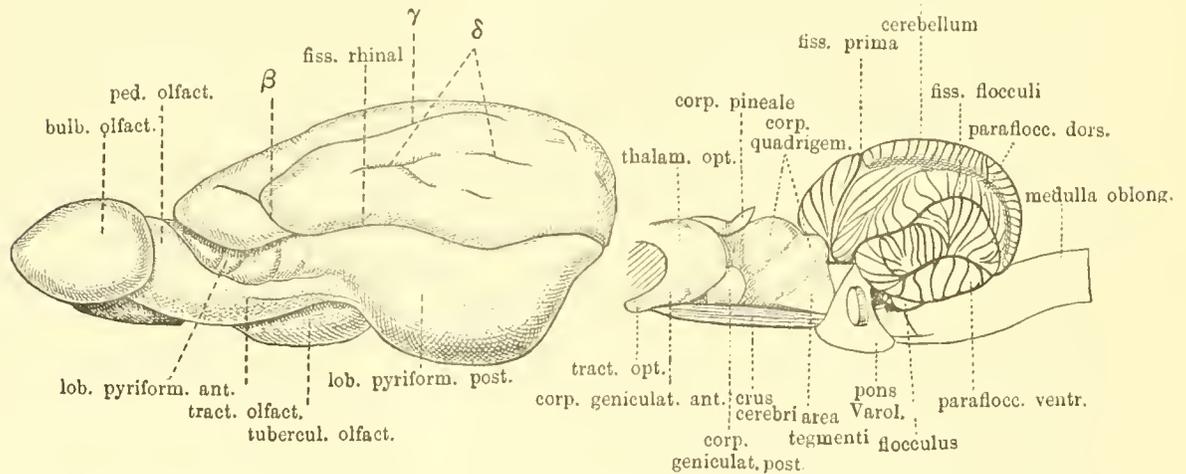
The terms "*lobus pyriformis*" and "*tractus olfactorius*" have been applied in a sense slightly different from that which the majority of writers attach to them. This attempt at a greater precision in description needs some slight explanation. It is customary to restrict the term "*lobus pyriformis*" to that expanded posterior area of the lobe (as we understand it) which is situated behind the *vallecula Sylvii*, and for which the terms "*natiform eminence*," "*hippocampal lobule*," and many other variants of these terms are regarded as alternative names.

The anterior tapering part of the same histological formation, which we have already

included in the pyriform lobe (*lobus pyriformis anticus*), is generally referred to as the "*tractus olfactorius*." This confusion may be avoided if we restrict the term olfactory tract to its literal meaning as the group of nerve-fibres lying on the surface of a cortical area, which is the cephalic extension of the pyriform lobe. [To be strictly accurate we should say that the *lobus pyriformis posticus* is the greatly expanded caudal extension of the *lobus pyriformis anticus*, but as the name "*pyriformis*" is usually associated exclusively with the former, I have spoken of extending it (the name) to the latter.] I have deliberately avoided the use of the term "hippocampal lobule," or any of the many variants of this term, because such expressions introduce a most undesirable confusion with the true "hippocampus," a structure quite distinct from the pyriform lobe, but one which in literature is frequently mistaken for it as a result of the confusing nomenclature in common use. This is an interesting example of the widespread misconception to which such loose nomenclature can lead in comparative anatomy: for the student of the literature relating to the fore-brain in Reptilia and Dipnoi (more especially Burckhardt on *Protopterus*) has had but too clear a demonstration of the utterly chaotic state of the morphology of the fore-brain which the confusion of pyriform lobe with hippocampus can produce. If we consider the base of the hemisphere as a whole, it will be found to present a pyriform shape. It is broadest at its posterior extremity, and contracts gradually as it extends forward, so that it passes insensibly into the large rounded stalk of the huge olfactory bulb which caps the anterior extremity of the hemisphere.

The *bulbus olfactorius* is a large conical cap of grey substance of about the size and shape of a filbert nut. The contour of the ventral surface is not unlike the conventional heart-shape, with the apex pointing forward. This surface is indented by a deep

Fig. 2.

Left lateral surface of brain of *Oryzopsis*. Nat. size.

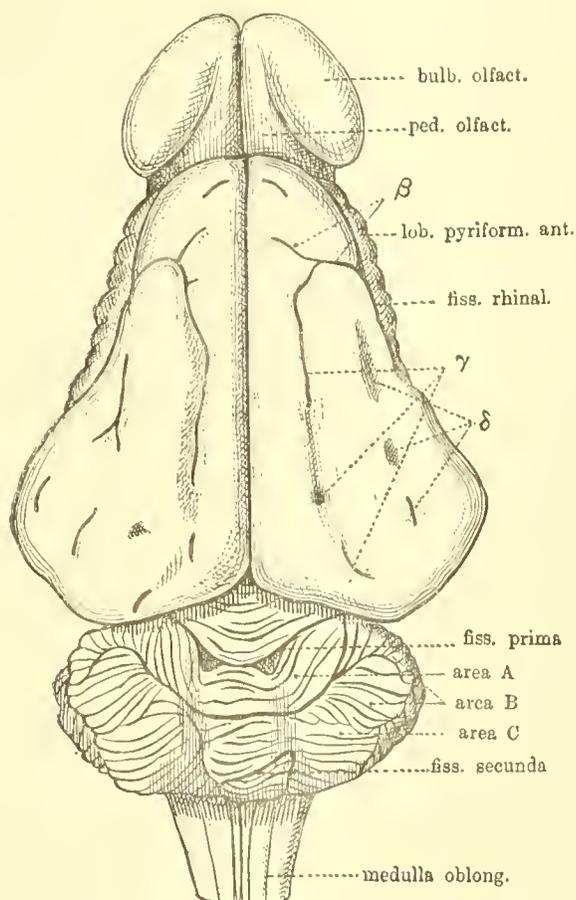
The cerebral hemisphere has been separated from the rest, by cutting the junction of the optic thalamus and corpus striatum so as to expose the lateral aspect of the thalamic and mid-brain.

sagittal fissure which is placed nearer the lateral than the mesial border. This fissure indents the whole thickness of the wall of the olfactory bulb, so that when we examine

the large cavity or ventricle of the bulb we find a very prominent longitudinal ridge in the floor, which is the result of this indentation (fig. 19).

The olfactory bulb is connected with the rest of the hemisphere by a large rounded peduncle, which is visible upon the base of the brain in the interval between the *tuberculum olfactorium* and the *bulbus olfactorius*. Even in a view of the dorsal aspect of the brain the peduncle is visible, because the apex of the cerebral cortex does not overlap it to so great an extent as in most mammals. On the lateral aspect of the hemisphere the massive olfactory peduncle extends backward and becomes directly continuous with the cephalic extremity of the pyriform lobe. The medullary covering which whitens the surface of the peduncle converges to form the compact olfactory tract, and immediately above this we find the vermiform anterior pyriform lobe. The narrow

Fig. 3.

Dorsal surface of brain of *Orycteropus*. Nat. size.

Based on a pencil sketch by the late Rt. Hon. T. H. Huxley.

band of grey substance which constitutes this part of the pyriform lobe is deeply constricted in many places, so that it appears to consist of a series of round knobs. These knobs are so prominent that they produce correspondingly deep depressions on the cranial wall, and hence we can readily recognize them in cranial casts. A beautiful

demonstration of this is given by Pouchet's figure of a cranial cast of *Orycteropus*\*. In a dorsal view of the actual brain the tuberculated *lobus pyriformis anticus* is very distinctly seen at the lateral border of the anterior part of the cerebral hemisphere (fig. 3).

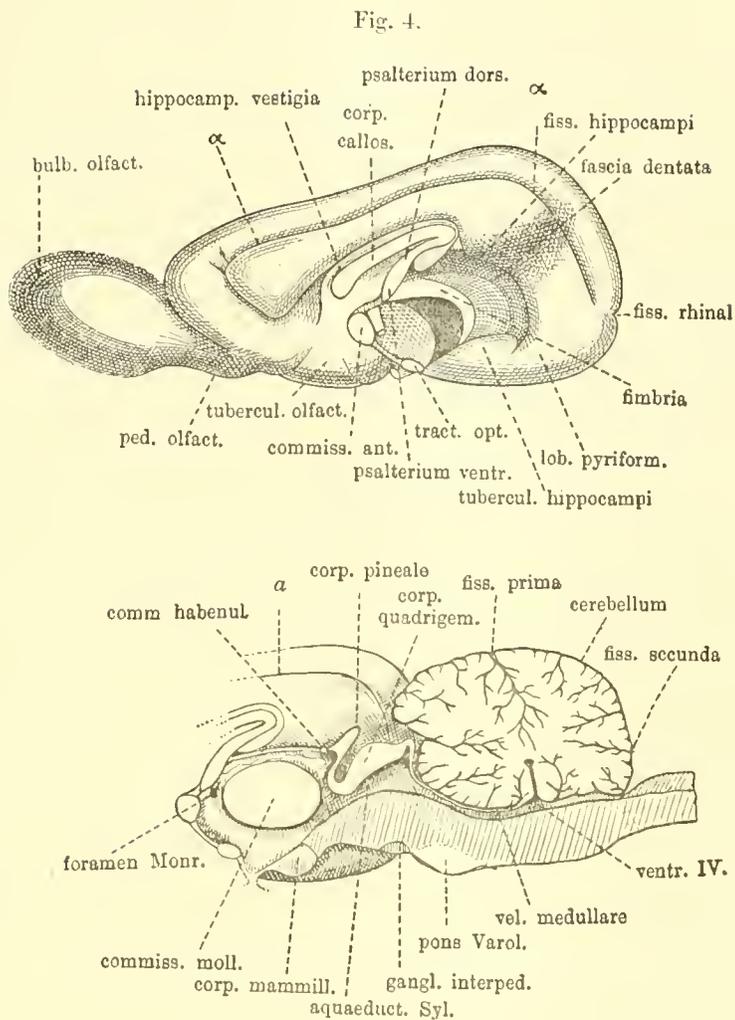
In the specimen of *Orycteropus* which we have so far been considering, the upper boundary of the pyriform lobe is very definitely indicated in its whole extent by a deep and clearly-cut rhinal fissure, which begins anteriorly in the cleft between the apex of the hemisphere and the olfactory peduncle, and proceeds backward in a direction which is practically horizontal (fig. 2). The posterior half of the fissure describes a very slight arc whose convexity is directed ventrally. Upon being traced backward the rhinal fissure extends on to the caudal surface of the hemisphere and proceeds transversely inward, as we may observe in a view of the ventral surface of the brain (fig. 1). The fissure ultimately reaches the mesial surface of the hemisphere and then ceases abruptly (fig. 4). In the whole of its course the fissure lies about midway between the upper and lower surfaces of the hemisphere.

The term *fissura rhinalis* may be most conveniently employed to designate the whole of this extensive fissure, as I have applied it in the above description, and not only to the anterior part as Krueg uses it †. The anterior part of the fissure, which forms the upper boundary of the *lobus pyriformis anticus*, may be distinguished as the *fissura rhinalis anterior*, and for the posterior part of the fissure we may adopt Krueg's name "*fissura rhinalis posterior*." The term "rhinal fissure" may be used to apply to the combination of these two fissures. The deep cleft between the olfactory peduncle and the apex of the hemisphere is sometimes regarded as part of the rhinal fissure. If we admit this, the rhinal fissure begins and ends on the mesial surface of the hemisphere in *Orycteropus* (fig. 4).

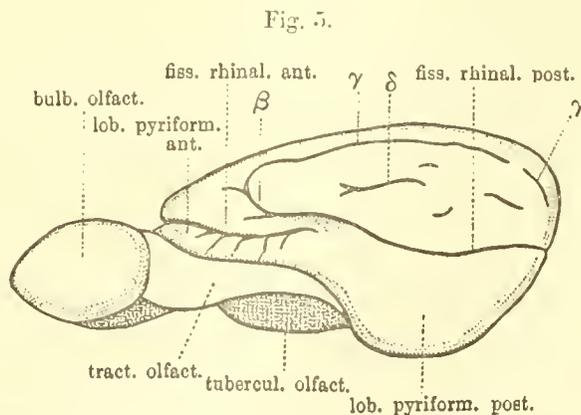
In the brain which I have hitherto been describing, the features of the extensive undivided rhinal fissure were clearly defined in its whole extent, and presented an exactly similar appearance in both hemispheres. But both of the brains in the Museum of the Royal College of Surgeons present a peculiarity in the disposition of the rhinal fissure, in which, while they agree the one with the other in both hemispheres, both differ from the type specimen which we have been so far considering. This peculiarity consists of a separation of the anterior from the posterior rhinal fissure. The anterior rhinal fissure begins anteriorly in the ordinary manner, and forms the upper boundary of the anterior pyriform lobe in the whole of its extent, but then ceases without joining the posterior rhinal fissure. The posterior rhinal fissure extends forward above the anterior rhinal and pursues a course for some distance parallel to the anterior fissure. Thus the cortex of the pyriform lobe is connected to the cortical area lying above the rhinal fissure, now generally known as *pallium*, by a narrow process of cortex lying between the overlapping extremities of the two parts of the rhinal fissure. This condition has been somewhat schematically represented in fig. 5.

\* G. Pouchet, *op. cit.*, 'Journal de l'Anatomie,' &c. tom. vi. pt. v. fig. 3.

† Julius Krueg, "Ueber die Furchen auf der Grosshirnrinde der zonoplacentalen Säugethiere," *Zeitschr. f. wissensch. Zoologie*, Bd. xxxiii. 1880, p. 610.



Mesial surface of the brain of *Orycteropus*, exposed by mesial sagittal section. Nat. size.  
The hemisphere above separated from the rest of the brain, and below in part attached to the brain-stem.

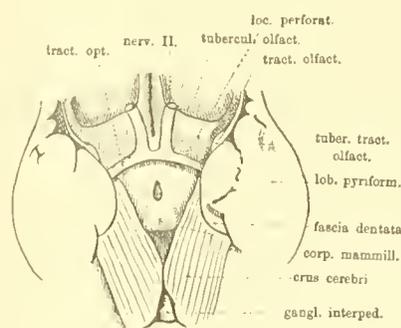


Scheme of the lateral aspect of the cerebral hemisphere of *Orycteropus*, to show a variation in the arrangement of its fissures.

The rhinal fissure thus forms a very clear boundary in the whole extent of the lateral and caudal extremities of the hemisphere between the pyriform lobe and the histologically and morphologically distinct area of pallium. But upon the mesial surface of the hemisphere (fig. 4) the upper margin of the pyriform lobe blends with the pallium without any clear external indication of the line of junction. In this part of the hemisphere the pyriform lobe extends around the postero-inferior angle, and is partly limited in front by the lower part of an arcuate cleft—the *fissura hippocampi*. But below the hippocampal fissure the pyriform lobe seems to be continuous with a peculiar oval body, which, for reasons to be subsequently explained, will be distinguished as the “*tuberculum hippocampi*” or “hippocampal tubercle.” The height to which the *lobus pyriformis* extends upon the mesial surface is indicated by the indentation upon the posterior margin of the hemisphere, which is the termination of the rhinal fissure (fig. 4).

If we compare these basal regions of the cerebral hemisphere of *Orycteropus* with those of the Great Ant-eater, *Myrmecophaga jubata*, which in size and general mode of life presents some resemblance to the African representative (*Orycteropus*), we find a general agreement between the two forms, but at the same time a number of interesting points of difference. Although the figures and descriptions of Forbes\* have added much in clearness and exactness to the earlier observations of Gervais †, we still lack a faithful representation of these basal regions of the hemisphere of *Myrmecophaga*. The *bulbus olfactorius* is relatively almost as large as that of *Orycteropus*, but it is not so pointed, nor is it indented by any fissure such as we have seen in the latter. It is also attached to the hemisphere by a large rounded peduncle, whose relations are analogous in the two forms. The *tuberculum olfactorium* is not so elongated as it is in the Aard-vark (*Orycteropus*), and presents a somewhat quadrilateral form. The *tractus olfactorius* presents the same general features, but in *Myrmecophaga* ends in a prominent elliptical nodule, which is situated in the *vallecula Sylvii* immediately in front of the *eminentia natiformis* and at the lateral margin of the *locus perforatus* (fig. 6). This

Fig. 6.

Part of the ventral surface of the brain of *Myrmecophaga jubata*. Slightly reduced.

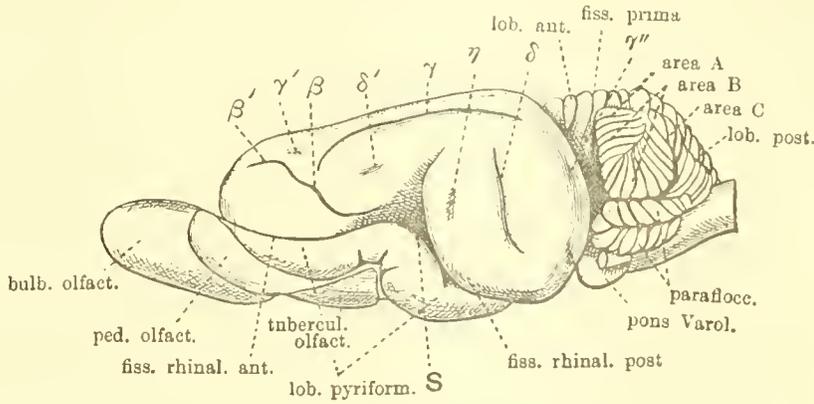
little nodule, which has been indicated in the figures by the name *tuberculum tractus olfactorii*, has been described in the Hedgehog (*Erinaceus*) by Ganser ‡, and is found in

\* *Op. cit.* Proc. Zool. Soc. London, 1882.† *Op. cit.*, Nouvelles Archives, t. v.

‡ S. Ganser, "Ueber das Gehirn des Maulwurfs," Morphologisches Jahrbuch, Bd. vii, 1882.

a well-developed form in *Tamandua* (fig. 9), the *Dasypodidæ* and *Bradypodidæ*, and possibly in other representatives of the Edentata. A very well-defined *fissura rhinalis* is present to indicate the upper boundary of the pyriform lobe, but it differs very distinctly from that of *Orycteropus* in that the posterior rhinal fissure joins the anterior rhinal, with which it is continuous, at an angle (fig. 7), while the anterior rhinal fissure

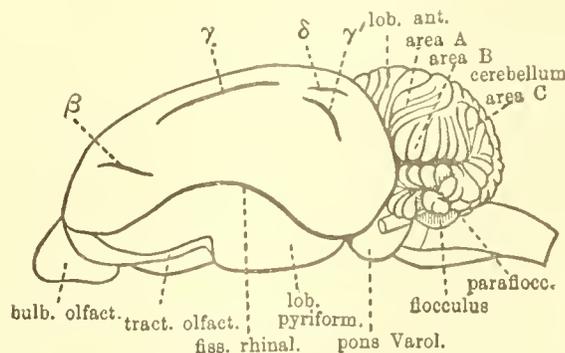
Fig. 7.



Lateral aspect of a brain of *Myrmecophaga jubata*. Very slightly reduced.  
S, Fossa Sylvii.

is still horizontal; the posterior rhinal inclines obliquely downward and backward, so that it reaches the ventral margin at a point about midway between the *vallecula Sylvii* and the posterior extremity of the hemisphere; it then curves inward upon the inferior surface, and ultimately ends upon the postero-inferior part of the mesial surface at a point just behind the lower part of the hippocampal fissure. This mode of termination of the rhinal fissure in *Myrmecophaga* has been well figured by Forbes\*, and presents a close analogy to the disposition which is represented in *Tamandua* in this memoir (fig. 10). The rhinal fissure in *Tamandua* (fig. 8) presents a less acute bend than is the

Fig. 8.



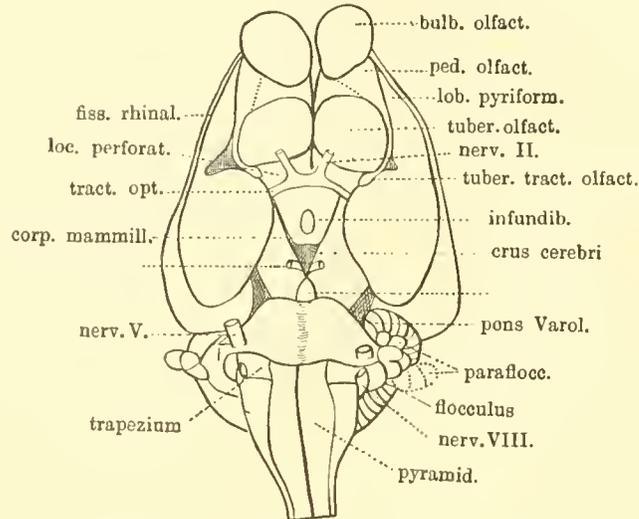
Lateral surface of brain of *Tamandua tetradactyla*. Nat. size.

case in the larger Ant-eater, and as a result it approaches much nearer the posterior margin of the hemisphere, but otherwise its disposition closely agrees with that of

\* *Op. cit.* Proc. Zool. Soc. London, 1882, fig. 4.

*Myrmecophaga*. In both representatives of the *Myrmecophagidæ* the rhinal fissure is nearer the base of the brain than it is in *Orycteropus*, so that in a view of the ventral surface practically the whole of the fissure is visible (fig. 9).

Fig. 9.

Ventral surface of brain of *Tamandua*. Nat. size.

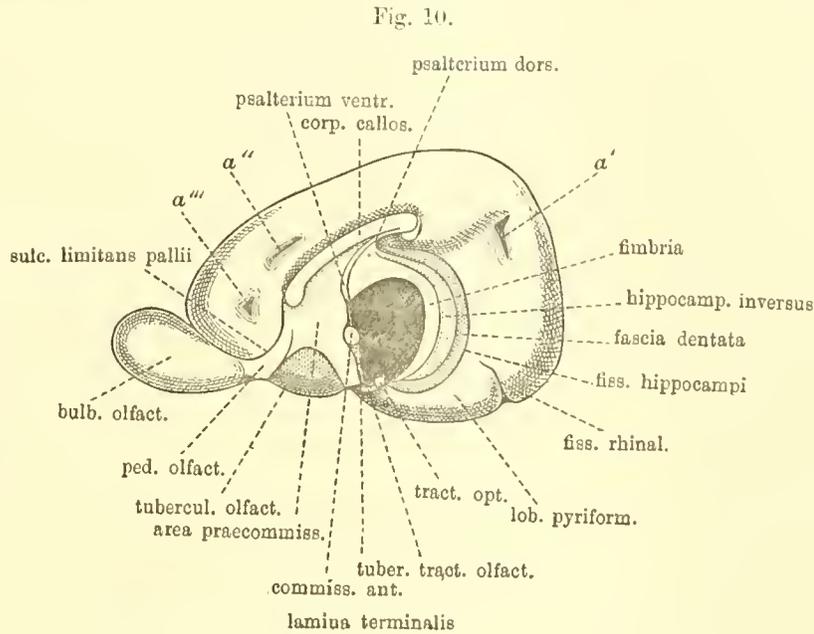
It follows from the above remarks that the shape of the pyriform lobe is very different in the American Ant-eaters, and especially the Great Ant-eater, from that which we have found in the African Aard-vark. Thus in *Myrmecophaga*, and to a less degree in *Tamandua*, there is a very distinct flexure in the pyriform lobe which is wanting in *Orycteropus*. The pyriform lobe is besides relatively smaller in the American forms. In these brains also the anterior limit of the pyriform lobe upon the mesial surface of the brain is more distinct, because the peculiar hippocampal tubercle which we found in *Orycteropus* is lacking in the *Myrmecophagidæ*, and the hippocampal fissure, as a consequence, extends much lower (fig. 10). As a result of the flexure of the pyriform lobe in *Myrmecophaga*, the *vallecula Sylvii* is deepened and a number of deep clefts or puckerings indent the surface of the pyriform lobe in this region. They are probably mere mechanical results of the bending (fig. 7).

In *Tamandua* the *tuberculum olfactorium* presents the same quadrilateral shape which we noted in *Myrmecophaga*. The olfactory bulb is relatively smaller than it is in the larger brains, and its peduncle is not so prominent because its dorsal surface is completely hidden by the anterior pole of the hemisphere.

My knowledge of the conformation of the brain in the small arboreal Ant-eater *Cycloturus* has, in the absence of any material, been derived mainly from the imperfect notes and illustrations which Pouchet (*op. cit.*) has contributed, and the even less complete observations of Tiedemann (*op. cit.*) and Gervais (*op. cit.*). It is not clear from Pouchet's work whether any rhinal fissure is present in the small arboreal Ant-eater. He says in the text that the brain of *Cycloturus* (which he calls *Dionyx*) is smooth, and he does not represent a rhinal fissure in his figure. But since he does not represent

the clearly defined rhinal fissure in *Tamandua*, the non-delineation of a corresponding fissure in his figure of *Cycloturus* cannot be regarded as any indication of its absence.

The illustrations which the earlier observers (Tiedemann, Lenret, and Rapp) have given of the brain in the Sloths convey practically no information concerning those regions of the brain which we have just been considering in the Aard-vark and Ant-eaters, and the figures which Pouchet (*op. cit.*) has given of the *Bradypodidae* do not represent even a feature so fundamental as the rhinal fissure. Professor Turner's representation\* of the brain of *Cholæpus Hoffmanni*, so far as I am aware, is the only figure which represents this feature



Mesial surface of right central hemisphere of *Tamandua*. Enlarged  $\frac{3}{2}$  diam.

in the brain of the Sloths. Of the two brains of *Bradypus tridactylus* at my disposal, one had almost reached the adult state, whereas the other was much younger, since it was taken from an animal measuring only 34 cm. from the nose to the anus. In the former the anterior rhinal fissure begins in the ordinary manner and extends obliquely upward and backward, and when it reaches a point midway between the anterior and posterior poles of the hemisphere it joins the posterior rhinal fissure almost at a right angle (fig. 11).

The posterior rhinal fissure forms an arc, the posterior extremity of which crosses the posterior border of the hemisphere at about the same horizontal level as the cephalic extremity of the anterior rhinal fissure.

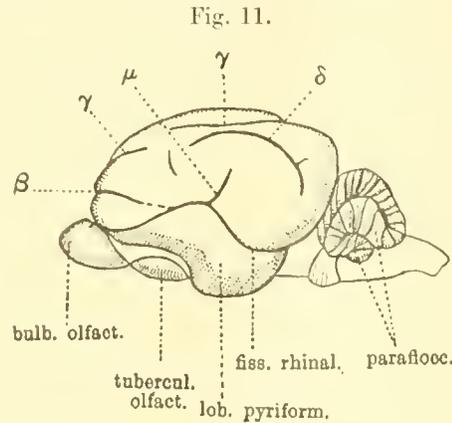
In the younger brain the two parts of the rhinal fissure approximate much more closely to the horizontal, so that their angle of junction is very obtuse. The posterior rhinal fissure is represented merely by a very shallow furrow.

In *Cholæpus didactylus* and, judging from Turner's figure (*op. cit.*), also *Cholæpus Hoffmanni*, the angle of meeting of the two parts of the rhinal fissure is quite as obtuse

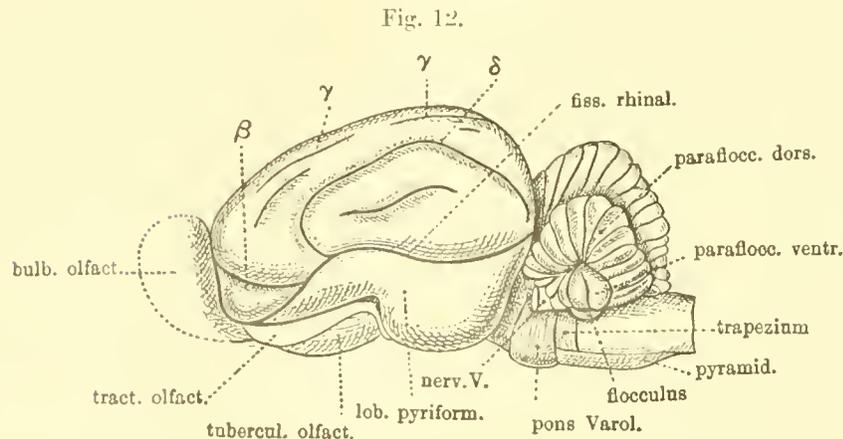
\* W. Turner, *op. cit.*, Journal of Anatomy and Physiology, vol. xxv.

as it is in the younger *Bradypus*. The anterior rhinal fissure is very oblique, but the posterior rhinal fissure is almost horizontal (fig. 12).

The conformation of the base of the brain in the *Bradypodidae* is so like that of *Tamandua* that it is unnecessary to give special illustrations, nor is it requisite to describe these features in detail. The general shape of the base of the brain in *Bradypus* is very



Lateral surface of brain of *Bradypus didactylus*. Nat. size.



Lateral surface of brain of *Choloepus didactylus*. Slightly enlarged.

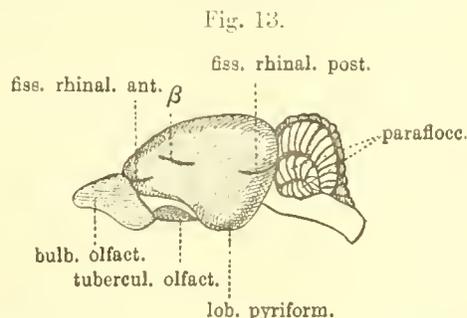
much like that of *Tamandua* (fig. 9), but in the former more of the pallium is visible along the lateral margin of the anterior part of the pyriform than is the case in the Ant-eater. This means that the proportion of pyriform lobe to pallium is less in the Sloth than in the partially arboreal Ant-eater. In *Choloepus* the base of the brain appears to be relatively broader than it is in *Bradypus*, but otherwise it presents a close resemblance.

In none of the Armadillos (with the possible exception of *Priodon*) do we find a complete rhinal fissure. Nothing is known of the brain of *Priodon*, except such information as we can gather from the examination of cranial casts, such as Gervais has represented (*op. cit.* pl. ii. fig. 12). But it is quite possible and even probable that in such a large brain a complete rhinal fissure will be found, because we find among mammals that an increase in bodily dimensions is accompanied by an increased extent

of pallium: in other words, an increasing disproportion between the sizes of the pallium and the pyriform lobe. It is such inequalities in the rate of growth of these fundamentally distinct cortical areas that give rise in all probability to the rhinal fissure.

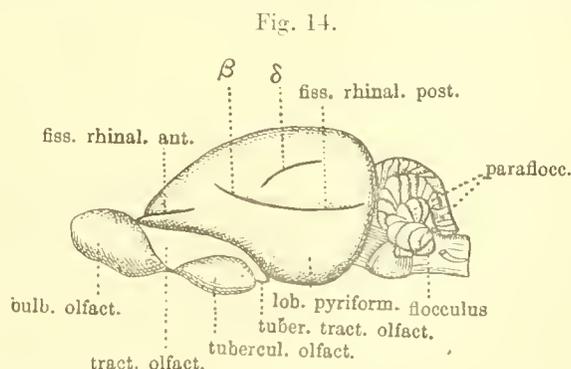
In *Chlamydophorus* there is no rhinal fissure whatever, but in all the other Dasypodidæ there are small anterior and generally also posterior rhinal fissures, which are separated by a varying interval in different genera.

In *Tatusia noremeincta*, two specimens of which I have had the opportunity of examining, we see the arrangement of these fissures in a typical manner. A short anterior rhinal fissure begins in the cleft between the olfactory bulb and the apex of the pallium, and extends horizontally backward for less than a third of the length of the hemisphere. A posterior rhinal fissure, which is very shallow, extends from just below the middle of the posterior border of the hemisphere and passes forward for less than a third of the length of the hemisphere. In the figure which Pouchet gives of a young *Tatusia* (*op. cit.* pl. vi. fig. 1), these fissures are only indicated very faintly. As both of the specimens which I examined were distorted, I have modified this figure of Pouchet so as to indicate the features present in my specimens (fig. 13).



Scheme of lateral surface of brain of *Tatusia pba.*

In the pallium, just above the wide gap between the anterior and the posterior rhinal fissures, we find a short oblique fissure which may be distinguished as  $\beta$ .



Lateral surface of brain of *Dasypus sexcinctus.* Nat. size.

In *Dasypus sexcinctus* (fig. 14) and *Dasypus villosus* we find practically the same arrangement of the rhinal fissures, with the difference that the more extensive posterior rhinal fissure enters into uninterrupted continuity with the pallial fissure  $\beta$ .

In the figures which Turner (*op. cit.*), Gervais (*op. cit.*), and Pouchet (*op. cit.*) give of the brain of *Dasypus* we find the same arrangement as I have just described in my specimens.

In *Tolypeutes* and *Xenurus* we find essentially the same arrangement, but the caudal extremity of the posterior rhinal fissure may fail in both these forms. Garrod (*op. cit.* Proc. Zool. Soc. London, 1878) gives figures of the brain in both of these Armadillos.

In all of the Armadillos the olfactory bulb and all the parts of the brain which are intimately associated with it reach relatively enormous dimensions. Visual acuteness is a matter of subsidiary importance to animals which burrow in the ground for their means of subsistence, and hence the importance of a sense like that of smell, which enables these animals to detect objects which they cannot see, becomes considerably enhanced. Thus the macrosmatism which characterizes all mammals, except those whose pallium has become sufficiently specialized to be something more than a mere sensorium, becomes very much exaggerated in these burrowers, who are guided in most of their pursuits mainly by olfactory impressions.

The large olfactory bulb varies considerably in shape in the different genera of this family. As the soft bulb is more liable to distortion than any other part of the brain, it is safer to rely upon the evidence of cranial casts than upon the examination of actual specimens when these have not been seen in the fresh state. Gervais has fortunately provided us with a complete series of cranial casts of the Dasypodidæ (*op. cit.* pl. ii.).

From the shape of the cranial casts, as well as from all the figures of Gervais, Pouchet, Turner, and Garrod, and from my own observations, it is evident that the large olfactory bulbs of both species of *Dasypus* and also of *Tolypeutes* assume a conical shape such as I have already had occasion to note in the Ant-eaters, Sloths, and Aard-varks. This form of bulb is also found in the extinct Ground-Sloths *Mytodon*, *Scelidothorium*, and probably also in *Megatherium*. It is equally found in the great extinct Armadillos *Glyptodon* (in which the olfactory bulb assumes enormous proportions), and probably *Eutatus*. In *Xenurus* and *Tatusia* the projection of the olfactory bulbs is still a feature of the brain, but it is not so developed as it is in *Dasypus*. There is a certain amount of antero-posterior flattening of the lower part of the bulb in these forms. In *Chlamydochorus* there is a very distinct antero-posterior flattening of the bulb, just as there is in the larger brain of the Pangolin (*Manis*). But the shape of the olfactory bulb is a matter of slight importance.

We can better appreciate the high degree of macrosmatism of the Armadillos if we compare their brains with that of the little arboreal Ant-eater *Cycloturus*, the shape and size of which is admirably shown by the figures of Tiedemann, Pouchet, and Gervais. When *Cycloturus* relinquishes a terrestrial life, such as its near relative *Myrmecophaga* leads, the olfactory sense diminishes in importance, and hence we have a reduction in the size of the olfactory bulbs and the rest of the apparatus pertaining to the function of smell.

In the brain of the Armadillos the predominance of the sense of smell manifests itself in other ways in addition to its direct effect upon the olfactory bulb. The *tuberculum olfactorium* is uniformly very large and of relatively greater prominence than it is in the



(*op. cit.*) have already called attention as resulting from the upward projection of the bony semicircular canals in the petriotic bone. Pouchet has already given a figure of the ventral surface of the brain, which indicates the situation of this depression.

The imperfect descriptions of the brain of *Manis* which Pouchet (*op. cit.*) and Gervais (*op. cit.*) had given have recently been supplemented by the concise and well-illustrated description by Max Weber (*op. cit.*). I have been able to confirm the accuracy of his brief description by the examination of two specimens of this genus. The basal regions of the hemisphere present in a typical manner the characteristic features which we have met in all the other forms. The base of the brain is very broad. The large olfactory bulb forms a thick buffer-like pad upon the flattened cephalic extremity of the hemisphere. The large *tuberculum olfactorium* presents an almost circular outline. The posterior part of the pyriform lobe is most markedly dependent, and descends to a much lower level than the rest of the hemisphere. This feature is much more pronounced than it is in any other individual in this heterogeneous group of mammals, and is probably a result of the obvious restriction to the expansion of the brain in the longitudinal direction.

The rhinal fissure is interrupted in a manner which suggests an analogy to the arrangement in the Armadillos. There is a very short horizontal anterior rhinal fissure, which is quite independent of the posterior rhinal fissure. The latter begins at the posterior margin of the hemisphere and arches forward, but just before reaching the anterior rhinal fissure it extends upward into continuity with a pallial fissure, in a manner not unlike the posterior rhinal fissure in *Dasypus*.

The fundamental features of the regions of the base of the brain which we have just been considering vary within relatively narrow limits in the Mammalia, although both Monotremes exhibit features in common which readily distinguish them from all other mammals. Such variations as we have found among the different representatives of this order are characteristic of the changes which the basal region of the hemisphere undergoes in the wider range of the Mammalia generally, and are in the main associated with the habits of life rather than with the systemic position of the individuals. For we find among other mammalian orders, more especially the Marsupialia, Insectivora, Rodentia, Carnivora, and Ungulata, parallel modifications which indicate the more or less direct causal relationship to the mode of life. All the areas which we have been considering are intimately associated with the olfactory apparatus, and, whatever other functions they may subserve, there can be no question that their predominant rôle is to constitute a receptive area for incoming impulses of smell. The importance of the sense of smell varies considerably in the different members of this order, although in all it reaches a very high degree of acuteness, as the great development of the olfactory bulb and its associated cortical areas demonstrates. But in this macrosomatism the Edentata are like all other lowly-organized mammals, in which the sense of smell has a larger function than in higher mammals, in which an intelligence dispenses with the necessity of any such predominant and guiding sense as the impressions of smell convey.

In Edentates like *Orycteropus* and the *Dasypodidae*, which spend their lives mainly in digging and burrowing in the ground for objects as to the position of which the sense of

smell is the main determinant, it is not surprising to find that the olfactory areas of the brain reach a relatively larger development than in the arboreal *Bradypodidae* and *Cycloturus*, in which the smell-sense is not of such vital importance. And in such a form as *Chlamydophorus*, which lives mainly underground and depends to a very slight degree upon its feeble visual organs, it is natural that the importance of the olfactory apparatus should be still further enhanced, as finds expression in a relatively enormous olfactory bulb and *tuberculum olfactorium*, and a pyriform lobe which includes more than half the lateral surface of the cerebral hemisphere.

In a short memoir upon the basal regions of the hemisphere, Gustav Retzius last year called attention to certain features of the pyriform lobe and the adjoining areas in some Edentates, among other mammals\*. He makes special mention of the little "tubercle of the external olfactory tract" in Marsupials and Edentates. He dignifies this little body with the name *gyrus intermedius rhinencephali* (p. 107), but although he carefully describes its situation, he does not give us any information concerning its structure.

It will prove a source of considerable confusion if the term "gyrus" is applied to such structures as this, involving as it does a considerable distortion of the generally accepted idea of the meaning of this term. Retzius goes on to state that in the same animals (*Didelphys*, *Macropus*, *Myrmecophaga*, *Dasyppus* among others) two or three sagittal "gyri" are found behind the "*gyrus intermedius*." He calls these the "*gyrus lunaris*" and "*gyrus ambiens (medialis and lateralis)*," in conformity with a nomenclature he had previously applied to the human brain †.

He further mentions that in the Insectivora (*Erinaceus*) there is a very large "*gyrus lunaris*" and a "*gyrus ambiens*."

Retzius does not make any mention of the fact that, in *Erinaceus* and many of the Edentates, the fascia dentata (as we shall explain subsequently) extends on to the base of the brain in the region of his "*gyrus lunaris*." Its relation to the latter structure is well shown in the figure of the base of the brain in *Myrmecophaga* (fig. 6).

#### THE CEREBRAL COMMISSURES.

In all vertebrates, series of nerve-fibres proceed from one cerebral hemisphere to the other, and serve to bring into functional association brain areas which are otherwise quite separate the one from the other. These fibres, whether they connect strictly homologous areas or constitute a symmetrical bond between heterologous parts of the two hemispheres, are generally known under the comprehensive title of "commissures."

In all except the lowliest vertebrates there are two compact and well-defined bundles of these crossing fibres forming ventral and dorsal commissures of the cerebral hemisphere. Within the class of mammals the constitution of these two commissures becomes rearranged in order to more readily accommodate the enormously increasing number of fibres which

\* Gustav Retzius, "Zur Kenntnis der Windungen der Riechhirns," Verhandl. Anat. Gesellsch. 1897, p. 105 *et seq.*

† Gustav Retzius, 'Das Menschenhirn,' 1896.

are proceeding from that essentially mammalian cortical area, the pallium. In all mammals except the Monotremata and Marsupialia (in which the pallial fibres cross the mesial plane in the ventral commissure) a large and increasing proportion of these pallial fibres invade the dorsal commissure and form the *corpus callosum*. When we remember that this structure has been acquired in its present form within the mammalian class, we naturally turn with great interest to the examination of the commissures in such an enigmatical order of mammals as the Edentata.

Pouchet says\* that the Edentates, considered as a whole, present a remarkable diminution in the size of the corpus callosum. He says that in a young *Choloepus*, which was 19 cm. long, the corpus callosum was 7.5 mm. long and 0.5 mm. thick. In the specimen of *Choloepus Hoffmanni* which Turner figures† the corpus callosum is represented as being 11 mm. long and 1 mm. thick in a hemisphere whose maximum length (without the olfactory bulb) is 36 mm.

In Flower's memoir there is an enlarged figure of the mesial surface of the brain of a *Choloepus didactylus*‡, but unfortunately the degree of magnification is not indicated. In a hemisphere 70 mm. long, he represents a corpus callosum 23 mm. long and 2.8 mm. thick. Judging from the average dimensions of the adult hemisphere of *Choloepus*, these measurements are probably about twice the actual size of the objects. In my specimen of *Choloepus didactylus* (which had been in alcohol for some years) the cerebral hemisphere is barely 35 mm. long, and the corpus callosum measures 10.75 mm. long and 1 mm. thick.

We may safely conclude that the corpus callosum in the adult Two-toed Sloth is about 11 mm. long and about 1 mm. thick. We cannot speak with the same degree of certainty of the measurements in *Bradypus*, because there is no information upon the subject in the past records, and my only specimen available for measurement is not fully grown. In the brain of *Bradypus tridactylus* which Professor Max Weber generously gave me, the cerebral hemisphere is 26 mm. long, and possesses a corpus callosum which is 6.75 mm. long, and 1 mm. thick. In the adult brain the cerebral hemisphere attains a length of about 32 mm. In this young Three-toed Sloth we have a corpus callosum which is much shorter, both absolutely and relatively (to the length of the hemisphere), than is the case in the Two-toed Sloth, but this shortness is compensated by a greater thickness, for in this small brain of *Bradypus* the corpus callosum has already attained to the same thickness which it reaches in the much larger brain of the adult *Choloepus*.

Pouchet §, after describing the corpus callosum in the Sloths, proceeds to describe that of the Ant-eaters. He says that in *Cyclothurus* and *Myrmecophaga* it presents similar features to that of the Sloths.

This is a very loose and utterly misleading statement, for, as we shall see subsequently, there is a very marked contrast between the features presented by the two families in this respect. He gives the measurements of the corpus callosum in *Myrmecophaga* as

\* *Op. cit.*, Journal de l'Anatomie et de la Physiol. tm. vi. p. 308 *et seq.*

† Turner, *op. cit.*, Journal of Anatomy and Physiology, vol. xxv. fig. 15.

‡ Flower, *op. cit.*, Phil. Trans. 1865, pl. xxxvii. fig. 5.

§ *Op. cit.* p. 308.

26 mm. in length and 2.5 mm. in thickness. The corpus callosum in the specimen which Forbes figures is about the same length, but not quite so thick. The cerebral hemisphere in *Myrmecophaga* is usually about 54 mm. long, so that the corpus callosum is almost half the length of the hemisphere.

In a specimen of *Tamandua*, whose hemisphere is 34 mm. long, the corpus callosum increases 14 mm. in length, and its narrowest part 1 mm. in thickness.

Pouchet \* represents the mesial surface of the cerebral hemisphere of a *Cycloturus*, the corpus callosum of which is very narrow and 6.5 mm. long, the hemisphere itself being 17 mm. long.

Thus we see that in the brains of the Myrmecophagidæ the corpus callosum is relatively shorter in proportion as the animal is smaller, the corpus callosum measuring respectively 48 per cent., 41 per cent., and 38 per cent. of the length of the hemisphere in the three genera.

In all the Armadillos the corpus callosum is very small. Pouchet describes the corpus callosum in a young *Dasyppus*, whose cerebral hemisphere is about 23 mm. long, as being 6 mm. long and 1 mm. thick. Turner represents † in *Dasyppus sevincetus* the cerebral hemisphere 30 mm. long, possessing a corpus callosum 6 mm. long and 1 mm. thick. In the brain of *Xeurus*, the cerebral hemisphere of which is 25 mm. long, we find a corpus callosum measuring 5 mm. in length and barely 1 mm. in thickness (in a specimen preserved in alcohol). In *Tolypeutes* the proportion is about the same. In a cerebral hemisphere of *Chlamydophorus*, 11.5 mm. in length, we find a diminutive corpus callosum of 2.25 mm. length and about .25 mm. thickness.

In all the Armadillos, in spite of the small dimensions of the cerebral hemisphere, the proportion between the lengths of the corpus callosum and the hemisphere is much smaller than it is in the Sloths, and, *a fortiori*, than in the Ant-eaters.

In his figures of the brains of a *Manis*, Max Weber represents ‡ a corpus callosum 6 mm. long and 1.5 mm. thick in a hemisphere whose maximum length is 24 mm. Pouchet represents § a corpus callosum 4.5 mm. long and 0.75 mm. thick in the brain of a young *Manis*, the hemisphere of which is 20 mm. long. In a cerebral hemisphere of the same length as Weber's specimen I have found a corpus callosum 6 mm. long, but barely 1 mm. thick. The disparity between these measurements of the thickness is probably explained by the fact that Max Weber has not figured the supracallosal vestige of the hippocampus, but represented it, together with the corpus callosum, as one structure.

In *Orycteropus* I have found that the corpus callosum measures 21 mm. in length and 2 mm. in thickness in a hemisphere whose maximum length is 60 mm.

Although the corpus callosum becomes reduced in some families, especially in the Armadillos, to very diminutive proportions, it is very misleading to state as a general rule that the corpus callosum is small in the Edentata. To appreciate the full significance

\* *Op. cit.*, pl. iv. fig. 4.

† *Op. cit.*, vol. xxv. fig. 13.

‡ Max Weber, *op. cit.*, tab. ix. fig. 69.

§ Pouchet, *op. cit.*, pl. iv. fig. 10.

of the evidence to be gained by a study of the cerebral commissures, it is of much greater importance to investigate their constitution and morphology than to judge them on a purely quantitative basis.

In separating the two cerebral hemispheres the one from the other by means of a mesial sagittal section, we cut through the large white masses of the cerebral commissures, which will be seen to consist of a small ovoid ventral commissure and a large elongated dorsal commissure of a peculiar shape. This dorsal commissure in *Oryzeteropus* is composed of two divaricated limbs, which meet and fuse posteriorly. The larger dorsal limb is the corpus callosum. Arching downward and backward from the ventral surface of the caudal extremity of the corpus callosum, there is to be found a peculiarly modified cortical area known as the *hippocampus*. The greater part of this peculiar structure is submerged below the general level of the cortex, and its position is indicated upon the surface by the hippocampal fissure. The cephalic margin of the hippocampus is fringed by a band of white fibres—which is known either as *fimbria* or *fornix*—and which is plainly visible upon the mesial surface of the hemisphere.

After these preliminary remarks we are in a position to appreciate the features of the cerebral commissures.

If we examine the mesial surface of the brain of *Oryzeteropus* which is exposed by a mesial sagittal section (fig. 1, p. 291), we find the *lamina terminalis* extending obliquely upward and forward from the optic chiasma to reach the ventral or anterior commissure, which consists of a large mass of transverse fibres presenting an oval outline in section and measuring 4·5 mm. by 3·5 mm. From the dorsal aspect of the ventral commissure the upper part of the *lamina terminalis* proceeds obliquely backward and upward to the inferior extremity of the ventral limb of the great bilaminar dorsal commissure. The ventral limb of this dorsal commissure consists of fibres which are proceeding from the hippocampus of one hemisphere through the fornix to the other hemisphere, and it is customary to call these crossing fibres of the fornix the *psalterium*\*, from a fancied resemblance in the arrangement of their homologues in man to a stringed instrument.

The *psalterium* in *Oryzeteropus* consists of a large ventral fusiform mass of fibres, which form the *psalterium ventrale*, and a slightly narrower upper part, the *psalterium dorsale*, placed immediately below the dorsal limb of the great commissure, which latter is best known by the designation *corpus callosum*. The *psalterium dorsale* joins the caudal extremity of the corpus callosum, which consists of a large rounded mass of fibres known as the *splenium*. The corpus callosum is a larger structure than the *psalterium*, and, unlike the latter, is of fairly uniform thickness, except at its cephalic and caudal extremities, which are thicker than the rest of the commissure. It is placed obliquely, and its posterior part is parallel to the *psalterium dorsale*; but as the *psalterium ventrale* bends downward toward the ventral or anterior commissure, a triangular interval is left between the psalterium and corpus callosum. This interval is filled by a mass of grey substance which will be subsequently described as the *corpus paracommissurale*, and which in part represents the *septum lucidum* of human anatomy.

\* *Psalterium*, = *lyra*, = *commissura fornicis*, = *commissura hippocampi*.

If we compare the commissures in *Orycteropus* with those of *Myrmecophaga*, we find that the ventral (anterior) commissure is approximately of the same size or even slightly smaller in *Myrmecophaga*, but the dorsal commissure presents a marked contrast. The *psalterium* is much longer and more markedly attenuated than it is in the African genus, while the corpus callosum is greater, more especially in length, and more nearly horizontal than is the case in *Orycteropus*.

The anterior commissure in a representative of the latter genus measures  $4.5 \times 3.5$  mm., and in a specimen of *Myrmecophaga*  $3.5 \times 3$  mm.; while the respective measurements of the psalterium are about  $12 \times 2$  mm. in *Orycteropus* and about  $17 \times$  less than 1 mm. in *Myrmecophaga*. The corpus callosum of the latter, measuring about 26 mm. long and with an average thickness of about 2 mm., greatly exceeds in size that of *Orycteropus*, which is only 21 mm. long, and about the same thickness as that of *Myrmecophaga*.

The condition of the commissures in these two genera points to a most decided superiority in the brain of *Myrmecophaga*, when we recollect that the two brains are approximately equal in size. The anterior (ventral) commissure is larger in *Orycteropus* because the olfactory bulb and pyriform lobe, from which it is mainly derived, are larger than they are in *Myrmecophaga*. But the larger corpus callosum in the Great Ant-eater points to a marked superiority in pallial development, *i. e.* a distinctly higher state of cerebral organization, in this animal than in the African *Orycteropus*. The psalterium of *Myrmecophaga* is more attenuated than that of *Orycteropus*, partly because it has been subjected to a greater amount of stretching\* by the larger corpus callosum, but partly because it is actually smaller in the former, a result of the smaller dimensions of the hippocampus.

In the cerebral commissures of *Tamandua* we find a considerable family resemblance to *Myrmecophaga*, making due allowance for the smaller size of the former (fig. 10). The anterior commissure, measuring about  $1.5 \times 1.25$  mm., is placed in a vertical *lamina terminalis*, which is attached dorsally to the ventral extremity of the *psalterium ventrale*. The psalterium is elongated and attenuated as it is in *Myrmecophaga*, being about 9 mm. long, and reaching a maximum thickness of 0.75 mm. in the plumpest part of the *psalterium ventrale*; but the *psalterium dorsale* consists of an extremely thin sheet of crossing fibres. The elongated corpus callosum is more oblique than it is in *Myrmecophaga*, and is nearly 14 mm. long and 1 mm. thick. The anterior and posterior extremities of the corpus callosum are distinctly thickened.

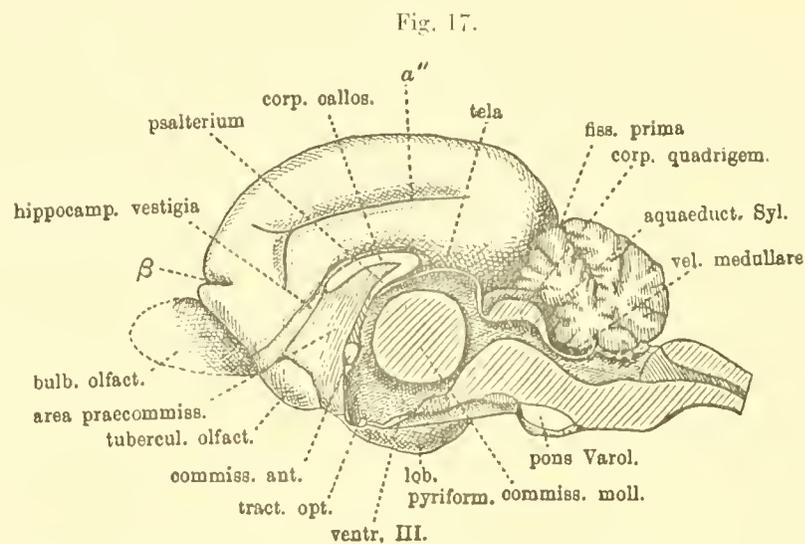
As far as Pouchet's figure allows us to express an opinion. *Cycloturus* also presents the typical elongated corpus callosum which seems to be the distinctive character of the family of *Myrmecophagidae* among the Edentata. In brains of approximately the same shape the proportion between the lengths of the corpus callosum and the cerebral hemisphere may be taken as a rough estimate of the degree of functional perfection of the pallium. Increase in extent of pallium and an increasing richness of texture will find expression in an increased number of crossing fibres.

\* Concerning this stretching influence of the corpus callosum, see 'Journal of Anatomy and Physiology,' vol. xxxii. p. 41.

In *Myrmecophaga* the length of the corpus callosum is about 48 per cent. of the length of the hemisphere; in *Tamandua* it is about 41 per cent., and in *Cycloturus* it is about 38 per cent.

In *Orycteropus*, an animal of similar habits and approximately equal size to *Myrmecophaga*, the corpus callosum, which is about the same thickness as it is in *Myrmecophaga*, is only 35 per cent. of the length of the hemisphere.

The cerebral commissures in the Sloths present a marked contrast both in appearance and in size to those of their relatives—the American Ant-eaters. We have just seen that the characteristic feature of the corpus callosum in the latter is its great length; the effect of this elongation is most noticeable in the caudal direction, and as the upper extremity of the psalterium is attached to this extremity of the corpus callosum it follows that the *psalterium dorsale* becomes markedly attenuated.



Brain of *Bradypus tridactylus*, juv.: surface exposed by mesial sagittal section. Enlarged 2 diam.  
Tela refers to roof of third ventricle.

In the *Bradypodidae* we find a very short corpus callosum; in three specimens of *Choloepus* the average length is 30 per cent. of the length of the hemisphere; and in a young specimen of *Bradypus* the proportion is as low as 26 per cent. These proportions are all the more noteworthy if we recall that the hemisphere in the Sloths is itself relatively short compared with that of the Ant-eaters.

The shortness of the corpus callosum explains the peculiar shape of the psalterium. For, being free from the stretching influence of a caudally elongating corpus callosum, the psalterium remains as a small plump mass of fibres, with no division into *psalterium dorsale* and *ventrale*. This little mass of fibres is thickest at its junction with the corpus callosum, and rapidly tapers to a rounded point as it extends downward and forward, forming an angle of about 30° with the corpus callosum. It is about half the length of the latter. Flower says \* that “the anterior end [of the corpus callosum] is simple

\* Flower, Phil. Trans. 1865, p. 639.

and obtusely pointed, without a trace of the reflected rostrum." In my specimen of *Choloepus*, as well as in the representative of *Bradypus*, the anterior extremity of the corpus callosum is fuller and not pointed as seems to have been the case in Flower's specimen. There is, as Flower remarks, no reflected rostrum or *genu* in *Choloepus*, but in my specimen of *Bradypus* there is a most decided genu, for the plump anterior extremity of the short corpus callosum presents a considerable curve in the ventral direction.

The shape of the psalterium and its relation to the corpus callosum in the Sloths recall that peculiar reversion to a simpler type of corpus callosum which we have previously met in *Nyctophilus* and other Bats\*. The difference is a considerable increase in the size of the corpus callosum in the *Bradypodidae*.

In the Sloths the anterior commissure is relatively smaller than it is in either *Myrmecophaga* or *Orycteropus*, probably because the pyriform lobe is relatively smaller in the former.

In three schemes which I have prepared to illustrate the variations in the hippocampus in the three American families (*vide infra*, fig. 23), the shapes of the commissures are clearly demonstrated and their marked contrast shown more forcibly than any description can picture them.

In the Armadillos we meet with yet another type of dorsal commissure which markedly contrasts with both of the types—those of the *Bradypodidae* and *Myrmecophagidae*—which we have just described. A representative of this type is seen in *Dasyppus villosus*. Here we find a dorsal commissure composed of two limbs—corpus callosum and psalterium—of approximately the same size, but of different shapes. Both of these limbs are placed very obliquely and in contact one with the other for the greater part of their extent, only a very small part of the extreme anterior end of the corpus callosum being separated by any interval from the psalterium. As a result, there is practically no septum lucidum, in the sense in which that term is applied in human anatomy.

The anterior extremity of the diminutive corpus callosum is pointed and depressed. The psalterium and corpus callosum each consist of a club-shaped mass of fibres of approximately the same size. The thick end of the club in the case of the psalterium consists of the cut edge of a vertical wall of crossing fibres, which are placed above the anterior commissure. This mass is the *psalterium ventrale*. At its upper extremity it tapers to the handle of the club, which is composed of the *psalterium dorsale*. This is short and is inclined slightly backward, and becomes continuous with the thick end of the club-shaped mass of the corpus callosum, which is placed upon the dorsal aspect of the *psalterium dorsale*. The corpus callosum is extremely oblique, and rapidly tapers to a point anteriorly and below. A very slight interval is left between the anterior extremity of the corpus callosum and the *psalterium ventrale*.

In Turner's description and figure of the brain of *Dasyppus sexcinctus* † there is no indication of any distinction between the *psalterium dorsale* and *ventrale*, and the whole

\* Cf. this Vol. p. 47.

† Turner, *op. cit.*, 'Journal of Anatomy and Physiology,' vol. i.

dorsal commissure is represented as an obliquely-placed, inverted, U-shaped structure, with symmetrical limbs of approximately the same shape and size. It seems probable, however, that there is a very definite attenuation and bending of the upper part of the psalterium in both species of *Dasyppus*.

In *Tolypteutes trilineatus*, Garrod\* represents a dorsal commissure of the same shape as that represented by Turner in *Dasyppus*, but with a corpus callosum slightly larger than the psalterium. The specimen of *Tolypteutes* at my disposal was not sufficiently well-preserved to permit me to supplement Garrod's brief notes.

The commissures in the brain of *Xenurus unicinctus* have not hitherto been described or figured, so far as I am aware. In the well-preserved specimen representing this genus in the College of Surgeons, the dorsal commissure very closely resembles the appearance figured by Turner in *Dasyppus* †.

We can say that in the three genera *Dasyppus*, *Tolypteutes*, and *Xenurus*, the corpus callosum is very small and pointed, obliquely situated, and of approximately the same size as the psalterium.

In the specimen of *Tatusia* in the College of Surgeons, the psalterium presents features similar to those which we have described in *Dasyppus villosus*, but the corpus callosum is considerably larger than the psalterium, and is plumper, longer, and of more uniform thickness than the corpus callosum of the other Armadillos. In this specimen the dorsal commissure as a whole was not unlike that found in the Hedgehog (*Erinaceus*) and in the Manidae. Such being the case, it is surprising to find the following observations of Pouchet ‡:—" Sur la coupe du cerveau de l'Encoubert [*Dasyppus*] le corps calleux mesure 6 millimètres de long et 1 millimètre d'épaisseur; c'est chez un jeune Cachicame [*Tatusia*] qu'il nous a montré les proportions les plus exigües. Nous l'avons vu aussi, sur cet animal, nettement recevoir des fibres de la partie antérieure et de la partie postérieure de l'hémisphère qui viennent s'y jeter en longeant la seissure médiane."

It is probable that the immediate ancestors of the *Dasyppodidae* possessed a considerably larger corpus callosum than the existing types, for otherwise it would be difficult to understand the stretching of the psalterium. If this be so, the corpus callosum has undergone a retrogressive diminution in size, and the condition in my specimen of *Tatusia*, rather than that of the other Armadillos, would be nearer the primitive one.

In *Chlamydophorus* we find a very peculiar dorsal commissure conforming to the same type as *Dasyppus villosus*, but in which the retrogressive changes resulting in the diminution of the corpus callosum have gone much further. We find a large psalterium divided in a typical manner into dorsal and ventral portions, and a corpus callosum so reduced in size that it is only slightly larger than the *psalterium dorsale*. This is one of the most extreme forms of reduction of the corpus callosum met with in the Eutheria. If this process of reduction were to be carried much further in *Chlamydophorus* we should reach a state of cerebral modification which we find in the Marsupial *Notoryctes*.

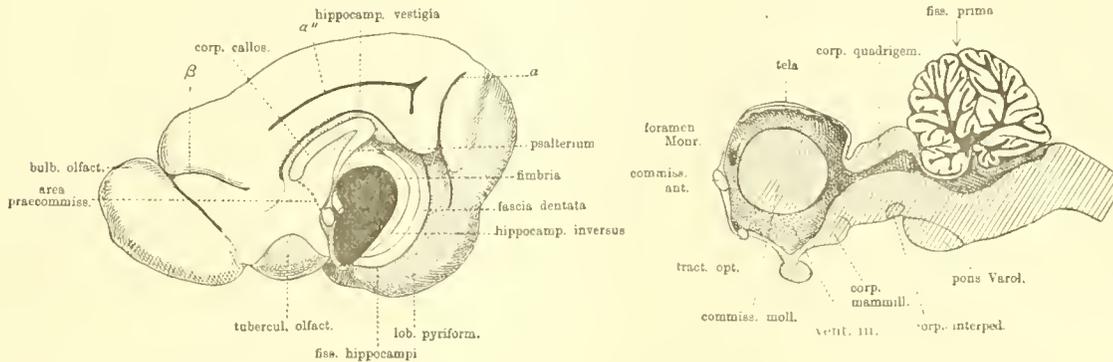
\* Garrod, *op. cit.*, Proc. Zool. Soc. London, 1878.

† Unfortunately, in the process of mounting, a glass rod had been pushed through the junction of the psalterium and corpus callosum, thus rendering impossible an accurate description of this region.

‡ Pouchet, *op. cit.* tom. vi. p. 309.

There is a marked contrast between the family type of dorsal commissure met with in the *Bradypodidae* and the equally well-defined family type of the *Dasypodidae* (fig. 23, p. 320). In the latter we find that specialized form of psalterium which we have seen in the *Myrmecophagidae* and *Orycteropus*, and which is found in the vast majority of Eutheria—a form of psalterium which we associate with a fully-developed corpus callosum. The diminutive size of the corpus callosum in the Armadillos therefore suggests a retrogressive development from some form with a large corpus callosum.

Fig. 18.



Brain of *Choloepus didactylus*; surface exposed by mesial sagittal section. Enlarged  $\frac{1}{3}$  diam.

The brain-stem has been cut away from the hemisphere.

In the *Bradypodidae* we find a marked contrast in the shape of the commissures. Here we have a corpus callosum which has attained a much larger size than in the *Dasypodidae*, though we must still regard it as relatively small and primitive. The psalterium presents a simple form in the Sloths, which a comparison with the marsupial would point out as a primitive type. In other words, we might regard it as the result of a progressive development from some simpler type rather than a retrogressive modification of a more highly organized form, as may have been the case in the Armadillos.

In all the Armadillos the ventral or anterior commissure is relatively very large, just as we should expect from the large size of the pyriform lobe.

In the brain of *Manis* the corpus callosum is very short, being barely 6 mm. long in the specimen at my disposal, and almost of uniform thickness throughout. It does not taper anteriorly, nor, on the contrary, is it thickened or bent anteriorly to form a *genu*. In my specimen the corpus callosum was not nearly so thick and plump in proportion to its length as that figured by Max Weber\*.

Max Weber has not figured the whole of the psalterium, but this structure in my specimen appears to be clearly composed of two parts—a ventral and a dorsal, neither of which is very plump. So that, on the whole, the dorsal commissure of *Manis* is much more like that of *Erinaceus* than any of the Edentates; for, while the psalterium resembles that found in the *Dasypodidae*, the corpus callosum is more like that of the *Bradypodidae* in shape, size, and position.

The anterior commissure is moderately large.

\* Max Weber, *op. cit.*, 'Zool. Ergebnisse,' ii. tab. ix. fig. 69 *cc.*

In reviewing the features presented by the cerebral commissures in the Edentata, we find that, while each family presents a more or less distinct type of dorsal commissure, all of the commissures conform to the type prevailing in the Eutheria generally, and an analogue for almost any Edentate type may be found among the Eutheria.

There is no feature in the arrangement of the commissures which indicates a transition stage between the primitive Sauropsidan-like type which prevails in the Prototheria and the Eutherian brain with a well-formed corpus callosum. It may be that the gradual dwindling of the corpus callosum which is obviously going on in the Armadillos may indicate the mode by which the Marsupials might have lost their corpus callosum, when their dorsal commissure assumed a resemblance to that of the Monotremes in being purely hippocampal. For the possibility of the Marsupials having once had a corpus callosum and subsequently lost it is forced upon our consideration by the dwindling of the anterior and dorsal parts of the hippocampal arc—changes which we associate causally in the Eutheria with the development of a corpus callosum. But the discussion of the question whether the ancestors of the Marsupialia originally had a corpus callosum must be postponed for a future memoir.

There are certain general questions relating to the cerebral commissures which may be discussed to better purpose after we have considered the cerebral cortex.

#### THE HIPPOCAMPAL FORMATION.

We have seen elsewhere\* that in the Monotremata and Marsupialia the hippocampus retains a peculiarly simple arrangement with relation to the margin of the hemisphere, which it has inherited from the ancestors of the Mammalia.

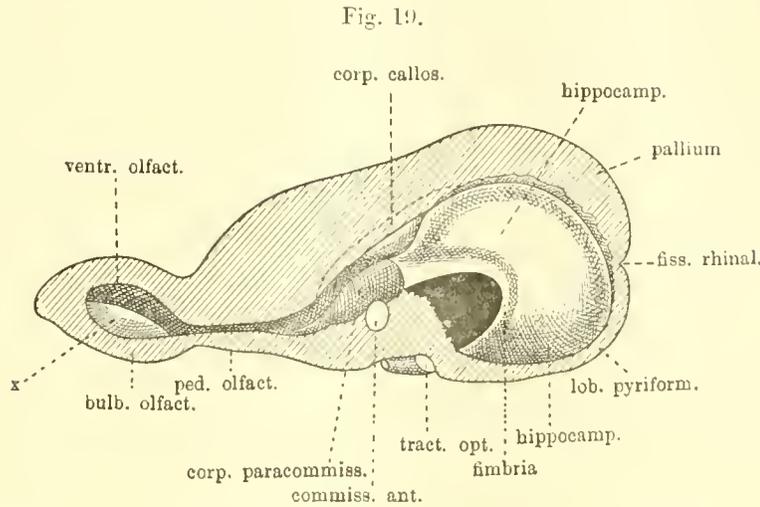
In approaching the study of this region of the brain in the Edentata, I have deemed it important to enter with some detail into the exact arrangement of the hippocampus, in the hope that some indication of the affinities of the Order might be obtained.

Extending downward and backward from the postero-inferior aspect of the psalterium, we find upon the mesial surface of the hemisphere (fig. 4, p. 291) two or more peculiar arcuate bands, which represent all that can be seen upon the surface of the peculiar hippocampal formation—the homologue of the hippocampus major of human anatomy. If, before beginning the study of these peculiar surface areas of the hippocampal formation, we examine this structure from within by opening up the cavity (lateral ventricle) of the hemisphere, we shall gain a much clearer conception of the region than would be the case otherwise.

If we dissect away the lateral wall of the hemisphere of *Orycteropus* so as to expose the mesial wall of the lateral ventricle, we find a large crescentic white mass bulging in the posterior part of the ventricle, looking not unlike the pupa of a silkworm lying in its cocoon. This large curved swelling is the hippocampus. Its concave anterior border is fringed by a prominent ridge of compactly arranged fibres—the *fimbria*. The lower extremity of the swollen mass is pointed, and the upper extremity, which extends slightly

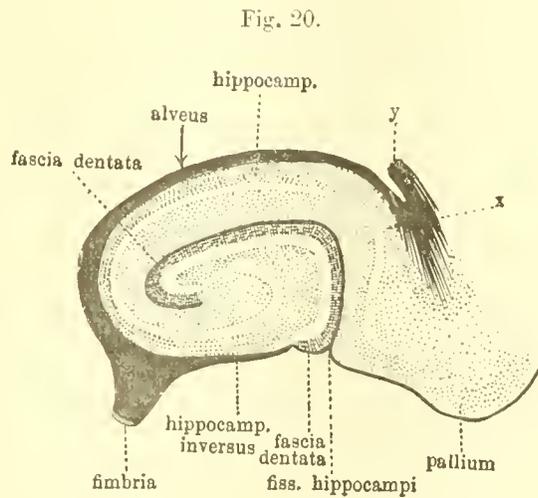
\* Cf. this Vol. p. 47.

further forward than the lower, is rounded and is placed upon the dorsal side of the broad anterior end of the fimbria.



Left hemisphere of *Orycteropus*; the lateral wall removed and the lateral ventricle opened. Nat. size.  
 x. "Complete" invagination of the ventral wall of the olfactory bulb.

If we make a horizontal section through this hippocampal swelling at about the middle of its extent, we gain a more exact idea of the extent of the prominence and the relationship between those parts of the hippocampal formation which make their



Semi-schematic representation of a transverse section through the hippocampal formation in *Orycteropus*.  
 Enlarged 4 diam.  
 x. Hippocampo-pallial junction. y. Corona radiata.

appearance upon the surface and the deeper-lying parts which produce the large ventricular bulging.

In such a section the hippocampal formation presents, roughly speaking, an elliptical

outline, and the greater part of its free surface is covered by a very definite layer of medullated nerve-fibres—the *alveus*.

The anterior border of the formation is rounded, and from the antero-mesial part of the curve a small triangular mass of fibres—the *fimbria*—projects. This spur serves to indicate the line of demarcation between the ventricular and extraventricular surfaces of the hippocampus. The whole of the ventricular and the greater part of the extraventricular surfaces (in this section) are covered with a very well-defined layer of medullated nerve-fibres—the *alveus*. Extending in the lateral direction from the fimbria, the alveus extends outward and then sweeps in a large curve caudally and extends backward as far as the posterior aspect of the ventricle, of which it forms the mesial wall. From the extent and degree of curvature of this large alveus-coated surface in the figure, we can appreciate more readily the great size of the bulging of the hippocampus into the ventricle (fig. 19). The alveus gathers fibres from the whole of the deep or ventricular surface of the hippocampus and conveys them by an oblique course to the fimbria, which is composed of a large mass of such fibres gathered into a compact bundle. But the alveus is not confined to the ventricular aspect of the hippocampus. For we find an extraventricular alveus extending backward from the fimbria upon the mesial surface of the hemisphere for a considerable distance until it meets a grey band of peculiar constitution—the *fascia dentata*.

The fascia dentata is morphologically the extremely specialized margin of the costa, which has undergone a peculiarly modified hypertrophy in its superficial layers, resulting in that curiously folded layer which is known in human anatomy as the fascia dentata. [It is not advisable to apply the term *gyrus* to this structure, as many writers, following Huxley, are in the habit of doing, because it is not a gyrus in the ordinary sense of the term, but merely the peculiarly modified superficial region of a cortical area.]

An exceedingly small fragment of the fascia dentata makes its appearance upon the surface in the section we are considering, since almost the whole of its real surface is hidden from view by being opposed to the morphological surface of the hippocampus and the adjoining cortical area.

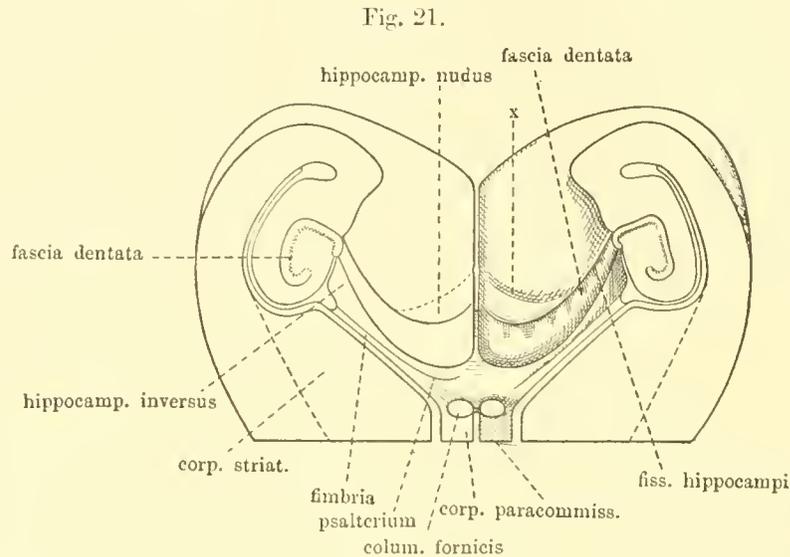
In the section we find the superficial fragment of the fascia dentata at the posterior extremity of the extraventricular alveus; from this point the fascia dentata extends for a considerable distance in the lateral direction and in apposition with the area of cortex which adjoins the hippocampus proper. The fascia dentata then bends forward, its surface now coming into contact with the morphological surface of the hippocampus; in the rest of its course the fascia dentata pursues a course parallel to the alveus: that is to say, it proceeds forward and then curves mesially and then slightly backward. The potential cleft which extends into the cortex in the interval between the fascia dentata and the general cortex and separates the morphological surface of the fascia dentata from the surfaces of the hippocampus and the adjoining cortex is the *fissura hippocampi*. The deeper parts of this "fissure" are merely potential, because the surface of the fascia dentata becomes adherent to the opposed surfaces, especially that of the hippocampus. The hippocampal fissure is unique in its nature and mode of formation, and cannot be classed with any other fissures of the brain.

Behind the hippocampal fissure, in the section we are considering, we find the general cortex forming the posterior lip of the fissure. If we trace this cortex toward the hippocampus, we find that its superficial layer becomes directly continuous with that of the hippocampus. The change from general cortex to hippocampus takes place opposite the bend in the hippocampal fissure, and consists essentially in the levelling down of the scattered cell-elements of the general cortex into a regular column of cells of peculiar shape, which characterizes the hippocampal formation. We may call this region the *hippocampo-pallial junction*. From this point the hippocampus proper extends forward, its deep surface coated with alveus forming the mesial wall of the ventricle, its real surface being in apposition with that of the fascia dentata. The hippocampus, still maintaining these relations, extends forward, then curves around so that its "deep" alveus-coated surface sweeps beyond the fimbria and thus makes its appearance upon the surface of the hemisphere. In this manner the morphologically deep aspect of the hippocampus actually forms part of the surface area of the hemisphere; in other words, part of the hippocampus becomes completely invested, with its "superficial" area excluded from the actual surface and its "deep" aspect exposed. This area of the surface of the brain, which is placed between the fascia dentata and the fimbria, and is covered by extraventricular alveus, may be termed the "*hippocampus inversus*." The whole of the "morphological surface" of the hippocampus proper is hidden from view in this section because it is submerged in the depths of the hippocampal fissure.

After these considerations we may better appreciate the appearance of the mesial surface of the hemisphere.

In a mesial view of the hemisphere of *Orycteropus* (fig. 4) we see the fimbria beginning below at a point just behind the optic chiasma as a very narrow band and extending obliquely upward and backward, then curving upward and ultimately horizontally forward to the situation of the psalterium ventrale. It rapidly increases in breadth during its course from below upward. If, instead of examining this region from its lateral aspect, we look at it from below (fig. 21), we find that for its upper half the fimbria follows a very oblique course forward and inward, so that anteriorly it approaches close to the mesial plane, and a large proportion of its fibres extend across to the other side of the brain, thus forming the *psalterium ventrale*. The fimbria presents analogous features in all the other Edentates, in common with most lowly mammals. Lying behind the fimbria, we find in *Orycteropus* the area of inverted hippocampus which separates the fascia dentata from the fimbria. As we trace these structures upward, we find that the area of inverted hippocampus rapidly tapers, and at the same time the fascia dentata broadens and approaches the fimbria. The exact arrangement of the upper endings of these three bands will be discussed after the inferior endings are considered. In *Orycteropus* the inverted hippocampus and the fascia dentata appear to end suddenly below in a deep arcuate furrow (fig. 4) which marks the upper limit of the peculiar *hippocampal tubercle*, to which a brief reference has already been made. As this hippocampal tubercle exists among the Edentata in *Orycteropus* only, we may with advantage consider the mode of termination of the hippocampus in the other forms first. In all Edentates we find the three superficial bands—*fimbria*, *hippocampus inversus*, and *fascia dentata*—which we have noted

in *Orycteropus*. As we trace these bands downward and forward in any Edentate other than *Orycteropus*, they will be found to taper and end simply just behind the optic chiasma. This mode of ending is shown in the figure of *Tamandua* (fig. 10), and Max Weber's figure shows it in *Manis*. In his account of the state of the hippocampus in



Dissection to expose the ventral surfaces of hinder parts of the cerebral hemispheres in *Orycteropus*.

Enlarged  $\frac{3}{2}$  diam.

x. Furrow corresponding to hippocampo-pallial junction.

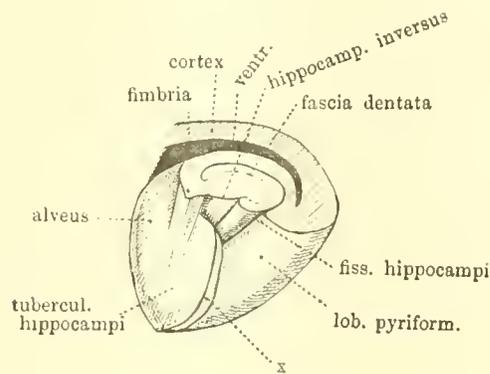
*Cholapus*, Flower\* mistakes the inverted area of hippocampus for part of the fascia dentata. In many of these brains the inferior extremity of the fascia dentata may be seen, upon the ventral surface of the brain, in direct continuity with that part of the pyriform lobe which Gustav Retzius calls the "*gyrus lunaris*." This is shown in our figure of *Myrmecophaga* (fig. 6), in which the antero-inferior extremity of the fascia dentata makes a peculiar bend toward the fimbria and almost at right angles to the rest of its course.

In *Orycteropus*, however, we find the region of the ventral extremity of the hippocampal formation occupied by the peculiar large oval swelling which I have called *tuberculum hippocampi*. We may at a glance appreciate the significance of this peculiar structure if we remove the lower extremity of the hippocampal formation from the rest of the brain and examine it from the front, so that we may at the same time see part of the ventricular surface of the hippocampus and the whole of the extraventricular parts (fig. 22). We then see the fimbria descending and rapidly vanishing as a distinct ridge by the scattering of its fibres over the lower parts of the hippocampus. In front of the fimbria we can see the lower part of the ventricular surface of the hippocampus, which we have already seen in profile (fig. 19). We see this alveus-coated surface of the hippocampus sweeping around the lower extremity of the fimbria and becoming extraventricular as the *tuberculum hippocampi*. The latter structure is obviously nothing else

\* Flower, *op. cit.*, Phil. Trans. 1865.

than a prominent boss of inverted hippocampus covered with an exceedingly attenuated coat of extraventricular alveus, and therefore serially homologous with the flattened

Fig. 22.



Dissection to expose ventral extremity of the hippocampal formation in *Orycteropus*. Nat. size.

x. Attenuated lower extremity of fascia dentata.

band of inverted hippocampus which separates the fascia dentata from the fimbria. But the lower extremity of the fascia dentata has not entirely disappeared, for it is represented by an extremely attenuated band which separates the hippocampal tubercle from the pyriform lobe just as the "band of Giacomini" does in the human brain. The *tuberculum hippocampi* is exactly analogous to the tip of the uncus in human anatomy, which Retzius has recently called the *gyrus intralimbicus*\*.

Such an arrangement, so far as I am aware, exists nowhere else outside the Primates.

As the hippocampal formation proceeds upward toward the psalterium and splenium of the corpus callosum it at the same time rapidly approaches the mesial plane, so that a perspective view, such as a representation of the mesial surface of the hemisphere affords, gives a very distorted picture of the hippocampal region. To gain an accurate idea of this region we must examine from below those large opercula-like cortical folds which form a dome-like roof above the optic thalamus and corpora quadrigemina. Such a view may be obtained by making a horizontal section immediately above the anterior commissure and inverting the upper part of the cerebral hemispheres (fig. 21). In this view we may start from the typical section of the hippocampus which has been described above (fig. 20), and which is now exposed once again. We see the fimbria extending obliquely forward and inward toward the *columna fornicis*, the elliptical section of which is seen on each side of the mesial plane. Many fibres of the fimbria enter the *columna fornicis* of the corresponding side; many other fibres of the fimbria cross the mesial plane just behind the *columnae fornicis* and thus form the *psalterium ventrale*.

The area of inverted hippocampus which in the cut surface is placed immediately behind the fimbria may be observed to rapidly taper and soon disappear as the mesial plane is approached.

But as the fascia dentata approaches the mesial plane it increases considerably in

\* Gustav Retzius, *op. cit.*, 'Das Menschenhirn.'

breadth: in other words, an increasing area of that part of the fascia dentata which is in contact with the cortex (*vide* figure 20) becomes exposed. *Pari passu* with this uncovering of the fascia dentata, the opposed surfaces of pallium and hippocampus, which hide it from view elsewhere, also become exposed. There is a general unrolling, as it were, of the hippocampal formation. So that, as the fascia dentata becomes more and more exposed, we also find that the hippocampo-pallial junction approaches and ultimately appears upon the surface as a shallow furrow separating the pallium, which lies behind it, from the exposed surface of the hippocampus, which now makes its appearance on the surface in front of the furrow (fig. 21, *x*).

This exposed hippocampus (*hippocampus nudus*) is the true morphological surface of the hippocampus which elsewhere is submerged, hidden in the depths of the hippocampal fissure\*. Near the mesial plane it appears to emerge from the hippocampal fissure, and under the name "*Balkenwindung*," which Zuckerkandl introduced, it has given rise to much discussion. Zuckerkandl's "*Balkenwindung*" is nothing else than our "*hippocampus nudus*."

As the fascia dentata becomes more exposed and apparently broader it bends transversely inward, and when quite close to the mesial plane it bends suddenly backward and rapidly tapers to a point below the splenium of the corpus callosum. These recurved portions of the fascia dentata upon the two sides of the mesial plane are in close proximity the one to the other, and in many animals (*e. g.* the Rabbit) they actually meet and fuse in the course of development †. But the two structures are developmentally independent, and each is derived wholly from its own cerebral hemisphere.

If we now return to the consideration of the mesial surface of the hemisphere (fig. 4), we readily recognize the mesial border of this infrsplenial bent part of the fascia dentata as a pear-shaped body proceeding backward upon the under surface of the *psalterium dorsale* and *splenium*, and appearing to be directly continued around the splenium on to the dorsal surface of the corpus callosum as a rounded white cord. But the fascia dentata really ceases, as a definitely recognizable entity, upon the ventral surface of the splenium. The rounded white cord which surrounds the splenium, and *appears* to be merely the attenuated fascia dentata, is more directly the upward continuation of the *hippocampus nudus*, i. e. the hippocampus proper.

The fascia dentata, as its mode of development indicates, is a comparatively late specialization of the margin of the hippocampus proper. As it develops it rolls itself, as it were, over the surface of the hippocampus and hides this from view. On the inferior aspect of the splenium the hippocampal formation unrolls, the hippocampus proper becomes once more exposed, the fascia dentata tapers and disappears almost entirely, and a remnant of the more primitive hippocampus proper surrounds the splenium and extends along the whole length of the upper surface of the corpus callosum as a rounded white cord.

This cord-like remnant is a vestige of the anterior part of the more extensive hippo-

\* The true significance of this will be appreciated at a glance from fig. 21 of my short memoir in the 'Journal of Anatomy and Physiology,' vol. xxxii. p. 49.

† Compare in this connection the comparative observations of Stieda in *Zeitsch. f. wissensch. Zoologie*, 1870.

campal arc which we find in Marsupials and Monotremes\*. In *Orycteropus* this circumcallosal hippocampal vestige is a very prominent rounded strand which we can readily follow with the naked eye around the splenium, along the whole length of the corpus callosum, and around its anterior extremity. But beyond this we cannot thus follow it. We shall see that in most of the other Edentates the mode of termination of this vestige of the anterior part of the hippocampal arc is more clearly exhibited than it is in *Orycteropus*.

Turning to the consideration of the brain of *Tamandua* (fig. 10), we find a typical hippocampal formation, three concentric bands of which—fimbria, inverted hippocampus, and fascia dentata—appear upon the surface. These three bands end simply below, *i. e.*, without that peculiar modification which in *Orycteropus* was described under the name hippocampal tubercle. At its upper extremity we find the same series of circumsplenic modifications of the hippocampal formation as we have already described above. But the infrsplenic bending of the fascia dentata is much further removed from the *psalterium ventrale* than is the case in *Orycteropus*: in other words, the corpus callosum has grown relatively further backward, carrying the infrsplenic hippocampal flexure (*flexura hippocampi*) with it, and has extended the *psalterium dorsale* to permit this separation from the *psalterium ventrale*.

A large supracallosal vestige of the hippocampus may be recognized upon the dorsal aspect of the corpus callosum in *Tamandua*, but it is relatively smaller than the corresponding vestige in *Orycteropus*. The deep cleft which separates the hippocampal vestige from the overhanging pallium corresponds to the callosal fissure of human anatomy. It is not, as is often erroneously stated, the continuation of the hippocampal fissure, because the latter always ceases in the Edentates, as in most Eutheria, immediately below the splenium of the corpus callosum when the hippocampus unrolls. The hippocampo-pallial limiting furrow, which emerges from the upper extremity of the hippocampal fissure, surrounds the splenium, and joins the *fissura callosalis*, is often mistaken for the hippocampal fissure itself, and hence the belief in the continuity of hippocampal and callosal fissures. Unlike the condition of affairs in *Orycteropus*, the *fissura callosalis* in *Tamandua* becomes continuous anteriorly with a well-defined fissure which arches downward and forward to disappear in the deep cleft which separates the upper surface of the olfactory peduncle from the apex of the hemisphere. This is the ventral boundary of the pallium, and hence may be called *fissura limitans pallii*. It serves to indicate to the naked eye the upper limit of the hippocampal vestige which we can discover along this line by histological examination.

In *Myrmecophaga* we find a close agreement with the condition just described in *Tamandua*. There is also a large and clearly-defined hippocampal vestige, which Forbes has failed to indicate in his figure of the mesial surface. However, he speaks of the fascia dentata "being continued, as described by Professor Turner in *Dasypus*, as a thin layer of longitudinally-disposed fibres over the *corpus callosum* to near its *genu*" †.

\* Cf. this vol. p. 50; also 'Journal of Anatomy and Physiology,' vol. xxxii.

† W. A. Forbes, *op. cit.*, Proc. Zool. Soc. London, 1882, fig. 4, and p. 294.

As a description of the mere appearance of the hippocampal vestige in *Myrmecophaga* this account is lucid enough, but if we literally interpret either it or the expression of Turner (which it somewhat travesties) as a statement of the actual constitution of the parts we shall gain a very erroneous conception. For, as the hippocampal formation surrounds the splenium, the fascia dentata dwindles and practically disappears, leaving the diminutive remnant of the simple hippocampus proper upon the surface of the corpus callosum. This hippocampal vestige is very rich in longitudinal medullated fibres, which in human anatomy are called the *stria Lancisii* (as well as an immense variety of other names). This explains the statement of Turner that the fascia dentata is prolonged into the upper surface of the corpus callosum as a narrow band\*, which, to the naked eye, it *appears* to be. It also explains the statement, which Forbes wrongly attributes to Turner, that the fascia dentata is "continued forward as a thin layer of longitudinally-disposed fibres."

Histological examination enables us to exactly interpret the puzzling macroscopic appearances and to state definitely that the hippocampal formation, a complex of fascia dentata and hippocampus (in the narrow sense), extends up to the splenium of the corpus callosum and becomes continuous around the splenium with a diminutive band which represents the dwindled hippocampus from which the fascia dentata has practically vanished; as this vestigial hippocampus contains a large number of medullated nerve-fibres, it is often mistaken for a purely fibrous structure.

Although the figure of the mesial surface of the brain of *Cycloturus* which Pouchet gives † is lacking in detail, it suffices to show that a *sulcus limitans pallii* exists in a form exactly analogous to that of the other two representatives of the *Myrmecophagida*; and the fact that his figure represents a vestigial hippocampus at all shows that this structure is more prominent than is usual among Eutheria.

Flower has given a useful figure and a description of the hippocampal region in *Choloepus* ‡, but the corresponding region in *Bradypus* has not, so far as I am aware, been properly figured or described.

In the brain of both of the Sloths the hippocampus presents the typical features in the greater part of its extent, such as we have already described in *Tamandua*, and which we find in most mammals. But in the upper part of its extent the hippocampus presents in both *Bradypodida* certain features in common which distinguish it from that of the other Edentates. We have already observed that in this family the corpus callosum has not grown backward even to the same extent as it has in *Orycteropus*. As a result the psalterium, as we have already seen, is short and simple, and in addition the upper part of the hippocampal formation has undergone very slight disturbance. In both Sloths the fascia dentata appears to extend directly toward the splenium without such a marked infrasplenic flexure as we find in the other Edentates. To the naked eye no area of exposed hippocampus makes its appearance behind the splenium, and the

\* W. Turner, *op. cit.*, 'Journal of Anatomy and Physiology,' vol. i.

† G. Pouchet, *op. cit.*, 'Journal de l'Anatomie et de la Physiologie,' tome vi. pl. iv. fig. 4.

‡ W. H. Flower, *op. cit.*, Phil. Trans. 1865.

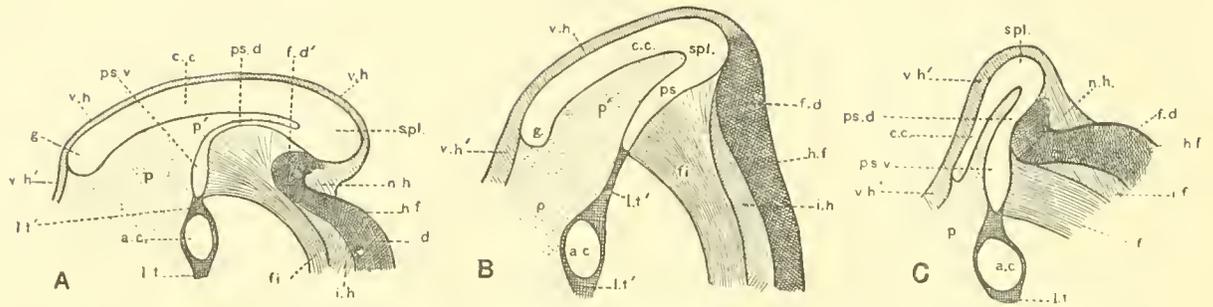
hippocampal fissure even appears to extend into continuity with the callosal fissure. Looking at the mesial surface of the hemisphere, the upper part of the fascia dentata appears to accompany the fimbria right up to the splenium and then to pass without any marked bending into the vestigial hippocampus which covers the dorsal surface of the corpus callosum.

A large supracallosal hippocampal vestige is found in both Sloths, and in my specimen of *Bradypus* we have an interesting demonstration of the precallosal course of the hippocampal vestige. Thus we find extending obliquely downward and forward from the front of the corpus callosum two shallow furrows which slightly diverge as they approach the olfactory peduncle (fig. 17). The upper of these furrows corresponds to the limiting fissure of the pallium in the *Myrmecophagidae*. The area included between these two furrows is the precallosal part of the hippocampal vestige. It appears broader than the supracallosal part of the vestigial arc because the latter is flattened horizontally upon the corpus callosum, while the precommissural vestige is vertical, being a constituent part of the mesial wall of the hemispheres.

In representing the hippocampus from any one point of view it is impossible to convey an accurate idea of its exact disposition, because it bends about in various planes during its course so that in a perspective drawing it appears distorted. As it is a matter of great importance to clearly understand the behaviour of this important and peculiar part of the brain, I have drawn three schemes (fig. 23): one of *Tamandua*, representing the Ant-eaters; one of *Choloepus*, representing the Sloths, which we have already discussed; and one of *Dasypus villosus*, representing the Armadillos, which we shall consider almost immediately. These schemes represent the actual relations of the hippocampal formation to the commissures in the three American families of Edentates.

After the preceding descriptions these schemes are almost self-explanatory. In the Ant-eater (A) we see the three bands of fimbria (*f.*), inverted hippocampus (*i.h.*), and fascia dentata (*f.d.*) ascending in front of the hippocampal fissure (*h.f.*), just as they do in the Rabbit or any of the common Eutheria. As they ascend, the intermediate band (inverted hippocampus) disappears and the fascia dentata comes into contact with the fimbria. The main portion of the latter continues its forward course to the *psalterium ventrale* (*ps.v.*), but a few of its uppermost fibres become widely scattered in the triangular interval between the subsplenic flexure of the fascia dentata (*f.d.*) and the fibres going to the ventral part of the psalterium. From these scattered fibres the thin membranous *psalterium dorsale* (*ps.d.*) is formed. The fascia dentata (*f.d.*) suddenly diverges from the fimbria and bends backward beneath the splenium (*spl.*) of the corpus callosum. As it does so it rapidly tapers and fades away. As this is taking place a part of the true hippocampus (*n.h.*) (using that term in the strict and exclusive sense) crops out of the upper part of the hippocampal fissure (*h.f.*). This little fragment of naked hippocampus (*n.h.*) becomes directly continuous with its atrophied serial homologue, the vestigial hippocampus (*v.h.*), which surrounds the corpus callosum (*c.c.*) and extends forward not only as far as the genu (*g.*), but beyond this point toward the situation of the olfactory peduncle.

Fig. 23.



Three schemes to represent the relation of the hippocampal formation to the commissures in the *Myrmecophagidæ* (A), the *Bradypodidæ* (B), and the *Dasypodidæ* (C).

## Reference letters.

*c.c.*—Corpus callosum.  
*g.*—Genu corporis callosi.  
*spl.*—Splenum corporis callosi.  
*ps.v.*—Psalterium ventrale.  
*ps.d.*—Psalterium dorsale.  
*a.c.*—Commissura anterior.  
*l.t.*—Lamina terminalis.  
*l.t'.*—Lamina terminalis (the intercommissural copula).  
*p.*—Arca precommissuralis.  
*p'.*—Arca precommissuralis (pars dorsalis = septum lucidum).

*f.d.*—Fascia dentata.  
*f.d'.*—The fascia dentata at the *flexura hippocampi*.  
*fi.*—Fimbria.  
*i.h.*—The inverted hippocampus.  
*h.f.*—Fissura hippocampi.  
*n.h.*—Hippocampus nudus—the exposed surface of the hippocampus proper.  
*v.h.*—The vestiges of the hippocampus (supracallosal part).  
*v.h'.*—The vestiges of the hippocampus (precallosal part).

In the *Bradypodidæ* we have a peculiarly simple arrangement of hippocampal formation, which is all the more remarkable because it forms such a marked contrast to the typically Eutherian type we have just found in the Ant-eaters. The small corpus callosum has produced a minimum disturbance in the circumsplenic parts of the hippocampal arc. There is practically no *flexura hippocampi*, no appearance of the naked hippocampus. On the other hand, the fascia dentata extends directly toward the splenium and gradually tapers and fades away without bending. The other changes in this scheme are self-explanatory.

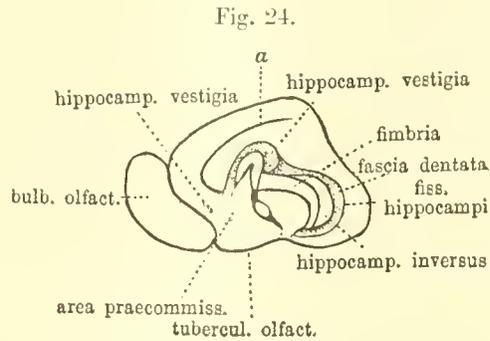
We will now turn to the consideration of the hippocampal formation in the Armadillos, the type of which is represented in the third scheme (C).

In all the *Dasypodidæ* examined we find the typical arrangement of the hippocampal formation such as is common in the Eutheria. The vestigial hippocampus (*v.h.*) is relatively very large.

In *Xenurus* we have a beautifully clear demonstration of the arrangement of the parts under consideration. The vestigial hippocampus is a plump arcuate cord, which surrounds the diminutive corpus callosum, and then bends downward and forward in front of the commissure.

It is equally prominent in *Dasypus sexcinctus* and *Dasypus villosus* (fig. 23, C) and in

*Tolypentes*; and in the small brain of *Chlamydochorus* (fig. 16) we again find an admirable demonstration of the arrangement of this archaic hippocampal arc. In the small brain of *Chlamydochorus* I have traced in a complete series of sections the series of changes in the hippocampus as it surrounds the splenium of the corpus callosum and joins the supracallosal vestige, and found that they agree in all points with the transition region in such simple Eutherian brains as those of *Erinaceus*. These changes need no description if we compare the schemes C and A in fig. 23.



Mesial surface of right cerebral hemisphere of *Xevurus unicolor*. Nat. size.

In *Manis* we find an exactly analogous arrangement. The large vestigial hippocampus which I found in my specimen is not shown in Max Weber's figure (*loc. cit.*), but probably goes to swell the thickness of the corpus callosum.

In the preceding pages I have entered into considerable detail concerning the exact disposition of the hippocampal formation in *Oryzeteropus* and the Ant-eaters for several reasons.

In the first place, if the Ant-eaters occupy the lowly position near the bottom of the mammalian phylum which is usually assigned them, we might expect some indication of this fact in that region of the brain which has undergone such a striking modification within the Eutheria, namely in the hippocampal formation. Instead of this, we find the typical Eutherian plan in as fully developed form as that of the Ungulata and Carnivora.

In the Sloths, it is true, we find an arrangement of hippocampus which is as simple as it is possible to be in the presence of a corpus callosum. But the resemblance of the condition in the Sloths to that which we have found in certain small bats\*, and which is obviously a reversion-type, suggests that the simplicity of the Sloth brain may possibly not be primitive. At the same time we must recognize the possibility of the archaic simplicity of type being retained, just as it is, for instance, in the case of the auditory ossicles according to Kitchen Parker. In the Armadillos, again, we have the typical Eutherian plan exemplified.

The relatively large vestigial hippocampus in these Edentata invited a minute study in the hope of finding some definite indications of its original structure; but here again

\* Cf. this vol. p. 58.

we find that the structure is quite as atrophic as the relatively much more insignificant vestiges of the hippocampus in the more highly-organized mammals.

There is another reason of quite different nature for entering so minutely into the anatomy of this region in the Edentata. The clear demonstration of the hippocampal region which the Edentate brain affords renders it a particularly suitable object upon which to demonstrate the typical features of a region which has given rise to greater perplexity, perhaps, than any other of the brain.

For many years the question of the mode of ending of the dorsal extremity of the hippocampus has excited a great deal of controversy. Several investigators have from time to time given an accurate account of its behaviour in different mammals. Thus Henle and Giacomini long ago demonstrated that the hippocampal formation extends on to the dorsal aspect of the splenium in Man. Other writers, on the other hand, have emphatically denied this and affirmed that the hippocampus is always subcallosal. Other writers, again (such as Zuckerkandl, who has a large following), have stated that the fascia dentata extends on to the upper surface of the corpus callosum. Then, again, Ganser says that in the Mole the fascia dentata ceases upon the ventral aspect of the corpus callosum, but that the layer of pyramidal cells (*i. e.* the hippocampus proper) becomes continuous with the rudimentary supracallosal *indusium*. We have, then, in the literature of this subject four mutually contradictory beliefs concerning the mode of termination of the upper extremity of the hippocampus, each maintained by its own supporters with much cogency.

We have already seen in the different Edentates that the manner in which the hippocampus terminates can be clearly demonstrated, and we can also see with the naked eye the cephalic extension of the hippocampal vestige, not only to the anterior extremity of the corpus callosum, but also as far as the olfactory peduncle. No other writer upon this subject seems to have even suspected the presence of this cephalic extension of the hippocampus. For it has been possible, upon the evidence of comparative data, to definitely state that the *indusium* is not only continuous with the hippocampus, but *is* itself atrophied hippocampus\*.

#### “THE PARACOMMISSURAL BODY.”

In examining the mesial surface of the hemisphere we find, in front of the psalterium and ventral commissure, a region to which passing reference has been already made as the *area præcommissuralis*. This term was originally introduced by the writer as a purely descriptive title for a region of doubtful identity in front of the cerebral commissures in *Ornithorhynchus*. This was subsequently shown to be the surface of a large ganglionic mass to which the name *corpus præcommissurale* was given †. In the course of further investigations which were carried on after the introduction of the

\* For the evidence of this point see ‘Journal of Anatomy and Physiology,’ *op. cit.* vol. xxxii.

† Cf. “The Origin of the Corpus Callosum,” this volume, p. 47.

former term, I was able to clearly establish the identity of the *area precommissuralis* with those surface-areas corresponding to *septum lucidum* and *gyrus subcallosus* (Zuckerkandl) of the human brain. Taking into consideration the fact that these two areas are merely parts of one and the same formation, the separation of which into two parts is purely arbitrary in most mammals, it seemed desirable to retain the term "*area precommissuralis*" for the whole surface-region, even though the term may not be so apt elsewhere as it is in the case of *Ornithorhynchus* and the Submammalia.

The term "precommissural area" sufficiently explains the locality of the region to which it is meant to be applied in all vertebrate brains. The term "*precommissural body*," however, is not nearly so appropriate a title for the ganglionic mass whose surface is the precommissural area, and in many cases it is singularly inappropriate. By substituting for it the name "*paracommissural body*" we shall obtain a term which may justly be applied to this important ganglionic mass in any vertebrate. Unlike the term "precommissural area," which was introduced much earlier, the term "precommissural body" has not yet been adopted by other writers, and hence there can be no objection to the substitution of the more apt title "*corpus paracommissurale*" for the ganglionic mass which I had previously called the "*corpus precommissurale*."

The need for some definite name for this mass of grey matter which forms so prominent a constituent of the brain in the Reptilia, Amphibia, and Dipnoi has been felt for a considerable time. The terms "*septum lucidum*" and "*gyrus subcallosus*" are not only meaningless but inaccurate when applied to any other brains than the most highly organized of the Mammalia, and their application to such brains as the Prototherian, Saurian, or Amphibian cannot fail to give rise to great misconception. Nor can these terms be applied with any more propriety to the *Dasypodidae*.

In the dissection of the lateral ventricle of *Orycteropus* (fig. 19) the paracommissural body makes its appearance in the interval between the anterior commissure and the corpus callosum as a very plump mass of grey matter which forms a most marked contrast to the surrounding areas because they are all lined with white medullated fibres. The posterior margin of this body is abrupt and rounded, and appears as though it were placed on the lateral aspect of the fimbria. Anteriorly the paracommissural body gradually shades away toward the tunnel in the olfactory peduncle.

The paracommissural body is separated from the *corpus striatum* by the slit-like lateral ventricle. It is unnecessary to enter into a description of the corpus striatum or lateral ventricle in this place. These features of the brain do not appreciably differ from those of common Rodents such as *Lepus*.

The essential features of the paracommissural body are similar in all the Edentates. The shape of the body, however, is modified considerably by the growth of a corpus callosum, and hence it is very variable in the different families. These changes in shape are best appreciated from a study of the mesial surface of the hemisphere, where the paracommissural body enters into the constitution of the wall of the brain forming the precommissural area.

In the Sloths (figs. 17, 18, and 23 B) we see the typical arrangement of the precom-

missural area. It forms a broad tract lying in front of the *lamina terminalis* (*l.t.*), which contains the anterior commissure: it extends forward to become continuous with the mesial surface of the olfactory peduncle; it is separated above from the pallium by the precommissural vestige of the hippocampus (*r.h.*'), and below it extends into continuity with the tuberculum olfactorium. The dorso-caudal angle of the paracommissural body has been drawn upward and backward as a long pointed process (*p.*'), which fills up the gap between the psalterium (*ps.*) and corpus callosum (*e.c.*). This process is somewhat stretched, and is the homologue of the *septum lucidum* of human anatomy. With the corresponding lamina of the other hemisphere it encloses a narrow median slit—the *cazum septi*, which opens forward and downward. The only important difference in the *Myrmecophagidæ* (fig. 23 A) is that the "septal" part (*p.*') of the paracommissural body has been stretched to a much greater extent.

In the Armadillos (fig. 23 C) there is practically no septal part of the paracommissural body.

In the Pangolins the condition most nearly approaches that of the Sloths.

#### THE PALLIUM.

It is convenient for descriptive purposes to associate together all the surface-areas which we have so far discussed — *bulbus* and *pedunculus olfactorius*, *tuberculum olfactorium*, *lobus pyriformis*, *lobus perforatus*, *hippocampus*, and *area precommissuralis*—in contradistinction to the rest of the surface of the hemisphere, which it is customary to call *pallium*.

The histological structure and the morphological relations of each of the structures which have just been enumerated are quite distinct, and present little, if anything, in common to those of any of the other areas. But while they present so little in common they are clearly distinguished from the rest of the cortex or pallium by the fact that they are phylogenetically older, and at the dawn of the mammalian epoch had reached the height of their histological differentiation and morphological importance. The pallium, on the other hand, is phylogenetically quite recent, seeing that it can be first definitely recognized as a very insignificant element in the cerebral hemisphere of reptiles. In the Mammalia for the first time it develops its distinctive features, and continues to increase in morphological importance and in histological elaboration. There is, therefore, a very clear line of demarcation between the behaviour of the pallium and the rest of the surface of the brain which deserves to be clearly reflected in any system of nomenclature which we may adopt. From the fact that all the surface-areas, apart from the pallium, are more or less intimately associated with the olfactory apparatus, it has become customary to apply the term "*rhinencephalon*" to this group of surface-areas. This application of the term "*rhinencephalon*" was suggested by Sir William Turner\*, although at that time the exact limits of the region—more especially with regard to the precommissural area—could not be mapped out. The suggestion of Schäfer† to include

\* W. Turner, *op. cit.*, 'Journal of Anatomy and Physiology,' vol. xxv, 1890.

† E. A. Schäfer, Quain's 'Anatomy,' 10th ed. vol. iii. part 1, 1893, p. 160.

the gyrus fornicatus in the rhinencephalon, in conformity with Broca's idea of a limbic lobe, would, if adopted, destroy the whole value of the term "rhinencephalon" as a contradistinction to the term "pallium."

In employing the term rhinencephalon we must always bear in mind that this heterogeneous collection of surface-areas is not exclusively a "smell-brain," but that the association of all these parts with the olfactory apparatus is much more intimate than it is with any other sensory organs. This will explain the apparently paradoxical statement that smell-less animals, like certain Cetacea, possess a "smell-brain" or rhinencephalon, since the pyriform lobe and hippocampus do not entirely vanish in such animals.

The pallium is the progressive part of the cerebral hemisphere, and therefore the region to which we must attach most importance in the study of the mammalian brain. For in the lowest mammal the rhinencephalon has already reached as high a stage in the evolutionary process as it ever will reach, and its essential features change but little in mammals. The slight change that does occur is principally a process of retrogression in the more highly-organized members.

In the following description I have departed from the usual custom by employing the term "sulcus" for all the pallial furrows instead of the more usual term "fissure," not only because the former is a much more accurate name, but also in order to introduce a distinction between the strictly intrapallial furrows and the pallial boundaries, which we still call "*rhinal fissure*," "*hippocampal fissure*," and "*callosal fissure*." To this usual distinction the only exception will be made in the case of the *Sylvian fissure*, which in its fully-developed form deserves the name "fissure." The mesial surface of the pallium presents much greater uniformity in the arrangement of its sulci than the cranial surfaces, and hence we may preferably begin an examination of the pallium in this region.

Upon the inner aspect of the hemisphere of *Orycteropus* the pallium forms a broad strip of cortex which extends from the corpus callosum to the dorsal edge of the hemisphere. This strip of pallium bends downward in front of the corpus callosum, and becomes continuous along an ill-defined line with the precommissural area. Behind the corpus callosum it bends downward and becomes continuous with the pyriform lobe. The whole extent of this strip of pallium is divided into two approximately equal areas, a central or circumcallosal and a peripheral or marginal respectively, by a single deep and well-defined sulcus (fig. 4). This sulcus, which we may at present distinguish as  $\alpha$ , begins posteriorly in close proximity to the caudal extremity of the rhinal fissure: that is, at the extreme ventral limit of the mesial pallium. As it ascends it follows a course parallel to the peripheral margin of the hemisphere, and bends forward midway between the corpus callosum and the upper edge of the hemisphere until it reaches the anterior pole; still following its course parallel to the peripheral margin, it bends downward in front, then after a short course suddenly bends again upward and backward, *i. e.* parallel to the pallio-precommissural junction, and ultimately terminates in a triangular depression formed by the opening up of the anterior extremity of the callosal fissure. From the antero-superior bending of this sulcus one or two small but deep branches are usually

given off, which are probably the expression of a puckering of the cortex at the seat of flexure.

The posterior ascending part of the sulcus is very deep, and indents the whole thickness of the cortex, *i. e.* is a "complete fissure." The possible significance of this observation will be discussed later.

The arrangement of sulci upon the mesial surface of the hemisphere in *Myrmecophaga* has been well represented by Forbes\*. The extensive sulcus  $\alpha$  of *Orycteropus* is represented by an analogous arrangement of three independent sulci:—a posterior vertical ( $cm''$  of Forbes), which we may distinguish as  $\alpha'$ ; a longitudinal ( $cm'$  of Forbes), which we may call  $\alpha''$ ; and an oblique anterior ( $cm$  of Forbes), which we may call  $\alpha'''$ . The longitudinal sulcus ( $\alpha''$ ) extends beyond the corpus callosum at each end, and separates the supracallosal pallium into two longitudinal strips.

The posterior vertical sulcus ( $\alpha'$ ) appears to be much more extensive than the corresponding part of the sulcus  $\alpha$  in *Orycteropus*. This apparent difference serves to accentuate the constant relationship which the sulcus  $\alpha$  maintains to the *fissura rhinalis*.

In *Myrmecophaga* the rhinal fissure terminates at the ventral border instead of high up on the posterior border of the hemisphere as it does in *Orycteropus*, and the sulcus  $\alpha'$  descends to the ventral limit of the pallium, *i. e.* in close proximity to the *fissura rhinalis*.

In *Tamandua* there is no definite sulcus representing the  $\alpha$  series of *Myrmecophaga*, but merely three deep pit-like depressions, which are probably the rudiments of the corresponding three sulci in the Great Ant-eater. The sulcus  $\alpha'$  is represented by a short deep sulcus, merely 3 mm. long, which rises as high as the level of the splenium of the corpus callosum. The sulcus  $\alpha'''$  is represented by a deeply-incised triangular depression a short distance in front of the genu of the corpus callosum. Above the anterior extremity of the corpus callosum there is a short shallow furrow which is partially analogous to the sulcus  $\alpha''$  in the Great Ant-eater.

In the figure of the mesial surface of the brain of *Cycloturus* which Pouchet gives † there is no trace of any pallial sulcus.

In the *Bradypodidae* the mesial surface of the pallium presents an arrangement of sulci which is analogous to the  $\alpha$ -system in the Ant-eaters. In addition the mesial extremity of a sulcus, which belongs more especially to the cranial aspect of the pallium, extends on to this surface of the hemisphere in both *Choloepus* and *Bradypus*. This sulcus, which we shall describe later under the designation  $\beta$ , deeply notches the anterior border of the hemisphere.

A sulcus, which we may distinguish as  $\alpha'$ , begins upon the mesial surface of the hemisphere in *Choloepus didactylus*, just in front of the termination of the posterior rhinal fissure, and opposite the midpoint of the hippocampal fissure. Its relation to the rhinal fissure is exactly similar to the sulcus we have similarly designated in *Myrmecophaga*. As it ascends it pursues a course which is approximately parallel to the upper half of

\* Forbes, *op. cit.*, Proc. Zool. Soc. London, 1882, p. 293, fig. 4.

† Pouchet, *op. cit.*, tom. vi. pl. iv. fig. 4.

the hippocampal fissure, and upon reaching the dorsal part of the hemisphere it does not bend forward but continues its course as far as the dorso-posterior corner of the hemisphere, where it ceases just before reaching the dorsal surface of the hemisphere. In the right hemisphere this sulcus just crosses the upper edge to reach the cranial surface. In his description of the brain of *Cholæpus Hoffmanni* Turner says\* that this sulcus, which he does not name, extends on to the cranial surface above. Flower† does not represent any sulcus corresponding to  $\alpha'$  in his specimen of *Cholæpus didactylus*.

In my young specimen of *Bradypus tridactylus* there is a very well-developed sulcus  $\alpha'$ , which presents an arrangement exactly analogous to that which Turner has described in *Cholæpus Hoffmanni*. It begins below just in front of the rhinal fissure, and ascends vertically; in its upward course it is placed upon the caudal rather than upon the mesial aspect of the hemisphere, as was the case in *Cholæpus*, and crosses the postero-superior border of the hemisphere at a distance of about 3 mm. from the interhemispherical cleft; it, or more strictly a sulcus  $\gamma$  with which it is in uninterrupted communication, extends forward for a distance of 10 mm. on the dorsal or cranial surface of the hemisphere (left). On the right hemisphere of this brain the sulcus  $\gamma$ , which is in continuity with  $\alpha'$ , is much shorter, while in the brain of *Bradypus* in the College of Surgeons this sulcus  $\gamma$  extends for more than half the length of the hemisphere.

In the brain of *Cholæpus* a longitudinal sulcus divides the area of pallium which lies above the corpus callosum into two horizontal bands, of which the lower is slightly the narrower. In my specimen of *Cholæpus didactylus* this sulcus, which we may call  $\alpha''$ , begins slightly in front of the corpus callosum and terminates close to the upper extremity of the sulcus  $\alpha'$  by bifurcating so as to form a short vertical sulcus parallel to  $\alpha'$ . In Flower's specimen of the same species the sulcus  $\alpha''$  begins slightly further forward and extends considerably further backward before it ends simply without bifurcating. In Turner's specimen of Hoffmann's Sloth this sulcus, which Turner calls by Krueg's designation of "*splenialis*," begins far forward and with a bifurcated extremity; posteriorly it bends downward into a direction parallel to the sulcus  $\alpha'$ , and, according to Turner, is "apparently continuous with the hippocampal fissure." Such apparent junctions between the hippocampal and other fissures are of absolutely no importance, because the *fissura hippocampi* is quite *sui generis*, and of a nature entirely different from all other fissures or sulci.

In my specimen of *Bradypus* the sulcus  $\alpha''$  begins far forward in a bifurcated extremity in much the same manner as it does in Turner's specimen of *Cholæpus Hoffmanni*. In the right hemisphere it ends simply at the posterior extremity, but in the left hemisphere there is a slight bifurcation, and in addition a small independent vertical sulcus midway between the adjacent extremities of  $\alpha'$  and  $\alpha''$ .

In all the specimens representing the brains of Sloths we find a well-defined family type in the mode of disposition of the mesial surface of the pallium.

Among all the Armadillos we find some arrangement of sulci analogous to the series  $\alpha$ , except in *Chlamydophorus*, which, like *Cycloturus*, has a smooth pallium.

\* Turner, *op. cit.*, Journal of Anat. & Physiol. vol. xxv. p. 122. † Flower, *op. cit.*, Phil. Trans. 1865, fig. 5.

In *Dasypus sexcinctus* and *Dasypus villosus* there is a sulcus which we may refer to as simply  $\alpha$ . This consists of a small slightly arched sulcus, about 10 mm. long, which imprints the pallium about midway between the corpus callosum and the superior border in such a manner that the centre of the arc is placed above the prominent splenium of the corpus callosum.

In *Xenurus* the sulcus  $\alpha$  is much more extensive, and exhibits a peculiar resemblance to the fissure  $\alpha$  in *Orycteropus*, excepting that it lacks the posterior descending part, which we have called  $\alpha'$  in *Myrmecophaga* and the Bradypodidæ.

It is not improbable, however, that this defect is more apparent than real. In speaking of *Myrmecophaga* we had occasion to point out how much lower the sulcus  $\alpha'$  descends in this form than the corresponding part of the sulcus  $\alpha$  does in *Orycteropus*, and we associated this with the fact that the sulcus  $\alpha$  presents a constant relationship to the rhinal fissure, which is placed higher up on the cerebral surface in the latter. The rhinal fissure is placed much higher still in the Armadillos, and hence it is not improbable that the apparently incomplete sulcus  $\alpha$  in *Xenurus* may be analogous to the whole of the extensive sulcus  $\alpha$  in *Orycteropus*.

In *Manis*, Pouchet\* has figured an extensive longitudinal sulcus analogous to the sulcus  $\alpha''$  in the Bradypodidæ and *Myrmecophaga*. It is considerably longer than the corpus callosum, but quite simple. More recently Max Weber has given an excellent figure of the mesial surface of the brain of *Manis* †, in which he represents under the title "*fissura splenialis*" a longitudinal sulcus which extends the greater part of the length of the mesial surface, and ends in front in a T-shape. In his figure there is a faint line proceeding from the neighbourhood of the hippocampal fissure around the posterior margin of the hemisphere on to the dorsal surface of this in a manner similar to the sulcus  $\alpha'$  in *Bradypus*. There is, however, no mention of any such sulcus in his description. Moreover, Ziehen, who has recently examined the brains of four representatives of this genus, makes no mention of any such sulcus. He simply states ‡ that in *Manis* he found a *fissura splenialis* 15 mm. long, which extended further forward than the genu of the corpus callosum, and ended in a T-shape, 4.5 mm. from the frontal pole.

The specimen of *Manis* to which I had access in the College of Surgeons presented on the mesial surface a sulcus exactly resembling that which Weber figures and describes under the name "*fissura splenialis*."

Before passing on to the consideration of the cranial surface of the pallium we may briefly consider, in the light of the imperfect data at our command, the significance of this  $\alpha$ -system of sulci, which in some form or other is present in all the heterogeneous representatives of this order, with the exception of the smooth-brained *Chlamydophorus* and *Cycloturus*.

If we examine the mesial surface of the brain of the Sheep (*Ovis aries*) we shall find a clearly-defined series of sulci presenting an arrangement analogous to the  $\alpha$  series in the

\* Pouchet, *op. cit.*, tom. vi. pl. iv. fig. 10.

† Max Weber, *Zool. Ergebnisse*, ii. tab. ix. fig. 69.

‡ Ziehen, 'Das Centralnervensystem der Monotremen und Marsupialier,' Jena, 1897. p. 156.

Edentata. We find a deep sulcus beginning just in front of the termination of the rhinal fissure, and following a course upward and then forward, parallel to the corpus callosum. Before reaching quite as far as the genu this deep sulcus stops as such, but it may be continued as a shallow furrow obliquely upward on the dorsal surface. To this Krueg has applied the name "*fissura splenialis*," from its relation to the *splenium corporis callosi* \*. An independent sulcus pursues a course parallel to the anterior extremity or *genu* of the corpus callosum, and is hence known as the *fissura genualis*.

In the important memoir of Krueg to which reference has just been made, the presence and essential uniformity in the arrangement of this splenial sulcus in all the Ungulata is clearly demonstrated by means of a beautiful series of illustrations and a lucid description. Two years later the same investigator earned our further gratitude by showing, in the same clear manner, the existence of an analogous sulcus in a large series of other mammals, including the important order of Carnivora †.

From these valuable series of observations we learn that in a very considerable number of widely-separated mammals we find a constant arrangement of sulci corresponding to those which we have called  $\alpha'$  and  $\alpha''$  in *Myrmecophaga*, and which together form a feature for which Krueg has introduced the term *fissura splenialis*. We also learn that a *genual sulcus* surrounds the anterior extremity of the corpus callosum, but its shallowness and inconstancy point to the fact that it is of considerably less importance than the splenial sulcus.

The high importance of the splenial sulcus is shown not only by its depth, its constancy, and its well-defined features, but also by the fact that it is the first pallial fissure to make its appearance in the Cat and probably also in the Sheep ‡. In the foetal Cat it begins as a small arcuate sulcus behind the corpus callosum, which is analogous to the permanent condition of this sulcus in *Dasypus* §. As the hemisphere grows, the *sulcus splenialis* extends forward. In the development of this sulcus in the Edentata it is highly probable that a similar mode of development would be found in *Myrmecophaga* and *Orycteropus*, for the posterior vertical part of the sulcus which we have called  $\alpha'$  is deeper than the rest, and in *Orycteropus*, if not in others, it is "complete." It is this postero-ventral part of the sulcus, moreover, which is the most constant. We have already had occasion to observe the constancy of its relation to the rhinal fissure not only in *Orycteropus* and *Myrmecophaga*, but also in the *Bradypodidae* and possibly in the *Dasypodidae*.

In many families of Marsupials we find a sulcus upon the mesial surface of the hemisphere, which presents the typical relationship to the *fissura rhinalis* which characterizes the *sulcus splenialis*. In many Marsupials (e. g. *Phascolarctos*) this sulcus is quite short, and is confined to the situation corresponding to that in which the early splenial sulcus

\* Julius Krueg, "Ueber die Furchung der Grosshirnrinde der Ungulaten." Zeitsch. f. wiss. Zool. Bd. xxxi. p. 308.

† Julius Krueg, "Ueber die Furchung auf der Grosshirnrinde der Zoonplacentalen Säugethiere," Zeitsch. f. wiss. Zoologie, Bd. xxxiii.

‡ Vide Krueg, *op. cit.*, Zeitsch. f. wiss. Zoologie, Bd. xxxi. & xxxiii.

§ Vide Krueg, *op. cit.*, Bd. xxxiii. Taf. xxxiv.

first makes its appearance in the kitten's brain. But in other Marsupials (e. g. *Macropus*, *Thylacinus*) the sulcus extends upwards, and frequently crosses the upper border to reach the dorsal surface of the hemisphere.

In the larger Chiroptera we find a very extensive and fully-developed splenial sulcus in a brain which lacks a genual fissure. Turner has figured it in *Cynonycteris collaris* and *Pteropus medius*\*. I have examined and found practically the same arrangement in *Pteropus poliocephalus*.

There is a general tendency, therefore, in most of the mammalian orders to the formation of a definite splenial sulcus upon the mesial surface of the hemisphere. We find this tendency clearly expressed in the Edentata as well as in the Marsupialia, Ungulata, Cetacea, Carnivora, and Chiroptera. It is therefore the expression of a very general tendency among the Mammalia, and the fact that this fissure develops upon parallel lines in the different families of Edentates must not be considered as an indication of their mutual affinity, but rather of their wider kinship with the general body of mammals. In the Monotremata, or rather in *Echidna*, which alone of the two genera possesses a convoluted brain, we find no definite splenial sulcus, and this absence seems rather to accentuate the closer interrelationship of the other mammals, in which the sulcus in question is never lacking in a convoluted brain.

If we examine the brain in the large series of mammals which possess some representative of this sulcus, we shall find in many and very diverse orders an extensive and regularly-arched sulcus extending forward in a "genual" manner such as we have met in *Orycteropus* and *Xenurus*. We have already noted the existence of such a splenial sulcus in *Pteropus* and other large Chiroptera; in many Cetacea we find a similarly extensive and regularly arcuate splenial sulcus, as for instance Turner's figure of *Balaenoptera* † shows; we find the same arrangement in many Ungulata, as for instance in *Equus*, and among the Carnivora we find an admirable example of the same arrangement in *Proteles cristatus* ‡. In the latter brain Krueg distinguishes the anterior part of the large arcuate sulcus as *genual*, and the rest of the fissure as *splenial*. The inconstancy and variability of the genual sulcus show that it is of very slight morphological importance, and in many cases it may be merely a mechanical product. The splenial sulcus, however, is a much more definite and constant feature, and is obviously of great morphological significance. But the most constant part of the splenial sulcus is that portion which lies behind and below the splenium of the corpus callosum. In a series of mammalian brains this part of the sulcus is absolutely constant in all hemispheres which have any pallial sulci whatever; it is also the deepest part of the sulcus; it is, as we have seen in the Cat, the first part of the sulcus to appear in ontogeny, and from comparative studies we find that many brains (e. g. *Phascolarctos*) which possess no other true pallial sulci have a small splenial sulcus in this situation. The posterior or ventral part of the splenial sulcus is the constant element, but the anterior part is much more

\* Turner, *op. cit.*, Journal of Anatomy and Physiology, vol. xxv.

† Fig. 33.

‡ W. H. Flower. "Anatomy of *Proteles*," Proc. Zool. Soc. London, 1869, fig. 4.

variable, often insignificant or entirely lacking, and altogether of quite minor morphological importance. In the Sloths we have seen that these two elements in the splenial sulcus, the constant element ( $\alpha'$ ) and the variable element ( $\alpha''$ ), are quite distinct the one from the other.

If we turn from the consideration of the splenial sulcus in the majority of mammals to its condition in the Primates, we are surprised to find that the sulcus which is usually described as the "splenial" is lacking in its most essential part, namely in that retrosplenial portion which we have just learned to regard as the only constant part of the sulcus. Thus Turner\*, in common with many other writers, uses the term "splenial fissure" as synonymous with "calloso-marginal fissure," tacitly implying a homology which is extremely questionable. We are quite prepared to admit that the calloso-marginal fissure of Man and the other Primates may represent the inconstant and morphologically unimportant ( $\alpha''$ ) element of the splenial sulcus, but it obviously does not represent the whole, nor in fact the most important part, of that fissure. Moreover, it seems highly improbable that the most constant sulcus of the pallium throughout the Mammalia, the earliest fissure to make its appearance in development and often the only "complete" sulcus present, should entirely vanish in the Primates.

One of the first, if not actually the earliest, sulci to make its appearance in the development of the human pallium is a short, oblique, and very deep furrow a short distance behind and slightly below the splenium of the corpus callosum. This important sulcus has been called by Professor Cunningham † the "*anterior calcarine*." The features of this sulcus in its earliest stage are so analogous to the earliest stage of the "splenial fissure" of Krueg in the developing brain in the Cat that the question of their homology naturally suggests itself. When we remember that the anterior calcarine sulcus is a complete and a very constant sulcus, of obviously great morphological importance, and that it makes its appearance in a situation analogous to that occupied in most mammals other than the Primates by a very constant sulcus which is sometimes complete and of undoubted morphological importance, there is sufficient evidence to justify us in suggesting, as a tentative working hypothesis, the morphological identity of the two structures, *i. e.* of the *anterior calcarine fissure* of Primates with the essential or caudal part of the *splenial fissure* of most other mammals. For it seems to me unlikely that such a deeply-imprinted feature, which, almost alone of all the pallial fissures, tends to make its appearance in all the mammalian orders, except the specialized Monotremes, should suddenly disappear in the Primates without leaving any trace behind. If we glance at such a brain as that of *Lemur nigrifrons*, which Turner has reproduced ‡ from a memoir of Flower, the resemblance of the calcarine fissure to the  $\alpha'$  element of the splenial sulcus is indeed striking, since the sulcus in question presents the characteristic relationship to the rhinal fissure. In Man and the Man-like Apes the similarity is not so striking, not

\* Turner, *op. cit.*, Journal of Anatomy and Physiology, vol. xxv. p. 143.

† D. J. Cunningham, "The Surface Anatomy of the Primate Cerebrum," Cunningham Memoirs of the Royal Irish Academy, No. vii., 1892.

‡ Turner, *op. cit.*, Journal of Anatomy and Physiology, vol. xxv. fig. 38.

only because the rhinal fissure has vanished, but also because the "calcarine fissure" appears to branch backward and upward into two other sulci, the posterior calcarine (in Man) and the parieto-occipital respectively. But, as Cunningham remarks\*, these latter fissures are of vastly less morphological importance.

In many of the Carnivora we see the beginning of that backward extension of the occipital pole of the hemisphere which produces the occipital "lobe" of the Primates, and as a result of this growth the "*calcarine limb*" of the splenial sulcus (or in other words the  $\alpha'$  element) becomes acutely bent on the "*calloso-marginal limb*" or  $\alpha''$  element of the splenial sulcus. It is not difficult to understand that the continuation of such a process results in the separation of the calcarine from the less important and more unstable calloso-marginal element in the Primates. In this manner we would have produced the extensive calcarine sulcus which Cunningham describes† in the Anthropoid Apes.

[Since the above was written I have met with the following interesting remarks, which lend considerable support to the thesis I have independently put forward. In discussing the question "whether we are justified in saying that quadrupeds have a far less developed occipital lobe than the Primates," Professor Moriz Benedikt says‡:—

"The first argument for this view is that the quadrupedal classes of animals have no occipital fissure. This statement appears to me to be contrary to the real condition. The stem of the fork-shaped occipital fissure (the combined calcarine and parieto-occipital) of Man is characterized as an arc with its convexity directed towards the posterior pole, and it surrounds that part of the gyrus fornicatus which limits the splenium corporis callosi. When we search after this fissure in a great number of gyrencephalic animals, we find it, but only in connection with the fissura calloso-marginalis.

"It may be remarked that in certain anomalous human brains the fissura calloso-marginalis does not come to an end, as in typical cases, by being curved upwards, so as to form the posterior limit of the paracentral gyrus of Betz. It is continued towards the posterior part, forms a limit between the præcuneal gyrus and the corresponding part of the gyrus fornicatus, and unites with the stem of the fork-shaped fissure in such a manner that this stem becomes the most posterior part of the calloso-marginal fissure."

This is most important and valuable corroborative evidence; for what Benedikt calls "the stem of the fork-shaped fissure" is the same sulcus which Cunningham calls "anterior calcarine" and which I have already regarded as the caudal extremity of the splenial sulcus. Speaking of Benedikt's earlier expression of this view §, Professor Cunningham says, "Upon his further statement that the calcarine fissure is also developed in brains below the Primates we are not in a position at present to offer an opinion" ||.

\* Cunningham, *op. cit.*, Cunningham Memoirs, p. 41.

† Cunningham Memoirs, *op. cit.*

‡ Moriz Benedikt, "Some Points on the Surface-Anatomy of the Brain," *Journal of Anatomy and Physiology*, xxv. p. 211.

§ Moriz Benedikt, "Der Hinterhaupts-Lappen der Säugethiere," *Centralbl. f. d. med. Wissensch.*, 1877, No. 10.

|| D. J. Cunningham, "Complete Fissures of the Human Cerebrum," *Journal of Anatomy and Physiology*, vol. xxiv. p. 343.

It seems to me that the suggestive mass of evidence in favour of the view that the "retro-limbic fissure" of Quadrupeds is the homologue of the calcarine sulcus of Primates cannot be lightly gainsaid.]

The great bulk of the literature relating to the brain in the Edentata is mainly concerned with the cranial aspect of the pallium. But although this is the case, the information to be culled from a study of this mass of descriptive matter is of a very imperfect and in many ways an unsatisfactory nature, for our methods and ultimate aims in investigating the anatomy of the brain are now vastly different from those which inspired the authors of the records which we find so disappointing in their insufficiency. It would therefore be hardly justifiable to enter into a serious discussion of many aspects of the study of the surface of the brain which take a foremost place in the memoirs to which reference will be made.

It will conduce to clearness in the description of the surface of the pallium in this order if we begin with the consideration of *Myrmecophaga*, in which the fissures very clearly conform to a well-recognized type.

In the memoir of Gervais \* we find excellent representations of the conformation of the pallium in a specimen of *Myrmecophaga*, as well as a figure of a cranial cast of another specimen. In the more recent memoir of Forbes † we find some very useful semi-diagrammatic figures of the brain in two specimens of *Myrmecophaga*. My observations were made upon two specimens in the galleries of the Royal College of Surgeons; but, as one of these brains was still clothed with its membranes, practically only one was available for examination. A partially-dissected specimen of the brain of *Myrmecophaga* in the stores of the College enabled me to investigate many points in its internal anatomy. Figure 7 represents the left lateral aspect of one of the brains of *Myrmecophaga* in the College of Surgeons, and may serve as a type upon which to base our description.

The ventral boundary of the pallium is formed by the rhinal fissure, which consists of an approximately parallel anterior segment passing by a regular arcuate course directly into the posterior rhinal segment. The latter forms an angle of about 120° with the former, and hence the posterior part of the pallium descends to the base of the brain as a large dependent process behind the pyriform lobe. Above the point of junction of the anterior and posterior rhinal fissures we find a triangular depressed area of pallium, which we may distinguish as the *fossa Sylvii*. Its posterior border is formed by a vertical lip which begins below at about the mid-point of the oblique posterior rhinal fissure. As it ascends this lip diverges from the lip formed by the pyriform lobe at the posterior rhinal fissure, and when it has reached a point about 7 mm. from the dorsal surface of the hemisphere (viewed in profile) it curves backward for a short distance and terminates suddenly. Thus we find the *fossa Sylvii* limited below and behind by two prominent arcuate lips, the convexities of which face one another. These lips meet below, but above and in front they are widely separated. In this broad interval the depressed area of

\* P. Gervais, *op. cit.* pl. i. figs. 3, 3a, and 3b, and pl. ii. fig. 3.

† W. A. Forbes, *op. cit.*, Proc. Zool. Soc. London, 1882.

pallium gradually slopes up to the general level of the pallium without any definite lip to separate it from the rest of the surface. Toward the anterior extremity of the fossa, however, an ill-defined ridge of cortex or lip makes its appearance just above and parallel to the anterior rhinal fissure. In other words, a horizontal depression about 1.5 mm. broad is found immediately above the posterior half of the anterior rhinal fissure; from the anterior extremity of this depression a sulcus begins and extends obliquely upward and forward toward the antero-superior corner of the hemisphere, where it terminates at a point about 2 mm. from the apex and an equal distance from the mesial border of the pallium. We may distinguish this sulcus by the designation  $\beta$ . Upon the right hemisphere of the same brain the *fossa Sylvii* presents features which closely resemble those upon the left hemisphere, and the sulcus  $\beta$  arises in the same manner, but does not extend so near to the mesial plane. But in addition we find in this hemisphere a small oblique sulcus, 9 mm. long, upon the dorsal aspect of the apex, just in front of the termination of the sulcus  $\beta$ . In the brain which Gervais figures the two hemispheres appear to be perfectly symmetrical so far as the *fossa Sylvii* and the sulcus  $\beta$  are concerned. The lips which limit the *fossa Sylvii* appear to be more prominent, and in addition there seems to be a definite though faint lip bounding the *fossa Sylvii* in front. As a result of the existence of this anterior lip, the upper extremity of the *fossa Sylvii* seems to be converted into a definite fissure, which arches obliquely upward and backward and then pursues a course of about 10 mm. in the caudal direction parallel to the great interhemispherical cleft (*vide* Gervais, pl. i. figs. 3 and 3a). So far as we can judge from Gervais's figures, the sulcus  $\beta$  is quite independent of the *fossa Sylvii* and the fissura rhinalis, but begins at a distance of 2 mm. above the anterior rhinal fissure and extends obliquely forward to cross on to the mesial surface of the hemisphere at a distance of about 4.5 mm. from the apex of the pallium. Unlike the condition in our type-specimen, the sulcus  $\beta$  appears to be symmetrical in the two hemispheres. Forbes represents the sulcus  $\beta$  in one of his specimens extending into continuity with the rhinal fissure; but he remarks that the area in front of the sulcus  $\beta$  (which, in accordance with the extraordinary suggestion of Broca, he calls the "frontal lobe") is connected to the *fossa Sylvii* (Broca's "lobule sous-sylvien") by a small, sometimes deep, bridging fold.

At a distance of about 6 mm. from the mesial plane there is, upon the dorsal surface of each hemisphere, a longitudinal sulcus which we may distinguish as  $\gamma$ . The anterior extremity bends obliquely outward and downward, and is 13 mm. distant from the apex of the hemisphere. The posterior extremity approaches quite close to the posterior border of the hemisphere, and bends outward for a short distance parallel to it.

In the specimen figured by Gervais the anterior extremity of this sulcus does not bend laterally, but otherwise it agrees with our type-specimen. In all cases the sulcus  $\gamma$  approaches very close to the sulcus  $\beta$ , but without actually joining it.

The broad elliptical area which lies between the posterior lip of the *fossa Sylvii* and the posterior margin of the hemisphere is divided into two approximately equal parts by a deep vertical sulcus, which begins above at a point about 4 mm. (viewed in profile) below the sulcus  $\gamma$ , and ends below at about an equal distance above the ventral margin of the hemisphere. This sulcus, which we may call  $\delta$ , is approximately symmetrical

upon the two hemispheres. From the postero-ventral corner of the hemisphere a shallow furrow ascends upon the left hemisphere for three or four millimetres, and upon the right hemisphere a more definite sulcus in the corresponding place. We may call this the sulcus  $\epsilon$ .

Upon the right hemisphere of our type-specimen there is a faint trace of a vertical furrow midway between the sulcus  $\delta$  and the *fossa Sylvii*. We may refer to this as the sulcus  $\eta$ . There is no sign of it upon the left hemisphere.

In the figure of the lateral aspect of the brain which Gervais gives there are two extensive vertical sulci upon the postero-ventral area of pallium, and a trace of a third. The exact homologies of these sulci are somewhat doubtful. It is possible that the most caudal represents an exceptionally well-developed sulcus  $\epsilon$ , and the more anterior the sulcus  $\delta$ .

Upon the left hemisphere of our type, as well as in the specimens figured by Gervais and Forbes, there is a shallow horizontal furrow midway between the anterior part of the sulcus  $\gamma$  and the narrow tapering extremity of the *fossa Sylvii*. This may be distinguished as  $\delta'$ .

If we compare the arrangement of sulci upon the cranial surface of the hemisphere of *Myrmecophaga* with the principal and more constant fissures which are found upon the pallium in the Carnivora, we must admit that the resemblance is so close that it suggests something more than a mere coincidence. The similarity is so striking that we do not hesitate to compare one by one the sulci of *Myrmecophaga* with sulci which are obviously homologous in almost any Carnivore. The resemblance is perhaps more striking in the case of the small Carnivores, because smallness implies a simplicity in the arrangement of the sulci. In the larger Carnivores the pattern becomes complicated by the introduction of numerous subsidiary and morphologically unimportant sulci. But in such a brain as that of *Proteles*, of which Flower has provided us with admirable illustrations\*, we find hemispheres devoid of all the subsidiary sulci and only the important sulci remaining. In such a type we find the homologues of the sulci of *Myrmecophaga* preserved, while most of those not represented in the brain of the Ant-eater are also lacking in the small Carnivore. For purposes of comparison, however, I shall refer to the better-known brain of the Dog, of which many admirable descriptions are available.

In the Dog we find a fissure arising from the point of junction of the anterior and posterior rhinal fissures, and extending obliquely upward and backward. It is customary among writers to call this the "Sylvian fissure," but we must accept this term, which is borrowed from human anatomy, with some reservation. The so-called Sylvian fissure of the Dog's brain is rather an early expression of those factors which, in the human brain, produce large folds of pallium that overlap an intermediate area of sunken cortex, and by their meeting form a fissure.

The so-called Sylvian fissure in the Carnivora ought to be regarded as analogous rather than strictly homologous to the true or human Sylvian fissure. In the Carnivora

\* W. H. Flower, "Anatomy of *Proteles*," Proc. Zool. Soc. London, 1869.

the downward bending of the posterior part of the pallium, which results in the production of the large post-rhinal tongue-like process, necessarily implies a restriction to, or rather a tension on, the growing pallium at the seat of the bending. It is not unlikely that this flexure produces a kink—the *fossa Sylvii*—at the place of bending, and that the tension of the growing cortex in this region is relieved by the outgrowth of lips of pallium at the margins of the kink. In the human brain both of these factors become greatly exaggerated, and a much larger area becomes involved, but the process is probably analogous to that which takes place in the Dog.

In the Dog's brain the Sylvian fissure is formed by the meeting of two lips of the pallium, which extend toward their place of meeting by overlapping a depressed area of cortex. If these lips be cut away, we expose a triangular depressed area of exactly the same shape as the *fossa Sylvii* in *Myrmecophaga*. The anatomy of this region of the Dog's brain has been most lucidly demonstrated by Dr. Langley\*. In the dissection represented in his figure 16 we find a triangular depressed area or *fossa Sylvii* (which he calls the "Island of Reil"), limited on the ventral side by the convex junction of the two parts of the rhinal fissure; on the caudal side bounded by an almost vertical limiting furrow, which is formed by the outgrowth of overhanging lip (which has been cut away in the dissection); and bounded in front and dorsally by an oblique furrow which is formed by the overhanging anterior lip. The superior limiting furrow joins the posterior limiting furrow above, and the two are analogous to the *sulcus limitans insulae* of the human brain. It is also noteworthy that a narrow horizontal depression extends forward from the *fossa Sylvii* above the anterior rhinal fissure, just as we find in *Myrmecophaga*, but in the Dog this depression is overlung by the anterior extremity of the upper lip or operculum.

Thus the representative of the sulcus  $\beta$  in the Dog's brain appears in a superficial view to join the anterior rhinal fissure.

In *Myrmecophaga* there is no Sylvian fissure, even in the sense in which this term is applied to the Carnivore's brain. But we have a *fossa Sylvii*, which is limited posteriorly by an operculum that has not yet overlapped the depression, and anteriorly by the very faintest trace of an anterior operculum. Before we can say that a Sylvian fissure exists, these two lips must increase considerably in size, overlap the depressed area, and ultimately meet to form a fissure.

The exposure of the *fossa Sylvii* in the Edentata is indicative of the small extent of pallium as compared with the Carnivore.

The sulcus  $\beta$  is represented in the Dog by a sulcus which is called *supraorbital* by Flower † and others, or *pre-Sylvian* by Owen and others. The sulcus  $\gamma$  is represented in the brain of the Carnivora by a longitudinal sulcus known as the *coronal* or *sagittal* sulcus. In the Carnivora, however, the cephalic extremity of the coronal sulcus is usually bent in the lateral direction to accommodate the crucial sulcus, which is lacking in the Edentata. The caudal extremity of this sulcus is

\* J. N. Langley, "The Structure of the Dog's Brain," *Journal of Physiology*, vol. iv. See especially, in this connection, pl. vii. fig. 16.

† W. H. Flower, "Anatomy of *Proteles*," *Proc. Zool. Soc. London*, 1869, p. 479.

often bent downward, and in *Myrmecophaga* it is quite possible that this occasional feature of the Carnivorous brain may occur, for in our type-specimen we find a faint depression  $\gamma''$  in the situation where this more extensive sulcus occurs at times in the Dog.

The only sulcus in the post-Sylvian region of the Dog's brain which presents any constancy is one that Owen calls *post-Sylvian*, while Krueg distinguishes it as *posterior supra-Sylvian*. It corresponds to the sulcus  $\delta$  in *Myrmecophaga*. But in the Dog it usually forms part of a large arc, the anterior extremity of which may possibly be represented in *Myrmecophaga* by the small but constant depression  $\delta'$ .

In the Dog the growth of the Sylvian opercula covers up the Sylvian fossa and forms the fissure of Sylvius, and after that has taken place the tension of further growth is relieved by the formation of the large *supra-Sylvian sulcus*.

In the Dog a sulcus, which is not nearly so constant as the posterior supra-Sylvian, is sometimes found between the latter and the Sylvian fissure. The occasional furrow  $\eta$  in *Myrmecophaga* may represent this sulcus, which in the Dog is called the "*posterior ecto-Sylvian fissure*" by Langley (*op. cit.*), who has modified Wilder's nomenclature.

The furrow  $\epsilon$  in *Myrmecophaga* finds its analogue in a sulcus of the Dog's cerebrum, which Wilder and others following him have called *ecto-lateral*.

From this brief review we have seen that every sulcus or depression upon the pallium of *Myrmecophaga* finds an analogue to correspond with it upon the brain of the Dog. Moreover, we find that if a large number of Dogs' brains be compared, or if we compare the brains of a large number of different Carnivores, the constant and deepest sulci are those which we find represented in the brain of the Great Ant-eater.

There is, however, one important and very significant exception to this generalization. In the Dog, as in all Carnivores, we find a short deep sulcus extending transversely outward from the interhemispherical cleft near the cephalic extremity of the pallium. This sulcus, commonly known as the *crucial*, is a very characteristic feature of the brain in Carnivora, and is quite lacking in the brain of *Myrmecophaga*. This absence is very significant when we recall the fact that physiological experiment has shown that the pallium which immediately surrounds the sulcus in the Dog is the only "excitable" or "motor" area of the cortex. It may be that the brain of the Dog shows a marked superiority over the brain of the Ant-eater in that the central area, which presides over skilled movements, shows a sudden increase in extent, resulting in the formation of a new sulcus, the *crucial*.

On the other hand, the formation of the crucial fissure may be to some extent the expression of a general, rather than a local, increase in the extent of the pallium. For we find in the brain of the small Carnivore *Genetta tigrina*, which Mivart has described, an absence of a true crucial sulcus, whereas all the sulci found in the Edentata are well developed\*. In this small and very active Carnivore there are only some shallow pits to represent the crucial sulcus, and, as we have no reason to believe that skilled movements are less developed in this family than in the other Carnivores, it is possible

\* St. George Mivart, "Notes on some Points in the Anatomy of the *Eluroidea*," Proc. Zool. Soc. London, 1882, p. 516, fig. 11.

that the general growth of the pallium may have some influence in the production of the crucial sulcus.

Apart from this apparent difference in the extent of the excitable areas of the cortex, there are other differences between the pallia in the contrasted brains.

If we compare the size of the brain in *Myrmecophaga* and *Canis*, we shall find a striking contrast between the two organs. In his valuable monograph upon the weight of the brain in mammals, Max Weber\* gives the weight of the brain in grammes as compared to the body-weight in four specimens of the Great Ant-eater as follows:—

	Brain- weight.	Body- weight.	Percentage of Brain-weight to Body-weight.
<i>Myrmecophaga jubata</i> , ♀ .....	75	: 20,800	0·36 %
"    "    ♂ .....	84·5	: 25,500	0·33 %
"    "    ♀ .....	87	: 23,000	0·37 %
"    "    ♀ .....	84	: 28,086	0·29 %

From the same lists I select for comparison the brain-weights of four Dogs whose body-weights approximate to those of the Ant-eaters, and express them in a similar manner thus:—

	Brain- weight.	Body- weight.	Percentage of Brain-weight to Body-weight.
<i>Canis fam.</i> : <i>Bernhard</i> , ♀ .....	116	: 28,000	0·41 %
<i>Canis fam.</i> : <i>Sagax venaticus</i> + <i>Extrarius</i> <i>aquaticus terre nove</i> , ♂ .....	107	: 27,500	0·39 %
<i>Canis fam.</i> : ditto, ♂ .....	98	: 25,000	0·39 %
<i>Canis fam.</i> : <i>Molonossus</i> .....	95	: 21,000	0·45 %

In all of these Dogs there is a most decided superiority in the brain-weight over that of the Ant-eaters.

The brain-weight in Dogs is exceedingly variable, as Weber's tables amply demonstrate, but in all Dogs approaching the size of a *Myrmecophaga* there is a very decided superiority in the weight of the Dog's brain over that of the Edentata. Among other species and genera this superiority is even more striking. Thus in *Canis jubatus*, according to Weber, we find a brain weighing 160 grms. in an animal of only 23,600 grms., *i. e.* a brain 0·7 % of the body-weight, and in *Felis pardus* a brain of 130 grms. in an animal of 23,820 grms., or 0·54 % of the body-weight. On the other hand, in a *Hyæna striata* weighing 28,750 grms., or more than the heaviest of the four Ant-eaters, Weber found a brain weighing nearly 81 grms., or 0·28 % of the body-weight. This, however, must have been a very exceptional case, for in another specimen of the same species and of the same sex he found a brain of 89 grms. (*i. e.* heavier than the brain of any of the Ant-eaters), while the animal weighed merely 17,500 grms., thus giving a brain-weight which is 0·508 % of the body-weight.

\* Max Weber, "Vorstudien über das Hirngewicht der Säugethiere," Separat-Abdruck aus Festschrift für Carl Gegenbaur, Leipzig, 1896.

In the Dog the brain is, roughly speaking, more than 10% of the body-weight heavier than in the Ant-eater, taking into consideration only animals of approximately the same size.

We find upon examination that the difference in size of the brain in *Myrmecophaga* and *Canis* (in animals of approximately the same size) is almost wholly a question of the extent of the cerebral cortex.

Now in *Myrmecophaga* the rhinencephalon is both relatively and absolutely very much more extensive than it is in *Canis*, and hence the disproportion between the size of the pallium in the two brains is even greater than a comparison of the brain-weights might lead us to imagine. It becomes an interesting question to determine what effect this increase in extent has upon the configuration of the pallium.

I have already explained the effect of local hypertrophy of the excitable cortex in the production of the crucial sulcus and the lateral displacement of the anterior end of the coronal sulcus ( $\gamma$ ). I have also shown how two definite opercula form around the fossa Sylvii and ultimately expand so as to cover up that depressed area. In addition to this the homologues of the sulci which the pallium of *Myrmecophaga* presents become deeper and more extensive in the Dog, and large numbers of new sulci make their appearance to enable the more extensive pallium to accommodate itself in a minimum space.

Let us notice also some general results of the larger pallium. In the Ant-eater the posterior border of the hemisphere is vertical, and the hemisphere itself entirely in front of the cerebellum. In the Dog the general expansion of the cortex is relieved by the caudal extension of the postero-superior part of the hemisphere over the cerebellum, so that the posterior border becomes oblique. This backward or occipital extension has obvious effects upon the mesial surface, which need not be specifically detailed.

This occipital extension of the pallium in the Carnivores is analogous to the much more pronounced growth in the caudal direction which we find in the Primates.

I have discussed at some length the points of resemblance and of contrast in these two brains in order to explain more clearly the salient characters of the brain in the Ant-eater. We have thus been able to estimate those features which constitute the superiority of the Dog's brain over that of the Ant-eater, and have been impressed with the important conclusion that the two brains are built upon essentially the same plan, or, in other words, that the same factors which are at work in moulding the pallium in the Carnivora are fashioning the homologous part of the brain of *Myrmecophaga* in the same likeness.

The significance of these facts will be considered later. At present I merely note the resemblance. The records of any observations which have hitherto been made upon the brain of *Tamandua* are of the scantiest nature. Gervais gives a figure representing the dorsal aspect of a cranial cast\*, and Pouchet gives figures of the dorsal and lateral aspect of the cerebral hemispheres†, but these figures are very unsatisfactory, because they lack all detail. Even a landmark so well-defined as the rhinal fissure is represented only in a small part of its course.

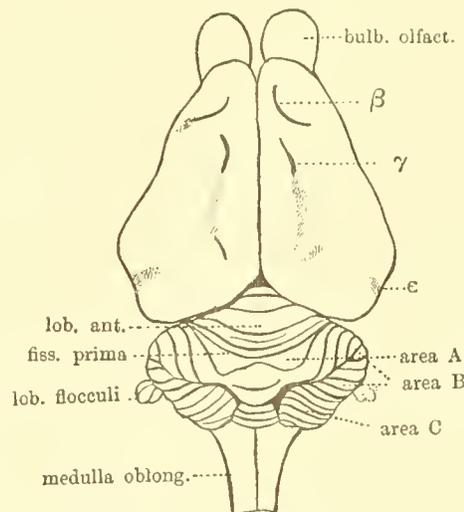
\* P. Gervais, *op. cit.* pl. ii. fig. 2.

† G. Pouchet, *op. cit.* pl. v. figs. 1 & 2.

Forbes has given us an exceedingly crude scheme of the dorsal aspect of one hemisphere of *Tamandua* \*. My own observations were made upon these brains, one of which had been left to the Royal College of Science by Professor Huxley, and the other two are at present in the galleries of the Royal College of Surgeons. To illustrate my description I have constructed a semischematic drawing (fig. 8) from one of the specimens in the College of Surgeons.

If we imagine an extension of the process of simplification which would be necessary to reduce the brain of *Canis* to the condition of *Myrmecophaga*, so that in a smaller brain all the less pronounced features in the brain of the latter became eliminated, and the more deeply-impressed characters became more faintly marked, we should gain some idea of the appearance of the brain of *Tamandua*. We have seen that in *Canis* the faintly-marked lips which serve to denote the boundaries of the fossa Sylvii of *Myrmecophaga* have become definite opercula which cover up the fossa Sylvii. In *Tamandua* the lips entirely disappear, so that we find no trace of a fossa Sylvii, for the pallium above the regular arc formed by the rhinal fissure is smooth. The sulcus  $\beta$ , which we have seen to correspond to the supraorbital sulcus of the Dog, is represented by

Fig. 25.

Dorsal surface of brain of *Tamandua tetradactyla*. Nat. size.

a short oblique sulcus which does not approach nearer than 4 mm. to the rhinal fissure in our type-specimen. This sulcus is constant in the six hemispheres which I have examined, as well as in the figures of Pouchet and Forbes. It is even visible as a depression upon the cranial cast which Gervais represents. This is the most constant sulcus upon the cranial surface of the pallium in *Tamandua*. In this connection it is not without interest to note that, according to Krueg †, it is one of the earliest fissures to make its appearance in the development of the pallium in the Cat, as well as in the Sheep and Ox.

\* W. A. Forbes, *op. cit.* fig. 5.† Julius Krueg, *Zeitsch. f. wissensch. Zool.* Bd. xxxiii.

A *sagittal sulcus* ( $\gamma$ ) pursues a course parallel to and at a distance of about 5 mm. from the interhemispherical cleft for about the middle two fourths of the margin of the hemisphere in our type-specimen. Just behind its caudal extremity there is another short sulcus which probably belongs to the same series. In a second brain this sulcus is also present in both hemispheres, but is interrupted and in parts very shallow on the right side. In the third specimen the sagittal sulcus is represented in each hemisphere merely by short sulci at the cephalic and caudal extremities of the position which the sulcus would occupy. These short sulci are united by a very shallow furrow. In Pouchet's and Forbes's illustrations continuous sagittal sulci are represented; while in the cranial cast figured by Gervais deep coronal grooves are indicated, and each apparently lodges a large blood-vessel.

Just below the caudal extremity of the sagittal sulcus ( $\gamma$ ) there is in our type-specimen a shallow, almost vertical sulcus, which probably corresponds to the sulcus  $\delta$  in *Myrmecophaga*. In one of the other two brains this sulcus is even more faintly marked still, but in the third we find an exceedingly interesting condition. In this brain there are indications of an arcuate sulcus resembling the suprasylvian sulcus in the Carnivora. A sulcus begins a short distance above the point of junction of the anterior and posterior rhinal fissures, and after arching upward and backward for a short distance it passes into a shallow furrow which curves backward and vertically downward in a situation exactly analogous to the sulcus  $\delta$  in *Myrmecophaga*. It seems as though this represented a more complete arcuate or *suprasylvian sulcus* than is present in *Myrmecophaga*. It may be that the depression  $\delta'$  in the latter represents the cephalic extremity of the arc. Upon the left hemisphere of this brain of *Tamandua* we find the upper part of the arcuate sulcus without the descending part.

The cranial cast of *Tamandua* which Gervais has represented\* is considerably larger than any brain which I examined or of which there is any record. From this cast we might gather that the sagittal ( $\gamma$ ) and supraorbital ( $\beta$ ) sulci were deeper and more definitely mapped out than they are in the brains we have examined.

In the absence of any fossa Sylvii it would have been difficult to detect in the brain of *Tamandua* any resemblance to the Carnivorous type of brain, but *Myrmecophaga* provides for us the needful connecting-link. For, while clearly exhibiting the family type which binds it to *Tamandua*, it shows us how the Sylvian fissure becomes obliterated, so that the transition from the Carnivorous to the simple *Tamandua* type is easy to follow.

A notable demonstration of this resemblance is given by the developing brain of *Felis*, which Krueg has figured †. At a period just before the Sylvian fossa makes its appearance, the configuration of the pallium of the foetal kitten presents a surprising resemblance to the adult *Tamandua*, with its supraorbital ( $\beta$ ), sagittal ( $\gamma$ ), and suprasylvian ( $\delta$ ) sulci.

At the same time *Tamandua* demonstrates the superiority of the Carnivore's brain. For in the latter order a brain of the dimensions of that of *Tamandua* would certainly

\* P. Gervais, *op. cit.* pl. ii. fig. 2.

† Julius Krueg, *op. cit.*, Zeitsch. f. wissensch. Zool. Bd. xxxiii. Taf. xxxiv.

be more richly furrowed even than that of *Myrmecophaga*. We know that the pallium increases in extent in any order with the added bulk of the animal. A Carnivore as small as *Cycloturus* would have a pallium with as complex a pattern as the Great Ant-eater.

I have not had an opportunity of examining the brain of the small arboreal Ant-eater *Cycloturus*, but, judging from the figures of Tiedemann, Pouchet, and Gervais, its pallium must be quite smooth and devoid of sulci. The transition from *Tamandua* with its shallow and faintly-marked sulci to the smooth condition is quite simple, and amply justified by the difference in size between these two Ant-eaters.

One cannot fail to be struck by the resemblance in the configuration of the hemisphere of *Tamandua*, and especially *Cycloturus*, to the Rodent type. Moreover, the exact shape of the corpus callosum and the behaviour of the hippocampal formation, which we have found so variable elsewhere, are closely reproduced in the Rodentia. When we compare the brain in the Rodentia with that of the Myrmecophagidæ, we can confidently affirm that any superiority of type that may exist certainly does not favour the Rodent. Unfortunately no collection of brain-weights is available for comparing the two groups on the basis of relative size of brain. The solitary brain-weight of *Tamandua* which Max Weber gives\* is much higher than that of any Rodent of approximately the same body-weight. But a large mass of data is necessary before we can confidently compare the two groups.

It is sufficient at present to note that there is an interesting series of transition stages in pallial modification in the Carnivora, Myrmecophagidæ, and Rodentia. But while the evidence at our disposal conclusively shows the distinct superiority in cerebral organization of the Carnivore over the Ant-eater, it does not permit us to say that the latter is in any way inferior to the Rodent.

All the information we possess clearly and decisively points to the undoubted kinship of the Ant-eaters with the Sloths and Armadillos. But for several reasons I propose to consider next the pallium of the Aard-vark. From the writings of Pouchet and Gervais one might conclude that there is a close resemblance between the brains of *Myrmecophaga* and *Orycteropus*. I shall demonstrate that such a belief is utterly illusory and erroneous, and shall discuss *Orycteropus* in this place in order to show the strong contrast between the two forms, and in this way to accentuate the importance of the agreement we have found between *Myrmecophaga* and the Carnivora.

In our brief review of the literature relating to the brain in different families of Edentata, we found that practically nothing was known of the brain in the Orycteropidæ beyond its general shape. Leuret published some observations† upon the brain of *Orycteropus* sixty years ago, but, acting under the mistaken idea that mammals might be classified according to the relative richness of their cerebral convolutions, he included in one group three such dissimilar brains as those of *Orycteropus*, *Macropus*, and *Pteropus*, without giving us any information of lasting value.

\* Max Weber, *op. cit.*, Gegenbaur's 'Festschrift,' 1896.

† Leuret, 'Anatomie comparée du Système nerveux,' Paris, 1838.

Writing thirty years after Leuret's original memoir, Pouchet says \* that the Ant-eaters form with *Orycteropus* a separate group, in which we find an agreement in the arrangement of the convolutions and in the general form of the brain. The same writer says (p. 16), in reference to a late fœtus of *Orycteropus*:—"Quant aux circonvolutions, leur analogie est complète avec celles du Tamandua." He proceeds to state that in the adult the resemblance to *Myrmecophaga* becomes more marked. In giving details to support the latter statement, Pouchet gives a free rein to his imagination. Probably the culminating instance of this is his statement that the fissure of Sylvius is well marked (p. 17). There is not the faintest trace even of a *fossa Sylvii*.

Gervais also insists in equally decided terms upon the close resemblance between the brain, and especially the cerebral cortex, in *Myrmecophaga* and *Orycteropus* †. He concludes his remarks upon this subject with the following words:—"Je lui [l'*Oryctérope*] trouve une analogie incontestable avec celui du grand Fourmilier, c'est à dire du Tamanoir. L'un et l'autre ont dans leur forme quelque chose du cerveau des Carnivores, mais avec moins de circonvolutions, et le type en reste distinct à certains égards." And Forbes adds his testimony to this fancied resemblance, which Pouchet and Gervais had previously described, in the following terms:—"Orycteropus in its cerebral characters seems to approach *Myrmecophaga* more nearly than any other form, the sulci and gyri of the brains of the two forms, as well as their conformation, being very similar" ‡.

In two animals which follow similar modes of life and whose dimensions are not widely different, it would be strange if there were not some points of resemblance, but there is not so much justification for pointing resemblances in the pallium of *Orycteropus* and of *Myrmecophaga* as there would be in a comparison of *Ovis* with *Canis*. It is perhaps only just to the authors of the remarkable statements quoted above to mention that there is no evidence to show that any of them ever saw the brain of an adult *Orycteropus*.

In spite of a somewhat illusory resemblance in general shape, which naturally obtrudes itself in the examination of cranial casts, the configuration of the actual brain of *Myrmecophaga* presents a decided contrast to that of *Orycteropus*. To begin with, the shape of the pallium is very different in the two forms. For in *Orycteropus* the ventral boundary of the pallium, which of course is formed by the rhinal fissure, is horizontal; and hence there is no caudal downgrowth of pallium such as we find in the brain of the Ant-eater. There is no trace of a *fossa Sylvii* in *Orycteropus*, for the pallial area immediately above the mid-region of the rhinal fissure is quite smooth.

In my specimen of *Orycteropus* a sulcus, the arrangement of which is analogous to that of the *supraorbital* or *presylvian* sulcus of the Dog and to the sulcus  $\beta$  in *Myrmecophaga*, springs from the mid-point of the anterior rhinal fissure, and extends obliquely forward and upward to within a distance of about 5 mm. from the interhemispherical cleft. In the two brains of *Orycteropus* in the College of Surgeons, this sulcus springs from the cephalic extension of the posterior rhinal fissure, which is independent of the anterior rhinal fissure.

\* G. Pouchet, *op. cit.* tom. vi. p. 15.

† P. Gervais, *op. cit.* pp. 47 & 48.

‡ W. A. Forbes, *op. cit.* p. 295.

From about the mid-point of the sulcus  $\beta$  another sulcus takes origin, and after arching mesially and caudally, extends directly backward as far as the posterior extremity of the hemisphere. This sulcus is exactly analogous to the *sagittal sulcus* ( $\gamma$ ). In parts this sulcus is very shallow and sometimes interrupted. In my specimen the sulcus is more complete upon the left than upon the right hemisphere.

The relations of the sulci  $\beta$  and  $\gamma$  the one to the other are constant in the three brains to which I had access. This arrangement differs but slightly from that obtaining in *Myrmecophaga*, and which is generally prevalent among the quadrupedal Mammalia having convoluted brains. The appearance of the combined sagittal and supra-orbital sulci and the relation of the latter to the rhinal fissure present even greater resemblance to the arrangement prevalent in the Ungulate brain than that of the Carnivore.

Midway between the sagittal sulcus and the rhinal fissure we find a series of fragmentary sulci whose extent is variable in different brains. The horizontal sulcus of which they constitute the rudiment is the homologue of that which Krueg calls the *fissura suprasylvia* in the Ungulata\*. This sulcus is the homologue of the suprasylvian sulcus of the Carnivora, and of the rudimentary representative ( $\delta$ ) of this in *Myrmecophaga*.

In many Ungulata the "fissura suprasylvia" is horizontal, just as it is in *Orycteropus*, but in others the more definite formation of a Sylvian fissure becomes associated with an arcuate arrangement of the suprasylvian sulcus. In the Carnivora and *Myrmecophagide* the representatives of the suprasylvian sulcus always present a deep ventral concavity. At the same time we must not lose sight of the fact that in many Ungulata the suprasylvian sulcus is decidedly arcuate. But we associate this arcuate condition of the sulcus in question with a relatively much higher degree of pallial development than is necessary to give rise to an arcuate condition in the Carnivora. In other words, an arcuate suprasylvian sulcus is a characteristic feature of the Carnivore's brain, whereas in that of the Ungulate it is an indication of a high state of pallial development.

The fact that *Orycteropus* possesses supraorbital ( $\beta$ ) and sagittal ( $\gamma$ ) sulci, which are analogous to those I have already described in *Myrmecophaga*, is not to be considered as an indication of a close kinship, but merely signifies that both of these peculiar animals belong to the great group of mammals which also includes all the Ungulate and Unguiculate animals, as well as, in all probability, the Rodentia and Chiroptera.

The fact that *Orycteropus* possesses a horizontal rhinal fissure, and consequently exhibits no tendency towards the formation of a pallial downgrowth at the posterior part of the hemisphere, distinguishes this peculiar mammal from the Ant-eaters and Unguiculata, and suggests a *rapprochement* with the Ungulata.

But, it may be argued, the absence of a fossa Sylvii in *Orycteropus* clearly distinguishes it from the Ungulata, in which a Sylvian fissure (in the same sense in which this term is used in speaking of the Carnivora) is well developed. But there are distinctions between the Sylvian fissure of the Carnivore and the Ungulate. In the Ungulata it is

\* Julius Krueg, *op. cit.*, Zeitsch. f. wissensch. Zool. Bd. xxxi.

unusual to find the fossa Sylvii, or the fissure which is formed by the meeting of its lips, so well defined in the neighbourhood of the rhinal fissure as is customary in the Carnivora. Sometimes, it is true, the posterior lip is as well defined as it is in Carnivora, as, for instance, in the brain of the Pig (*Sus*); but very often the posterior lip, which we have already noted as the most important boundary of the fossa Sylvii, is not so well formed, and in many Ungulates the Sylvian fossa becomes reduced to insignificant proportions. In some Ungulates it becomes so far reduced as to be a mere horizontal depression above the caudal extremity of the anterior rhinal fissure, with no attempt at the formation of a fissure. The most extreme instance of this reduction with which I am acquainted is the Musk-Deer (*Moschus moschiferus*), excellent figures of which have been provided for us by Flower\*.

In this animal we find a brain of peculiar simplicity, which presents a remarkable resemblance to that of *Orycteropus*. If we compare Flower's fig. 12 with the representations of the lateral aspect of the hemisphere of *Orycteropus* (figs. 2 and especially 5), this similarity will be at once apparent. In the two brains of *Orycteropus* in the College of Surgeons we have already observed that the anterior is distinct from the posterior rhinal fissure, and that the latter extends forward for some distance above and parallel to the former. This arrangement becomes more intelligible when we compare it with the condition in *Moschus*. In this interesting brain the posterior rhinal fissure also *appears* to extend forward above and parallel to the anterior rhinal for a considerable distance. But the anterior rhinal fissure joins the posterior rhinal, before the *apparent* anterior extension of the latter overlaps the former; and in addition the area between the two overlapping fissures is depressed, so that by comparison with *Myrmecophaga* or any of the common Carnivores or Ungulates we find in this depression the representative of the fossa Sylvii. In *Orycteropus* it is probable that the apparent cephalic extension of the posterior rhinal fissure is intrapallial and represents the upper boundary of the fossa Sylvii, the relation of which to the sulcus  $\beta$  is identical with that which obtains in *Myrmecophaga* (fig. 7).

The configuration of the pallium in *Orycteropus* is analogous to that which is found in the simplest form of Ungulate brain. The pallium in *Orycteropus* is relatively much smaller than it is in *Myrmecophaga*, and this fact probably explains the great difference in the size of the corpus callosum in the two brains. It is also much smaller than the pallium in any Ungulate with which I am acquainted.

Tiedemann, Pouchet, and Turner, in the memoirs to which I have frequently referred, have given figures and brief descriptions of the brain of the Two-toed Sloth, and in Gervais's excellent figure of the cranial cast of *Choloaps* the shape and size of a brain of this genus are accurately represented. Leuret and Pouchet have figured the brain of the Three-toed Sloth, and Gervais has represented a cranial cast of this genus.

While these contributions to our knowledge relieve me from the necessity of describing

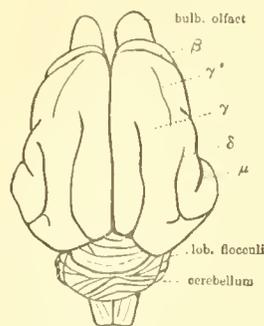
\* W. H. Flower, 'On the Structure and Affinities of the Musk-Deer,' Proc. Zool. Soc. London, March, 1875.

the shape and size of the brain in this family, they unfortunately convey a very imperfect idea of the exact configuration of the pallium of *Cholapus* and *Bradypus*. This is all the more unfortunate because the state of preservation of my specimens does not permit me to describe the pallium with that amount of detail which is desirable. My observations have been made mainly upon two representatives of each of the genera *Bradypus* and *Cholapus*.

In all the representatives of both genera to which I have had access, as well as all those to which reference is made in the memoirs quoted by me, there is a very well-defined supraorbital sulcus ( $\beta$ ) presenting peculiar yet constant features.

In *Bradypus tridactylus* the supraorbital sulcus ( $\beta$ ) appears to spring from the anterior rhinal fissure near its middle, and proceed almost horizontally forward. At its apparent origin from the rhinal fissure this sulcus is very shallow, and may even fail (fig. 11), but it rapidly deepens as it extends forward. It proceeds transversely inward across the anterior pole of the hemisphere (fig. 26), and deeply notches the mesial surface of the hemisphere at its anterior border (fig. 17  $\beta$ ).

Fig. 26.

Dorsal surface of brain of *Bradypus tridactylus*. Reduced to  $\frac{5}{6}$  nat. size.

In *Cholapus didactylus*, and apparently also in *Cholapus Hoffmanni* (judging from Turner's figures), this sulcus presents a disposition exactly analogous to that I have described in *Bradypus* (figs. 12 & 18  $\beta$ ).

In *Bradypus* the sagittal sulcus ( $\gamma$ ) is variable. In the specimen I have represented (fig. 26) there is an extensive sagittal sulcus which is almost two thirds of the length of the hemisphere. It crosses the posterior border to become continuous with the sulcus  $\alpha'$  on the mesial surface. On the dorsal aspect of the anterior pole of the hemisphere there is another sulcus which probably belongs to the same ( $\gamma$ ) series. It begins just behind the sulcus  $\beta$ , and extends backward for a short distance laterally to the main part of the sulcus  $\gamma$ . The representatives of the  $\gamma$  series of sulci present a slightly different arrangement on the smaller brain of *Bradypus*. On the left hemisphere the fissure  $\gamma$  is divided into two parts, just as we have noted in the first brain. Of these the posterior, which is in continuity with the sulcus  $\alpha'$ , extends forward for only about half the length of the hemisphere. The anterior fragment of the sulcus

begins on the *mesial* side of the posterior fragment and extends forward towards the sulcus  $\beta$ , but just before its termination it gives off a peculiar hook-like lateral branch.

On the right hemisphere the sulcus  $\gamma$  is split up into three parts, of which the anterior and posterior are very short and laterally placed. The intermediate segment, which occupies about the middle two fourths of the hemisphere, overlaps both of the other fragments on their mesial side.

In the admirable representation of the dorsal aspect of a cranial cast of *Bradypus* which Gervais gives, the sagittal sulcus is represented by a single and very definite furrow which extends almost the whole length of the hemisphere. After comparing the condition of the  $\gamma$  series of furrows in *Bradypus* with the analogous sulci in *Choloepus*, it seems possible that the fragmentary sulci which we have found in the former may represent the two sagittal sulci which we find in the Two-toed Sloth.

In one of my specimens of *Choloepus didactylus* a sulcus begins near the lateral margin of the posterior surface, and after pursuing a mesial course along the superior border of the hemisphere it bends forward, at a distance of 7 mm. from the mesial plane, and extends the whole length of the hemisphere till it meets the sulcus  $\beta$ . At a distance of 9 mm. from its cephalic limit this sulcus takes a sharp bend toward the mesial plane and continues its course at a distance of about 4 mm. from the great inter-hemispherical cleft. From the caudal extremity of the more mesially placed part of the sulcus a much shallower sagittal sulcus arises and proceeds backward almost to the posterior border of the hemisphere, dividing the area between the sagittal sulcus ( $\gamma$ ) and the interhemispherical cleft into two equal areas. This condition is practically symmetrical in the two hemispheres.

In the second brain there were also two sagittal sulci, but they were apparently not so complete (fig. 12) as those just described.

In a figure which Pouchet gives of the dorsal aspect of the brain of a young Two-toed Sloth two very complete and independent sagittal sulci are represented, of which the lateral unquestionably represents the *sulcus sagittalis* of other forms. Again, in the cranial cast of *Choloepus* which Gervais figures there are two very distinct sulci.

In the brain of *Choloepus Hoffmanni* which Turner has figured, we find fragmentary sulci representing these two sulci. The proper sagittal sulcus crosses the posterior margin of the hemisphere and bends to the lateral side of the mesial or subsidiary sagittal sulcus, where it suddenly ceases. Further forward we find traces of the anterior portion of this sulcus.

The question as to the nature of the mesial sagittal sulcus naturally suggests itself. It seemed at first not unlikely that this sulcus might represent the anterior part ( $\alpha''$ ) of the splenial sulcus, taking into consideration the course of the  $\alpha'$  element of the splenial sulcus and the fact that it is not uncommon for this sulcus to extend on to the dorsal aspect of the pallium in many Ungulates and other mammals. But the existence of a very deep sulcus on the mesial surface in the usual position of  $\alpha''$ , and the extreme shallowness of the mesial sagittal sulcus, lead me to discard this suggestion and to regard the additional furrow as a mere mechanical product of the peculiar pallial growth of *Choloepus*.

When we consider the close resemblance in shape between the brains of the Sloths and the gigantic extinct Ground-Sloths, and in view of the fact that increase in bodily dimensions in any group of mammals usually implies a more extensive pallium, we might expect to find in the brains of *Megatherium*, *Myiodon*, and *Scelidotherium* some signs of a richer pattern of sulci and perhaps a definite medial sagittal sulcus. So far as can be judged from the figures which Gervais gives of the cranial casts of these extinct monsters, the brain of *Myiodon* appears to have been richly convoluted after the analogy of the brain of the rhinoceros. While we can readily recognize the sagittal sulcus, we cannot be sure of the presence of a definite mesial sagittal sulcus after the manner of *Choloepus*. In *Scelidotherium*, whose brain is just like a very much enlarged brain of *Bradypus*, there is a typical sagittal sulcus, but we can recognize no mesial sulcus. The same remarks might apply to the brain of *Megatherium*; but the observer cannot fail to be struck with the apparent simplicity of these two brains. In the brains of such large animals, when we consider the well-developed sulcal pattern in the minute *Bradypus*, we might have expected an extremely rich and complex pattern of sulci. There appears to be some indication of this in the cranial cast of *Myiodon*.

On the lateral aspect of the sagittal sulcus there is, in the brain of *Bradypus*, a strongly-arched sulcus whose features are very constant in all the brains which I have examined, and of which there are records as well in the cranial casts. It is unquestionably the homologue of the suprasylvian sulcus of the Carnivores, to which we have referred as  $\delta$  in the other Edentate brains. It is interesting to note that it is strongly arcuate, like the corresponding sulcus in the Carnivores and its rudiments in the Ant-eaters; for it therefore contrasts in a marked manner with the corresponding sulcus in the lowlier Ungulates and the Aard-vark, in which it is horizontal.

In both of the brains of *Bradypus* which I have examined, a deep furrow springs from the angle of junction of the anterior and posterior rhinal fissures and extends obliquely upward, with a slight inclination backward toward the central point of the concavity of the sulcus  $\delta$ . This furrow we may for the present distinguish as the sulcus  $\mu$ . If we were considering the brain of a Carnivore or an Ungulate, there should be no hesitation in calling the sulcus  $\mu$  the fissure of Sylvius (as that term is generally applied outside the Primates), but there are reasons for some hesitancy in adopting this title in *Bradypus*, because no other Edentate whatever has a Sylvian fissure.

There is a considerable resemblance between the brains of *Bradypus tridactylus* and the small Carnivore *Genetta tigrina*, of which Mivart has given some useful illustrations\*. The cranial aspect of the pallium of *Genetta*, the brain of which is not unlike that of *Bradypus* in shape, is impressed by sagittal, suprasylvian, and supraorbital sulci, which in simplicity are comparable with those of the Three-toed Sloth. The shape and appearance of the suprasylvian sulcus and its relation to the simple oblique Sylvian fissure are exactly comparable to the arcuate sulcus  $\delta$  and its relation to the enigmatical sulcus  $\mu$  in *Bradypus*. A comparison of my fig. 11 with Mivart's fig. 11 demonstrates this, but the similarity of our younger brain is much more surprising. The resemblance

\* St. George Mivart "On the *Æluroidea*." Proc. Zool. Soc. London, 1882, p. 516.

between these two brains is rendered all the more patent from the fact that the crucial sulcus has almost disappeared from the brain of *Genetta*. In making this comparison with the Carnivora, it is interesting to note that in its developmental history the pallium of *Bradypus* (judging from the data Pouchet has provided) closely agrees with such carnivores as *Felis*. Krueg has shown that the arcuate suprasylvian sulcus ( $\delta$ ) makes its appearance very early in the Cat, and the illustrations of foetal brains which Pouchet gives clearly show that the sulcus  $\delta$  is a deep and well-defined furrow before any other furrow makes its appearance on the cranial aspect of the pallium. The later appearance of the sagittal ( $\gamma$ ) and supraorbital ( $\beta$ ) sulci also agrees in the two forms, and there is nothing (so far as I know) in the developmental history to prevent the adoption of the view that the sulcus  $\mu$  of *Bradypus* is the homologue of the Sylvian fissure of the *Æluroidea*.

The sulcus  $\delta$ , which corresponds to the suprasylvian sulcus in brains possessing a Sylvian fissure, presents some interesting points of difference in the two genera of Sloths. We have already noted the constancy of this sulcus in *Bradypus*. It appears to be equally constant in *Cholapus*, for all specimens—the two I have examined, those which Pouchet and Turner represent, as well as the cranial casts—exhibit features which are in agreement, while they all differ somewhat from the equally constant *Bradypus* type.

In *Cholapus* the sulcus  $\delta$  begins anteriorly (fig. 12) either from or in close proximity to the anterior rhinal fissure, a short distance behind the sulcus  $\beta$ . It then arches upward, then backward parallel to the sulcus  $\gamma$ , and finally bends downward on the posterior aspect of the hemisphere to terminate in the neighbourhood of the end of the rhinal fissure. In this manner an extensive arc is formed, which is also well shown in Pouchet's young *Cholapus didactylus* and Turner's *Cholapus Hoffmanni*.

The most puzzling feature of the brain of *Cholapus* is the absence of the sulcus  $\mu$ . In none of the series of brains to which I have had access is there any evidence of the presence of this sulcus. This absence is the principal reason for hesitancy in proclaiming the sulcus  $\mu$  in *Bradypus* the homologue of the fissure of Sylvius in the Carnivore. For if this sulcus is the fissure of Sylvius in the Three-toed Sloth, it is very strange that such an important feature should vanish in the larger brain of the Two-toed Sloth, the pallium of which is more complex. Between the arcuate sulcus  $\delta$  and the rhinal fissure there is an additional horizontal or slightly arcuate sulcus which is lacking in *Bradypus*.

In all the gigantic Ground-Sloths there is a very deep and extensive sulcus  $\delta$  forming a huge arcuate suprasylvian sulcus, after the manner of the Carnivora. There seems to be in addition a well-defined Sylvian fissure, or rather sulcus  $\mu$ . There is therefore in all the Sloths a striking analogy in the configuration of their pallium to that of the smaller Carnivores.

In the smaller and more highly macrosomatic brains of the Armadillos we find a much simpler pallium than among the other families. The series of variations in general form and actual size which characterize the brain in the *Dasyproctidae* are admirably shown by the figures which Gervais has given of *Chlamydomorphus*, *Tatusia*, *Tolypeutes*, *Xenurus*, *Dasyproctus sercinctus*, *Dasyproctus villosus*, and *Priodon* \*.

\* P. Gervais, *op. cit.* pl. ii. figs. 6, 7, 8, 9, 11, 10, and 12 respectively.

In this family we find almost a complete series of intermediate forms between the small brain of *Chlamydomorphus*, which is but 17 mm. long and broader than it is long, and the large brain of *Priodon*, which is not very different in size from those of *Myrmecophaga* and *Orycteropus*, and has cerebral hemispheres not unlike those of the larger Ant-eaters in shape. Between the short broad type of hemisphere of *Chlamydomorphus* and the long and relatively narrow type of *Priodon*, we find within this family all intermediate gradations. In *Xenurus* and *Tatusia* the short square form is not yet lost, while in *Tolypeutes* and *Dasypus*, especially the species *sexcinctus*, we find a decidedly elongate type of hemisphere making its appearance. The transition from the hemisphere of *Dasypus sextinctus* to that of *Priodon* is practically a question of mere increase in size.

In spite of these great variations in external form, there are obvious signs of the family resemblance in the configuration of the pallium. Such being the case, it is of interest to note how much cerebral form may become modified in one homogeneous family. This fact emphasizes the extreme caution which should be exercised in drawing conclusions from the mere shape of the cranial cavity of fossil forms.

In the small brain of *Chlamydomorphus*, which lacks even a rhinal fissure, it is not surprising to find a complete absence of sulci in the small pallial area. The only fissure in the hemisphere of this peculiar Armadillo is the hippocampal, which is absolutely constant in all mammals, and is never found outside the Mammalia.

I have already had occasion to call attention to a small pallial sulcus, distinguished as  $\beta$ , which is present in all the Armadillos except *Chlamydomorphus*. This sulcus is sometimes continuous with the posterior rhinal fissure, as, for instance, in *Dasypus*; at other times it is separate, as in *Tatusia*. It is not unlikely that this small sulcus is the homologue of a more extensive supraorbital sulcus ( $\beta$ ), which the ancestors of the *Dasypodidae* possessed. In this case a small area immediately below the point of junction of the sulcus in question and the posterior rhinal fissure might be regarded as the analogue of the fossa Sylvii.

The disposition of this sulcus (fig. 16), its position on the hemisphere, and its relation to the rhinal fissure all support the analogy to the sulcus  $\beta$ , which I have suggested.

In addition to the pallial sulcus  $\beta$ , there is in *Dasypus* (fig. 14), *Tatusia* (fig. 13), and sometimes in *Xenurus* a second pallial sulcus, which extends obliquely upward and backward from a point just above the junction of the posterior rhinal fissure with the sulcus  $\beta$ . The presence of this sulcus in the genera *Dasypus* and *Tatusia* and its constancy, indicate that it is a feature of some morphological importance. It is not improbable that we must look to the suprasylvian sulcus ( $\delta$ ) of other families for the homologue of this, which we have distinguished as  $\delta$  in the Armadillo. In a brain with a reduced pallium such as that of the *Dasypodidae* the suprasylvian sulcus, which we have already learned to regard as having considerable morphological importance and as appearing early in phylogeny, would probably occupy the situation which the sulcus  $\delta$  occupies in *Dasypus*.

It is particularly unfortunate that the only brain of the *Dasypodidae* with which we are not acquainted is that of the Giant Armadillo (*Priodon*), because it is highly probable

that in this large brain the pallial sulci would be sufficiently well developed to settle these difficult morphological problems\*.

The most noteworthy feature of the brain of the gigantic extinct Armadillo is the relatively diminutive proportions of the cerebral hemispheres. In *Glyptodon* we find hemispheres only slightly larger than those of *Priodon*; and the relatively small pallium appears to be almost, if not quite, smooth. The extreme macrosmatism of the living Armadillo is even more exaggerated in the extinct forms, and especially *Glyptodon*, which exhibits enormous conical olfactory bulbs attached to the hemispheres by means of large peduncles.

Thanks to Max Weber, we have now a more exact knowledge of the brain of the Pangolin than the works of Pouchet and Gervais provide. For in his important monograph upon *Manis* Weber gives us some excellent figures of the brain, accompanied by a brief concise description. I have examined two brains illustrative of this genus.

As I have already pointed out, the anterior rhinal is quite distinct from the posterior rhinal fissure. The latter becomes continuous, as we found to be the case in *Dasyppus*, with a pallial sulcus which extends obliquely upward and forward toward the anterior pole of the hemisphere. Weber calls this the "*fissura præsylvia*," but says that its homology must remain doubtful. I think that we may, without hesitation, regard it as the homologue of the sulcus  $\beta$ , which corresponds to the *præsylvian* (Owen) or *supra-orbital* (Flower) sulcus of other mammals. In Weber's specimen this sulcus becomes directly continuous with a well-defined and typical sagittal sulcus ( $\gamma$ ), in a similar manner to the arrangement we have already noted in *Orycteropus* and in some of our specimens of *Cholpanus* (vide Weber's figures 67 and 68). In the better-preserved of my two specimens the supraorbital sulcus ( $\beta$ ) is not connected to the sagittal sulcus ( $\gamma$ ).

We may, in agreement with Max Weber, regard the area just below the junction of the posterior rhinal fissure with the supraorbital sulcus ( $\beta$ ) as the fossa Sylvii; but I must entirely disagree with him when he describes a Sylvian fissure in addition to this.

Thus he says:—"Aus der Fossa Sylvii ziehen zwei weitere Furchen: die eine [ $\beta$ ] nach vorn und oben, um in die später zu nennende Fissura sagittalis einzutreten, die andere vertikal nach oben, um weiterhin nach hinten umzubiegen. Letztere möchte ich als Fissura Sylvii deuten, während die Homologie der ersteren mir zweifelhaft geblieben ist." † This region of the brain is unfortunately not shown clearly in Weber's figures, because it is not easy to determine which are true sulci and which merely vascular depressions. In the only brain of *Manis* upon which I have been able to examine this region there is a large arcuate fissure, which appears to spring from the lowermost part of the supraorbital sulcus, and behaves in a manner exactly similar to the suprasylvian sulcus ( $\delta$ ) in the Sloths. The homology of this sulcus with the suprasylvian sulcus of

\* In a popular work edited by Martin Duncan (Cassell's 'Natural History': London) a figure, entitled "Brain of the Armadillo," accompanies a description of *Priodon* (vol. iii. p. 183). The brain is as richly convoluted as that of the Sloths, but is utterly unlike that of any Armadillo I know, and is certainly not the brain of *Priodon*; for, apart from the configuration of the cerebrum and cerebellum, the olfactory bulb is relatively as small as that of *Cycloturus*, while all the Armadillos have enormous bulbs.

† Max Weber, *J. Zool. Ergebnisse*, p. 87.

other mammals seems to be much more likely than with the Sylvian fissure, as Weber suggests.

The arrangement of the sulci in this brain presents a peculiar resemblance, in respect to different points, to the brain of the Armadillos and Sloths. On the one hand, the general plan, the arcuate suprasylvian sulcus, the sagittal sulcus, and the supraorbital sulcus considered together, strongly recall the brain of the Sloth. And yet we must at the same time admit that these features are the common inheritance of widely different mammalian families. On the other hand, the condition of the rhinal fissure and its relation to the supraorbital sulcus shed an interesting light upon the brain of the Armadillo. More especially is this the case in the fœtal *Manis* (*vide* Pouchet, *op. cit.* pl. v. fig. 9), in which the combined posterior rhinal fissure and sulcus  $\beta$  form an exact facsimile of the arrangement of these sulci in *Dasyppus*. Then, again, the relation of the suprasylvian sulcus ( $\delta$ ) to the sulcus  $\beta$  in *Manis* is identical with that of the sulcus which we have called  $\delta$  to the sulcus  $\beta$  in *Dasyppus*.

In a brief note Huntington sums up\* the features of the brain in the Edentata (*Myrmecophaga*, *Tamandua*, *Arctopithecus*, *Dasyppus*, *Tatusia*, and *Manis*) in the following terms:—"In the brain (hemispheres) the uniform presence of a more or less modified longitudinal sagittal sulcus parallel to the great longitudinal fissure, the tendency to the formation of a transverse frontal sulcus, and the absence of a distinct Sylvian fissure, are to be noted as Edentate characters."

Taken as it stands, this statement is very misleading. In the first place, "the presence of a modified longitudinal sagittal sulcus" and "the tendency to the formation of a transverse frontal sulcus" are no more entitled to be called "Edentate characters" than they are to the designations "Carnivore" or "Ungulate." Instead of being the special and exclusive characteristic of the Edentata, these sulci are the common property of the whole Mammalia, excluding probably the Monotremata only.

This writer also refers to the absence of the Sylvian fissure as an "Edentate character." In the strict application of the term it may be correct to say that the Edentata possess no Sylvian fissure. But to baldly make this statement with no word of explanation cannot fail to give rise to serious misapprehension. Even admitting, for the sake of argument, that the sulcus  $\mu$  of *Bradypus* is not as much entitled to the name "Sylvian fissure" as the topographically analogous depression in *Genetta*, it seems to me to be distinctly misleading to say of *Myrmecophaga* that it possesses "no distinct Sylvian fissure." This may be literally true enough, but some explanation is surely necessary to indicate that although the Great Ant-eater's brain possesses "no distinct Sylvian fissure," yet, at the same time, it differs only in degree from the brain of the Dog, in which a typical Sylvian fissure exists.

The fuller discussion of the data relating to the pallium will be left for consideration in the concluding remarks. At present we may pass to the consideration of the other parts of the brain.

\* G. S. Huntington, *op. cit.*, Trans. New York Acad. of Sciences, Jan. 13, 1896, p. 98.

## THE BRAIN-STEM.

By the term "brain-stem" we understand that part of the brain which remains after the removal of those morphological excrescences, the cerebral hemispheres and the cerebellum. It is a term which is used merely as a convenience in description, and has no claim to morphological accuracy.

It is unnecessary to discuss in detail the features of this part of the brain, because its morphology is practically unchanged in the main body of mammals, if we make due allowance for purely functional modifications and variations in size. We shall therefore consider this part of our subject in as brief a space as is consistent with lucidity.

The ventral surface of the thalamic region and mesencephalon forms in *Orycteropus*, in common with most other mammals, a broad exposed area (fig. 1) extending from the optic tract in front to the prominent pons Varolii behind. The lateral part of the subthalamic region is hidden by the anterior part of the crus cerebri, which is itself partially overlapped by the *lobus pyriformis posticus*. The mesial border of the anterior extremity of the crus cerebri is about 6 mm. from the mesial plane, but as it proceeds backward it inclines obliquely inward, so that when it reaches the transverse strand of the pons Varolii it is in close proximity to the crus cerebri of the other side.

Thus a triangular interval is left between the anterior extremities of the crura cerebri. A large prominent mass of pale colour occupies this interval. The posterior part of this mass consists of two large ellipsoidal bodies, each 6 mm. long and 3 mm. thick, which are placed so close the one to the other that it is necessary to examine them very closely to discover the slight median groove which indicates their line of separation. They are the *corpora mammillaria*. The interval between these bodies and the optic chiasma is occupied in the mesial plane by the thin floor of the third ventricle—the *infundibulum*—from which the pituitary body is suspended in the normal state. In this specimen of *Orycteropus*, however, the pituitary body has been torn off, leaving an elliptical aperture, which opens into the cavity of the third ventricle (compare fig. 1).

Extending backward from the corpora mammillaria to the pons Varolii there is a deep mesial cleft between the two crura cerebri.

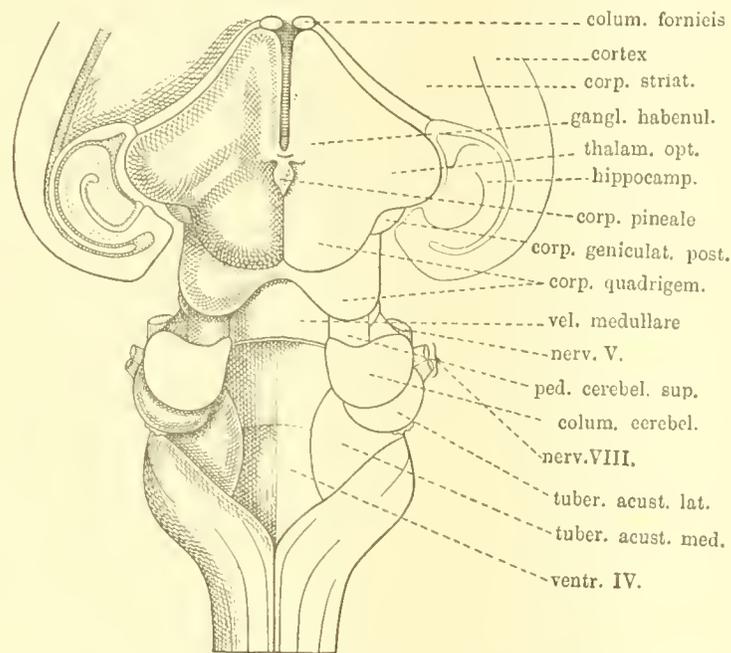
When the crus cerebri makes its first appearance upon the base of the brain by coming from under cover of the optic tract it consists of a strand of fibres 10 mm. broad, but as it extends obliquely backward it becomes narrower and plumper, and when it disappears under the fibres of the pons it is only 5 mm. broad, but 2.5 mm. thick. In many of the other Edentates (figs. 6 and 9) the crus cerebri is a more prominent strand, and this is doubtless a result of the relatively greater size of the pallium than is the case in *Orycteropus*.

The interpeduncular cleft is occupied immediately in front of the pons Varolii by an ellipsoidal nodule of grey substance—the *corpus interpedunculare*—in all the Edentata (figs. 1, 6, and 9). This body is 5 mm. long in *Orycteropus*, and of correspondingly large dimensions in all the other Edentates.

Along the lateral border of the crus cerebri in *Orycteropus*, parts of the optic thalamus

and the mesencephalon may be seen cropping out in a view of the ventral surface of the brain. In the angle between the lateral part of the pons Varolii and the crus cerebri we find a triangular area which we may call the *area tegmenti*, because it is the surface of the *tegmentum*, i. e. the essential part of the basal region of the mesencephalon. In Man the corresponding region is called the *area lemnisci*, because an important nerve-tract in the tegmentum known as the fillet or lemniscus appears on the surface in this situation. In front of the *area tegmenti* we find a very prominent hemispherical boss of grey substance, the *corpus geniculatum posticum* [vel *mediale*]. This body is partly hidden from view by the overlapping fold of cortex (pyriform lobe). If we remove this cortical operculum we shall be able to see the optic tract extending obliquely backward and outward across the crus cerebri, and then expanding to cover a small ill-defined boss of grey substance which is placed just in front of the posterior geniculate body. This is the *corpus geniculatum anticum* [vel *laterale*]. In a view of the base of the brain with the cerebral cortex undisturbed, the anterior geniculate body and the lateral part of the optic tract are hidden from view.

Fig. 27.

Dissection to expose dorsal surface of brain-stem in *Oryzeteropus*. Enlarged  $\frac{1}{3}$  diam.

In a profile view of this region (fig. 2) we can better appreciate the large dimensions of the prominent posterior geniculate body, which seems to rest on the crus cerebri, and by contrast we can see how ill-defined are the boundaries of the anterior geniculate body, which appears as a slight swelling that can only with difficulty be distinguished from the optic tract in front and the optic thalamus on the dorsal side. Above and behind the posterior geniculate body we see the corpora geniculata in profile. But these bodies can be more satisfactorily studied in a dorsal view (fig. 27).

The dorsal surfaces of the optic thalami and the anterior pair of the corpora quadri-

gemina form a large flattened area of a quadrilateral shape. The optic thalami are separated the one from the other by a median slit, which is the third ventricle. A shallow furrow begins on each side near the posterior extremity of the third ventricle and proceeds obliquely outward and backward at an angle of about  $60^\circ$  with the mesial plane; this furrow on each side serves as a line of demarcation between the optic thalamus, which is placed in front of it, and the corpora quadrigemina behind it. The anterior pair of the corpora quadrigemina form two broad flattened eminences (fig. 27) which rise to a slightly higher level than the optic thalami and posterior corpora quadrigemina. Together they form a sector of about  $120^\circ$  of a circle of 9.5 mm. radius. In the mesial line they are separated by a shallow furrow. A small body shaped like an arrow-head lies free in the anterior part of this mesial furrow. This is the pineal body. It is solid, but is attached anteriorly to the thin walls of a pouch-like diverticulum of the third ventricle. A very deep furrow extends across the mesial line under the corpus pineale (fig. 4), and from this the furrows which separate the corpora quadrigemina from the optic thalamus start. If these furrows be traced laterally they will be found to dip down upon the lateral surface of the brain-stem (fig. 27), and in the deep groove thus formed we find the large projecting posterior geniculate body (figs. 27 and 2).

The dorsal surface of the optic thalamus presents a quadrilateral outline. Its anterior and posterior boundaries are two parallel obliquely-placed grooves, both of which begin at the mesial plane and extend outward and backward, the anterior boundary for about 16 mm., and the posterior boundary (which is the thalamo-mesencephalic groove) for 9.5 mm. The postero-lateral extremity of the optic thalamus consists of a large rounded knob, the outline of which resembles, both in extent and degree of curvature, the postero-lateral boundary of the quadrigeminal body. From a profile view (fig. 2) we can readily understand how this large lateral knob of the optic thalamus is related to the ill-defined anterior geniculate body and the optic tract. The oblique antero-lateral boundary of the optic thalamus consists of a deep groove which separates it from the corpus striatum (fig. 27). Upon each side of the posterior part of the third ventricle, and just in front of the attachment of the pineal diverticulum, we find a large pear-shaped area very faintly marked off from the rest of the dorsal surface of the optic thalamus by shallow furrows. This is the *ganglion habenulae*. It extends about as far forward as the mid-point of the slit-like third ventricle and then gradually shades away. A very prominent ridge of nerve-fibres is connected with this ganglion, and forms the dorso-mesial lip of the third ventricle in the whole of its extent: this is the *tania thalami*.

The posterior quadrigeminal bodies form a pair of large rounded projections upon the postero-lateral aspects of the anterior quadrigeminal bodies. They are placed a considerable distance apart, and are connected across the middle line by a tapering narrow bridge of grey substance (fig. 27). Upon the lateral aspect of the mesencephalon each posterior quadrigeminal body is prolonged into an oblique column of a greyish colour which extends downward and forward toward the prominent, somewhat triangular, posterior geniculate body (fig. 2). This column is called the *brachium* of the posterior geniculate body. In the angle between it and the crus cerebri we find the irregularly quadrilateral region of the *area tegmenti*.

In a mesial sagittal section of the brain the ventricles are opened up, but as their features agree with those of the Rodentia, Carnivora, Ungulata, and the main body of Mammals, we merely need review them very briefly.

The third ventricle is a vertical slit-like cavity between the optic thalami. These bodies, however, meet in the mesial plane and fuse so as to form a large elliptical bridge of grey substance—the *commissura mollis*—which therefore causes the disappearance of a large part of the third ventricle. In fact the third ventricle becomes reduced to a narrow channel which surrounds the soft commissure (figs. 4, 17, and 18). The roof of this ventricle is formed by a thin epithelial layer which extends from the upper part of the *psalterium centrale* to the upper part of the pineal body. At the situation of its attachment to the pineal body a little transverse strand of nerve-fibres is found crossing the middle line in the roof of the pineal recess. This consists of fibres proceeding from the *ganglion habenulae* and *tania thalami* of each side to the *ganglion habenulae* of the other side, and is hence known as the *commissura habenularum*. It is sometimes called the *commissura superior*, but Zichen has recently caused some confusion by calling the dorsal commissure in Monotremes and Marsupials by this name\*.

Between the roof of the third ventricle and the posterior superior part of the soft commissure the ganglion habenulae may be seen in the lateral wall of the ventricle as a pear-shaped projection (figs. 4, 17, and 18). The anterior wall of the third ventricle is formed by the lamina terminalis, which extends from the epithelial roof above to the optic chiasma below, and contains the *psalterium centrale* and the anterior commissure.

Between the soft commissure and the *intercommissural copula* (*i. e.* the part of the lamina terminalis [fig. 23, 17.] which links the anterior commissure to the psalterium) a small elliptical aperture will be found in the lateral wall of the ventricle. This is the foramen of Monro, leading into the lateral ventricle. The floor of the ventricle is formed by a thin lamina extending from the optic chiasma to the *corpora mammillaria*. This floor is drawn downward into a funnel-shape—the *infundibulum*—and to its apex the pituitary body is attached (figs. 4 and 18).

The posterior walls of the third ventricle are formed by a very solid mass composed of the anterior end of the mesencephalic tegmentum and the *corpora mammillaria*. The anterior surface of this mass presents a regular curve which leads back to the floor of a narrow channel opening out of the third ventricle. This is the aqueduct of Sylvius. The roof of the anterior aperture of this channel is formed by a large mass of nerve-fibres presenting a sickle-shape in section. This is the posterior commissure. This broad funnel-shaped anterior opening rapidly contracts to a narrow canal, which extends backward, with a slight obliquity upward, and tunnels the mesencephalon between the anterior quadrigeminal bodies and the tegmentum, which forms its floor. As the aqueduct approaches the posterior extremity of the anterior quadrigeminal bodies it gradually expands not only in vertical extent, but even more markedly in the lateral direction, so that an elongated funnel is produced, the wide mouth of which looks in the caudal

\* Zichen, *op cit.*

direction. This mouth is closed by a very thin vertical film—the anterior medullary velum—which proceeds upward to be attached to the upturned edge of the narrow bridge of grey substance which connects the two posterior quadrigeminal bodies

Upon being traced downward this medullary velum (called by the older anatomists the valve of Vieussens) descends until it reaches the tegmentum, upon which it rests, without, however, becoming attached to it. It proceeds backward, forming the anterior part of the roof of the flattened fourth ventricle, and becomes attached to the ventral surface of the cerebellum (figs. 4, 17, and 18).

The aqueduct of Sylvius presents similar features in all the *Myrmecophagidæ*, and in *Choloepus*, *Manis*, and in the majority of mammals included in the Carnivora, Ungulata, Rodentia, Marsupialia, and allied Orders.

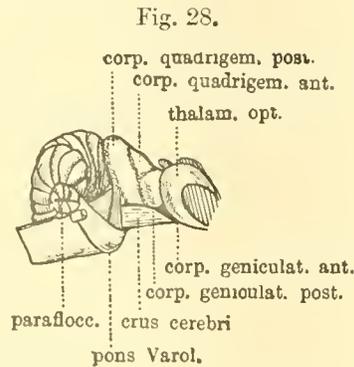
In my specimen of *Bradypus* the wide anterior mouth of the aqueduct gradually tapers as it proceeds backward, so that there is no tubular anterior constriction. Thus the Sylvian aqueduct appears relatively larger than it does in other Edentates (fig. 17).

In the *Bradypodidæ* the posterior part of the roof of the mesencephalon becomes very much elevated, for reasons which we shall consider immediately. As a result of this the posterior infundibular expansion becomes greatly exaggerated. The aqueduct of Sylvius opens out of the third ventricle by a fairly wide opening and rapidly expands, so that the posterior opening becomes very wide and the direction of the canal very oblique. These modifications become most pronounced in *Chlamyphorus*, although they are already very well-marked in *Dasyppus*.

In *Myrmecophaga* and *Tamandua* the anterior corpora quadrigemina become relatively smaller and flatter in comparison to the optic thalamus than is the case in *Orycteropus*, and the posterior quadrigeminal bodies, instead of being lower than the anterior, now rise to a considerably higher level than any other part of the mesencephalon or thalamencephalon. In *Tamandua*, in addition to this, these elevated posterior quadrigeminal bodies now become somewhat flattened between the cerebellum and the cerebral hemispheres. In the *Bradypodidæ* the anterior quadrigeminal bodies become still further reduced, but the posterior geniculate bodies, which in the Ant-eaters and the Aard-vark are already very large, now attain enormous proportions. Compared with the size of the corpora quadrigemina the optic thalamus is proportionately larger than it is in the *Myrmecophagidæ* and *Orycteropus*. I have unfortunately been unable to examine these parts of the brain of *Manis*. But in the *Dasypodidæ* we again find modifications of this region. The anterior quadrigeminal bodies become even further reduced in size than they are in the Sloths, but in addition the optic thalamus is extremely small. In marked contrast we find a large and prominent pair of posterior quadrigeminal bodies which project upward as an elevated ridge between the cerebellum and the cerebral hemispheres. The posterior geniculate bodies attain such large proportions that in a profile view they would appear to be almost half the size of the optic thalamus (fig. 28).

In *Chlamyphorus* these changes become much more pronounced. The anterior quadrigeminal bodies become extremely reduced and the region of the corpora quadrigemina converted into a transverse vertical plate which is interposed between

the cerebellum and the cerebral hemispheres. The posterior geniculate bodies still retain their relatively large dimensions.



Right lateral aspect of brain-stem and cerebellum of *Dasypus villosus*. Nat. size.

In spite of all these variations in form and the relative proportions of different parts, the mesencephalic region in all the Edentates conforms to the same type, which is practically constant in the Marsupialia, Insectivora, Rodentia, Chiroptera, Ungulata, and Carnivora. All the changes which take place are probably the direct expression of functional adaptation to different modes of life. In animals which lead a life such as all the Edentates follow, the sense of sight is of considerably less importance than the sense of hearing and the all-important sense of smell. For most of the animals of this group are nocturnal, and many of them are burrowing animals. They seek their food and pursue the other objects which constitute the sum of their life's exertions at a time or in a manner in which visual sensations must be of subsidiary importance. Even to the dog and cat, who seek their visible prey with the directing aid of a highly-developed visual area of the pallium, the sense of sight is quite subsidiary to that of smell and possibly also of hearing. It is only natural, therefore, to expect in the Edentata, which are not so well provided with a pallial visual mechanism and which pursue their ends under circumstances in which sight can avail them nothing, that the visual sense should be of even more subsidiary importance. We have already seen that the olfactory parts of the brain reach a very great development in this group. The auditory regions of the brain are also exceptionally well-developed, as we shall see later; but it is quite possible that the enormous size of the posterior geniculate body and the large dimensions of the posterior quadrigeminal bodies may also be witnesses to the high importance of the auditory sense.

The waning importance of the visual sense is markedly reflected in the anatomy of the mesencephalon. The anterior quadrigeminal bodies, which are so well-developed in *Orycteropus* and almost equally so in the *Myrmecophagidae*, undergo a conspicuous reduction in the *Dasypodidae*, and in *Chlamyphorus*, in which the visual activity has become so slight as to have earned for it the name "Pichi-ciégo" or "Blind Armadillo." While the anterior quadrigeminal bodies are undergoing this retrogression, the posterior bodies remain, because their chief function is certainly not visual, and hence we get that peculiar transverse ridge-like condition of the mesencephalon in the Armadillos.

I have already had occasion to refer to the pons Varolii in *Orycteropus*. It is a prominent transverse strand (fig. 1) of nerve-fibres which crosses the ventral surface of the brain-stem, and, after bending up on the lateral aspect of the brain-stem on each side, dips into the cerebellum, forming its middle peduncle. In the mesial plane the pons Varolii is 10 mm. broad and 3 mm. thick. It expands slightly on each side of the mesial plane, and then contracts again so that at a distance of 10 mm. from the mesial plane it is merely 6 mm. broad. At this point it splits into two strands to enclose the large fifth nerve, the great majority of the fibres passing in front of the nerve. At the lateral margin of the nerve the fibres collect again to form a rounded cord, the middle peduncle of the cerebellum, which bends round the lateral aspect of the brain-stem, and after a course of 13 mm. in the dorsal direction disappears in the cerebellum.

In *Tamandua* (fig. 9), *Myrmecophaga*, and the *Bradypodidae*, the pons presents similar features, but is relatively larger than it is in *Orycteropus*. In *Manis* and the *Bradypodidae* its features are similar. In *Chlamydomorphus* the pons is a very insignificant bundle of fibres.

On the ventral surface of the medulla oblongata a very prominent band of fibres makes its appearance in *Tamandua* (fig. 9), by coming from under cover of the pons Varolii on each side of the mesial plane. These are the pyramidal tracts or anterior pyramids. They are equally well-developed in *Myrmecophaga*, and only slightly less prominent in the Sloths and Armadillos. But in *Orycteropus* (fig. 1) the pyramidal tracts are flattened bands, the position of which is indicated by the emergence of the roots of the hypoglossal nerve along their lateral borders. The contrast between these insignificant bands and the prominent cords in the Ant-eaters is probably explained by the larger pallium in the latter, because the fibres of the pyramids are derived from it.

Just behind the pons a transverse band of nerve-fibres, the *corpus trapezoideum*, emerges from under cover of the pyramid on each side and pursues a course to the lateral border of the brain-stem. Just behind the situation of the fifth nerve, another and much smaller nerve—the seventh or facial—separates this *trapezium* (or trapezoid) body from the pons Varolii. Upon tracing the trapezium a little beyond the seventh nerve it leads to another nerve or pair of nerves, each of which is larger than the seventh. This is the auditory or eighth nerve, composed of two parts, cochlear and vestibular respectively. These nerves immediately dip into a large mass of grey substance, which we may distinguish as the *tuberculum acusticum laterale* (fig. 27). This lateral acoustic tubercle is an elongated band of grey substance, of a somewhat crescentic shape, which is placed mainly upon the lateral aspect of the brain-stem, at the junction of the medulla oblongata and the pons. It begins ventrally just opposite the lateral margin of the emerging fifth nerve, and is placed in the groove behind the middle peduncle of the cerebellum: it proceeds obliquely upward and backward, and upon reaching the dorsal aspect of the brain-stem it extends directly inward, closely embracing the middle peduncle of the cerebellum in the whole of its course. The greater part of this tubercle lies within the fourth ventricle, since the line of attachment of the epithelial roof of this cavity crosses over the extreme lateral margin of the acoustic tubercle.

Three large and compact bundles of nerve-fibres enter the cerebellum on each side of

the mesial plane. These are known as its peduncles. The superior cerebellar peduncles issue from the mesencephalon and proceed directly backward, at a distance of 9 mm. the one from the other. They soon meet the middle peduncles extending dorsally from the pons and the fibres of the inferior peduncles which ascend from the medulla oblongata and spinal cord. Together the three peduncles of each side form a large and massive column-like support for the cerebellum, and hence the combined mass may be called the *columna cerebelli*. The fourth ventricle is a broad and very shallow cleft which lies upon the expanded dorsal surfaces of the region of the pons Varolii and the upper open part of the medulla oblongata. Its anterior part is placed between the two parallel superior peduncles of the cerebellum, and is roofed by the medullary velum which stretches between these peduncles. The posterior part of the ventricle is triangular in outline, the lateral angle of the triangle extending widely behind the *columna cerebelli* on each side and forming the lateral recess. In the floor of this lateral recess we find the crescentic *tuberculum acusticum laterale*. On the mesial side of this, we find in the floor of the fourth ventricle a larger rounded and very prominent mass of grey matter, which we may call the *tuberculum acusticum mediale* (fig. 27). In the writings of different anatomists the nomenclature of this region is often responsible for much ambiguity. The term "*tuberculum acusticum*" is commonly applied to that body which I have distinguished by the adjective "*laterale*," and the name "*trigonum acusticum*" to my "mesial tubercle"; but these terms are very confusing. For the difference in the name leads writers to regard the tubercle sometimes as part of the trigone, at other times as a separate body, or even to confuse the trigone with the tubercle. For the sake of clearness of description I have introduced the qualifying adjectives "*laterale*" for the tubercle which is probably cochlear, and "*mediale*" for that which is probably vestibular, and called them both "tubercle."

In all the Edentates the features of this region are practically constant and call for no fuller description.

#### THE CEREBELLUM.

We might with almost equal justification begin the description of the cerebellum in the Edentata at the present time with the same remarks which Pouchet employed in introducing the same subject thirty years ago. But if Pouchet found reason in his time to deplore the obscurity which anatomists had allowed to enshroud the comparative anatomy of this important organ, we at the present day have infinitely more reason to bemoan our ignorance. For while the subject of cerebellar morphology has received little more illumination than it had in Pouchet's day, the feverish activity which has prevailed in all other fields of neurological investigation has thrown such a clear light upon the anatomy of the rest of the nervous system that by contrast our ignorance of cerebellar morphology seems to-day greater than ever.

When this investigation was begun two years ago, I found it necessary to study for myself the comparative anatomy of the cerebellum in an extensive series of vertebrates before it was possible to intelligently appreciate the Edentate types of cerebellum, and understand the morphological plan to which these types conform. Perhaps the greatest

hindrance in this study was the stumbling-block which human anatomists have erected in the shape of a cerebellar anatomy which is devoid of a rational morphological basis. The investigator of a large series of mammalian cerebella will appreciate at an early stage in his labours that underlying the apparently irreconcilable differences and seemingly divergent designs exhibited in cerebellar architecture there is, in all the Eutheria and Metatheria, one common fundamental plan which becomes variously elaborated in different animals. It thus becomes possible for him to compare upon a sure and sound basis any cerebellum, ranging from the simplest bifoliate structure of *Notoryctes*, to the most complexly elaborated organ in Man; and it is possible to construct a simple plan for descriptive purposes which will equally apply to any representative of this large series of mammals.

Since this work has been accomplished I have become acquainted with three memoirs dealing with this *terra incognita* of cerebellar anatomy which have recently appeared.

Thanks to the kindness of the author, I have recently received a brief introductory memoir by Stroud, who has studied the development of the cerebellum in the Cat and in Man\*.

This important and interesting communication insists upon the uniformity of the fundamental plan of the cerebellum in *all* mammals, even including the Monotremata. [The writer does not refer to the distinct specialization of the Prototherian cerebellum, which should exclude it from this generalization.]

A most important memoir dealing with the development of the cerebellum in the Sheep and in Man appeared at about the same time as Stroud's contribution, and in many points confirms, and in some other respects tends to refute, Stroud's results. For this important contribution to this much-neglected field of research we are indebted to Walther Kuithan †.

Theodor Ziehen has recently given us a pure description (unilluminated by any suggestions of a general or morphological nature) of the cerebellum in the Monotremata and Marsupialia ‡.

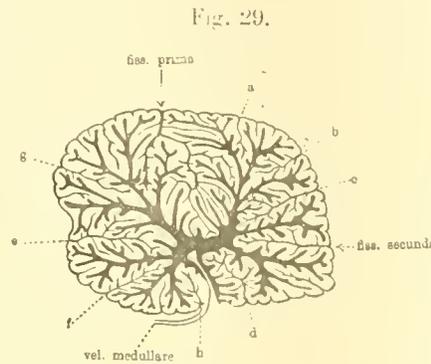
The cerebellum in *Orycteropus* is a large, solid, ellipsoidal mass, the major diameter of which is transverse, and measures (in a specimen which had been for some years in alcohol) 47 mm.; the maximum diameter in the sagittal is 27 mm., and the maximum height is 20 mm. This large, somewhat flattened mass completely covers and hides from view the fourth ventricle, and it is supported on two large columns which are 11 mm. apart: in other words, are 5.5 mm. from the mesial plane on each side. Each of these columns is 9 mm. in diameter, and consists of the combined cerebellar peduncles of its own side. It is obvious from the measurements that the cerebellum must project on each side far beyond these columns of support; but not only is this so, but its ventrolateral extremities are wrapped, as it were, around the lateral aspects of the peduncles so

\* B. B. Stroud, "The Mammalian Cerebellum.—Part I. The Development of the Cerebellum in Man and the Cat," *Journal of Comparative Neurology*, vol. v. 1895.

† Walther Kuithan, "Die Entwicklung des Kleinhirns bei Säugetieren," *Münchener medicinische Abhandlungen*, vii. Reihe, 6. Heft, 1895.

‡ T. Ziehen, *op. cit.*

that the combined peduncular masses are not visible in a profile view. In the exuberance of its growth the mesial cephalic and mesial caudal parts of the cerebellar mass bend in the ventral direction, and become tucked in between the two pillar-like masses formed by the cerebellar peduncles. These cephalic and caudal cerebellar processes come into apposition between the *columnae cerebelli* (as we may call the combined peduncles) and thus produce a deep vertical transverse slit, which we may call the superior recess of the fourth ventricle (*recessus superior*) (*vide* fig. 29).



Mesial sagittal section of the cerebellum of *Orycteropus*. Enlarged  $\frac{4}{3}$  diam.

Anteriorly the cerebellum is in close contact with the posterior extremities of the cerebral hemispheres, and this contact adapts the configuration of the anterior margin of the cerebellum, so that a prominent rostrum is formed projecting forward from its antero-superior margin in the mesial plane. This rostrum projects into the interhemispherical cleft, and partly roofs over the posterior corpora quadrigemina.

Although the surface of the cerebellum is evenly rounded in *Orycteropus* and does not present any of those sudden projections which are found in many mammals, it cannot be considered even or smooth. On the contrary, the surface of the organ will be found on all sides to present slight gradual elevations and gentle depressions, and these hills and vales give the organ an irregularly-corrugated appearance. The surface of the cerebellum is everywhere marked with an exceedingly complicated pattern of lines, labyrinthine in its intricacy. These lines, the arrangement of which we shall find to conform to a more or less definite and orderly plan, represent the situation of the deep fissures, which cut up the whole mass of the cerebellum into a complex mass of narrow leaf-like folds. These folds are mutually adaptive, and are so closely packed that the whole complex of *folia* forms a solid organ.

The lateral poles of the cerebellum are formed of two large bodies, each composed of a complex mass of *folia*. These masses are almost completely separated from the rest of the cerebellum by fissures which cut deeply into the organ until they reach the medullary matter. As the area thus separated off on each pole from the rest of the cerebellum includes the homologue of the *flocculus* of human anatomy, and is a natural division of the organ, we may distinguish it as the *lobus flocculi*, and the deep limiting fissure as the *fissura flocculi*. The latter corresponds to the *parafloccular sulcus*

of Stroud\*, who has shown that it arises at an early period of development in Man and the Cat.

The *lobus flocculi* consists of two morphologically distinct parts, which, adopting Stroud's nomenclature, we may call the *flocculus* and *paraflocculus* respectively. Of these the latter is very much larger than the former, which it flattens against the cerebellar peduncles and completely hides from view. The *paraflocculus* is a large mass of an oval outline, which forms the greater part of the lateral pole of the cerebellum, being adapted to the lateral aspect of the *columna cerebelli*. It is 20 mm. long and 16 mm. broad, and is placed obliquely, and more especially upon the caudal aspect of the pole of the cerebellum. In a view of the cerebellum from above the *paraflocculus* is visible as a crescentic area fringing the lateral and postero-lateral margins of the organ. In a caudal view of the organ the *paraflocculus* is seen as an obliquely-placed tapering mass extending from the lateral pole downward and mesially. The *paraflocculus* is divided by an arcuate fissure into two parts, which we may distinguish as the *paraflocculus ventralis* and the *paraflocculus dorsalis*. The former is crescentic, and consists of eight simple folia, and behind these of a bunch of three folia on one stalk. The *paraflocculus dorsalis* consists of four branches of radiating fissures, together forming an arc above the ventral part of the *paraflocculus*. The *flocculus* consists of a broad flattened group of folia which are hidden under the posterior part of the ventral *paraflocculus* and adapted to the dorsal surface of the *tuberculum acusticum laterale*.

After subtracting the two *lobi flocculi*, the rest of the cerebellum may be divided for descriptive purposes into three azygos lobes, a cephalic, a caudal, and an intermediate or central.

The cephalic lobe, which we may call the *lobus anticus*, is separated from the rest of the cerebellum by a fissure which we may distinguish as the *fissura prima*. This is the deepest fissure which crosses the mesial plane of the organ; it is the most constant fissure in the mammalian series, and is ever present, separating the two simple folia which form the greater part of the simple cerebellum of *Noloryctes*, and in addition it is the first of the fissures which cross the middle line to make its appearance in the course of development, as Stroud and Kuithan have independently demonstrated. It is a fissure of the greatest morphological importance, ranking in this respect with the *fissura flocculi* only. It corresponds to the "*sulcus furcalis*" of Stroud, the "*sulcus primarius cerebelli*" of Kuithan. In human anatomy quite subsidiary importance is attached to this fissure under the name "*fissura preclivalis*."

In a mesial sagittal section this *fissura prima* may be seen cutting very deeply into the organ from the dorsal surface, and extending almost to the *recessus superior* of the fourth ventricle. In this plane it divides the organ into two approximately equal areas, the anterior of which corresponds to the *lobus anticus*. Regarding the dorsal surface of the organ, this fissure may be seen to cross the middle line slightly in front of a point midway between the cephalic and caudal limits of the organ. It extends transversely for about

\* Stroud, *op. cit.*, p. 95.

4.5 mm. on each side of the mesial plane, and then bends obliquely forward and outward to reach the anterior surface of the organ. In this way it cuts off a lozenge-shaped area on the dorsal surface, which forms part of the anterior lobe. On the anterior surface the fissure extends obliquely downward and with a slight lateral inclination, and ultimately reaches the situation where the middle peduncle dips into the cerebellum.

By means of this deep cleft a lozenge-shaped area on the dorsal surface, a large central semicircular area on the cephalic surface, and a long caudally-extending worm-like intercolumnar process on the ventral surface are completely separated from the rest of the cerebellum to form the *lobus anticus*. Stroud, following the precepts of Burt Wilder as regards nomenclature, calls this lobe by the mononym "*preramus*." Kuithan calls it "*Vorderlappen*." Thus both Stroud and Kuithan, on embryological grounds, support the suggestion, which I am advancing for comparative reasons, to separate the region in front of the *fissura prima* from the rest of the cerebellum as a natural primary division, which we may appropriately distinguish as the *lobus anticus*.

The part of the cerebellum which is left after removing the *lobus anticus* and the two *lobi flocculi* is the most complex part of the organ, and, as its subdivisions are not so clearly defined as those of the other lobes, opinions are divided as to the most natural method of subdivision. We may at once neglect Kuithan's subdivision, because he fails to recognize the upper part of the *paraflocculus* in the Sheep, but simply calls it *vermis lateralis*, without suggesting any homology. Otherwise he says little about the region behind the *fissura prima*. Stroud calls the whole of this area "*postramus*." He calls each of the lateral areas of the "*postramus*" a *pitem*, and divides each into a "*prepileum*" and a "*postpileum*."

The objections to the acceptance of this suggestion of Stroud are twofold. In the first place, this mode of dividing up the lateral areas is not sufficiently constant in the lowlier mammals to be fundamental, and if it were it is not sufficiently comprehensive; in other words, this lateral area falls more naturally into three (or perhaps four) subdivisions. In the second place, there is, in the area behind the *fissura prima*, a fissure of higher morphological importance and of greater stability than Stroud's "*interpilar sulcus*." This fissure I shall call the *fissura secunda*, because, of the fissures that cross the mesial plane, it is second in importance only to the *fissura prima*. The *fissura secunda* corresponds to the cleft which separates the pyramid from the uvula in the human brain. Stroud calls it the *uvular sulcus*, and demonstrates its early appearance in the Cat, for he confesses (p. 106) that he does not know whether it or the *fissura prima* develops the earlier. Kuithan's figures show the precocious appearance of the *fissura secunda* soon after the *fissura prima* in the Sheep. But my main reason for adopting this fissure as an interlobar boundary is a comparative one. In all the various types of cerebellum which form a complete gradation from that of *Notoryctes* to that of Man, this fissure is constant, and separates a small caudal area of cerebellum from the complex central mass. Its morphological importance is undoubtedly considerably inferior to that of the *fissura prima*, but to the student of the lowlier mammalian types the adoption of the *fissura secunda* as an interlobar fissure will facilitate descriptive work very considerably.

I propose, therefore, to divide the mesial or "interfloccular" area of the cerebellum

into three azygos lobes by means of the two fissures *prima* and *secunda*. These three lobes will be called *lobus anticus*, *lobus centralis*, and *lobus posticus* respectively. The convenience and clearness of the term "*centralis*" induce me to adopt it, for there is little danger of this term ever being confused with that denoting the small "*lobulus centralis*," a term applied in human anatomy to the cephalic part of the *lobus anticus*.

The *fissura secunda* cuts deeply in a horizontal direction into the cerebellum in the mesial plane, from a point upon the caudal surface a short distance above the sharp ventro-caudal angle. It follows a transverse course of 10 mm., *i. e.* about 5 mm. on each side of the mesial plane, and then bends suddenly at a right angle into the vertical direction, and reaching the ventral surface it extends in the cephalic direction as far as the posterior medullary velum, *i. e.* into close proximity to the cerebellar peduncles.

By means of this peculiar fissure, a little mesial tongue-like process—the *lobus posticus*—is completely cut off from the rest of the cerebellum.

The *posterior lobe* is divided by a deep fissure upon the ventral surface into two main groups of folia. The anterior of these is a small insignificant group of three folia intimately associated with the posterior medullary velum and corresponding to the *nodulus* of human anatomy. The rest of the lobe is a large, complex, triangular mass, which includes the postero-ventral angle of the cerebellum and corresponds to the *uvula* of human anatomy.

The *lobus centralis* constitutes the chief part of the cerebellum. It is limited in front by the *fissura prima*, behind by the *fissura secunda*, and laterally by the *fissura flocculi*. It is a large, irregular, and complicated region, which, in the exuberance of its growth, has bulged obliquely forward and laterally on each side, and, wedging its way between the lateral part of the *lobus anticus* and the front of the *lobus flocculi*, it has extended on the anterior surface as far in the ventral direction as the *columna cerebelli*.

In the caudal direction it shows a similarly exuberant growth, for the lateral parts of the *lobus centralis* bulge downward upon the caudal surface of the organ between the *lobus posticus* and the *lobus flocculi*.

Thus the *central lobe*, which is comparatively narrow in the mesial plane, expands considerably in its lateral parts and embraces the *lobus flocculi*.

This expanded lateral part of the *lobus centralis* on each side may be distinguished as the *area crescens*, for it will be found that in the higher mammals it is the exuberant increase of this part of the cerebellum which is the main factor in the evolutionary process.

The most caudal part of the *lobus centralis* in the mesial plane is naturally separable from the rest as a distinct wedge-shaped sector, which is probably the homologue of the *pyramid* of human anatomy. In *Oryzeteropus* this *pyramid* does not appear to belong to the central lobe, but to be quite distinct from it; and we shall see subsequently that in many mammals the pyramid is quite a subsidiary twig of the large tree-like branch which forms the central lobe. This view is, moreover, supported by developmental evidence, in the case of animals the pyramid of which is independent in the adult.

We shall see later that in the simpler cerebellum of small mammals the pyramid is directly continued in the lateral direction, on each side, into the caudal extremity of the

*paraflocculus dorsalis*, by means of a band of grey substance. This arrangement also exists in *Orycteropus*, but the larger dimensions of the *area crescens* have hidden the connecting band. Bulging downward upon the lateral side of the pyramid, the *area crescens* seems to cut off the pyramid from all connection with the lateral parts of the organ; but if the *area crescens* be raised, a narrow flattened band will be found arching downward from the *pyramid* into continuity with the *paraflocculus dorsalis*.

We are now in a position to understand the course of the *fissura flocculi*, of which little has been said. The floccular fissure separates the floccular lobe from the *area crescens* of the central lobe. It begins anteriorly at the *columna cerebelli*, proceeds in the caudal direction around the lateral pole, then obliquely backward on the dorsal surface of this pole until it reaches the posterior surface; it then proceeds obliquely toward the mesial plane, at the same time inclining downward; after reaching the ventral margin of this surface it bends sharply upward on the mesial side of the *area crescens*, and crosses the mesial plane as the upper limiting furrow (*e*) of the *pyramid*.

The *area crescens* is divided into three chief subdivisions by means of two deep fissures which begin at its lateral margins and extend toward the mesial plane. The more anterior of these fissures, which we may distinguish as *a*, begins on the anterior surface of the cerebellum, in close proximity to the point where the *fissura prima* reaches the *columna cerebelli*. From a surface-view the two clefts, *fissura a* and the *fissura prima*, would appear to arise from a common stem, but a submerged folium really separates them in the whole of their extent. The fissure *a* extends vertically, and hence it diverges from the *fissura prima*. The two fissures thus come to be separated by an anterior district which we may call the *area A*. The fissure *a* ascends vertically on the anterior surface, and then proceeds directly backward on the dorsal surface, and then arches mesially, and at a point about 6 mm. from the mesial plane it joins a much shallower transverse fissure, which we may for convenience of description regard as part of the fissure *a* (fig. 29). The region included between the fissure *a* and the *fissura prima* consists of the two laterally placed, oblique fusiform areas *A* and a mesial quadrilateral area. The latter is joined to the area *A* on each side by a narrow neck.

A second very deep fissure cuts into the lateral border of the *area crescens*, and this we may distinguish by the letter *b*. The fissure *b* starts from the postero-lateral margin of the *area crescens* at a point which roughly corresponds to the middle of the *fissura flocculi*. It cuts transversely into the central lobe, but suddenly comes to a termination at a point about 5 mm. from the mesial plane. At this point we find a shallow depression, which we may call the *medullary area*, for reasons which will be evident later. For the sake of convenience of description, we may denominate a shallow fissure which crosses the mesial plane at this point as part of the *fissura b*.

By means of the fissures *a* and *b* the broad expanded lateral part of the central lobe, which we have called the *area crescens*, is divided into three regions, which we may distinguish as the areas *A*, *B*, and *C* respectively. The area *C*, the most caudally placed of the three regions, is a large amygdaloid mass which projects backward between the *lobus flocculi*, on the lateral side, and the pyramid and *lobus posticus* on the mesial side

and upon the posterior surface of the organ it extends as far as the ventral surface. Mesially it becomes continuous, by means of a very narrow stalk, with the small folium which extends across the mesial plane above the pyramid and is included between the fissures *a* and *c*. The surface of the area C is deeply incised by about 12 fissures, which are obliquely placed and converge toward the mesial stalk.

The area B is by far the greatest of the three subdivisions of the *area crescens*. It is attached to the mesial parts of the organ by a narrow stalk, composed of a single folium, which is wedged in between the areas A and C, but it rapidly expands in the lateral direction and forms a large oval mass, which extends obliquely forward between the *lobus flocculi* on the lateral side, and the area A and the *lobus anticus* on the mesial side, and reaches as far as the *columna cerebelli*. The surface of this area, which forms the nucleus of the large lateral mass of the cerebellum, is deeply scored by numerous fissures, which converge toward the axis of the area, and thus this region becomes split up into innumerable folia, which are arranged like the barbs on a feather. The single folium which forms the stalk of this large mass expands in the middle line to form a little cuneiform mass which is interposed between the mesial continuations of the fissures *a* and *b*.

We find, therefore, that it is possible to divide the *lobus centralis*, according to the conventional mode, into a distinct central part, or *vermis*, and lateral areas. In the case of the *lobus anticus* there is no such natural division. And in the case of the *lobus posticus* the whole lobe belongs to the *vermis*.

The importance of this mode of dividing up the cerebellum into *vermis* and lateral lobes is very much exaggerated by the customary mode of describing the organ.

The bilateral symmetry of the *vermis* is disturbed by bending to the right side, which affects the upper part of the pyramid and the adjacent supra-pyramidal part of the central lobe.

The study of the configuration of the cerebellum as it is demonstrated in a mesial sagittal section is especially instructive. In *Orycteropus* the mesial sagittal section of the cerebellum exhibits an oblong figure with all the angles, except the postero-inferior, rounded off. The dorsal and ventral surfaces are horizontal and considerably longer than the vertical anterior and posterior surfaces.

The arrangement of the lobes and their subdivisions, which is exposed in a mesial sagittal section of the cerebellum in *Orycteropus*, presents the closest analogy to that of the human cerebellum. If we overlook the fact that the general shape of the sections is so different, and that the diameters of the former section are only about one half those of the latter, we might confidently say that the sections are in all essentials identical. This fact is so impressive and significant that we may be pardoned for examining the points of this resemblance more closely.

We may begin at the velum medullare and follow the folia in the caudal direction in the two forms, employing the terms in common use in human anatomy at the present time (cp. Quain's, Schwalbe's, or any of the ordinary anatomy text-books).

The most caudal part of the velum is thickened by transverse bands of grey matter to form the *lingula* in both brains. The rest of the *lobus anticus* presents a very close

resemblance to the combined *lobulus centralis* and the *culmen monticuli* of the human brain, and is quite as complex and built upon the same morphological plan in *Orycteropus* as it is in Man. We find that the area which lies behind the *fissura prima* (*præclivalis* of Man) is strikingly similar in the two forms. This large area is divided into four primary divisions in both cerebella. These fissures are respectively (adopting Schäfer's nomenclature in Quain's 'Anatomy') the *sulcus prægracilis*, corresponding to our fissure *c*; the *sulcus præpyramidalis*, corresponding to our *fissura secunda*; and the *sulcus postnodularis*, corresponding to our fissure *d*. The resemblance between the several areas into which these fissures subdivide the region behind the *fissura prima* is extremely close, and is carried even further than the general shape of the main divisions. The large triangular mass between the *fissura prima* and the fissure *c* is subdivided into three parts by the relatively shallow fissures *a* and *b*, just as the analogous region in the human brain is split up into the *clivus*, the *folium cacuminis*, and the *tuber valculæ* by the *sulcus postclivalis* and the *sulcus horizontalis magnus*.

The area included between the fissures *c* and *d* in the brain of *Orycteropus* presents exactly the same shape which has earned the name *pyramid* for the apparently analogous region of the brain of Man.

It is unnecessary to do more than refer to the *urula* and *nodulus*, for they are obviously homologous in the two cerebella.

In the whole section, then, we find a most striking and surprisingly close resemblance between the two cerebellar types. And, even more surprising still, the degree of complexity of the mesial section in *Orycteropus* is certainly no less rich than it is in Man. It is not surprising, when we find this parallelism between two such distantly-related forms as *Orycteropus* and *Homo*, to find that the same pattern is widely prevalent among the larger mammals, being found equally in the *Carnivora*, *Ungulata*, and *Myrmecophagidæ*.

A mere resemblance between two sagittal sections, even when it is so close and so apparently beyond question as are those of *Orycteropus* and *Homo*, is not, however, a sufficient guarantee of the morphological identity of the similar parts. We need some further corroborative evidence before we can admit their homoplasy. This evidence is to be sought in the behaviour of the lateral extensions of these central parts in a series of cerebella, and also in the developmental history of the parts in the brains under comparison.

The behaviour of the lateral extensions of the *lobus anticus* and the *lobus posticus* amply confirms their suggested homologies in the two forms, and although we cannot supply the embryological evidence to support this view, we can have little hesitation in adopting it as accurate.

While there can be little doubt as to the homologies of most of the segments which present an analogous arrangement in the two sagittal sections, we must confess to grave doubts as to the homology of the *pyramid* of Man with the part we have tentatively called by this name in *Orycteropus*. If we admit that the appearance of a sagittal section is valid and sufficient evidence, we would not hesitate to state the homology at a glance, for the disposition, the relationships, and even the shape of the two parts are exactly

alike. Kuithan has unhesitatingly called the analogous part of the Sheep's brain by the name "*pyramid*," although its disposition agrees exactly with the corresponding part in *Orycteropus*. In the meantime I shall use the term *pyramid* with the reservation that the validity of its homology with the similarly-named part of the cerebellum in Man remains to be proved. This point can be satisfactorily settled only by embryological investigation, and neither Kuithan nor Stroud has attempted to solve the problem.

After we have learned how closely the cut surface of the cerebellum which is exposed in a mesial sagittal section in *Orycteropus* agrees with the arrangement in the brain of Man and the Sheep, it is not surprising to find the closest agreement between *Orycteropus* and *Myrmecophaga* in this respect. So exact is this resemblance that fig. 29 would need only very slight modification to represent a section from the Great Ant-eater. But the agreement is not confined to the mesial section. For in the behaviour of the lateral extensions of the parts we again find a close resemblance between the two organs. In *Myrmecophaga* the lateral parts are not so full and rounded as they are in *Orycteropus*, and hence the organ approaches nearer to a lozenge-shape. The descriptions we have given of the *fissura prima* and the *lobus anticus* in *Orycteropus* apply equally well to *Myrmecophaga*. The *lobus flocculi* is relatively smaller in the Ant-eater, and does not rise nearly so high as it does in the Aard-vark. Both the dorsal and ventral parts of the paraflocculus are horizontal worm-like bands, and the dorsal part especially is much narrower than it is in the Aard-vark. In addition it is much simpler (fig. 7). The *flocculus* is more exposed than it is in the Aard-vark.

The area A of the *lobus centralis* is moreover somewhat simpler than it is in *Orycteropus*. As a result of the smaller size of the *lobus flocculi*, the area B overlaps it to a greater extent than is the case in the Aard-vark. The area C closely resembles the corresponding region in our type, but the mesial region with which it is connected is submerged.

The lateral extensions of the pyramid have more obvious bands than is the case in *Orycteropus*, and thus they appear to form the lowermost folia of the area C.

The cerebellum of *Tamandua* is smaller and simpler, and presents several slight differences to mar the otherwise close resemblance to the organ in the Great Ant-eater. The main features of the anterior lobe are unchanged, but its structure is simplified by a reduction in the number and complexity of the folia.

The general features of the *lobus flocculi* resemble those of *Myrmecophaga*, but the band connecting the posterior extremity of the dorsal part of the paraflocculus to the pyramid now appears to be quite aborted. In a superficial view the folia of the posterior extremity of the paraflocculus appear to be in series with the folia of the area C of the *lobus centralis*. The posterior extremity of the ventral paraflocculus is peculiarly modified to form a projecting tuft of about six folia on a common stalk. This is lodged in a special cavity of the periotic bone, and in the loose nomenclature in common use would be called simply "flocculus."

The area A of the central lobe is a single folium which is cut up by a few shallow sulci, not visible on the surface. The area B is a simplified copy of the corresponding

area of the Great Ant-eater. The pyramid is now simply a branch of the main stem of the central lobe.

In size and general appearance, the cerebellum of *Tamandua* is not unlike that of *Canis*. This resemblance is also borne out to a considerable extent in the detail of most parts of the organ, but the floccular lobe presents a number of differences. The only one of these which we need mention here is the fact that the projecting part of the lobe is formed from the junction of the dorsal and ventral parts of the paraflocculus, and hence is not strictly homologous to the projecting part in *Tamandua*, which is the most caudal part of the *paraflocculus ventralis*.

In spite of the extraordinary difference in size in the cerebella of the Sloths, they present a close structural agreement. The much smaller organ of *Bradypus* is slightly simpler than that of *Choloepus*, but it will suffice to describe the latter. There are very considerable differences between the appearance of the mesial sagittal sections of the brain represented in figure 18 and one in the stock of the College of Surgeons. The latter is larger and much more richly foliated, and, by contrast, the simplicity of the brain represented in figure 18 suggests immaturity. In the latter the pyramid is a very small branch of the central lobe, and forms a peculiar lip which overlaps the medulla oblongata and quite hides the uvula from view. In the specimen in the College of Surgeons the uvula is much larger and forms the ventro-caudal angle of the hemisphere, and the pyramid is a large and independent lobule.

The mesial section has lost the quadrilateral shape it has in the other Edentates we have considered, being now much less angular. A large *lobus flocculi* forms a large mass on each lateral pole. This floccular lobe has a similar appearance in the two Sloths (figs. 11, 12). The *paraflocculus dorsalis* consists of a large inverted V, composed of deep but simple folia. The *paraflocculus ventralis* consists of simple angular folia filling up the space between the limbs of the V. There is a typical anterior lobe, but it presents a quadrilateral shape from being wedged between the two large floccular lobes. The area A of the central lobe resembles that of *Tamandua*. The area B in *Choloepus* is expanded to a much less extent than it is in *Tamandua*, and in *Bradypus* the expansion is even less. As a result, the whole central lobe is simpler and has a more distinctly quadrilateral shape, which is increased by the large floccular lobes which form its lateral boundaries. The area B is only about three times as broad as the central area, with which it is in direct and uninterrupted continuity. Consequently there is merely a very simple arrangement of radiating fissures in the area B, which forms a marked contrast to the feather like grouping in the Ant-eaters. The area C is also much simpler, and, as a result of the lesser expansion of the area B, much broader than it is in *Tamandua*. The pyramid is connected laterally with a group of very broad folia which proceed to the dorsal paraflocculus. These folds may be regarded as part of the area C.

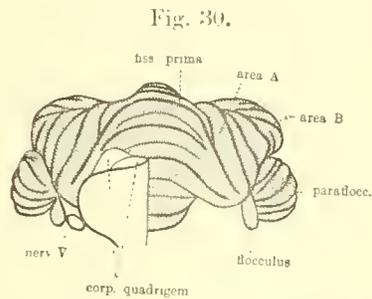
The posterior lobe needs no comment, as it is as constant as the anterior lobe.

In section the cerebellum of *Manis* is definitely quadrilateral, but in structure it is very simple and not unlike the organ in *Bradypus*, excepting that the floccular lobe is relatively smaller in the Pangolin.

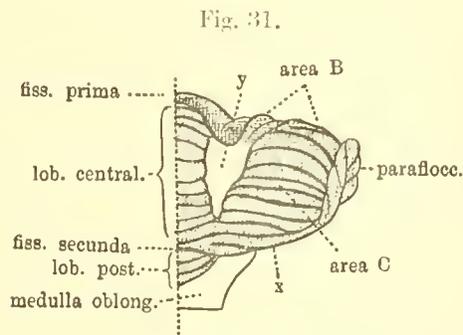
The cerebellum in the Armadillos apparently differs in such a marked manner from that of the other Edentates that we must consider it in more detail.

I shall describe the cerebellum of *Xenurus*, which is typical of the family.

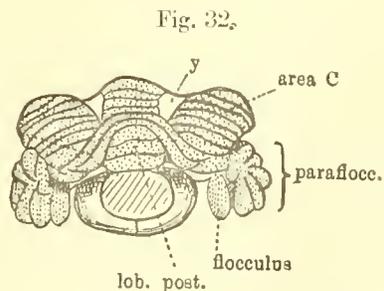
The cerebellum of *Xenurus*, which is apparently constituted so differently from the cerebellum in the other families of Edentata, is really built upon the same plan. Its most marked peculiarity is due to the fact that the *lobus centralis* extends forward like a hood and completely hides the *lobus anticus* from view. But if we remove the cerebral hemispheres and the anterior part of the brain-stem, and examine the anterior surface of the cerebellum (fig. 30), we shall find a typical anterior lobe bounded by a *fissura prima*.



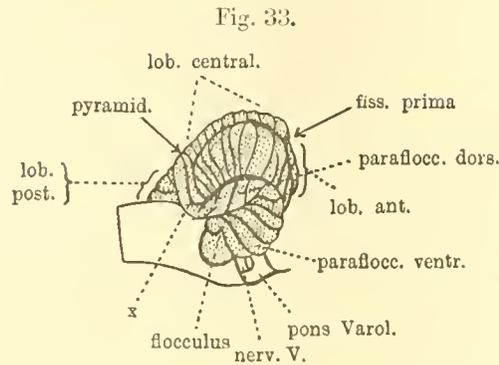
Anterior surface of cerebellum of *Xenurus*. Nat. size.  
The right half of the mesencephalon is delineated *in situ*.



Right half of dorsal surface of cerebellum of *Xenurus*. Enlarged  $\frac{5}{3}$  diam.  
*x.* Grey band connecting *pyramis* to *paraflocculus dorsalis*. *y.* Bare area of medullary substance.



Caudal surface of cerebellum of *Xenurus*. Nat. size.



Lateral (right) surface of cerebellum of *Xenurus*. Slightly enlarged.

The *fissura prima* is a simple areuate fissure strictly limited to the anterior surface. It limits a simple anterior lobe which is subdivided by a few areuate fissures (fig. 30).

The *lobus flocculi* is a prominent and much more independent part of the cerebellum than it is in the other Edentates. In other words, it is not packed so closely.

The paraflocculus is divided, as usual, into dorsal and ventral parts (fig. 33). The *paraflocculus dorsalis* is a narrow worm-like series of simple folia, which caudally become continuous with two broad grey bands (fig. 33, *x*), which arch mesially and then upward to become continuous with the *pyramid*, which is here a small and insignificant twig of the central lobe. The cephalic extremity of the dorsal paraflocculus becomes serially continuous with the *paraflocculus ventralis*, which is composed of much deeper and broader folia than the dorsal segment (fig. 33). Upon the mesial side of the ventral part of the paraflocculus we find the flattened cake-like *flocculus* (figs. 30, 32, and 33), which occupies the interval between the medulla oblongata and ventral part of the paraflocculus, and projects further backward (*i. e.* in the caudal direction) than the latter. The flocculus is connected to the *nodulus* (*i. e.* the foremost part of the posterior lobe) by means of a band of medullary substance. The posterior lobe is a very simple median band of grey substance which is subdivided into two parts, *nodulus* and *uvula*, by a deep transverse fissure, and in addition it is subdivided by three or four shallow furrows (figs. 33 and 31). It is separated from the small "pyramid" and its lateral connections by a shallow areuate *fissura secunda* (fig. 32).

Practically the whole of the dorsal surface of the organ is formed by the central lobe, which has extended forward over the anterior lobe. The lobe appears to have been stretched in this process and the grey matter separated into a median band and two lateral areas, which are separated by regions in which the medullary matter is exposed (fig. 31, *y*). The median band is subdivided into about ten simple folia by a number of transverse shallow furrows. The subdivision of the *area crescens* or lateral part of the central lobe is very imperfect.

The representative of the area A consists of the simple narrow folium which overhangs the anterior lobe (fig. 30). Its lateral parts are quite hidden in the *fissura prima*. The area C consists of the obliquely-placed lateral grey band which begins at the lateral extensions of the pyramid (figs. 31 and 33), and extends upward to the antero-lateral corner of the organ. It is subdivided by about ten simple transverse furrows. Wedged

in between the areas A and C we find at the dorso-lateral corner of the anterior surface (fig. 30) a little group of about six folia which converge in a mesial direction toward the lateral corner of the medullary area on the dorsal surface (fig. 31). The resemblance between the cerebellum in *Xenurus*, the Rodent *Lepus*, and the Marsupial *Dasyurus* is very striking.

In *Dasyppus* we find that the *lobus centralis* does not cover the *lobus anticus* so completely as it does in *Xenurus*. Thus the *fissura prima* and part of the anterior lobe become visible upon the dorsal surface. The area B of the central lobe, instead of being almost confined to the anterior surface, now forms the extreme lateral angle of the dorsal surface. In other words, the organ becomes much more like the cerebellum in the *Manidæ* and *Bradypodidæ*. We see the same process occurring in the Rodents. For while *Lepus* is like *Xenurus* in this respect, we find that in *Atherura*\* a cerebellum in many respects like that of *Tamandua* is found.

In *Dasyppus* the *paraflocculus dorsalis* is relatively larger than in *Xenurus*.

In *Chlamydomorphus* the cerebellum presents a very peculiar appearance (fig. 15). It is a flattened plate closely applied to the vertical posterior extremities of the hemispheres, and appears at a cursory glance to be utterly unlike any of the other forms we have so far considered. But when we study its anatomy more closely, by means of sections, we find that it is merely a simplified type of the cerebellum of *Xenurus* which has become flattened between the vertical occipital plane of the skull and the posterior extremities of the hemispheres. An exactly similar flattening takes place in the Marsupial *Notoryctes*. A *lobus flocculi* composed of about six simple folia is placed like a buttress against the lower part of each lateral edge of the cerebellum (figs. 15, 35, and 36).

Fig. 34.

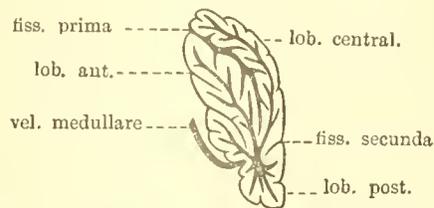
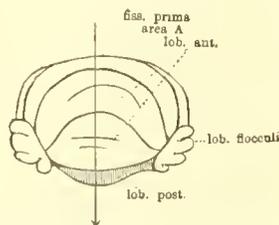
Mesial sagittal section of cerebellum of *Chlamydomorphus*. Enlarged 3 diam.

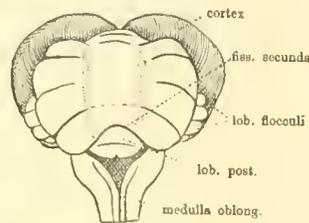
Fig. 35.

Anterior surface of cerebellum of *Chlamydomorphus*. Enlarged 2 diam.

\* F. G. Parsons, "On the Anatomy of *Atherura africana*," Proc. Zool. Soc. London, 1894, p. 687, figs. 5 & 6.

In a mesial sagittal section (fig. 34) we can correlate the organ with that of *Xenurus*. The deep *fissura prima* cuts into the anterior surface and separates the anterior lobe from the central lobe. Upon the anterior surface (fig. 35) we find the anterior lobe bounded by the semicircular *fissura prima* and subdivided by a few subsidiary sulci.

Fig. 36.

Caudal surface of brain of *Chlamydothorus* to show the cerebellum. Enlarged 2 diam.

Toward the lower part of the posterior surface we find the *fissura secunda* separating the small posterior lobe from the central lobe. In a view of the posterior surface (fig. 36) we see this *fissura secunda* as a small semicircle. A few shallow furrows begin at the lateral margin and extend for a short distance toward the mesial plane.

The meaning of all these data will be briefly discussed in the concluding part.

#### GENERAL CONSIDERATIONS.

In reviewing all the data which I have been able to collect and examine in the foregoing pages, the many imperfections of the record are only too patent. Our knowledge of the adult brain, even so far as its macroscopic features are concerned, is far from perfect, and we have only the merest scraps of information concerning its developmental history in the different genera. Yet this knowledge, in spite of its fragmentary nature, is not altogether lacking in importance. For if it does not permit us to positively localize the members of this group in the mammalian series, the evidence of cerebral anatomy enables us to definitely refute many beliefs concerning the position of the Edentata which even the wealth of paleontological discovery within recent years has been unable to shatter. In addition to this negative value, the testimony of the brain indicates with some degree of probability the direction in which we must look for the nearest allies of the heterogeneous group which we are discussing.

While recognizing that the evidence of cerebral anatomy often possesses a decisive taxonomic value, we cannot be blind to the fact that in many cases, without the support of the testimony of other anatomical systems, we could only vaguely hint at the position of a mammal from the character of its nervous system. Thus, while we attach considerable importance to the exact configuration of the brain in *Myrmecophaga*, we could not suggest any kinship of the Armadillos with this Ant-eater upon the evidence of its cerebral anatomy, if we were not aware of the peculiar Xenarthrous nature of its vertebræ. At the same time it is quite possible that, if we were acquainted with the pallial configuration of *Priodon*, we might be able to say decisively that the Giant Armadillo is a relative of the Great Ant-eater upon the evidence of the brain alone. The merest tyro could recognize at a glance the brain of a member of either of the great Ungulate or

Unguiculate groups, but the task of deciding whether some of the smaller mammalian brains belong to the Insectivora, Rodentia, Chiroptera, or possibly Edentata, would tax the ingenuity of the most learned anatomist. However much importance we may attach to the value of the evidence presented by the brain, we cannot afford to disregard the testimony of the other systems upon which, in many cases, we must rely for decisive data for classificatory purposes.

In attempting to form a just estimate of the value and full significance of our data, we cannot take too wide a view of the field of enquiry. We must strive to clearly appreciate the distinctive features of the mammalian brain and the factors which are at work in modifying it, before we attempt to estimate the taxonomic value of the features of any given type of brain. The brain indicates, perhaps more than any other system, the immense superiority of the mammal over all other forms of life. For, in virtue of the possession of such an organ, the mammal is able to very readily adapt itself to more complex conditions of existence than is possible among any other class of animals, without the most profound modifications of structure which take extremely long periods of time for their accomplishment. Mammals may, on the other hand, in comparatively very short periods of time and by means of changes which are so slight as not to fundamentally interfere with the distinctly mammalian type of body, adapt themselves to almost any mode of aquatic, terrestrial, or aerial life such as among other vertebrates it takes whole geological epochs to acquire, and then only at the expense of most fundamental modifications of their bodily structure.

The part of the brain in which this superiority most strikingly manifests itself is the cerebral hemispheres. In all vertebrates the incoming olfactory nerves are inserted into an olfactory bulb, which is connected by a peduncle with the cerebral hemisphere, which at first consists of little else than a small, simple, undifferentiated basal ganglion. At a very early stage in the evolution of the brain, we can recognize the primordial elements of the rhinencephalon making their appearance. Even in the Dipnoi and Amphibia we can recognize a differentiation of the mesial wall of the primitive hemisphere into the paracommissural body and the forerunner of the hippocampus, while on the basal and lateral aspects the undifferentiated primordial tuberculum olfactorium and lobus pyriformis may be localized. In the Sauropsida the primordial hippocampus and pyriform lobe advance a further stage in the process of differentiation, although they are still far removed from the final stage of elaboration which we find in even the lowest mammal.

It is only in the Mammalia that the pyriform cortex becomes fully differentiated and the hippocampus assumes its typical characters. Now, for the first time, the margin of the hippocampal formation becomes strangely modified to form the fascia dentata, and in association with this the region undergoes a peculiar mechanical involution which gives rise to the hippocampal fissure. These two regions—the pyriform lobe and the hippocampus—not only reach the acme of their elaboration within the Mammalia, but they increase considerably in size, so that in the early mammal they form a large and complicated mechanism in which olfactory impulses are received and possibly blend with the impulses of other sense-organs.

These peculiar changes which have been just briefly outlined are distinctive of the Mammalia; they are never found outside the class, and there is no mammal in which these features are lacking. Moreover, these changes appear to have practically reached their consummation even in the lowliest mammal.

Although the rhinencephalon is thus much larger and much more highly developed in the mammal than it is elsewhere, it at the same time takes a relatively much greater share in the formation of the cerebral hemisphere in the non-mammalian vertebrates. The simple primordial hippocampus of the reptile forms not only the greater part of the mesial wall, but also a large part of the dorsal wall or roof of the hemisphere; and its lateral margin is thus brought into proximity with the simple representative of the pyriform lobe which forms part of the lateral wall. All that separates these two parts of the rhinencephalon in the reptile is an insignificant area of simple cortex on the dorso-lateral aspect of the hemisphere. It is difficult to appreciate the fact that this apparently unimportant and almost undifferentiated patch represents the forerunner of that highly specialized and elaborately complex cortex which we know as the pallium, and which in the mammal produces such profound and far-reaching modifications and attains to a morphological importance which exceeds that of the rest of the nervous system.

In this imperfect sketch of some of the salient features in the evolution of the cerebral cortex we have wandered some distance from our main theme, in order to emphasize the fact that the pallium is practically a new structure in the mammal: it is something that has been added to the old Saurian brain, and immediately exercises so marked an influence upon its possessor that it is perhaps not an exaggeration to say that the possession of a pallium made mammals possible. Before its appearance the central nervous system might be compared to a series of autonomous governments, of varying importance and influence, united into a harmoniously working federation, with no very decided centralized control beyond the slightly dominant sway exercised by the insignificant cerebral hemispheres. In the mammal this federation comes under the domination of the almost absolute power of the dictatorial pallium. The pallium, in a sense, represents within itself the whole body, because nerve-paths proceeding from all regions of the body ultimately lead to the pallium, which is the Rome of the neural empire; but it also dominates and controls the whole of the nervous system, and through it the whole of the body.

It is of the utmost importance, therefore, to study the features of this organ, which may truly be regarded as a reflection of the whole body. Keeping constantly in view the fact of its recent appearance, its obvious influence on the rest of the organism, and the multiplicity of factors which determine its size and configuration, we may the better appreciate the meaning of its changing features which we are about to consider.

But before doing so we must briefly discuss the nature and constitution of the pallium.

The governing organ of the submammalian brain is probably the simple basal ganglion, which is generally influenced in all probability to a predominant degree by the precociously developed olfactory areas of the hemisphere. In the mammal the development

of the pallium (probably by differentiation from the basal ganglion) provides a cortical area with a free scope for expansion, in connection with which paths from all the lower sensory centres become established. Thus the primitive pallium becomes a field in which the retina, the sensory lining of the internal ear, and all the tactile surfaces of the body become represented, so that the impulses of these various senses may meet and mutually react the one upon the rest. Thus the primitive pallium is essentially a "sensory area," but it is at the same time a "projection area." For all of these centres may exercise a combined influence upon the pallial nerve-cells, from which efferent impulses proceed to the lower executive centres. Complex groupings of nerve-cells are also formed within the pallium, representing potential muscular acts of increasing degrees of complexity, which may become kinetic when the activity of the pallium stimulates, through its projection-fibres, the lower executive centres in the brain-stem and spinal cord.

The pallium, then, is essentially a place where afferent impulses from all parts of the body may meet and combine and exert a direct influence upon the mechanism which initiates bodily actions. It is for this reason that the mammal is able to execute movements of a more complex order, of greater precision and variety—in a word, can perform more skilful and purposeful acts than the animal without a pallium. The direct result of this is a marked advancement in the development of the limbs in order to execute the movements which the possession of a pallium makes possible. The way is opened for all kinds of specialization of movements, and the limbs and the other muscular parts of the body rapidly adapt themselves to special kinds of activities. Following in the train of these neuro-muscular modifications and specializations, the skeletal and alimentary organs rapidly accommodate themselves to the changing mode of life of the individual.

The small early pallium may be regarded as being entirely composed of sensory areas, which rapidly increase in size and complexity, as the intermediate sensory stations, such as the corpora geniculata and optic thalamus, grow, and produce richer and more abundant sensory paths to the pallium. With the increasing size and complexity of sensory areas the demand for association-elements which shall link together in functional unity the various sensory areas and the various parts of each area becomes imperative. Of necessity, therefore, a new set of elements springs up, consisting of nerve-cells whose nerve-fibre processes serve to bring into functional co-operation all the scattered elements of the sensori-projection pallium. A time comes at an early period in the evolution of the mammal when the various sensory areas become fully represented in the pallial growth. Up till this time any variation in the acuteness of a sense-organ has an important and obvious effect upon the size of the pallium.

The diminution or extinction of the visual element in the cortex, such as occurs to a high degree in *Notoryctes*, *Chrysochloris*, *Talpa*, and *Chlamydomorphus*, causes a most profound difference in the size of the pallium, and any interference with the tactile or auditory acuteness would doubtless have considerable influence upon the pallial region. But after the sensory areas are fully represented the pallium still continues to increase in extent.

Inextricably intertwined with the sensori-projection elements, the association-elements

increase in number, so as to unite into a more exquisitely delicate machine the sensori-projection cortex. The increase in number of these elements causes an insidious growth of the sensory areas in which they are so intimately mingled with the sensory and projection elements. But as these association-elements increase in number in the formation of intricate groupings which determine increasingly complex and "skilful" movements, they extend far beyond the limits of the "sensory" or "projection" areas, and constitute regions which Flechsig calls "areas of association."

In an interesting memoir upon the weight of the brain in mammals, Eugène Dubois\* calls attention to and discusses the influence of the size and richness of the sensory surfaces of the body upon the cerebral cortex. Flechsig, who introduced the terms "Projection-centre" and "Association-centre," has shown that the former develop very late in the ontogeny of the mammalian brain; and the sensory fibres, which are the first to develop in the cortex, only receive their medullated sheaths after the lower executive and phylogenetically ancient parts of the brain are fully developed.

The facts which we have discussed above to show the appearance of the pallium for the first time in the mammal give a demonstration of the late phylogenetic appearance of the more primitive pallium (*i. e.* the centres of projection), which is quite in harmony with their late appearance in ontogeny. The "centres of association" naturally make their appearance after the "centres of projection" are laid down.

Flechsig says † that in Rodents (the House-Mouse and the Marmot) association-centres are entirely lacking. In other words, the sensory centres are in close contiguity ("Sinnesphäre stösst an Sinnesphäre"), so that the whole pallium is one field of projection. It is difficult to conceive of a large pallial area like that of the Rodents as entirely devoid of association-elements, and we may with some reason interpret Flechsig's statements as meaning that the elements of association are not yet sufficiently numerous to form definite areas beyond the limits of the sensory. Such areas of association begin to make their appearance in the Carnivora, according to Flechsig. The association-elements which exist in the pallium of the Rodent are so intimately intermingled with the sensori-projection elements that they are not recognizable as such, but go to swell the dimensions of the sensory or projection areas.

The further discussion of these factors must be deferred until we can discuss the specific cases afforded by the pallium in the Edentata. In the meantime it is convenient to briefly discuss the brain-stem and cerebellum.

In the evolution of the mammal the features of the brain-stem change very slightly in comparison with the striking modifications which the cerebral hemisphere undergoes. Most of the changes which affect the brain-stem are more or less directly associated with the development of the pallium. Thus the fuller development of the optic thalamus and the corpora geniculata are probably integral factors in the elaboration of the sensory paths to the pallium. The changes which occur in the corpora quadrigemina are also in all probability expressions of the same series of changes.

\* Eugène Dubois, "Sur le Rapport du Poids de l'Encéphale avec la Grandeur du Corps chez les Mammifères," *Bulletins de la Société d'Anthropologie de Paris*, t. viii. (4<sup>e</sup> série) 1897.

† Paul Flechsig, "Gehirn und Seele," 2<sup>e</sup> Ausgabe: Leipzig, 1896, p. 84.

From the pallium a large mass of projection-fibres arises, and in its downward path invades the ventral part of the mesencephalon, where it is known as the crus cerebri. The caudal remnant of the same series of fibres in the medulla oblongata forms the pyramid. These series of fibres are lacking in the submammalia, and they increase in size with the growth and perfection of the pallium. On the ventral surface of the hind-brain a new series of fibres, the pons Varolii, makes its appearance. This is part of the association-system between the pallium and the cerebellum.

This leads us to the consideration of the cerebellum. This organ shows most marked signs of advance in the Mammalia, and, next to the cerebral hemisphere, indicates most strikingly the mammalian superiority of type. It is not improbable that the important changes in the cerebellum are to a large extent the result, partly direct and partly indirect, of the development of the pallium.

In the immediate ancestors of the mammal the cerebellum was in all probability a most insignificant and simple organ, but *pari passu* with the development of the pallium the organ rapidly increases in size and complexity and becomes intimately connected with the new pallium. It is in the highest degree probable that the sudden and contemporaneous progression of these two parts of the brain is a single correlated phenomenon, and not two coincident but independent acts. There can be little doubt that the increased activity of cerebellar evolution is one of the expressions of the all-powerful pallial influence.

We have already briefly and somewhat crudely indicated how the possession of a pallium may permit the mammal to execute movements of greater variety, of increased nimbleness and immeasurably greater delicacy: in a word, of infinitely greater complexity than is possible in an animal without a pallium. In the execution of such complex movements it becomes of the highest importance that the relative activity of the different muscles which perform the act should be delicately adjusted and nicely balanced in order that the complex movement may be "co-ordinate" and purposeful. It seems not unlikely, taking into consideration the two-fold connections of the cerebellum on the one hand with the incoming nerves from the sensory surfaces and the muscles, and on the other with the pallium, that this organ may be a complex executive machine which in some way controls and renders possible the delicately-adjusted co-operation of wide groups of muscles.

If such be the case, we might expect the cerebellum to be modified by two, among in all probability many other, factors.

In the first place afferent fibres which enter the cerebellum from sensory areas or muscular apparatus would presumably need a co-ordinating machine proportionate to their number—or, in other words, the size of an animal would influence the dimensions of the cerebellum.

In the second place, the pallial connection would undoubtedly influence the dimensions of the cerebellum. For a large and highly differentiated pallium, which betokens complex potential movements, would presumably need a much richer cerebellar associate than a small and simple one.

There are unquestionably many other factors at work, such as the possible influence of

the eighth nerve on the size of the lobus flocculi; but, from a careful comparison of a large series of mammals, these two hypothetical factors impress me as being the most potent influences which determine the size and complexity of the cerebellum.

There is one other point regarding the cerebellum which does not directly concern us in this memoir, but may be mentioned *en passant*. The growth of the cerebellum is almost purely an increase in the superficial extent of the cortex, for, so far as we are aware, the cerebellar cortex does not appreciably advance in the richness of its histological elaboration in the Mammalia. In other words, the resultant nerve-fibres do not become appreciably more abundant per unit of surface area. Therefore the problem of the mutual adaptation of the rapidly increasing cortical sheet, which is growing in terms of the square, to the proportionate increase of the white or medullary core, which from the nature of the case must grow in terms of the cube, becomes much more purely mathematical than is the case in the cerebral cortex. Consequently the surface of the cerebellum becomes exceedingly complex in order that the surface of the medullary matter may approximately be equal to that of the cortical matter. In a large mammal the cerebellum is much larger, and correspondingly more complex, than it is in a smaller mammal of the same family. While all parts of the cerebellum share in the increase, its effects become especially noteworthy in the region which I have called "*area creescens*." Among the factors which cause the rapid expansion of the *area creescens*, however, the pallial influence takes a predominant share. A glance at the cerebellum in the Primates conclusively demonstrates this.

In *Chlamydomorphus* we find a small and simple cerebellum which is constructed according to the same plan that prevails in many members of the Rodentia and Chiroptera, and in most Insectivores and Marsupials. There is the most remarkable apparent resemblance between the general shape of the organ in *Notoryctes* and *Chlamydomorphus*. But we find a much higher degree of complexity in the Edentate than in the Marsupial, which is all the more impressive when we consider the similar modes of life of these two animals, and their not dissimilar bodily dimensions. Even in the much larger Marsupial *Perameles* the cerebellum is not so richly folded as it is in the small *Chlamydomorphus*.

In *Xenurus* we find a cerebellum conforming to the same type, and quite as highly elaborated as that of the Rabbit, and in the larger Armadillos (such as *Dasyppus*) we find the same kind of progressive uncovering of the anterior lobe as in certain Rodents\*. This demonstrates the gradual transition from the simpler type of flattened cerebellum to the more complex type found in all the other families of Edentata, as well as in the Ungulata and Carnivora.

This plumper type of cerebellum with an exposed anterior lobe may possibly represent a higher type of cerebellum. We find that it is gradually attained in the Armadillos as the animal increases in size, *i. e.* as the somatic factor increases. It seems not improbable, however, that some other factor, such as the size and degree of complexity of the pallium, enters into this change. For in the Kangaroo (*Macropus*), in which the somatic

\* *Vide* Parsons's figures, *op. cit.*, Proc. Zool. Soc. London, 1894, p. 687.

factor must be much greater than it is in any Armadillo or Rodent, we still find the anterior lobe covered by the hood-like central lobe. In view of these facts and the marked contrast between the cerebellum in *Chlamydophorus* and *Notoryctes*, we are justified in attaching some importance to the degree of development of the cerebellum as an index of the status of its possessor.

The enormous growth of the "*area crescens*" of the central lobe in the Primates, and the very different configuration and size of the corresponding part of the cerebellum in the Monotremata, show us that there is some other very definite factor besides bodily dimensions which determines the size of the cerebellum. The quantity and quality of the pallium undoubtedly have a marked effect upon the proportions of the cerebellum.

If we regard the evidence of the cerebellum as having a definitive taxonomic value—and in view of the configuration of this organ in Monotremata and Primates, in comparison with the large group of other mammals, it is difficult to do otherwise—then we must attach some importance to the extremely close resemblance in configuration and proportions which exists between the cerebellum of the Ant-eaters and Aard-vark and of the Carnivora and Ungulata. The fact that such a highly specialized organ as the cerebellum should develop along such exactly analogous lines and attain such similar proportions in these different groups of animals most conclusively shows, when we remember how wide a scope for variation there is, that here we have an instance either of a most remarkable case of convergence or parallelism (which is exceedingly improbable), or an unassailable indication of the close genetic relationship which exists between the Edentates and the commoner quadrupedal mammals.

The idea of separating the Edentata from such other mammals as the Rodentia, Ungulata, and Carnivora, implied in the introduction of the term "*Paratheria*," or the belief that "they suddenly shot up from the Prototheria"\*, is entirely shattered by the evidence of the cerebellum, even if we had not the testimony of the other anatomical systems to the same purpose.

Among the extinct Armadillos we find in *Eutatus* a cerebellum of the simpler Armadillo-type, while in *Glyptodon* we find an enormous cerebellum which probably resembled that of *Dasypus*.

It is an interesting problem to determine what may have been the reason for a cerebellum of such huge dimensions in *Glyptodon*, for the organ is as large as a cerebral hemisphere. While the pallial factor must have been very slight, it may be that the somatic factor explains the large dimensions of the organ. For it is conceivable that an animal of such large proportions would need a large organ to co-ordinate its great muscular system, even though the commanding pallium, which renders such a co-ordinating mechanism necessary, should be so diminutive.

In describing the brain of *Myrmecophaga* I had occasion to call attention to the undoubted fact of its being fashioned in the likeness of the Carnivorous type. At the same time it was shown from Max Weber's statistics that Carnivores of similar body-

\* W. K. Parker, 'Mammalian Descent.'

weight possess a much heavier brain. We have unfortunately only a single record of the brain-weight in *Tamandua*:—a *Tamandua tetradactyla*, ♀, weighing 1168 gr., has a brain of 17.35 gr.\* This is an extremely high brain-weight for an animal of this size, far exceeding that of any of the Rodentia, Chiroptera, or Marsupialia of similar size, although it is still much below the Carnivore. Max Weber, who is extremely careful in stating when his measurements refer to young animals, makes no comment upon this measurement. His specimen, if not young, is apparently very small for a *Tamandua*, its body-length (without the tail) being only 37 cm. Dr. Selater gives † the corresponding measurement of a *Tamandua* which was in the Zoological Gardens as 20 inches (about 50 cm.). Rengger gives the length of a *Tamandua* which is still larger than Selater's specimen, being 22 inches (about 55 cm.) long ‡. But even admitting that Weber's measurement refers to a young animal, the brain-weight which he records would be considered large even for an animal of the dimensions of Rengger's specimen. For even then the brain would be relatively larger than that of many Rodents of a corresponding size. When we recall the fact that the brain of *Tamandua* is not unlike that of a Rodent, and may therefore be legitimately compared with it, we must admit that the brain of the Ant-eater is at least as highly developed as that of the Rodent.

We have unfortunately no record of the brain-weight in *Cycloturus*, although Pouchet § assures us that the brain of this small Ant-eater (which he calls *Dionyx*) is much larger than that of Rodents and Insectivores || of a similar size.

Taking all these facts into consideration, we are safe in concluding that the Ant-eaters are equipped with brains which, so far as size is concerned, are certainly not inferior to those of Rodents, and in all probability show a decided superiority.

According to Flechsig, the "centres of association" are as yet small in Carnivores, while in Rodents they are entirely wanting. This statement may be interpreted to mean that the insidious growth of association-elements within the pallium is not yet sufficiently great in Rodents to make itself manifest, but that it has increased to such an extent in Carnivores as to be recognizable beyond the limits of the areas of projection. It is in the highest degree probable that the distinction between the pallium in *Myrmecophaga* and a Dog of a corresponding size is wholly due to the more abundant development of association-elements in the Carnivore. For we have no reason to believe that any of the sensory areas of the Ant-eater are to any marked degree less rich in sensory elements than they are in the Dog. Nor are the primary end-stations, such as the *corpora geniculata*, the *corpora quadrigemina*, the *tubercula acustica*, or any other of the masses of grey matter from which sensory tracts may arise and proceed to the pallium, any smaller in the Ant-eater than they are in the Dog. In other words, so far as we can judge, the pallium of the Ant-eater is as abundantly supplied with sensory tracts as is the pallium of the Dog, and therefore we are, I think, justified in concluding

\* Max Weber, *op. cit.*, Gegenbaur's Festschr. p. 7. † P. L. Selater, Proc. Zool. Soc. London, 1871, p. 546.

‡ Rengger, 'Naturgeschichte der Säugethiere von Paraguay,' Basel, 1830, p. 309.

§ Pouchet, *po. cit.*, tm. v. p. 664.

|| He says Carnivores, but from the context there can be no doubt that he means Insectivores.

that any excess in cortical area of the Dog over the Ant-eater must be due to a richer supply of intrapallial elements, *i. e.* nerve-cells and their resultant nerve-fibres which associate the various sensory elements of the pallium the one with the other, as well as with the cells whose axis-cylinder processes become projection-fibres and carry impulses from the pallium to lower executive centres. In other words, the pallium of the Dog is a more perfect machine than that of the Ant-eater, in that it is more perfectly adjusted to the higher psychical needs of the animal, and the actions of its various parts are better co-ordinated by a richer association-system.

It is instructive to notice that the growth of the Dog's pallium has been a general expansion and not a local hypertrophy; in other words, the association-elements cannot be regarded as forming areas, as we might suppose from a too hasty application of Flechsig's ideas, but that they pervade the whole pallium, and with their increase there is a general pallial expansion. At the same time we had occasion to observe before that it is not unlikely that a localized expansion may have taken place in the area where we find the crucial sulcus in the Dog. In this region the mechanism which controls the movements of the limbs is being rapidly elaborated, so that the Carnivore can execute those complex, almost skilled, and rapid movements upon which its livelihood is dependent.

When we turn from the consideration of the Ant-eaters to the Sloths we at once encounter some difficult problems. For, while the pallium conforms to the Carnivore-pattern in quite as marked a degree (at any rate in *Bradypus*) as it does in the Ant-eaters, it seems strange that in these small brains there should be so many sulci of such a depth. Max Weber's tables contain a record of a *Bradypus tridactylus* ♀ of 2130 gr. weight with a brain weighing 16.5 gr. Thus this Sloth possesses a smaller brain than that of *Tamandua*, in spite of the fact that its body-weight is nearly double that of the Ant-eater. And yet, while the pallium of the latter, as we have seen, is almost free from sulci, the smaller pallium of the Three-toed Sloth is provided with a series of deep sulci even more complete than those of the Great Ant-eater. The slightly larger brain of the Two-toed Sloth has, in addition, a number of subsidiary sulci. It is quite possible that the extreme shortness of the head in the Sloths may have the effect of limiting the space for the brain, and that hence the expanding pallium becomes folded to adapt itself to its limited space.

From a careful comparison of the brains of *Tamandua* and *Cycloturus* (so far as this has been possible) with those of Rodents, we must admit that the Ant-eaters are certainly not inferior to the Rodents in the size of the pallium. Nor is the quality of the pallium inferior, if we may judge of its richness by the volume of commissural fibres and projection-fibres proceeding from it. In all that is of greatest significance as regards the superiority of a mammal, the Ant-eater is at least the equal of the Rodent. And yet it is customary to relegate the former to a much lower status than the latter. The evidence of the brain in the Great Ant-eater shows that this animal is not far removed from the Carnivora, and the whole tendency of our examination of this group is to bring them into very close relationship with such typical Eutheria as the Rodents and Carnivores.

In *Tamandua*, as a result of the elongated form of the head necessary for an Ant-eater, the brain has plenty of room to expand, and hence its cortex does not become folded like that of the Sloths.

If it be true that the surface of the pallium of *Bradypus* thus becomes folded in accordance with mechanical principles, it is somewhat remarkable that the arrangement of its sulci should follow a plan which is obviously the expression of an inherited tendency. That this does take place there can be no doubt, for when we examine a large series of mammalian brains we are surprised to find in organs of the most variable shapes convincing evidence that the arrangement of the sulci has been determined by some principle other than the purely mechanical factor which may have been the exciting cause of their development.

Max Weber records a brain weighing 11.3 gr. in a *Dasypus sexcinctus* ♂ of 2567 gr. There is a most decided fall both in the absolute and relative size of this brain when compared with those of the Sloths and Ant-eaters. Nor does a comparison of this record with those of members of the Rodentia, Chiroptera, or even Marsupialia, serve to brighten or place in a better light the degradation of the Armadillo. For in the Marsupial *Trichosurus* we find the record of a brain of the same size as that of *Dasypus* in an animal of merely 1724 gr. But at the same time it is only right to add that a *Didelphys* of 3480 gr. has a brain of merely 6.5 gr.

I think there is ample reason for hesitation before consigning the Armadillos to a lowly place, even if we admit, as is not improbable, that this single record is typical of the family.

In our consideration of the factors which may modify the size of the pallium we have already pointed out that the decadence or diminished acuteness of any sense-organ may exercise a marked effect upon the size of the pallium in those mammals in which the "areas of association" are not yet definitely established. In the consideration of the mesencephalon we have already had evidence to demonstrate that the visual acuteness of the Armadillos is on the wane. When we consider how large a share visual representation must take in the primitive pallium, we must admit that this is a potent factor in modifying its size. In addition to this, it is hardly to be believed that tactile impressions are of much importance, or find any scope for their exercise, in an animal encased in armour. The tendency of recent research is to recognize in the optic thalamus a station where not only the visual but also the general tactile path receives a relay on its way to the pallium. If this be so, we may perhaps be able to understand why the optic thalamus is reduced to such exceedingly diminutive proportions in the Armadillos. If we admit that the visual and tactile senses have a diminished importance in the Armadillos, I think that there is in this fact an ample reason for the diminutive size of the pallium. Pouchet tells us that the brain of *Chtamydophorus* is much larger than that of the Mole (*Talpa*). If this be a fact, it may be of value as evidence of the superiority of the Armadillo over the Insectivore.

We must regard the Armadillos as the descendants of mammals with a higher degree of visual and tactile acuteness, and a much more extensive pallial representation of these senses than they at present possess.

It is strange that in animals with such a small and insignificant pallium, which is not of sufficient extent to produce a complete rhinal fissure, we should find representatives of what we must regard as the supraorbital ( $\beta$ ) and sometimes also the suprasylvian ( $\delta$ ) sulcus. So far as we are at present capable of judging with our limited knowledge of the factors of pallial growth, there is little, if any, mechanical demand for any such sulci. If this be so, these fissures must have been inherited from ancestors of the Armadillos which possessed a more extensive pallium with fully-formed supraorbital and suprasylvian sulci.

The evidence of anatomy and palæontology, which has been carefully summed up by Sir William Flower\*, clearly points to the undoubted kinship of the Ant-eaters, Sloths, and Armadillos. There is nothing in the evidence of the brain which does not thoroughly harmonize with this view. *Myrmecophaga* exhibits a close resemblance to the brain of the Carnivora which we have already examined in detail. When we take into consideration the multiplicity of factors which are moulding the pallium into such varied forms in different groups of mammals, it is difficult to explain the resemblance between the pallial configuration of the Great Ant-eater and that which prevails in the great group of Unguiculata, as other than the expression of a genetic relationship, and not of fortuitous similarity.

We equally find in *Bradypus*, but to a less marked degree in *Choloepus*, signs of conformity to the Carnivore type of brain.

In the case of the *Dasyproctidæ*, the rudimentary sulci  $\beta$  and  $\delta$  may be the remains of a similar pattern, but it is so fragmentary that from the evidence of the brain alone we could not definitely locate these peculiar animals.

In spite of the obvious differences which exist between the brain of the Carnivora and that of the Ungulata, we find that among their most constant morphological features there is a very considerable amount of agreement, while other constant features coexist to point the contrast. The arrangement of the supraorbital and sagittal sulci, and to some extent the splenial sulcus, is so obviously homologous in the two types that we cannot regard this fact in any other light than the expression of an ultimate genetic relationship. If we trace the ancestry of the Ungulata and the Unguiculata back, we ultimately reach, according to the evidence of recent palæontology, a common Creodont stock, from which at the dawn of the Eocene the Condylarthrous progenitors of the modern Ungulata diverged from the forerunners of the Carnivora †. It is highly probable that in the simple brains of these primitive Creodonta those tendencies of growth were already impressed which equally manifest themselves in the pallium of the two diverging groups which spring from this common stock.

The divergence of these two stocks is manifested in the contrast between other features of the pallium in the two groups. The pallium in the Carnivore at a very early epoch bulges downward posteriorly, while this tendency is wanting in the Ungulata.

\* W. H. Flower, "On the Mutual Affinities of the Animals composing the Order Edentata," Proc. Zool. Soc. London, 1882, pp. 358-367.

† W. D. Matthew, "A Revision of the Pueroo Fauna." Bulletin of the American Museum of Natural History, vol. ix. 1897, p. 293, *Condylarthra*.

The effect of this is that in the Carnivore there is an early and most pronounced tendency in the suprasylvian sulcus to assume an arcuate form, whereas in the Ungulate the corresponding fissure is horizontal until, in a late stage in certain Ungulates, the perfection of the Sylvian fissure produces a secondary arching in the suprasylvian fissure. There is also, as we have already had occasion to remark, a correlative change in the early Carnivore and early Ungulate type of Sylvian fissure.

Among certain mammals, such as the Rodents, there is an ill-defined tendency toward a development along the Carnivore line of evolution, but it is never very pronounced. At the same time we find in some Rodents, as for instance *Lepus*, a decided caudal downgrowth of the pallium which is not unlike the condition in *Tamandua*. Among other Rodents \* we find evidences of a sagittal sulcus, a supraorbital, and occasionally a *Jossa Sylvii*, which in a vague manner suggest a tendency similar to that exhibited in the Carnivore's brain. The Chiroptera present a type of brain similar to the Rodentia with even fewer indications of their affinities, and they both gradually merge into the generalized type of the Insectivora, which gives no indication of the peculiar specializations of the higher groups. When we consider that the Carnivore type is so distinctly marked off from that of all other groups of mammals, and find in an enigmatical family of mammals such as the Ant-eaters an exact reproduction of all the salient features of this distinct type †, we are justified, I think, in attaching some taxonomic value to the resemblance.

If we admit that such a genetic relationship does exist, we must make the further concession that the Ant-eater stock branched off in all probability from the early Ungulate stock at a period subsequent to the splitting off of the Condylarthra or primitive Ungulata. Although the brain of the Ant-eater is far inferior to that of the Carnivore, it is immeasurably superior to that of the primitive Creodont. Arguing from the evidence afforded by the brain, we might surmise that the Ant-eaters branched off at an early epoch from the primitive Carnivore stock at a time when the peculiar and distinctive tendencies of pallial development had been fully determined. But while the Carnivores, leading an open life of free competition, have in the keen struggle for existence developed in a high degree the organ which permits them to successfully maintain the struggle, the Ant-eaters, on the other hand, have become peculiarly specialized to a particular kind of life in which their safety is assured, not by an exercise of a highly developed brain, but by leading a life of seclusion. They pursue a prey which does not call for that exercise of cunning and keen activity of muscle which alone can make a Carnivore's life possible.

According to the interesting palaeontological investigations of Wortman ‡, the early Eocene deposits of North America contain a series of peculiar extinct mammals, beginning from the earliest Puerco and continuing uninterruptedly into the Bridger, which seem to throw an interesting light upon the ancestry of the American Edentates.

\* Cf. F. E. Beddard, Proc. Zool. Soc. London, 1892, p. 596.

† Except for the crucial sulcus, which we have discussed elsewhere.

‡ J. L. Wortman, "The Ganodonta and their Relationship to the Edentata," Bulletin of the American Museum of Natural History, vol. ix. art. vi. pp. 59-110, 1897.

According to this writer, these peculiar mammals, which he calls *Ganodonta*\*, show a series of modifications which indicate the change from a typical mammal to a highly specialized form which is practically identical with the Edentate type. He concludes that the South-American Edentates of the present day sprang from this Ganodont stock, which began with *Hemiganus* and lead up to *Stylinodon*, and at the beginning of the Santa Cruz epoch they wandered from the Northern to the Southern continent. The distinctions between the members of this Ganodont stock and the Creodonta and Tillodontia are so slight, that we find different members of Wortman's group variously included in the Creodonta and Tillodontia by Cope, Marsh, and von Zittel, among other palæontologists.

It is not for me to express an opinion either for or against the evidence of a Ganodont origin for the Edentata; but this brief review of the recent tendencies of American palæontology makes it clear that in suggesting, upon the evidence of the data collected in this memoir, an origin of the Ant-eaters from some post-Creodont stock which has since then diverged from the Unguiculate stem, we are not contradicting palæontological evidence, but that, on the contrary, we are to a very considerable extent supported in our contention by this.

This leads us to the consideration of the position of *Orycteropus*. If the brain of *Orycteropus* were given to an anatomist acquainted with all the other variations of the mammalian type of brain, there is probably only one feature which would lead him to hesitate in describing it as an exceedingly simple Ungulate brain. That one feature is the high degree of macrosmatism. But we know how readily the degree of macrosmatism varies with the change of habit of the animal. Within the family of Ant-eaters we have seen the terrestrial *Myrmecophaga* exhibiting a high degree of macrosmatism, and the arboreal *Cycloturus* showing an equally noteworthy reduction in the size of its rhinencephalon. We may therefore associate the high degree of macrosmatism of *Orycteropus* with its peculiar mode of life, and regard it as a functional modification of little taxonomic value. Such being the case, the similarity of the brain to that of the macrosmatic *Moschus* is of exceptional interest, when we remember that the latter mammal retains "characters belonging to the older and more generalized types of ruminants" † and is a relative of the primitive hornless deer of the lower Miocene ‡. The characters of the brain of the Aard-vark which lead us to associate it with the Ungulate type are the horizontal direction of the whole rhinal fissure (*i. e.* the absence of a downgrowth of the pallium) and the horizontal arrangement of the representative of the suprasylvian sulcus. The features of the region where we find the *fossa Sylvii* in *Myrmecophaga*, and its similarity to the peculiar arrangement of the Sylvian fossa in *Moschus moschiferus* §, add further testimony to this Ungulate likeness.

At the same time we must admit that it is far inferior to existing Ungulates in regard

\* J. L. Wortman, "*Psittacotherium*, a Member of a New and Primitive Suborder of the Edentata," Bull. Amer. Mus. Nat. Hist. vol. viii. art. xvi. 1896.

† Flower and Lydekker, 'Mammals, Living and Extinct,' 1891, p. 314.

‡ A. S. Woodward, 'Vertebrate Palæontology,' Cambridge, 1898, p. 365.

§ W. H. Flower, Proc. Zool. Soc. London, 1875, p. 175.

to its pallial development, a fact which might be explained in the manner I have attempted to explain the shortcomings of *Myrmecophaga* when contrasted with the Carnivora. In the subsequent development of the post-Creodont mammals we find increasing complication and specialization of various anatomical systems, in correspondence with the varying conditions of life. This is seen in the jaws and other parts of the skull, in the structure of the limbs, in the modifications of the alimentary tract, but progress is especially noticeable in the brain. In all the existing descendants of the Creodont stock the brain has increased enormously in size, but in some groups to a much greater extent than in others.

In an interesting memoir, Max Weber has discussed the peculiar contrast between the size of the brain in the Hippopotamus and the Elephant\*. In two animals of approximately the same weight, one (the Hippopotamus) has a brain of 582 gr., while the other (the Elephant) has a brain of the enormous weight of 3370 gr. Max Weber says that the former reminds us of the Tertiary mammals, which Marsh has shown to have remarkably small brains, and he expresses the opinion (p. 6) that an animal with such a relatively small brain could have held its own in the struggle for existence only by its safe mode of life. It is of some significance in this connection that the Hippopotamus shows in other parts of its anatomy indications of a very primitive type †. It seems not improbable that in the case of the Hippopotamus and also of *Orycteropus* ‡ we have two "lonely creatures" who have become specialized, but only slightly removed from the primitive parent stock. They have early taken to eminently safe modes of life, and, by avoiding the fierce struggle for existence which "weeds out" most mammals that fail to keep pace with the rapid pallial growth, they have managed to linger on in spite of their inferior pallial equipment. The marvel is not that there should remain only solitary examples of these forms, but that even these few representatives of such stupid creatures should have escaped the fate of the imbecile *Glyptodon*.

To the student of brain-anatomy the name which the Dutchmen of the Cape have given to *Orycteropus* may not seem so singularly inappropriate as it is generally supposed to be; for in this simple and archaic "Earth-Pig" he may find an exceedingly early offshoot from the root-stock of the Ungulata or Condylarthra.

In Pouchet's memoir, to which we have so often referred, a doubt is expressed as to whether *Macrotherium* should not be included in the family of Aard-varks. Most observers, however, suggested an analogy between *Manis* and *Macrotherium*, until it was shown that the latter possessed vertebræ and teeth such as we find in a Perissodactyle Ungulate §. But to this Oldfield Thomas adds:—"One could not dare to suggest that the ancestors of *Manis* or *Orycteropus* were to be sought in that direction" ||. It would unquestionably be absurd to look for the ancestor of *Orycteropus* among the Perisso-

\* Max Weber, "Over het Hersengewigt der Zoogdieren," Koninklijke Akademie van Wetenschappen te Amsterdam, October 1896.

† A. S. Woodward, 'Vertebrate Palæontology,' p. 346.

‡ W. K. Parker, 'Mammalian Descent,' p. 97, wrote: "If ever there was a generalized type, this [the Aard-vark] is one."

§ H. F. Osborn, 'American Naturalist,' 1882, p. 725.

|| O. Thomas, *op. cit.*, Proc. Royal Soc. vol. xlvii. (1890) p. 248.

dactyla; but in view of its cerebral features we are justified in looking for its ancestry in the early Eocene Ungulate stem, long after the Carnivore stock from which the American Edentata are probably derived had branched off from the Creodonta, which the American palæontologists regard as the common progenitors of all these diversely specialized animals. Such a view does not necessarily conflict with the opinion of Kitchen Parker, who, in knowledge of many resemblances between the skulls of *Orycteropus* and *Rhynchocyon*, suggested that the former may be an offshoot from the Insectivorous stock\*. From the generalized structure of *Orycteropus* and the simplicity of its brain, we may infer that it has not advanced far beyond the stage of the primitive Creodonta, which are nearly related to the *Insectivora primitiva*, while all its near relatives have either been vastly changed in body, limb, and brain to meet the fierce competition by specialization of form and improvement of cerebral structure or have succumbed in the struggle and become extinct.

The evidence for this distant kinship with the primitive Ungulates is not absolutely conclusive, but it clearly demonstrates the distinctness of the Aard-vark from the Ant-eater, and suggests the relationship indicated in the foregoing paragraphs. In a memoir to which I have already referred, Oldfield Thomas remarks that "we are wholly in the dark as to what other mammals" *Orycteropus* "may be allied to" (p. 248). Under such circumstances it is important to place on record even such indecisive straws of evidence as I have herein supplied, as denoting which way the tide of evolution may have flowed in bringing down to the present generation this peculiar waif of a past age.

The brain of *Manis* is in many ways peculiar. Max Weber gives three records of the brain-weight which are singularly discordant:—

<i>Manis javanica</i> , ♂,	body-weight	1750 gr.,	brain-weight	9.5 gr.
" "	♀,	"	3500 gr.,	" 11 gr.
" "	"	"	8000 gr.,	" 13 gr. †

Unless these weights refer to animals of different ages we are at a loss to explain the extreme variations of the body-weight. Dubois says ‡ that the immense superiority in the brain-weight of *Myrmecophaga* over that of *Manis* is "a new reason for separating the American Edentates from those of the Old World." It seems to me that this is quite a fallacious argument. Among the American Edentates themselves, we find in the three families extreme variations in brain-weight, and in a natural group like the Rodentia we find contrasts § quite as marked as that which exists between the Great Ant-eater and the Pangolin ||. If we are going to separate these two animals we must find some more genuine distinction than that which Dubois suggests.

\* W. K. Parker, "On the Structure and Development of the Skull in the Mammalia.—Part. II. Edentata." Proc. Royal Soc. London, vol. xxxvii. p. 80.

† This weight we owe to Kohlbrügge, *Natuurkdg. Tijdschr. Ned.-Indië*, lv.

‡ Eugène Dubois, "Poids de l'Encéphale chez les Mammifères," *Bulletins de la Société d'Anthropologie de Paris*, t. viii. iv<sup>e</sup> série (1897) p. 374.

§ Dubois himself has noticed this fact in the Rodents, *op. cit.* p. 373.

|| *Vide* Max Weber's tables, *op. cit.*, Gegenbaur's Festschrift.

Considering the small size of the brain in *Manis*, the most impressive feature is the presence of so many pallial sulci. The reason for this may possibly be the resistance which the smallness of the cranial cavity offers to the expanding brain. The small size of the pallium in this peculiar animal is not necessarily a sign of its extreme inferiority, as Dubois seems to suppose. It may to a great extent be explained by the fact that the animal is encased in scales, since, if our introductory arguments are sound, the tactile element in the pallium may thus reasonably be supposed to be greatly reduced.

From a consideration of the cerebral features, it is difficult to add anything of a decisive nature to the enigmatical evidence of the other parts of the body. The configuration of the pallium exhibits in a well-defined form the distinctive features of all the progeny of the Creodonta, but it is very difficult to say whether it favours the Ungulate rather than the Unguiculate stem or *vice versá*. The fact that the supra-sylvian sulcus has a distinct tendency to an arcuate form may at first sight seem to point distinctly to a kinship with the Carnivore or American Edentate group, but it is not unlikely that the obvious limitation of growth in the longitudinal direction may account for this peculiarity. Then, again, the resemblance which the complex of the posterior rhinal fissure and the supraorbital and sagittal sulci bears to the corresponding feature in *Orycteropus* may point towards an affinity in this direction.

In considering the American Edentates, we have already learned that there was no feature or combination of features in the brain of the Armadillos which would lead us to associate them with the other American forms, if we had no knowledge of the other parts of the body, and especially the peculiarities of the spinal column. In such a simple type of brain as that of the Armadillos, which presents the typical Eutherian features, there is little of taxonomic significance. In the large brain of *Prodon* we should in all probability find some definite evidence, but while the other members of the family exhibit no cerebral features in opposition, they give no positive indication of the view, which the characters of the vertebral column seem to conclusively prove, that a genetic relationship certainly exists between the three American families.

The case of the evidence afforded by the brain in the Pangolins is exactly similar. For while it shows that the brain of *Manis* conforms to a simple type of architecture which agrees in many points with those of both *Orycteropus* and the American Edentates, there is not sufficient evidence to show decisively which type it really favours. When we consider how markedly the Pangolin differs from both the other groups in the anatomy of the other parts of its system, I think that we are fully justified in following Max Weber's suggestion\* of dividing the group Edentata into three orders:—

Order XENARTHRA (Gill).

- Family 1. *Bradypodidæ*.  
 2. *Myrmecophagidæ*.  
 3. *Dasypodidæ*.

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\* Max Weber, 'Zoologische Ergebnisse,' ii. p. 110.

## Order TUBULIDENTATA.

Family 1. *Orycteropodidæ*.

## Order SQUAMATA.

Family I. *Manidæ*.

Some confusion may arise from the use of the name *Squamata*, which is also applied to lizards and snakes.

The question which naturally arises in the consideration of such a division into orders, is whether the gain in pedantic accuracy is a sufficient justification for disturbing a well-known group, which everyone must now recognize as a mere conventional assemblage with no genuine bonds of union, and thus adding to the number of orders. The view which Oldfield Thomas takes concerning *Orycteropus*—that “it has been placed there [along with the American Edentates] rather on account of the inconvenience of forming a special order for its reception than because of any real relationship to them” \*—is endorsed by Flower and many other competent authorities. If *Orycteropus* is more nearly related to *Manis* than either is to the Xenarthra, as is not at all improbable, we must at present confess that we have no evidence to warrant such a contention. Such being the case, the adoption of the Nomarthra does not appear to me to help toward a clearer conception of this undoubtedly heterogeneous collection of mammals.

It seems possible to adopt a compromise which will avoid the disruption which Thomas dreads, as well as the anomalous course of including within one order animals which have nothing in common except certain functional modifications which are obviously adaptations to the peculiar mode of life.

In the light of our present knowledge, the group undoubtedly ought to be divided into three orders, as Max Weber suggests. But the meaning of the name “Edentata” is so well appreciated that it is not likely to fall into disuse, however much we might wish for such a consummation. The frank recognition of this fact may save us from the disturbing influence of new orders, if we retain the name “Edentata” on the distinct understanding that it consists of a heterogeneous “group” of three “orders,” which have no necessary relationship the one to the other.

The three existing families of Xenarthra are much more widely separated one from another than is usual among mere “families,” for they possess very little in common. The application of the term “suborder” to these three groups might express the distant relationship more effectively if it were not for the fact that, in view of the existence of only one family in each suborder, the additional names would merely add to the confusion †. On the whole it is desirable to adopt Max Weber’s suggested

\* Oldfield Thomas, Proc. Roy. Soc. vol. xlvii. (1890) p. 248.

† I have not discussed in this place the very marked distinctions, especially as far as the cerebral commissures are concerned, which separate the three families of Xenarthra. They have been sufficiently indicated in the body of this memoir. I may, however, remark that the apparent simplicity of the commissures in the Sloths is not necessarily an indication of a primitive condition, but may be merely a reversion to the archaic condition such as I have found in the Bat *Nyctophilus* (“The Origin of the Corpus Callosum,” this Vol., p. 47).

division into orders and retain the term Edentata as a convenient if unnatural expression.

The labours of palaeontologists have been amply rewarded within recent years, especially in North America, by exceptionally rich finds of extinct mammalian forms which enable us to trace the genealogy of many of the great groups which have survived until the present day. In the light of the knowledge gained from these records, we can trace the ancestry of the carnivorous clawed mammals (Unguiculata) and of the herbivorous hoofed mammals (Ungulata) back to generalized forerunners, which at the beginning of the Eocene period are with difficulty distinguishable the one from the other.

Not only is this so, but many of the contemporaries of these generalized forms which inhabited the earth at the beginning of the Tertiary epoch are equally difficult to distinguish from these ancestors of the Carnivores and Ungulates. At this time we find a huge multitude of primitive mammals—Creodonta, Condylarthra, Amblyopoda, Gano-donta, Tillodontia, among others,—and so generalized are all these forms, that it is not an easy matter to decide in the case of any whether we are dealing with the ancestor of the Primate, the Carnivore, the Ungulate, the Edentate, the Rodent, the Insectivore, or even the Marsupial.

One of the most noteworthy features which all these generalized and primitive mammals possess in common is the exceedingly small size of the brain. For at this epoch the pallium had just made its first appearance, and the cerebellum was yet in a very primitive condition. When we compare the diversely specialized forms which are rapidly evolved from this simple generalized type as the brain increases in size, we are able to appreciate how immense an impetus the forces of evolution received when a pallium first made its appearance in the brain of the Saurian ancestor of the Mammalia.

The profound effects of this important event almost immediately begin to manifest themselves in the body generally, and become recorded for all time in the modifications of the limbs which fossil forms present. For as complex muscular acts were rendered possible by the development of the pallium, the skeleton became modified in adaptation to these acts. The skeleton thus began "to assume characters and potentialities such as it had not exhibited before, and an entirely new set of modifications" became possible\*.

Under the potent influence of these new factors, which are so favourable to a rapid adaptation to any circumstances in which the individual may happen to be placed, the early mammal soon became specialized to various modes of life, and developed new forms of modifications with all the exuberance of its newly-discovered potentiality to excel. The effects of these modifications are most clearly demonstrated in the limbs and in the teeth, and, most important of all, in the brain.

In the keen struggle for existence, the mammal best equipped with a highly-developed brain, which endows its possessor with the cunning and nimbleness which are of more value than all the protective modifications, whether offensive or purely defensive, must prevail. In the increasing competition among mammals, the progressive perfection

\* A. S. Woodward, 'Vertebrate Palaeontology,' p. 246.

of the brain becomes a necessity if the individual is to survive. But after the brain has attained to a certain degree of development, and competition becomes keener, endless varieties of special modifications take place in different mammals in adaptation to special kinds of life. Those animals whose brains do not keep pace with the general advancement of the Class must either drop out of the race or adopt some special protective mechanism or habit of life which may save them from extinction. The Insectivora, which are the specialized remnants of one of the lowliest stages of mammalian development, are examples of this. The more generalized mammals continue their onward progress in virtue of their cerebral superiority, but from time to time groups branch off and, forsaking the fierce race for pallial supremacy, adopt habits of life and corresponding bodily modifications which will enable them to maintain the struggle against those of their relatives whose better brain-endowment enables them to endure without any marked bodily specialization for self-defence. But the individual which devotes all its energies to self-defence at the expense of its brain is bound before long to share the fate of the *Glyptodon*, even though it be "built like Rome," as the late W. K. Parker remarked.

The last descendants of the main generalized stem which never turned aside to adopt protective modifications or specialized habits of life, but prevailed in virtue of their brain-superiority, became the Primates. They have attained the loftiest position in the mammalian series, and at the same time retained much of the simplicity of the generalized type from which they sprang. It seems as though the adoption of specializations of an offensive or defensive nature is a confession of weakness.

The Ungulate lagged behind in the race for supremacy in cerebral organization at an early period, and by fleetness of limb and largeness of body has sought to compensate for its inferiority of brain. But in spite of this fact it still leads an open life, and the progressive development of its brain is still of vital importance. Hence we find that in the various offshoots from the primitive Condylarthra the growth and elaboration of the brain become conditions of survival. In all probability *Orycteropus* became specialized from the generalized type at about the same time as the Ungulata, and it is not improbable that it may even have branched off from the primitive Ungulate stock. The generalized type of its body and limbs shows that it must have adopted its protective habits of life at this period, and the configuration of its brain indicates that it may for some time have followed the Ungulate line of development. Innumerable modifications of the generalized type branched off at the same time as the ancestors of the Ungulata, and, either from lack of the capacity to develop their brain or to adopt some manner of protection, they succumbed in the struggle and became extinct. Of the few types which survived this process of extinction, *Manis* is probably an example. Although its brain has reached a very considerable degree of development, it has survived by virtue of its peculiar protective mechanism and of its mode of life. Soon after the branching-off of the Ungulata, it is probable that the Rodentia became specialized as a distinct group. They may have arisen from the common stem from which also the Carnivora and probably the Xenarthra sprang, but if so they branched off from this stem before the close of the Eocene, and by adopting a safe mode of life and

generally a small size of body, they were able to survive without that high degree of brain-development which became a vital necessity to the Ungulate, the Carnivore, and especially the Primate.

It is not improbable that the Xenarthra are more nearly related to the primitive Carnivora of the Eocene epoch than are the Rodents. Otherwise it is difficult to understand the features of the brain of *Myrmecophaga*. But if this is so, the Xenarthrous stem branched off from the Carnivore stock at an early epoch, and almost immediately it widely diverged into a number of distinct branches. The Armadillos separated themselves from the others at a very early period, and underwent extreme bodily modifications of a protective nature in order that they might be able to escape extinction, because their brains had become reduced to the lowly standard of the Insectivora.

The Sloths and Ant-eaters also diverged soon afterwards, and, although their brains are of no mean order, they would not be able to exist if it were not for the safe modes of life which they lead, and the peculiar specializations of limb and body which so admirably fit them for such habits.

We may conclude that the evidence of the brain clearly demonstrates that the Edentata are much more nearly related to the ordinary placental mammals than is commonly supposed to be the case. Not only so, but the brain has also reached a fairly high stage of development in *all* the representatives of this extremely heterogeneous group, and may certainly be placed upon a plane at least as high as that of the Rodentia.

The features of the brain conclusively show that *Orycteropus* is no more nearly related to the American forms than the Sheep is to the Dog.

The gradual loss of teeth, and the associated modifications of skull and limbs, do not necessarily imply a retrograde or degenerative process so much as extreme specialization and adaptation to particular modes of life.



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VIII. *Amphipoda from the Copenhagen Museum and other Sources.*—Part II.  
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(Plates 30-35.)

Read 3rd November, 1898.

## INTRODUCTORY REMARKS.

NO panegyrist of the Amphipoda has yet been able to evoke anything like popular enthusiasm in their favour. To the generality of observers they are only not repellent because the glance which falls upon them is unarrested, ignores them, is unconscious of their presence. The majority of the species keep themselves effectively concealed from all but pertinacious intruders, beneath stones and weeds and varying depths of water.

Of the families to be dealt with in these pages the first is the Orchestiidae, or, as some might prefer to call it from the genus first described, the Talitridae. This is of all the Amphipoda the family which has made the strongest effort to place itself in evidence and to overcome the disregard of a neglectful world. More than any of the tribe it has invaded the land, so that its representatives may be found, not only in the sand-hillocks above high-water mark, but in gardens, in woods far from the sea, on hills, in craters of extinct volcanoes. It has climbed higher than any of the Crustacea except a few woodlice, some of the freshwater forms having been taken by Mr. Whymper at a height of more than thirteen thousand feet in the Great Andes. Another mark of distinction may be found in the excessive trouble which nature and art have enabled it to give to the systematist. Not only are the descriptions and figures bequeathed to us by eminent naturalists and artists full of puzzles, but the creatures themselves have conspired in various ways to make the path of knowledge thorny and fatiguing.

Genera, the species of which have different habits, and which are separated by the unlikeness of the males, are in the females scarcely distinguishable (*Talitrus* and *Orchestia*). Genera which have been put apart by a decisive character provokingly join hands just when their separation is most needed. A great increase in the number of known species brings to light the missing links, which, as every one knows, are the curse of classification (*Orchestia* and *Talorchestia*).

Characters which at one time distinguished large groups, or were valid for the whole family, are gradually nibbled away by exceptions here and exceptions there till all the neatness and completeness of the arrangement they provided are muddled away and spoiled. For example, it can no longer be stated with precision that the Orchestiidae always have the first antennæ shorter than the second, and the third uropods with never more than a single branch. It is safer to say in the one case almost always and in the

other hardly ever. The clear division of the family into two groups by the palp of the maxillipeds is brought to nought. It is still true that there are some of the genera in which the joints of the palp in question are four, and others in which they are only three, but forms are now known in which they are not properly either three or four, but rather three and a fraction (*Parorchestia*).

The anomalous family of the Phliadidæ, with which this paper is next concerned, was introduced to scientific notice by that great pioneer in the zoology of the coast-line, Colonel Montagu. It was probably at Salcombe, in South Devon, that he found the typical species. To this he gave the name of *Oniscus testudo*, indicating by the generic name that he made the not unnatural mistake of supposing it to be an isopod. Some of its since found congeners have an even more striking likeness to some of the Isopoda. All the Serolidæ are broad and flat, but in them the tortoise-like and chiton-like appearance is generally impaired by projecting appendages. On the other hand, a New Zealand isopod genus, *Plakarthrium* Chilton, subsequently again described from South Georgia by Pfeffer under the name *Chelonidium*, has a facies with which that of some of the Phliadidæ is exactly comparable. Montagu's species has been found in the Mediterranean, and now a first cousin of it comes to us from Australia. From Australia and New Zealand together we are supplied, as will be shown, with four species of this family so remarkably alike in general appearance and in many conspicuous details of structure that one might readily take them for conspecific varieties. Minuter study brings to light the curious circumstance that they are not only specifically distinct, but that they are separated one from another by characters of generic value.

After one or two notes on the family Melphidippidæ, the paper concludes with the definitions of several new genera within the family of the Gammaridæ. The genus *Gammarus* may be regarded as antediluvian, because, since its institution by Fabricius in 1775, a whole flood of genera has issued from it. With successive restrictions it still remained unwieldy. The researches of Dybowsky in Lake Baikal added a hundred and fifteen species within the compass of a single treatise. Some of the Lake Baikal forms differ so strikingly that it requires either a very lax or a very lofty standard of generic value to allow the comprehension of their varied characteristics within a single genus. It is useless to apologize for the institution of new genera. Their fate not uncommonly is at first to be abused as needless, inconvenient, and ill-constructed. Attempts are sometimes made to ignore them and set them aside. Then, as time goes on, they are found to be necessary, they are recognized, and pass into circulation as current coin of the scientific realm.

The redistribution of species of Gammaridæ here offered would more naturally, as it seems to me, have appeared in that general account of the Amphipoda which is being prepared for 'Das Tierreich.' But the organizers of that vast scheme of zoological publication have passed a self-denying ordinance. Novelty is excluded. There are to be no surprises. The contributor is not to expand the sum of knowledge, but to condense it. From one point of view this is a wise and considerate arrangement, but it has a drawback. In surveying any large group of the animal kingdom, especially among

invertebrates, a reporter can scarcely pursue his studies very far without finding that there are new forms to be described, new names to be applied, new items of classification to be introduced. For all these the rule above mentioned requires double publication, and this, unlike the quality of merey, which blesses him that gives and him that takes, is an almost unmitigated nuisance to the writer and the reader.

It now remains for me to express my hearty thanks to Dr. Meinert and his colleagues at the Copenhagen Museum, and especially to Dr. H. J. Hansen, for entrusting me with the fine collection of Orchestiidae under their charge. To the Trustees of the Australian Museum, Sydney, I am indebted for 'co-types' of some of Professor Haswell's species sent me through the obliging intervention of Mr. R. Etheridge and Mr. Thomas Whitelegge. From America specimens of great service to my work have been sent me by Mr. James Benedict, of the National Museum, Washington; by Mr. S. J. Holmes, of the University of California; and by Mr. C. F. Baker, of the Alabama Polytechnic Institute. To Professor Möbius I owe my thanks for examples of several of the Lake Baikal Gammarids. Mediterranean specimens received from my friends M. Ed. Chevreux and Signor Della Valle have thrown light on various obscure parts of the subject. Lastly, I must refer to the special kindness of Professor Haswell, F.R.S., and Mr. Thomas Whitelegge, who have sent me miscellaneous gatherings of Australian Amphipoda, enabling me to dredge for southern rarities under the shelter of my own roof in the peaceful shallows of a watch-glass.

Fam. ORCHESTIIDÆ.

*Synoptic View of the Genera.*

- 1. { Maxillipeds, fourth joint of palp wanting or quite rudimentary, 2.  
 { Maxillipeds, fourth joint of palp distinct, 5.
- 2. { First gnathopods simple in the male, 3.  
 { First gnathopods subchelate in the male, 4.
- 3. { Second gnathopods feebly chelate in the male . . . . . 1. *Talitrus* Latreille, 1802.  
 { Second gnathopods strongly subchelate in the male . . . . . 2. *Orchestoidea* Nicolet, 1849.
- 4. { First gnathopods subchelate in the female . . . . . 3. *Orchestia* Leach, 1814.  
 { First gnathopods simple in the female . . . . . 4. *Talorchestia* Dana, 1852.
- 5. { Third uropods single-jointed, 6.  
 { Third uropods not single-jointed, 7.
- 6. { Telson partially cleft . . . . . 5. *Ceina* Della Valle, 1893.  
 { Telson entire . . . . . 6. *Chiltonia*, n. g.
- 7. { Third uropods with two rami, 8.  
 { Third uropods with only one ramus, 9.
- 8. { Telson divided . . . . . 7. *Parhyale* Stebbing, 1897.  
 { Telson entire . . . . . 8. *Neobule* Haswell, 1880.
- 9. { Maxillipeds, fourth joint of palp not unguiform . . . . . 9. *Parorchestia*, n. g.  
 { Maxillipeds, fourth joint of palp unguiform, 10.

10. { Second gnathopods of the male, fifth joint not produced between  
the fourth and the sixth . . . . . 10. *Hyale* Rathke, 1837.  
Second gnathopods of the male, fifth joint produced between the  
fourth and the sixth, 11.
11. { Telson undivided . . . . . 11. *Hyalella* S. I. Smith, 1875.  
Telson more or less divided . . . . . 12. *Allorchestes* Dana, 1849.

TALORCHESTIA TRIDENTATA, n. sp. (Plate 30 B.)

The back is not very broad. The first four pairs of side-plates are scabrous, the first shallower than the three following; the fifth is the widest. The eyes are roughly oval, rather more than their longer diameter apart.

*First antennæ.* Very small, not reaching the middle of the penultimate joint of the peduncle of the second antennæ.

*Second antennæ.* About one-third as long as the body; the last joint of the peduncle twice as long as the penultimate; the flagellum scarcely as long as the peduncle, flattened, slightly tapering, consisting of about twenty-four short transverse joints.

*First gnathopods.* Spinose, the fifth joint long, the subapical pellucid process of the hind margin narrow, very prominent; the sixth joint much shorter, rather narrow, the apical pellucid process prominent, the finger with sinuous inner margin, extending beyond the apical process of the sixth joint.

*Second gnathopods.* The second joint is channelled in front, the apices of the front margins being faintly lobed; the third joint is rather larger than the fourth, neither of them longer than broad; the fifth joint is exceedingly diminutive; the sixth very large, its hind margin fringed with spinules, the palm oblique, having near the finger-hinge a large triangular spinulose tooth, followed by a sinuous slope, and defined from the hind margin by two teeth side by side, only one of them being visible in a profile view; the finger very large, with swelling of the inner margin near the hinge; the rest of the margin concave, fringed with small spinules.

*Second pereopods.* This pair is much shorter than the first. The finger has a strong prominence near the base of the nail.

*Third pereopods.* This pair is very short, the second joint nearly as broad as long.

*Fourth and fifth pereopods.* These pairs are not very elongate, but much longer than the third pair. All the pereopods are spinose, with rather small branchial vesicles.

*First uropods.* Long, the rami much shorter than the peduncle, both carrying marginal spines.

*Second uropods.* The rami are not shorter than the peduncle, with stout spines.

*Third uropods.* The ramus is at least as long as the peduncle.

*Telson.* Short, spinulose.

*Length.* Less than half an inch, 11 mm.

*Hab.* California. The specimen described, a male, was sent me by S. J. Holmes, Esq., among specimens of *Orchestia traskiana*.

Without knowledge of the other sex this species can only conjecturally be assigned to

*Talorchestia*. But it shows considerable likeness to another member of that genus, *Talorchestia pravidactyla* Haswell, while also the sharply notched finger of the second peræopods and the long fifth joint of the first gnathopods are more commonly associated with *Talorchestia* than with *Orchestia*. The specific name alludes to the three-toothed palm of the second gnathopods.

TALORCHESTIA NOVE-HOLLANDIÆ, n. sp. (Plate 31 A.)

The body is stout. In the second pleon-segment the postero-lateral corners have an acute point; in the third segment they are quadrate.

*Eyes* round, dark, about their diameter apart.

*First antennæ*. They reach beyond the penultimate joint of the peduncle of the second antennæ; the joints of the peduncle are successively shorter, none of them elongate; the flagellum is shorter than the peduncle and consists of six joints.

*Second antennæ*. Verticillately spinulose, about one-third as long as the body, penultimate joint of the peduncle nearly four-fifths as long as the ultimate; the flagellum is rather shorter than the peduncle, and is composed of nineteen rather short joints.

*First gnathopods*. ♂. The second joint bulges considerably from the narrow neck and then narrows again slightly; the fifth joint is longer than the sixth, and has a prominent but narrow apical process of the hind margin; the sixth joint is rather short, much widened distally, the finger overlapping the true palm, but not the advanced rounded process of the hind margin, against which its apex impinges.

*Second gnathopods*. ♂. The second joint is comparatively narrow, the third rather larger than the fourth, the fifth diminutive; the sixth very large, slightly widening to the almost transverse palm, which, as so often occurs, has at the defining angle a small pocket, a broad convexity leading thence to a spinulose concave space near the finger-hinge, over which space the finger arches, leaving an interval, the convexity of its sinuous margin then touching the convexity of the palm and its apex passing into the defining pocket.

*First gnathopods*. ♀. The fifth joint has no apical process of the hind margin; the sixth is short, strongly spined, narrowing gradually to the short finger, the base of which occupies its rounded apex.

*Second gnathopods*. ♀. The second joint is membranous, well expanded; the sixth joint nearly as long as the fifth, rather narrow, produced as usual beyond the minute palm, to which the finger is adjusted in a rather oblique position.

*Second peræopods*. The finger is sharply notched near the nail.

*Third peræopods*. These are short, with the broadly expanded second joint almost as broad as long.

*Fourth peræopods*. Much longer than the third pair.

*Fifth peræopods*. These are longer than the fourth pair, and have the second joint broader, with subquadrate apex to its hind margin; the fourth and fifth joints rather broad, but at the same time elongate; the sixth joint long and narrow. All the peræopods have numerous spines on both margins.

*Uropods.* These all have marginal spines on the peduncles and rami.

*Third uropods.* The ramus is slender, shorter than the peduncle.

*Telson.* This is peculiar, much longer than broad, composed of separate halves, which appear to fold closely together, each carrying two apical spinules and two well-separated marginal spines.

*Colour.* Dusky in spirit.

*Length.* About two-fifths of an inch, 10 mm.

*Hab.* Australia, Manly Beach. Two specimens were forwarded to me by Mr. Thomas Whitelegge, of the Australian Museum, with the label, "*Talorchestia noræ-hollandiæ*. H. Manly Beach." The specimens were ♂ and ♀.

TALORCHESTIA DESHAYESII (Audouin). (Plate 30 A.)

1825. *Orchestia Deshayesii* Audouin, Explication des Planches de Savigny, Atlas, pl. 11. fig. 8.

1893. *Talorchestia Deshayesi* Chevreux, Bulletin de la Société Zoologique de France, vol. xviii. p. 127, fig. in text.

For the remainder of the synonymy of this well-known species reference may be made to the 'Challenger' Amphipoda and Della Valle's Gammarini. The specimen here figured is a young male. It exhibits a form of the second gnathopod closely agreeing with that which Barrois has figured as belonging to an individual with eighteen joints in the flagellum of the second antennæ. The individual here figured has that precise number of joints in the flagellum. Professor Th. Barrois was the first to call attention to the transformations through which the second gnathopod passes in the male of this species. It begins with a feebly chelate form. Gradually the palm becomes transversely excavate and defined by a blunt double tooth. The tooth becomes single, the palm becomes oblique, and finally in the adult stage there is an acute tooth, which, so far from chelately overlapping a small finger, has shrunk back to the very base of the hand, and a very long finger curves to meet it over a long straight extremely oblique palm.

The specimen was obtained for the Copenhagen Museum from Constantin, in Algeria, by Dr. Meinert.

I have a specimen with the adult form of the gnathopod on one side, and on the other the juvenile, the latter no doubt representing a limb that has been lost by some accident.

M. Ed. Chevreux was the first to show that in the female the first gnathopod is simple, so that the species is more properly referred to *Talorchestia* than to *Orchestia*.

The species is frequently to be met with on the sandy shores of North Devon. Its European distribution is very extended.

ORCHESTIA SULENSONI, n. sp. (Plate 30 C.)

The integument, as preserved in spirit, is membranaceous and iridescent. The third and fourth pairs of side-plates are little deeper than the fifth and sixth. The third pleon-segment has the postero-lateral corners quadrate, the point scarcely produced.

*Eyes* not very large.

*First antennæ.* The first joint is very small, at least as broad as long; the second and third joints are each slightly longer; the flagellum consists of four joints, together about as long as the third joint of the peduncle.

*Second antennæ.* The peduncle is large and stout, its penultimate joint about three-fourths as long as the ultimate, and not stouter. The flagellum is shorter than the peduncle, and on one side of the specimen contained twenty-one joints, on the other side eighteen.

*First gnathopods.* The second joint is narrow at the base, and then becomes rather broad; the fourth has no apical process; the fifth widens to a distal, pellucid, prominent but narrowly rounded process of the hind margin; the sixth joint, which is two-thirds the length of the fifth, is oblong, widening very slightly to the palm, which has no conspicuous process, and is overlapped by the small unguiculate finger. Both the fifth and sixth joints are beset with a moderate armature of spinules.

*Second gnathopods.* The second joint is not very wide, though for most of its length much wider than at the base. The third and fourth joints are very small, but larger than the almost evanescent fifth. The sixth joint is very large, fringed with spinules on the hind margin, widening to the palm, which is moderately oblique, spinulose, smoothly convex between a blunt defining tooth and a deep depression near the finger-hinge, the depression corresponding with a rounded process of the finger's inner margin; the large curved finger matches the palm.

*First and second pereopods.* These are slender, the first pair conspicuously longer than the second, the short finger of the second having, as usual in the genus, its inner margin indented.

*Third, fourth, and fifth pereopods.* Of these the third is much smaller than either of the others. In all the second joint is oval, but in the fifth pair, in which it is largest, the oval is modified by the comparative straightness of the hind margin. In the fourth and fifth pairs the joints following the third are rather long and narrow.

*First uropods.* The upper ramus has lateral as well as apical spines, and is rather shorter than the lower ramus, which has only apical spines.

*Second uropods.* The rami are equal, and both have lateral spines.

*Third uropods.* The ramus is not half as long or half as broad as the peduncle. It is armed with a row of three spinules.

*Length* two-fifths of an inch, 10 mm. From the size of the second gnathopods and powerful second antennæ in the single available specimen it may be inferred to be an adult male. It agrees with the imperfectly described *Orchestia lucuranna* of Fritz Müller in regard to the finger and the notched palm of the second gnathopods, but Müller lays stress on the fact that these characters are combined with incrassated fourth and fifth joints of the fifth pereopods in his species, the younger males with slender pereopods having also a smooth palm to the gnathopods and the second antennæ slender.

*Hab.* The specimen, which belongs to the Copenhagen Museum, was labelled "Madeira? Sulenson."

The specific name is given in compliment to the traveller who procured the specimen.

## ORCHESTIA GRILLUS (Bosc).

1802. *Talitrus grillus* Bosc, Histoire Naturelle des Crustacées, vol. ii. p. 152, pl. 15. figs. 1, 2 (called on the plate 'Thalitre terrestre').

It is not necessary here to discuss the synonymy of this species, which nearly resembles *Orchestia gammarellus* (Pallas). It is only mentioned for the sake of recording an abnormality in a male specimen belonging to the Copenhagen Museum. The second peraeopod on the right side has been cicatrized near the base of the fourth joint, but attached to the same side-plate that carries the damaged limb is a limb with the full number of joints, though these are less strongly developed than those of the limb on the left side or than the remaining joints of the broken limb.

*Hab.* The specimen is labelled "New York Omegn, L. Lund," meaning that it was obtained by L. Lund in the neighbourhood of New York.

## PARORCHESTIA, n. g.

Like *Orchestia*, except that the maxillipeds have a fourth joint to the palp, distinct, though small, conical, and carrying a spine on the truncate apex.

The name is derived from παρά, near, and *Orchestia*. The genus is formed to receive the species (1) *Orchestia tenuis* Dana, with which the *Allorchestes recens* of G. M. Thomson seems to be identical; (2) *Orchestia hawaiiensis* Dana; and (3) *Orchestia sylvicola* Dana.

## HYALE GALATEE, n. sp. (Plate 31 B.)

The species occurs both in the Atlantic and the Pacific, with the slight difference that in the Atlantic specimens the integument appears to be smooth, while in those from the Pacific the back and to some extent the appendages are scabrous, with little hairs or scales like a capital T inverted. The first side-plates are widened below, the second and third pairs are not very deep. The third pleon-segment has the postero-lateral corners quadrate.

*Eyes.* Large, oval, black, nearly meeting at the top of the head.

*First antennæ.* Much longer than the peduncle of the second antennæ; joints of the peduncle small, successively shorter; flagellum in ♂ with nine, in ♀ seven, distally widened joints.

*Second antennæ.* About one-third as long as the body; last joint of the peduncle considerably longer than the penultimate; flagellum of ♂ with twelve to fourteen, of ♀ nine joints.

*First maxillæ.* The palp has a small constriction.

*Maxillipeds.* The curved fourth joint of the palp is slender.

*First gnathopods.* ♂. The second joint is short and broad, with narrow base; the fourth is distally squared; the fifth is as broad as long, with a rounded lobe behind carrying spines along the somewhat flattened hind margin; the sixth joint is rhomboidal, distinguished by a small hump at the centre of the long front margin, the much shorter

concave hind margin making an angle before it joins the oblique spinuliferous palm, from which it is defined by a palmar spine that antagonizes with the apex of the curved finger.

*Second gnathopods.* ♂. The second and third joints are distally lobed in front; the fourth has the apex broadly rounded; the fifth is very short, with the little horny-looking process from the hind margin on either side more conspicuous than usual; the sixth joint is large, widest where the short, smoothly curved, hind margin meets the long, very oblique, nearly straight, spinulose palm, and narrowest at the hinge of the long curved finger, which has a strong bulb at the base of its inner margin.

*First and second gnathopods.* ♀. Small, the fifth joint short, the sixth oblong, slightly widened at the rather oblique, spinulose palm. The second pair are a little the longer.

*Percæopods.* These are moderately robust. The finger has a minute inner setule. In the last three pairs the second joint is broadly oval, nearly smooth on the hind margin, the lower part of the wing in the fifth pair being broadly produced downward.

*First and second uropods.* In both pairs there are lateral as well as apical spines on both rami.

*Third uropods.* The ramus is a little shorter than the peduncle, with spinules at or near the apex.

*Telson.* The lobes have the proximal half of nearly uniform width, the distal half triangular.

*Length.* About one-sixth of an inch, 4 mm.

*Hab.* Pacific and Atlantic. Specimens belonging to the Copenhagen Museum were taken at various localities, at different dates, by several naturalists, as appears from the labels, "‘Galatea,’ 6. 8. 46. Rhdt.;" "37° 32' N., 179° 43' E., 15. 3. 46. Reinhardt"; "4° 30' N., 137° E., 8. 11. 75," "Caspersen"; while in the Atlantic one specimen, ♂, was obtained from the Sargasso Sea by "Friis, 1861," and one specimen, ♀, "26° 20' N., 58° 40' W., 6. 2. 96. Chr. Levinsen," the last locality also corresponding with the Sargasso Sea.

#### HYALE DIPLODACTYLUS, n. sp. (Plate 31 C.)

The first and second side-plates are not very deep, and the first are but little widened below.

*Eyes.* Rounded, light-coloured in spirit.

*First antennæ.* Much longer than the peduncle of the second pair; the peduncle is short, the second joint much shorter than the first, and the third than the second; the flagellum in the ♂ has fourteen joints, in the ♀ nine.

*Second antennæ.* The last joint of the peduncle is rather longer than the penultimate; the flagellum in the ♂ has twenty-six joints, in the ♀ seventeen.

*First gnathopods.* ♂. The second joint is rather short, narrow above, broad below; the fourth joint is distally squared, supporting the spinose hind lobe of the fifth joint, which throws out this lobe beyond a short distal piece of its hind margin; the sixth

joint widens greatly to the palm, with the hind margin sinuous, much shorter than the smoothly curved front; the palm long, not very oblique, excavate, ending in a wide pocket, which receives the deeply furcate end of the finger, which is thus wider distally than at its base.

*Second gnathopods.* ♂. These scarcely differ from those of *Hyale Galatæa*, except that the expanded front margin of the second joint is closely fringed with setules, and the sixth is widest near to the base instead of at the junction of the hind margin with the long, very oblique palm.

*Telson.* *In situ* this is rather markedly upturned, with a slight twist to the blunt apex of each triangularly ending lobe. In other respects this species appears in both sexes to agree with *Hyale Galatæa*, except that the size is a little greater.

*Length.* ♂ rather over, ♀ rather under one-fifth of an inch, 5 mm.

*Hab.* St. Croix. The specimens belonging to the Copenhagen Museum were obtained by Oersted in the Danish West Indies.

The specific name refers to the double-ended finger in the first gnathopods of the male.

#### HYALE MACRODACTYLUS, n. sp. (Plate 31 D.)

The side-plates are not deep; the first is distally widened, the fourth is wide, with deep hind emargination. The third pleon-segment has the postero-lateral corners quadrate, the angle scarcely produced.

*Eyes.* Not large, rounded, wider apart than their diameter.

*First antennæ.* The peduncle is short, its first joint subequal to the second and third combined; the flagellum consists of thirteen joints, of which those near the base are short.

*Second antennæ.* More than half as long as the body; the last joint of the peduncle longer than the short penultimate; the flagellum containing twenty-five joints.

*First gnathopods.* ♂. The second joint is short and broad except at the base; the third has a small front lobe; the fourth an acute hind apex; the fifth is lobed much as in *Hyale diplodactylus*; the sixth is oblong oval, the palm oblique, spinulose, separated from the hind margin by a rounded angle carrying a palmar spine, against the inner side of which the apex of the finger closes.

*Second gnathopods.* ♂. The second joint is lobed at the distal end of the front margin; the third is lobed in front; the rounded apex of the fourth touches the base of the sixth; the fifth is small, triangular, with length and breadth subequal; the sixth is elongate, widest at the base, the front margin smoothly convex, the palm closely fringed with slender spinules and extending almost the whole length of the joint, its nearly straight line broken only by a shallow emargination between two slight swellings, one of which is close to the finger-hinge; the long, blunt, slightly sinuous finger can reach the apex of the fourth joint.

*First and second gnathopods.* ♀. The sixth joint is narrowly oblong.

*Peræopods.* In these the sixth joint at the apex of the inner margin carries a strong

blunt spine, with a similar but much shorter one below it; the finger curved, its inner setule minute. In the third and fifth pairs the second joint is somewhat orbicular; in the fourth pair it is oblong oval, rather wider above than below.

*First and second uropods.* Both rami have lateral spines.

*Third uropods.* The ramus is as long as the peduncle.

*Telson.* The lobes are bluntly triangular.

*Length.* About one-sixth of an inch, 4 mm.

*Hab.* St. Thomas's Harbour. The specimens, which belong to the Copenhagen Museum, were obtained in the Danish West Indies by Chr. Levinsen, and reached me mixed with specimens of *Hyale Perieri* (Lucas) and *Hyale media* (Dana).

A specimen in the same collection, from Rio Janeiro, is probably a younger form of the male of this species. It has a flagellum of ten joints to the first, and one of eighteen to the second, antennæ. The first gnathopods are without the strong bulging at the juncture of the palm with the hind margin. The second gnathopods have the long oblique palm smoothly curving and defined from the short hind margin by a small pocket, which the long finger reaches.

#### HYALE MAROUBRE, n. sp. (Plate 32 C.)

Body rather compressed, shining. Third pleon-segment with postero-lateral corners quadrate.

*Eyes.* Roughly rounded, about their diameter apart, moderately dark in spirit.

*First antennæ.* These reach well beyond the peduncle of the second pair. The peduncle is short, the first joint equal to the second and third combined; the flagellum has nine slender joints.

*Second antennæ.* About half the length of the body; the flagellum longer than the peduncle, slender, composed of nineteen joints.

*First gnathopods.* ♂. The fourth, fifth, and sixth joints are subequal in length; the fourth has a produced, broadly-rounded apex, carrying one or two spinules; this apex is separated from the sixth joint by the rounded hind lobe of the fifth, which is fringed with about eight graduated spines; the sixth joint is oblong, but scarcely longer than the width, which is rather greater at the palm than the base; the hind margin from near the base is fringed with spinules which pass round on to the surface and meet a transverse row of small spinules, across which the short finger closes, as though they represented the true course of the palm, but the hinder half of the distal margin of the sixth joint extends beyond these in a microscopically denticulate lobe at right angles to the hind margin, though the junction is rounded off.

*Second gnathopods.* ♂. The second joint is slightly lobed at the front apex, downward, not outward; the third joint has a small outward lobe; the fourth joint is small, a little produced at the hind apex; the fifth is very small, triangular; the sixth very large, oval, broadest proximally, the hind margin very short, the spine-fringed palm very oblique and long, well defined, the long finger nearly reaching the fourth joint, its

apex when closed passing on the inner side of the palmar spine into a pocket on the surface of the sixth joint. The branchial vesicles are very small.

*Peræopods.* These are of medium robustness and the usual relative proportions, but are distinguished by the apical spines of the sixth joint. As in various other species, the large distal spine which antagonizes with the finger is blunt-headed, with the margin partially serrate, but the smaller spine between this and the finger is bent up to meet it, and is not tapering or parallel-sided, but from the neck onward of fusiform appearance, with numerous lines or grooves parallel more or less to the outline; the setule on the inner margin of the finger is extremely small. In the last three pairs the second joint has the hind margin crenulate, but not strongly.

*First uropods.* The rami are as long as the peduncle, and neither of them is devoid of lateral spines.

*Second uropods.* The rami are unequal, longer than the peduncle.

*Third uropods.* The ramus is moderately slender, as long as the peduncle, both with apical spines only.

*Telson.* Cleft to the base, slightly broader than long, the lobes distally somewhat acutely triangular.

*Length.* One-fifth of an inch, 5 mm.

*Hab.* Australia; Maroubra Bay, near Sydney, New South Wales. The specimens occurred in a gathering sent me by Mr. Thomas Whitelegge, "obtained by washing the seaweeds from low tide-line."

By the structure of the first gnathopods and the peculiar spines of the peræopods this species seems to be easily distinguishable from all hitherto described.

#### HYALELLA WARMINGI, n. sp. (Plate 32 A.)

The body is rather robust; the sixth side-plates are deeply lobed behind; the third pleon-segment has the postero-lateral corners a little produced backward, acute.

*Eyes.* Small, dark, wider apart than their diameter.

*First antennæ.* The second joint is scarcely shorter than the first, the third a little shorter than the second; the flagellum has thirteen joints in the  $\sigma$ , ten in the  $\varphi$ .

*Second antennæ.* More than half as long as the body, the gland-cone prominent, the last joint of the peduncle a little longer than the penultimate; the flagellum shows nineteen joints in the  $\sigma$ , fifteen in the  $\varphi$ .

*First maxillæ.* The palp is minute.

*Maxillipeds.* Third joint of palp distally widened, fourth with curved spine on the blunt apex.

*First gnathopods.*  $\sigma$ . The fifth joint has a subapical group of spines on the front margin, and the bulging hind margin fringed with graduated spines; the sixth joint is shorter, widening, with sinuous hind margin to the transverse palm, which is defined by a process within which the finger closes; there is an oblique row of spinules on the surface.

*Second gnathopods.*  $\varphi$ . The second joint is slender, not lobed below; the fifth short,

the fringed cup-like process well produced; the sixth joint large, oval, the very oblique sinuous palm forming three lobes, of which the centre one is broadest, the finger closing at the third into a pocket which meets the hind margin at a well-defined angle.

*First and second gnathopods.* ♀. These are similar to the first in the ♂, but smaller, and the sixth joint of the second is rather longer and more slender than that of the first.

*Peræopods.* These are tolerably robust and spinose. In the last three pairs the second joint is broadly oval, considerably larger in the fifth than in the two preceding pairs. There are simple accessory branchiæ on the first four pairs of the peræopods.

*First and second uropods.* These have lateral spines on both rami.

*Third uropods.* The ramus is as long as the peduncle.

*Telson.* Squared at the base, then broadly rounded, with two distant setules on the broad apical margin.

*Colour.* Dusky in spirit.

*Length.* A fifth of an inch, 5 mm.

*Hab.* Lagoa Santa, from watercourse. The specimens belong to the Copenhagen Museum, and were obtained by Warming, after whom the species is named. The species seems most nearly related to *Hyalella Lubomirskii* (Wrześniowski), to judge by the description of that species, which is unhappily unaccompanied by figures.

#### HYALELLA MEINERTI, n. sp. (Plate 32 B.)

The first three pairs of side-plates are deeper than broad; the third pleon-segment has the postero-lateral corners acutely quadrate.

*Eyes.* Black, usually wider apart than their diameter.

*First antennæ.* Slender, more than half as long as the second pair; third joint of the peduncle nearly as long as the second, but by its slenderness resembling the joints of the flagellum; flagellum composed of nine or ten elongate joints.

*Second antennæ.* Slender, more than half as long as the body; penultimate joint of peduncle rather long, ultimate still longer, the flagellum consisting of thirteen to fifteen elongate joints.

*First gnathopods.* ♂. The fourth joint has a scabrous, rather prominently rounded apex; the fifth is strongly widened distally, with the projecting apex scabrous and rounded; the sixth joint is much shorter, scarcely widening to the transverse well-defined palm, and, as is so commonly the case in the genus, inclined athwart the preceding joint.

*Second gnathopods.* ♂. The second joint is narrow, the fourth as in the preceding pair; the fifth with the usual cup-like spine-fringed lobe; the sixth much longer than broad, its basal part narrow, rather abruptly widening at the boss which defines the oblique, slightly sinuous palm, the finger closing completely over the palm, with its apex on the surface within the boss.

*First and second gnathopods.* ♀. These are small; the fourth joint has a rounded

apex; the sixth in the first pair is shorter than the fifth, but in the second at least as long, in both narrow, oblong, narrowest at the base, with the short palm transverse or slightly tending to form an acute angle with the hind margin.

*Peræopods.* The fourth pair are rather longer than the third, and the fifth than the fourth. In the third and fourth pairs the second joint is oval, in the fifth pair it is much wider, with flattened front and very convex hind margin. There are accessory branchiæ to all the five pairs. The ordinary branchiæ were not perceived on the fifth pair.

*Uropods.* These are unusually slender. The first and second pairs have lateral spines on both rami. The third pair are comparatively long, the tapering ramus rather longer than the peduncle, and extending considerably beyond the telson.

*Telson.* Oblong oval, with a pair of spinules on the rounded apex.

*Length.* A fifth to a quarter of an inch, 5-6 mm.

*Hab.* Lago di Espino. Specimens belonging to the Copenhagen Museum, obtained by Dr. Meinert, in compliment to whom the species is named.

In regard to the first and second antennæ this species agrees closely with Faxon's "*Allorchestes dentatus*, var. *gracilicornis*," and in other respects with his "*Allorchestes longistilus*"; but for neither of these forms is any mention made of accessory branchiæ, nor do those appendages appear to be present in *Hyaella inermis* S. I. Smith, to which Faxon's species are closely related.

#### CHILTONIA, n. g.

First four pairs of side-plates deep. First and second antennæ equal in length. First maxillæ without palp, although distinctly notched at the palp's usual position. Maxillipeds with the fourth joint of the palp small, conical. Other mouth-parts as in the family character. First and second gnathopods subchelate, the second differing greatly in the two sexes. The third uropods one-jointed. Telson simple.

Name of the genus given in compliment to Dr. Charles Chilton, M.D., D.Sc., F.L.S.

#### CHILTONIA MIHIWAKA (Chilton).

1898. *Hyaella mihiwaka* Chilton, Annals and Magazine of Natural History, ser. 7, vol. i. p. 423, pl. 18.

The typical species has been very accurately described and figured by Dr. Chilton, who has obliged me with specimens. It seems possible that the pear-shaped third uropods may represent a peduncle and ramus coalesced into a single joint.

"*Colour.* Greyish or nearly white.

"*Size.* Largest specimens about one-fifth of an inch (5 mm.).

"*Hab.* Mountain-streams near Port Chalmers, up to about 1500 feet above sea-level (*Chilton*). In hillside stream at East Taieri; from spongy moss at top of Mount Cargill, 2200 feet, and on Swampy Hill, 2400 feet (*G. M. Thomson*)."

*ALLORCHESTES MALLEOLUS*, n. sp. (Plate 33 A.)

The body is moderately compressed. The first four pairs of side-plates are rather deep, without the projecting point of the hind margin found in many of the *Orchestiidae*. The third pleon-segment has the postero-lateral angles bluntly produced.

*Eyes.* Not large, rounded, dark in spirit, at least as far apart as their diameter.

*First antennæ.* About three-quarters as long as the second pair; the second joint a little shorter than the first; the third considerably shorter than the second; the flagellum longer than the peduncle, with ten to twelve joints.

*Second antennæ.* Not more than one-third as long as the body; the peduncle stout; the last joint a little longer than the penultimate; the flagellum shorter than the peduncle, consisting of ten to twelve joints. In young from the marsupium the first antennæ are not shorter than the second; the flagellum in each pair is limited to two or three joints.

*First maxillæ.* The palp is minute, on a well-defined interruption of the hind margin of the outer plate.

*Second maxillæ.* The principal seta on the inner margin of the inner plate is not very elongate.

*First gnathopods.* ♂. The second joint widens rapidly to the middle; the fourth is not longer than the third; the fifth little longer than the sixth, widest subapically, with spines on both margins at the widest part; the sixth widening to a sort of palmar angle, a part of the sinuous hind margin being adapted to rest on the hind process of the fifth joint, the margin then abruptly turning to join the short spinulose palm, which is exactly fitted by the stout two-pointed finger.

*Second gnathopods.* ♂. The second joint has no conspicuous distal lobe. The fourth is produced, but not acutely; the fifth is produced into a shallow, fringed, cup-like process; the sixth is oval, the finger closing over an oblique, almost straight palm into the usual pocket, armed with two palmar spines; the hind margin not at all bulging, carrying spinules at two points.

*First gnathopods.* ♀. The fourth and fifth joints are as in the male; the sixth is oblong, slightly widening to the transverse palm, the hind margin sinuous, the finger acute, closely fitting the palm.

*Second gnathopods.* ♀. These are larger than the first pair, though very small compared with the second pair in the male. The fourth joint is subacutely produced; the fifth is shorter than the sixth, distally wider than the length, the process fringed with spinules; the sixth joint is oblong, slightly widened distally, the hind margin straight, the finger acute, scarcely reaching the end of the transverse palm. In young, taken from the marsupium, the first and second gnathopods have a general resemblance to the first gnathopods of the adult female. The marsupial plates of the second gnathopods and first pereopods have one distal corner subacutely produced; those of the second pereopods end squarely; in all, the fringing setæ are short.

*Pereopods.* None are strongly spined. The finger is curved; in the last three pairs the second joint is oblong oval, the front margin nearly straight, the hinder produced

downward in a rounded lobe; in the fourth pair this joint is more oblong than oval, widest proximally, whereas in the fifth pair it is much broader and widest distally. In the female the last three pairs are shorter and stouter than in the male, with the fourth joint more widened distally.

*Pleopods.* There are two or three coupling-spines on the peduncle, and on the inner margin of the first joint of the inner ramus four to five spines, not cleft, but at the apex a little dilated and hooked.

*Uropods.* Small; first pair with lateral spines on only one of the rami; third with the small ramus shorter than the peduncle.

*Telson.* Nearly square when flattened out, with slightly convex sides, the cleft not reaching beyond the middle, its sides not divergent.

*Length.* About 7 mm.

*Hab.* Korean and Japanese waters: 31° 40' N., 125° 50' E., Tong-kai, in seaweed (*Studer collection*); 34° 14' N., 129° 34' E., in seaweed, Korea (*Andréa*); 34° 40' N., 129° 50' E., Japan (*Andréa*); 37° 0' N., 131° 20' E. (*Studer collection*); Wladiwostock? (*H. Koch*); all the specimens belong to the Copenhagen Museum.

The specific name refers to the hammer-like appearance of the first gnathopods of the male.

*ALLORCHESTES COMPRESSUS* Dana. (Plate 33 B.)

1852. *Allorchestes compressa* Dana, Proceedings of the American Academy of Arts and Sciences, vol. ii, p. 205.
1852. *Allorchestes australis* Dana, P. Amer. Ac. vol. ii. p. 206.
1853. „ *Gaimardii*? Dana, United States Exploring Expedition, vol. xiii. p. 884, pl. 60, fig. 1 *a-i*.
1853. *Allorchestes australis* Dana, U.S. Expl. Exp. vol. xiii. p. 892, pl. 60, fig. 7 *a-o*.
1862. „ *Gaimardii* Bate, Catalogue of Amphipodous Crustacea in the British Museum, p. 41, pl. 6, fig. 9.
1862. *Allorchestes australis* Bate, Catal. Amph. Brit. Mus. p. 45, pl. 7, fig. 6.
1881. *Aspidophoreia diemeuensis* Haswell, Proceedings of the Linnean Society of New South Wales, vol. v. p. 101, pl. 6, fig. 2.
1893. *Allorchestes (Hyale?) compressa* Della Valle, Fauna und Flora des Golfes Neapel, Monograph 20, p. 528 (see also pp. 519, 523).
1893. *Aspidophoreia (Hyale?) diemenensis* Della Valle, F. u. Fl. G. Neapel, Mon. 20, p. 530.

The body is compressed, especially at the pleon. The first four pairs of side-plates are deep, the fourth being also wide; the second to the fourth are quadrate, the fifth is shallow. The postero-lateral corners of the third pleon-segment are quadrate, with minutely-produced point.

*Eyes.* Oval, wider apart than the longer diameter.

*Antennæ.* In young from the marsupium the two pairs are equal; in the adult the proportions are rather variable. As Bate points out, Dana mistook a fused portion of the flagellum in the second pair for a joint of the peduncle.

*First antennæ.* Usually rather longer than the peduncle of the second pair; flagellum consisting of from ten to twenty joints.

*Second antennæ.* Flagellum much or not much longer than the peduncle, having from ten to twenty joints.

*Upper lip.* Broader than deep.

*First maxillæ.* Palp minute.

*Maxillipeds.* Second and third joints of palp broad.

*First gnathopods, ♂.* Fifth joint slightly longer than sixth, widest subapically, with spinules at projections of front and hind margins; sixth oblong, a little widened at the almost transverse convex palm; the finger matches the palm.

*Second gnathopods, ♂.* Robust, the second joint with small downward-produced lobe, the third also with the front lobed, the fourth apically produced behind, the fifth produced backward in a rather slender and not strongly spined lappet, the sixth large; the palm spinulose, very oblique, defined from the slightly bulging hind margin by palmar spines and the small hollow which receives the apex of the strong finger

*First gnathopods, ♀.* These are as in the male, except that the sixth joint is more elongate, equal to the fifth.

*Second gnathopods, ♀.* Rather larger than the first; the second joint not produced downward, the third without conspicuous lobe, the fourth as in the male, the fifth with its lappet stretching along part of the straight hind margin of the sixth, the sixth broader than in the first pair, slightly widening to the transverse palm, which the finger matches. The branchial vesicles are large, oval, with narrow neck. The marsupial plates are broad, oblong, produced at one corner, their setæ short.

*First and second peræopods.* Subequal, slender.

*Third peræopods.* The second joint is oblong oval, the front margin carrying spines, nearly straight, the hind margin nearly smooth; the fourth joint is widened, spinose on both margins.

*Fourth peræopods.* Considerably longer than the third, but with the second and fourth joints not quite so wide; the branchial vesicles in both these pairs have an accessory lobe.

*Fifth peræopods.* These are shorter than the fourth pair, especially in the male, but they have the second joint much larger and more rounded behind, widest subapically and broadly produced behind the third joint; the fourth joint not much widened; the finger, as in the other pairs, short and curved.

*First uropods.* The rami are decidedly shorter than the peduncle.

*Second uropods.* The rami are a little shorter than the peduncle.

*Third uropods.* The ramus is small, conical, shorter than the stout peduncle, tipped with a minute spinule.

*Telson.* Broad; the two quadrate lobes, separated by a linear fissure, are set at an angle one to another, gable-like.

*Colour.* For *Aspidophoreia diemenensis* Professor Haswell says: "surface (in the spirit specimen) ornamented with marbled spots of red, brown, and white, and with numerous, very minute, white dots, arranged in clusters of three or four."

*Length.* For *A. Gaimardii* Dana gives the equivalent of 14-16 mm., Bate 18 mm.; for *A. australis* Dana gives 12-13 mm.; for *A. diemenensis* Haswell gives 20 mm.; some

unnamed specimens kindly sent me by Professor Haswell, and which I refer to this species, measured about 11 mm.

*Hab.* Shores of Illawarry, New South Wales (*A. Gaimardii* and *A. australis* Dana); South Australia (*A. Gaimardii*, Bate); Tasmania (*A. diemenensis* Haswell); Jervis Bay, Australia (the specimens above-mentioned, received from Professor Haswell).

ALLORCHESTES PLUMICORNIS (Heller). (Plate 33 C.)

1866. *Nicea plumicornis* Heller, Denkschriften der k. Akad. d. Wissensch. math.-naturw. Cl. vol. xxvi. p. 5, pl. 1. figs. 8, 9.

1893. *Hyale Prevostii* Della Valle, F. u. Fl. Neapel, Mon. 20, Gammariini, p. 519.

The body is compressed and the back smooth. The first side-plates widened below.

*Eyes.* Elongate rounded, black.

*First antennæ.* They reach along nearly half the flagellum of the second pair. The first joint is longer than the second, the second than the third, which itself is not very short; the flagellum is much longer than the peduncle, of about eighteen successively lengthening joints.

*Second antennæ.* The flagellum is longer than the peduncle, of twenty-two joints; the terminal joints of the peduncle and first half of the flagellum are clothed below with long fascicles of setæ.

*First maxillæ.* The palp reaches the base of the spines of the outer plate.

*Maxillipeds.* The third joint of the palp is setose, the fourth long, acute.

*First gnathopods, ♂.* The second joint rapidly widens from the narrow base; the fourth has a bluntly-produced apex; the fifth forms a broad hind lobe, fringed along the hind margin with graduated spines; the sixth is oblong oval, rather longer than the fifth, widening slightly to the straight, oblique, spinulose palm; the finger thick, with outer margin abruptly curving to an acute apex.

*Second gnathopods, ♂.* The second joint is rather narrowly produced downward in front; the fourth bluntly produced behind; the fifth very short, but wide, embracing the base of the large oval sixth joint, which has a small group of spinules on the hind margin; the palm oblique, well defined by its angle and palmar spines; the finger strong, acute, much curved.

*Pereopods.* The fifth pair is like the fourth, but rather longer; the sixth joint slender, straight; the finger acute, little curved; the setule of its inner margin prominent, as in all the pereopods.

*Uropods.* All the rami have marginal spines. In the third pair the peduncle is rather shorter than the telson, the ramus nearly as long as the peduncle.

*Telson.* Cleft to the base; the lobes below the middle narrow to rounded, well-separated apices. As usual, the lobes *in situ* are inclined one towards the other.

*Length.* 9-11 mm.

*Hab.* Mediterranean, at Ragusa in the Adriatic, at Genoa, and at Villefranche.

Male specimens from Villefranche have been kindly sent me by the well-known carcinologist, M. Ed. Chevreux. According to Heller, only females were known to him;

but I feel convinced that his figures and description refer to the male sex. The hirsute second antennæ and the great difference in the size of the two pairs of gnathopods are strong evidence of this.

*ALLORCHESTES HUMILIS* Dana. (Plate 33 D.)

1852. *Allorchestes humilis* Dana, P. Amer. Ac. vol. ii. p. 206.

1853. „ „ Dana, U.S. Expl. Exp. vol. xiii. p. 890, pl. 60. fig. 6 *a-e*.

1862. „ „ Bate, Catal. Amph. Brit. Mus. p. 45, pl. 7. fig. 5.

1893. ? *Hyale Prerostii*, ♀, Della Valle, F. u. Fl. G. Neapel, Mon. 20, Gammarini, p. 528.

*Eyes.* A little oblong, according to Dana. In Saghalien specimens, small, round, light-coloured.

*First antennæ.* A little shorter than the second pair; the peduncle two-thirds as long as the peduncle of the following pair; the flagellum containing from six to eight joints, which are very distinct, with moniliform appearance, and long filaments on the widened apices.

*Second antennæ.* About one-third the length of the body; the last two joints of the peduncle subequal; the flagellum containing nine to ten joints, which are not very long nor distally widened; the setæ being in Dana's account all very short, but not very short in Saghalien specimens.

*First maxillæ.* The palp reaches the base of the spines of the outer plate.

*Maxillipeds.* The third joint of the palp is said by Dana to be narrow, nor is it wide in the Saghalien specimens; but this joint often looks much narrower than it is, unless specially flattened for examination.

*First gnathopods.* The fifth joint is scarcely longer than broad; the sixth is much longer, oblong, widening to the oblique, spinulose palm, which is shorter than the spinuliferous hind margin, and has a strong palmar spine.

*Second gnathopods.* These are very similar to the first pair, and the sixth joint, though considerably, is not exorbitantly larger; the fourth joint has the hind margin somewhat produced, which is not the case in the first pair; the fifth has a narrower hind lobe; the sixth is oblong oval, the closely-fringed palm more oblique, and subequal to the hind margin, which carries two groups of spinules. The finger, according to Dana, is "curved and short, and shuts close against" the palm; in the Saghalien specimens its outer margin is strongly convex, and the inner, which matches the palm, carries six minute setules.

*Percopods.* These are moderately stout, the finger curved, with the usual setule on the inner margin. In the last three pairs the second joint is nearly orbicular, with the hind margin slightly crenulate. In the Saghalien specimens the branchial vesicles are narrow at the base, then becoming inflated.

*Third uropods.* These are very short. In the Saghalien specimens the ramus is as long as the peduncle, each carrying apical spines.

*Telson.* This is not mentioned by Dana. It is short, divided beyond the middle, but not to the base, each half as broad as long; the apices are divergent, truncate, tipped with spinules.

*Length.* "Four lines," about 8 mm. (Dana); 5 mm. (Saghalien specimens). Dana prefixes "Female?" to his description; but, in my opinion, his description and figures refer to the male.

*Hab.* New South Wales, from shallow pools of water along shores of Port Jackson (Dana); Saghalien, 49° 30' N., 142° 8' E. (*Andréa*, specimens belonging to the Copenhagen Museum).

#### Fam. PHLIADIDÆ.

Antennæ short, first pair without accessory flagellum. Upper lip with distal margin undivided. Lower lip without inner lobes. Mandibles without palp. First maxillæ with the palp obsolete. Gnathopods simple or only feebly subchelate. Pleopods with the peduncles laterally produced in one or more of the pairs. Third uropods not biramous. Telson entire.

- |    |   |   |   |
|----|---|---|---|
| 1. | { | Palp of the maxillipeds three-jointed, 2.             |   |
|    | { | Palp of the maxillipeds four-jointed, 3.              |   |
| 2. | { | Second uropods with two rami. . . . .                 | <i>Phlias</i> Guérin, 1836.                 |
|    | { | Second uropods with one ramus . . . . .               | <i>Pereionotus</i> Bate and Westwood, 1862. |
| 3. | { | Third pleopods with rudimentary inner ramus. . . . .  | <i>Iphiplateia</i> n. g.                    |
|    | { | Third pleopods with well-developed inner ramus, 4.    |   |
| 4. | { | First four pairs of side-plates very deep. . . . .    | <i>Iphinotus</i> , n. g.                    |
|    | { | First four pairs of side-plates very shallow. . . . . | <i>Bircenna</i> Chilton, 1884.              |

The genus *Iphigenia*, G. M. Thomson, is represented as having a three-jointed palp to the maxillipeds, but in other respects its resemblance is so close to *Iphinotus* that its right to stand as a separate genus awaits confirmation.

All the genera of this family have representatives in the Southern Ocean; but *Pereionotus* pertains also to English and Mediterranean waters, and *Phlias* to the Mediterranean.

#### IPIIPLATEIA, n. g.

Body much depressed, pleon strongly flexed. Head immersed between the projecting side-plates, square, feebly rostrate, with the eyes on the prominent front corners. First four pairs of side-plates very large, outspread. Antennæ short, subequal in length, the first the broader, the second attached on the under surface of the head, some way to the rear of the first. Upper lip with entire convex distal margin. Mandibles without palp. Lower lip without inner lobes. First maxillæ without inner plate; palp obsolete, but the position for it marked; apical teeth of outer plate five in number. Second maxillæ with the small outer plate continuous with the base, the inner broader. Maxillipeds with palp extending beyond the outer plate; the fourth joint small, not unguiform. First and second gnathopods simple. Third, fourth, and fifth pereopods with widely-expanded second joint, and the fourth joint broad. Second and third pleopods with lateral expansion of the peduncle, the third with rudimentary inner ramus. First and

second uropods biramous, the second smaller than the first; third uropods one-jointed, very small. Telson entire.

The name is derived from the prefix *ίφι-*, signifying strength, and *πλατεία*, broad. Only one species is at present known.

*IPHIPLATEIA WHITELEGGEI*, n. sp. (Plate 34.)

The body forms a broad oval; the basal joint in the first antennæ, and the second joint in the last three pairs of peræopods, helping to complete the figure. It is dorsally a little convex and smooth, or feebly angular along the centre; the last segment of the peræon slightly upraised, and the first segment of the small pleon projecting backward in a prominent tubercle, the remainder of the pleon being rather tightly folded under the body, its sixth segment dorsally undeveloped. The head is embedded between the subtriangular first side-plates, which project forward beyond its rounded corners, these being almost on a level with the short obtuse rostrum. The second side-plates oblong; the third a little more widened distally; the fourth very broad, excavate behind; the fifth, sixth, and seventh small, bilobed, the front lobe the larger.

The *eyes* are small, oval, dark, close to the corners of the head.

*First antennæ.* First joint nearly as broad as long, with large advanced inner lobe; second similar in shape, but much smaller; third narrow, not lobed; flagellum very small, two-jointed, second joint minute.

*Second antennæ.* Basal joints, small, obscure, seemingly soldered to underside of head; penultimate joint of peduncle rather larger than ultimate, neither large; flagellum two-jointed, small, scarcely so long as last joint of peduncle, second joint scarcely visible.

*Epistome* rounded above. On either side of it is a small, rounded oval, pellucid space in the ventral surface of the head.

*Upper lip.* At the centre of the margin are two oval spaces, each enclosing a tuft of short hairs, the two tufts not convergent.

*Mandibles.* Cutting-edge quadridentate; spine-row consisting of three minute spinules; molar tubercle wanting, unless represented by a broad pellucid spine tipped with a setule.

*First maxillæ.* Of the apical spines four form a row, the fifth being set beside them near the centre.

*Second maxillæ.* Inner plate with truncate apical margin, fringed with five very short and small but rather broad spines, the innermost the largest; the outer plate very narrow, tipped with a few spinules. The mandibles and maxillæ are in this genus not only exceedingly small, but so closely compacted that it is difficult to separate them.

*Maxillipeds* comparatively wide. Inner plate with four minute spine-teeth on the truncate apex, outer plate rather broad, the inner margin carrying six widely-spaced insignificant spine-teeth; first three joints of palp not greatly differing in length; second much broader than third; fourth small, cylindrical, and so pellucid that its margins may easily be mistaken for a couple of setæ, its apex tipped with a very long seta.

*First gnathopods.* Second joint not nearly reaching the distal border of the side-plate; third as long as fourth, the latter, as usual, underriding the wrist; the wrist or fifth joint

a little longer than the sixth, which narrows to the apex, forming no palm; finger small, curved, with a setule on the concave margin, near to the nail. The hand and finger have a closely similar structure in both gnathopods and all five pereopods.

*Second gnathopods* like the first, except that the fifth and sixth joints are more nearly equal. Branchial vesicles narrow.

*First pereopods.* Second and third joints as in the gnathopods; fourth scarcely longer than wide, narrow at the base, then widening to a lobe in front; fifth joint a little shorter and narrower, as broad as long, much shorter than the sixth.

*Second pereopods* like the first.

*Third pereopods.* Second joint rounded oval, little longer than broad, the hinder expansion broadly produced below the third joint; fourth as broad as long, hind lobe well expanded and produced downward; fifth much narrower, a little longer than broad, distally narrowed, shorter than sixth.

*Fourth pereopods* like the third, but the second and fourth joints larger.

*Fifth pereopods.* Second joint shorter than in the two preceding pairs, but even wider, the great hind expansion having a somewhat three-sided margin; the remaining joints nearly as in the third pair.

*First pleopods.* Peduncle twice as long as broad, with five or six coupling-spines; rami with about ten joints, inner ramus the shorter, with no cleft spines.

*Second pleopods.* Peduncle much shorter, distally widened, so as to be fully as broad as long, with five or six coupling-spines on the projection; rami nearly as in first pair.

*Third pleopods.* Peduncle very short, with a long narrow projection, carrying at its apex three coupling-spines; inner ramus minute, oval, unjointed, without setæ; outer ramus normal, but with the divisions of the joints somewhat obscure.

*First uropods.* Peduncle longer than the straight inner, rather shorter than the curved outer ramus. The rami with obtuse apices, the *vis-à-vis* margins microscopically pectinate, the others finely ciliate.

*Second uropods* much smaller than first, otherwise similar.

*Third uropods* consisting of a small oval piece, nearly concealed by the telson. A minute setule projects from outer margin of the apex.

*Telson* semi-oval, with narrow apex projecting beyond the third uropods.

*Length* about a fifth of an inch, 5 mm.

*Hab.* Australian waters. Specimens sent me from Watson's Bay, New South Wales, by Mr. Thomas Whitelegge, who called attention to their peculiar appearance, and in compliment to whom I have named the species.

#### PEREIONOTUS Bate and Westwood.

1862. *Pereionotus* Bate and Westwood, British Sessile-eyed Crustacea, vol. i. part 5, p. 226.

1862. „ Bate, Catalogue of the Amphipodous Crustacea in the British Museum, p. 374.

1863. *Iceridium* Grube, Sitzungsberichte der Schles. Gesellsch. vom 18ten Februar 1863.

1864. „ Grube, Archiv für Naturgeschichte, Jahrg. 30, Bd. i. p. 209.

1888. *Pereionotus* Stebbing, 'Challenger' Amphipoda, pp. 81, 340, 348.

1893. „ Della Valle, F. u. Fl. G. Neapel. Mon. 20, Gammarini, p. 559.

Body depressed, pleon strongly flexed. Head square, feebly rostrate, with the eyes on the prominent front corners. Antennæ short, the second shorter and much more slender than the first, attached on the under surface of the head some way to the rear of the first. Mouth-organs in general like those of *Iphiplateia*, the maxillipeds excepted, in which the palp does not reach beyond the outer plate, and is only three-jointed. The limbs of the peræon also nearly as in *Iphiplateia*, except that the second joint of the fifth peræopods is very much smaller than that of the third and fourth pairs. All the pleopods with both rami well developed, the peduncle laterally produced in the third pair or in both the second and third pairs. The first uropods biramous; the second much shorter, uniramous; the third one-jointed, obscure, completely covered by the telson, which is entire.

The type species, *Pereionotus testudo* (Montagu), seems to be almost certainly identical with *Ieridium fuscum* Grube, while *Phlias serratus* Guérin is certainly distinct. I am indebted to M. Ed. Chevreux for a Mediterranean specimen labelled *Ieridium fuscum*, but which has the first and second uropods both biramous as in the genus *Phlias* of Guérin.

#### PEREIONOTUS THOMSONI, n. sp. (Plate 35 A.)

The *body* is a broad oval. The medio-dorsal line throughout the peræon and in the first two segments of the pleon is raised to a carina, formed by a succession of processes not quite so long as their respective segments, that on the first peræon-segment being preceded by an acute point directed forward.

*Head.* The lateral angles extend a little in advance of the small, but distinct, rostrum; and, though on the whole rounded, they have a minutely acute point on the inner side.

The first four pairs of side-plates are without conspicuous setules on the distal margin.

*Eyes.* Rounded oval, dark, situated on the lateral lobes of the head.

*First antennæ.* The inner margin of the broad first joint is indented; the second joint cylindrical, not lobed; the third conical; the flagellum small, two-jointed, with the long hyaline filaments common to all the species of this family.

*Second antennæ.* Very slender; the last joint of the peduncle is rather longer than the penultimate; the flagellum consists of one short joint with several setæ about thrice as long as the joint. On one side of the specimen the flagellum is possibly two-jointed.

*Upper lip.* The hairs on the distal margin are convergent.

*First maxille.* These show a small spinule in the position of the palp. This minute character may be generic; but in the other species only a slight bulge of the margin has been perceived at the point in question.

*Maxillipeds.* Inner plates with three or four apical spine-teeth; the outer plates rather large, minutely fringed on distal half of the inner margin; palp only three-jointed, and not quite reaching the apex of the outer plate.

*First and second gnathopods and first and second peraeopods.* All these are scarcely distinguishable from the corresponding limbs in *Iphiplateia Whiteleggei*. In common with the three following pairs of peraeopods they have on the inner margin of the sixth joint not only a tolerably strong apical spine, but a similar one nearer the middle.

*Third peraeopods.* The second joint is broader than long, with very convex hind margin; the fourth joint is not longer than the third, and is very broad by reason of the great hind lobe; the fifth joint is neither so long nor so broad as the third; the sixth and the finger are as in the kindred species in general, but the inner setule of the finger not very strong.

*Fourth peraeopods.* These are like the third, except that the lobe of the fourth joint is less expanded, and the second joint is smaller.

*Fifth peraeopods.* These are like the fourth, except in regard to the second joint, which is not only much smaller, but differently shaped, the hinder expansion not quite reaching, instead of overlapping, the third joint.

*First pleopods.* Peduncle about twice as long as broad, with two coupling-spines; the rami slender, with elongate first joint and six or seven short ones.

*Second pleopods.* Peduncle broader than long, with two coupling-spines on the convex but not otherwise projecting inner margin, the rami broader than in the first pair.

*Third pleopods.* Peduncle short, with the coupling-spines on a short but very distinctly produced process; the rami broad, subequal, differing little from those of the second pair.

*First uropods.* The peduncle is slightly longer than the longer (probably the outer) ramus, the other ramus shorter and somewhat curved; both are narrow, each with a spinule and short stout spine on the apex.

*Second uropods.* The peduncle does not reach the end of the telson; it has the apex armed with a spinule and short, stout spine; the narrowly oval, single ramus similarly armed.

*Third uropods.* Attached to the ventral plate, which represents the sixth pleon-segment, are two membranous, rather conical, plates, which together occupy the breadth of the telson, but do not reach its apex.

*Telson.* Triangular, with rounded apex.

*Length.* Less than 5 mm.

*Hab.* Watson's Bay, Australia. A single specimen, a female with eggs, occurred in the gathering from low-tide line, obligingly sent me by Mr. Thomas Whitelegge.

The species is remarkably like *Pereionotus testudo*, as figured by Della Valle, to whom I am indebted for a specimen from the Mediterranean. It differs by the absence of the lateral tubercles on the peraeon-segments, the want of any conspicuous setules on the distal margin of the first four pairs of side-plates, the presence of a submedian spine on the inner margin of the sixth joint of the limbs, and in having the peduncle of the second pleopods not outdrawn. The third uropods are obscure in both species, but apparently present and similar in both.

## IPHINOTUS, n. g.

Body much depressed, pleon strongly flexed. Head immersed between the projecting side-plates, square, feebly rostrate, with the eyes on the prominent front corners. First four pairs of side-plates very large, outspread. Antennæ short, subequal in length, the first the broader. Upper lip with the convex distal margin rather flattened. Mouth-organs in general as in *Iphiplateia*, the maxillipeds excepted, these having the fourth joint of the palp well-developed, unguiform. The limbs of the peræon nearly as in *Iphiplateia*, except that the second and fourth joints in the fifth peræopods are very much smaller than those in the third and fourth pairs. All the pleopods with both rami well developed, the peduncle in the second and third pairs laterally produced in a long and strong process. The first uropods slender, the second stout, both biramous, with the peduncle much longer than the rami. The third uropods membranous, not biramous, small. Telson entire.

The name is derived from the prefix  $\iota\phi\iota$ -, and  $\nu\omega\tau\omicron\varsigma$ , back.

## IPHINOTUS CHILTONI, n. sp. (Plate 35 B.)

The body is broad oval, with dorsal carina, of which the condition of the specimens no longer allows a minute description.

*Head and eyes* as in *Pereionotus Thomsoni*.

*First antennæ.* First joint large, distally widened; second cylindrical; third scarcely longer than broad; flagellum of three small joints, with the usual filaments.

*Second antennæ.* Moderately stout; the last joint of the peduncle longer than the penultimate; flagellum of five joints, of which the last four are very small, all setose.

*Upper lip.* Broader than deep, with converging hairs on the almost straight distal margin.

*Mandibles, lower lip, and maxillæ* as in *Iphiplateia*.

*Maxillipeds.* Inner plates with four apical spine-teeth, outer with minute setules along inner margin; palp four-jointed, reaching considerably beyond the outer plates; the fourth joint unguiform.

*First and second gnathopods and first and second peræopods.* These are in general as in *Pereionotus Thomsoni*, but the finger is abruptly narrowed at the sharp hooked nail, and the setule of the inner margin is strong.

*Third and fourth peræopods.* Second joint very large, only a little longer than broad, but rather longer in the third pair than in the fourth; the fourth joint greatly expanded, the great hind lobe being nearly double the length of the front margin; fifth joint a little longer than the third; sixth joint and finger as in the preceding pairs.

*Fifth peræopods.* These are much smaller than the third or fourth, especially in regard to the second and fourth joints; the second, with its hind expansion, not quite reaching the third joint; the hind lobe of the fourth scarcely longer than its front margin.

*First pleopods.* Peduncle not very long, and not expanded.

*Second pleopods.* Peduncle short, but produced on the inner side to a long and

powerful process, at the truncate apex of which are four coupling-spines; the rami are long, of eleven or twelve joints, the outer ramus the longer.

*Third pleopods.* These closely resemble the second pair, but the process of the peduncle appears to be a little less massive and the rami appear rather less strong.

*First uropods.* Peduncle slender, more than twice as long as the slender, subequal, finely ciliated rami.

*Second uropods.* Shorter, but much stouter, than the first; the peduncle about twice as long as the stumpy rami, and fringed near the outer margin with some eleven short spines.

*Third uropods.* Membranous, broad above, but together not so broad as the telson; the pointed apex projecting just beyond the telson. In the two specimens figured there is the appearance of a broad basal and a small triangular apical joint; but this may be due to an accidental folding, as in a third specimen these uropods are single-jointed.

*Telson.* Much wider than long, membranous, with a few slight setules at the sides; the apex slightly angular, the angle very obtuse.

*Length.* About 5 mm.

*Hab.* Lyttelton Harbour, New Zealand. Specimens, labelled "*Iphigenia typica*," kindly sent me many years ago by Mr. (now Dr.) Charles Chilton, F.L.S.

In 1882, Mr. G. M. Thomson, F.L.S., in the 'Transactions of the New Zealand Institute,' vol. xiv. p. 237, established under the family Corophiidae the genus *Iphigenia*, which he held to be allied to *Teiluis* Dana. He described and figured (pl. 18, fig. 6) the single species *Iphigenia typica*, from two specimens obtained by the dredge in Otago Harbour, New Zealand. He gives the length as "0.12 inch." Upon comparing his description and figures of this peculiar new form with the specimens sent me by his friend Mr. Chilton, I did not venture to suppose that there could be a question of more than one species. Nevertheless, one important feature obviously called for remark. The Lyttelton Harbour specimens were provided with a four-jointed palp to the maxillipeds (see 'Challenger' Amphipoda, p. 1638); while in Mr. Thomson's figure the palp is three-jointed. As this circumstance is not referred to either in his generic definition or description of the species, and as the figure itself is small and not very clearly printed, there might be some doubt as to what was really intended. But, to make up for the inadequacy of the printed figures, Mr. Thomson very kindly sent me clear tracings of the large original drawings of some of them. One tracing shows the palp of the maxillipeds considerably overlapping the outer plate, but unmistakably consisting of only three joints. In the accompanying manuscript, full of valuable notes on New Zealand Amphipoda, after explaining that he no longer possessed any specimens of *Iphigenia typica*, Mr. Thomson added, "I have a suspicion that the animal is only a young state of some different form, partly from the apparent absence of one of the thoracic legs and partly because the uropoda appear to be very incomplete." The apparent incompleteness of the uropods was no doubt only due to the difficulty of perceiving the membranous third pair lying closely beneath the telson. As the fifth pereopods are shown in the figure, the absence of one of the thoracic legs can only have been accidental, nor was the immaturity of the specimens likely to have affected the number of joints in the palp of the maxillipeds.

According to present information, therefore, it seems proper to place in different genera the Lyttelton Harbour specimens here described, and the original *Iphigenia typica* Thomson. It has been earlier pointed out by von Martens that the name *Iphigenia* is much preoccupied. The new name *Iphinotus*, therefore, will take its place, should it appear hereafter that the maxillipeds in Thomson's species were really four-jointed, but accidentally defective. On the other hand, if Thomson's figure show the true state of the case, when that is made clear, it will be necessary and time enough to give his genus a new name.

But the two species, *Iphinotus Chiltoni* and *Iphigenia typica* are in many points so closely alike that, while they perhaps belong to different genera, perhaps also they are but one species. In addition, however, to the recorded difference in the maxillipeds, there is a difference in the peræopods, the fourth pair having its second joint subequal to that in the third pair in the Lyttelton Harbour specimens, but considerably smaller in those described by Mr. Thomson. Again, the latter are said to have the "telson about as broad as long, nearly semicircular"; whereas in the Lyttelton Harbour specimens it is much broader than long and slightly angular at the apex. Apparently also in the first described specimen the dorsal line is much more strongly tuberculate. The validity of all these marks of distinction remains to be determined by future observation.

#### BIRCENNA Chilton.

1884. *Bircenna* Chilton, 'Transactions of the New Zealand Institute,' vol. xvi. p. 264.

Body broad. Head not rostrate. Antennæ short, subequal, both pairs very slender; second with prominent gland-cone. Mandibles without palp. First maxillæ with inner plate carrying an apical seta, outer plate having eight apical spines; position of palp marked, but no trace of palp apparent. Maxillipeds with outer plate not extending beyond the inner; palp four-jointed, fourth joint small, not unguiform. First and second gnathopods with the hinder apex of the sixth joint a little produced. Fifth peræopods larger than fourth, fourth than third. Pleopods all biramous, and all with the peduncles broadly produced laterally. First and second uropods with unequal curved rami. Third uropods each consisting of an apically bifid plate, not covered by the triangular telson.

This genus, represented by the single New Zealand species, *Bircenna fulvus* Chilton, stands apart from the rest of the family by many of its features. Among the less obvious are the characters of the first maxillæ and maxillipeds, the first maxillæ having an inner plate, which seems to be wanting in the other genera, and eight teeth instead of five on the outer plate, while in the maxillipeds the outer plate does not, as in the other genera, extend beyond the inner plate. I am indebted to my friend Dr. Chilton for the opportunity of dissecting a specimen of *Bircenna fulvus*.

## Fam. MELPHIDIPPIDÆ.

*Gammarus spinosus* Goës, 1866. transferred to *Melphidippa* by Bocck in 1871, is distinct from *Gammarus spinosus* Lamarck, 1818. It may now be called *Melphidippa Goësi*.

*Neohela serrata* Stebbing, 1888, should be called *Melphidippa serrata*.

## Fam. GAMMARIDÆ.

## PARACRANGONYX, n. g.

All the side-plates shallow. Eyes rudimentary. First antennæ longer than the second, with small accessory flagellum. The pleopods abnormal, having only one ramus. The third uropods with very small inner ramus. Telson entire.

The type-species is *Paracrangonyx compactus* (Chilton), 1882, from wells in New Zealand.

## APOCRANGONYX, n. g.

Eyes wanting. First antennæ longer than the second, with small accessory flagellum. The third uropods rudimentary, without rami. Telson entire.

The type-species is *Apocrangonyx lucifugus* (Hay), 1882, from a well in Illinois.

## HYALELLOPSIS, n. g.

Body smooth. Fourth to sixth pleon-segments very short. Antennæ short, first rather the longer, with one-jointed accessory flagellum. Fifth peræopod short, with very large second joint. Uropods short, the third uniramous. Telson small, rounded.

The generic name alludes to the likeness between this genus and the Orchestid *Hyaella* in the caudal part of the animal.

The type-species is *Hyalellopsis Czyrniański* (Dybowsky), 1874, from Lake Baikal.

## Gen. PALLASEA Bate, 1862.

In this genus I place:—1. *Gammarus asper* Dybowsky, 1874, distinct from *Gammarus asper* Dana, 1852, giving it the new name *Pallasea Dybowski*; 2. *P. Reisnerii* (Dybowsky), 1874; 3. *P. cancellus* (Pallas), 1772; 4. *P. Gerstfeldtii* Dybowsky, 1874; 5. *P. quadrispinosa* Sars, 1867; 6. *P. Kesslerii* (Dybowsky), 1874; 7. *P. baikali*, a new name for *Gammarus Lovenii* Dybowsky, 1874, which is distinct from *Gammarus Loveni* Bruzelius, 1858; 8. *P. Brandtii* (Dybowsky), 1874; 9. *P. Grubii* (Dybowsky), 1874; 10. *P. cancelloides* (Gerstfeldt), 1858. All these species of *Pallasea* occur in Lake Baikal.

## PARAMICRUROPUS, n. g.

One of the pleon-segments abruptly elevated above the next. Fifth and sixth pleon-segments very small. Antennæ short, the first the longer, with small accessory flagellum. Third uropods rudimentary, the rami not very unequal. Telson small.

The species are *Paramicruropus Solskii* (Dybowsky), 1874, and *Paramicruropus Taczanowskii* (Dybowsky), 1874, both from Lake Baikal.

## Gen. GAMMARELLUS Herbst, 1793.

Under the designation *Cancer* (*Gammarellus*) Herbst has grouped a large number of species, and for some part of the group it seems right that *Gammarellus* should be used as the generic name. The majority of the species are Amphipoda, so that it seems further not unreasonable to select an amphipod as type of the genus. The first species in Herbst's list that is an amphipod is the one which he calls *Cancer* (*Gammarellus*) *homari*. This is a species instituted by Fabricius in 1779. It was called *Amathia Sabinii* by Bate in 1862; but the name *Amathia*, due to Rathke in 1837, having been preoccupied by Lamarek in 1812, Bate and Westwood altered the generic term to *Amathilla*. Spence Bate, however, had previously called the young form of the above-mentioned species *Grayia imbricata*, so that *Grayia* has precedence of *Amathilla*. Since a change, then, in any case is necessary, the opportunity is favourable for restoring Herbst's *Gammarellus*, and there is an additional advantage in that we are thus enabled to dispense both with *Grayia*, which is inconveniently similar to the name of a reptilian genus, *Graia* Günther, 1858, and with *Amathilla*, which is equally near to the molluscan name *Amathella* Gray, 1859.

The two species coming under this revived generic name are *Gammarellus homari* (Fabricius), 1779, and *Gammarellus angulosus* (Rathke), 1843. A third nominal species, *Gammarellus carinatus* (Rathke), is not certainly distinct from *G. homari*.

## EUCRANGONYX, n. g.

Like *Crangonyx* in general, but with a small inner ramus to the third uropods. Telson emarginate.

The species assigned to this genus are:—1. *Eucrangonyx mucronatus* (Forbes), 1876; 2. *Eu. Vejdovskyi*, a new name for *Crangonyx subterraneus* Vejdovsky, 1896, which seems to me distinct from the species so named by Bate in 1859; 3. *Eu. Packardii* (Smith), 1888; 4. *Eu. gracilis* (Smith), 1871; 5. *Eu. antennatus* (Packard), 1881. *Eu. gracilis* is from Lake Superior and Lake Huron, the others from wells or subterranean streams.

## Gen. AXELBOECKIA, n. n.

The name is proposed as a substitute for *Bœeckia* Sars, 1894, preoccupied by Malm in 1870, and by G. S. Brady in 1871.

The generic name is given in honour of the late Axel Boeck, a distinguished carcinologist.

The species assigned to this genus are *Axelboeckia spinosa* (Sars), 1894, from the Caspian Sea, and *Axelboeckia Carpenterii* (Dybowsky), 1874, from Lake Baikal.

#### BRACHYUROPUS, n. g.

With median rostrate carina. Fourth side-plate with projecting tooth. First antennæ much the longer, with long accessory flagellum. First and second gnathopods similar, subchelate. Last three peræopods elongate. First and second uropods elongate, third rudimentary, with very unequal rami. Telson apically emarginate.

The generic name alludes to the shortness of the third uropods.

The species included are *Brachyuropus Grewingkii* (Dybowsky), 1874, and *Brachyuropus Reichertii* (Dybowsky), 1874, both from Lake Baikal.

#### Gen. BRANDTIA Bate, 1862.

In addition to the type-species *Brandtia latissima* (Gerstfeldt), 1858, there may be referred to this genus:—2. *B. lata* (Dybowsky), 1874; 3. *B. tuberculata* (Dybowsky), 1874; 4. *B. Morawitzii* (Dybowsky), 1874; 5. *B. smaragdina* (Dybowsky), 1874; 6. *B. fasciata*, a new name for *Gammarus zebra* Dybowsky, 1874, which is distinct from *G. zebra* Rathke, 1843. All these species occur in Lake Baikal.

#### MICRUROPUS, n. g.

Without carinæ or overarching segments. Antennæ short, with subequal peduncles, the first pair usually longer than the second; accessory flagellum one-jointed. First and second gnathopods with subequal hands. Third uropods small or very small; the rami unequal; outer ramus usually one-jointed. Telson cleft.

The generic name refers to the smallness of the third uropods.

The species referred to this genus are:—1. *Micruropus puella* (Dybowsky), 1874; 2. *M. inflatus* (Dybowsky), 1874; 3. *M. vortex* (Dybowsky), 1874; 4. *M. talitroides* (Dybowsky), 1874; 5. *M. littoralis* (Dybowsky), 1874; 6. *M. glaber* (Dybowsky), 1874; 7. *M. rugosus* (Dybowsky), 1874; 8. *M. Wahlii* (Dybowsky), 1874; 9. *M. Finsenii* (Dybowsky), 1874; 10. *M. perla* (Dybowsky), 1874; 11. *M. Klukii* (Dybowsky), 1874; 12. *M. pachytus* (Dybowsky), 1874. All from Lake Baikal.

#### NEONIPHARGUS, n. g.

First to fourth side-plates much deeper than those which follow. Eyes well developed (or wanting). First antennæ the longer; accessory flagellum very small, two-jointed. Mouth-parts nearly as in *Niphargus* (but first maxillæ in the type-species said to have six instead of seven spines on the outer plate). First and second gnathopods similar,

subchelate; fifth joint distally wide, sixth subquadrate. Fifth peræopods shorter than fourth. Third uropods not elongate; outer ramus one-jointed, inner minute. Telson partly (or wholly) cleft.

The type-species is *Neoniphargus Thomsoni*, a new name for Mr. G. M. Thomson's *Niphargus montanus*, 1893, from Mount Wellington, in Tasmania. As Costa's *Gammarus montanus*, 1857, appears to be a *Niphargus*, the name used by Thomson was pre-occupied. A second species, doubtfully assigned to this new genus, is the *Gammarus puteanus* of Moniez, 1889, from subterranean waters in France. It was renamed *Niphargus Moniezi* by Wrzeńskiowski in 1890.

#### IIAKONBOECKIA, n. g.

Near to *Axelboeckia* and *Gmelinopsis*. Segments of peræon with margins acutely produced. Head with rostral and lateral projections. Antennæ with equal peduncles, first pair the longer; accessory flagellum very small. Hand of first gnathopods like that of second, but larger. Third to fifth peræopods with the second joint broad, not produced downward. Third uropods with subequal rami, the outer ramus (seemingly) one-jointed. Telson cleft nearly to base.

The generic name is given in compliment to Hakon Boeck, who edited his brother's well-known work on the Amphipoda of the North.

The type-species is *Hakonboeckia Strauchii* (Dybowsky), 1874, from Lake Baikal.

#### BAIKALOGAMMARUS, n. g.

Near to *Gammarus*. Pleon-segments, from the second, third, or fourth to the sixth, with a few dorsal setules or spinules. First antennæ longer than second, but with a shorter peduncle; accessory flagellum very short. Hand of first gnathopods not smaller than that of second. In third to fifth peræopods the second joint broad, the wing produced downward in a long rounded lobe. Third uropods rather elongate; the peduncle as long as the two-jointed outer ramus. Telson cleft.

The generic name alludes to Lake Baikal, so prolific in Gammaridæ.

The type-species is *Baikalogammarus pullus* (Dybowsky), 1874, from Lake Baikal.

#### Gen. MELITA Leach, 1814.

Besides the accepted species of this genus, there may be referred to it with more or less probability *Maera confervicola* Stimpson, 1857; *Amphitoe Gayi* Nicolet, 1849; and *Gammarus tenuicornis* Stimpson, 1856.

Stimpson's Chinese species may or may not be the same as Dana's *Melita tenuicornis*, 1852, from New Zealand. Dana's *M. tenuicornis* is a synonym of his own *Melita inaequistylis*; but it will be time enough to consider what should be the designation of Stimpson's species when its distinctness has been proved.

## PARACERADOCUS, n. g.

Side-plates not deep, the first larger than the fourth. First antennæ longer, but not stouter than the second, and with shorter peduncle. Upper lip transversely elliptic. Under lip with principal lobes deliscent. Palp of mandibles elongate; third joint not short. First maxillæ with large inner plate, carrying setæ only on the apex; the palp broad. Second maxillæ having the inner plate fringed along inner margin. Limbs of peræon, uropods, and telson as in *Ceradocus*.

The type-species is *Paraceradocus Miersii* (Pfeffer), 1888, from South Georgia.

## Gen. CERADOCUS Costa, 1853.

The species belonging to this genus are:—1. *Ceradocus orchestipes* A. Costa, 1853, which includes the preoccupied *Gammarus fasciatus* O. G. Costa, 1844; 2. *Ceradocus Torelli* (Goës), 1866; 3. *Ceradocus rubro-maculatus* (Stimpson), 1856; 4. *Ceradocus semiserratus* (Bate), 1862; of which the first and last are both named *Ceradocus fasciatus* by Professor Della Valle.

## Gen. MAERA Leach, 1814.

In this genus I propose the name *Maera Westwoodi* for *Gammarus Kröyeri* Bell and Westwood, 1855, which is distinct from the earlier *Gammarus Kröyeri* Rathke, 1843, and add to the accepted species Haswell's *Megamoera Mastersii*, 1880; Dana's *Gammarus asper*, 1852; his *Gammarus? indicus*, 1853; Gerstfeldt's *Gammarus kürgensis*, 1858; and Dana's *Amphithoe pubescens*, 1852. The last four are involved in some obscurity.

## Gen. ELASMOPUS A. Costa, 1853.

To the species already accepted in this genus may be added Haswell's *Megamoera snensis*, 1880; his *Moera viridis*, 1880; his *Megamoera Boeckii*, 1880; the *Moera crassimana* of Miers, 1884, the specific name becoming *crassimanus*; and the *Maera Miersi* of Wrzeźniowski, 1879. The last two are rather obscure.

## PLESIOGAMMARUS, n. g.

Near to *Gammarus*. Many of the segments have a marginal swelling. The pleon carries dorsal setæ, but no dorsal spines. Peduncle of first antennæ longer than that of second. Third to fifth peræopods with the second joint long and narrow. First uropods reaching to the end of the short third pair. Telson not cleft to the base.

The type-species is *Plesiogammarus Gerstaeckeri* (Dybowsky), 1874, from Lake Baikal.

## PHREATOGAMMARUS, n. g.

Without eyes. Upper lip broader than deep. First joint of mandibular palp not very short. First and second gnathopods equal. First and second peræopods much shorter than third. Fifth peræopods the longest, with sixth joint much longer than any of the other joints. Third uropods long, with equal, one-jointed, cylindrical rami. Otherwise like *Gammarus*.

The generic name means a well-*Gammarus*.

The type-species is *Phreatogammarus fragilis* (Chilton), 1882, from wells in New Zealand.

## OMMATOGAMMARUS, n. g.

Near to *Gammarus*. Dorsal spines only on fourth to sixth pleon-segments. Eyes of irregular form, with indented outline. First antennæ longer than second, but usually with shorter peduncle; accessory flagellum of more than one joint. Upper lip narrowed to a rounded apex. Under lip with inner lobes rudimentary. Third joint of mandibular palp not very elongate. First maxillæ having inner plate fringed with numerous setæ, outer carrying eleven spines; second joint of palp with about ten spine-teeth on one maxilla, and short spines on the other. Maxillipeds with outer plate reaching far along second joint of palp; spine-teeth and setæ numerous. Hand of first gnathopods not smaller than that of second. Third uropods having outer ramus about twice as long as inner, with simple setæ on its inner margin; inner ramus with feathered setæ on both margins. Telson cleft to the base.

The generic name alludes to curious character of the eyes.

The species included are:—*Ommatogammarus albinus* (Dybowsky), 1874; 2. *O. flavus* (Dybowsky), 1874; 3. *O. carneolus* (Dybowsky), 1874; 4. *O. amethystinus* (Dybowsky), 1874; all from Lake Baikal.

## ODONTOGAMMARUS, n. g.

In general like *Gammarus*, but lower front angle of fifth side-plates produced into a tooth; peduncle of first antennæ not shorter than that of second, its third joint as long as its second; hand of first gnathopods not smaller than that of second; third to fifth peræopods having second joint produced at lower hind angle into a tooth; third uropods not very long, but, as in *Gammarus*, the two-jointed outer ramus longer than the inner.

The generic name alludes to the tooth on the fifth side-plates.

The species included are *Odontogammarus calcaratus* (Dybowsky), 1874, and *O. margaritaceus* (Dybowsky), 1874, both from Lake Baikal.

## DIKEROGAMMARUS, n. g.

Fourth and fifth pleon-segments each raised dorsally to a spiniferous tubercle. First antennæ the longer; accessory flagellum well developed. The gnathopods larger in the male than in the female; the second larger than the first. The form agrees in general with *Gammarus*.

The generic name alludes to the two horn-like elevations on the pleon.

The species included are:—*Dikerogammarus macrocephalus* (Sars), 1896; 2. *D. hæmobaphes* (Eichwald), 1842; 3. *D. Grimmi* (Sars), 1896; 4. *D. Verreauxii* (Bate), 1862; 5. *D. fasciatus* (Say), 1818. The first three are found in the Caspian, the fifth in streams and ponds of the United States of America. The fourth is said to have been found by M. Verreaux in New Holland, Spence Bate ascribing the species to "Edwards, Ann. des Sc. Nat.," a vague reference which has not yet been verified.

## Gen. GAMMARUS J. C. Fabricius, 1775.

For *Gammarus tenellus* Sars, 1896, which is distinct from *Gammarus tenellus* Dana, 1852, I propose the equivalent name *G. ischnus*. For *G. marinus* Risso, 1826, which is distinct from *G. marinus* Leach, 1815, it is useless to propose a new name while the species remains unidentified.

## PÆKILOGAMMARUS, n. g.

All segments of peræon and pleon usually having dorsal hairs or spinules. Head rostrate. First antennæ with peduncle longer than that of the second pair, its third joint longer than the second. Upper lip with wide, almost straight, apical margin. Under lip, as in *Axelboeckia*, having the principal lobes separated by what may be rudimentary inner lobes. First maxillæ with about six setæ on the inner plate. Outer plate of maxillipeds not reaching far along the second joint of the palp. Hand of first gnathopods larger than that of second. Third uropods with equal rami, both carrying plumose setæ; outer ramus one-jointed. General character like *Gammarus*.

The generic name alludes to the variegated colouring of the several species.

The species included are:—*Pækilogammarus pictus* (Dybowsky), 1874; 2. *P. orchestes* (Dybowsky), 1874; 3. *P. talitrus* (Dybowsky), 1874; 4. *P. araneolus* (Dybowsky), 1874; all from Lake Baikal.

## ECHINOGAMMARUS, n. g.

In general like *Gammarus*, but with dorsal spines on segments anterior to the fourth of the pleon; the first antennæ longer than the second, though with shorter peduncle; the hand of the first gnathopods almost always larger than that of the second.

The generic name alludes to the numerous spines on the body.

The species included are:—1. *Echinogammarus Berilloni* (Catta), 1875, in certain fresh waters of Western Europe; 2. *E. verrucosus* (Gerstfeldt), 1858; 3. *E. Maackii* (Gerstfeldt), 1858; 4. *E. ochotensis* (Brandt), 1851, from Ochotsk Bay; and the following twenty-three, all instituted under the generic name *Gammarus* by Dybowsky in 1874, and all, like the second and third, found in Lake Baikal:—*saphirinus*, *Czerskii*, *lividus*, *viridis*, *cyaneus*, *testaceus*, *Sophiæ*, *fuscus*, *murinus*, *aheneus*, *sarmatus*, *capreolus*, *Uzzolzewii*, *strophthalmus*, *schamanensis*, *leptocerus*, *toxophthalmus*, *vittatus*, *Petersii*, *violaceus*, *ibex*, *Parcevi*, *polyarthrus*. Here, too, may perhaps be placed the obscure *Gammarus mulilus* of Abildgaard, 1789.

#### HETEROGAMMARUS, n. g.

In general like *Gammarus*, without dorsal teeth or carinæ or noticeable processes of head- or side-plates; accessory flagellum of first antennæ more than one-jointed; outer ramus of third uropods two-jointed; but separated from *Gammarus* by one or more of the following characters:—the peduncle of first antennæ longer than that of the second; the hand of the first gnathopods larger than that of the second; the first uropods very short.

The generic name alludes to the character of the genus as a second self to *Gammarus*.

The species included are the following eight, from Lake Baikal, instituted by Dybowsky in 1874, under the generic name *Gammarus*:—*Stanislavii*, *Sophianosii*, *capellus*, *ignotus*, *Flori*, *bifasciatus*, *branchialis*, and *albulus*; the last being given by Dybowsky as a var. *albula* of *Gammarus Flori*.

#### PARAPALLASEA, n. g.

Median carina not represented on peræon or first to third segments of pleon. Fourth side-plates broader and not less deep than the preceding, emarginate behind. Flagellum of first antennæ longer than the peduncle; accessory flagellum elongate. Third to fifth pereopods with second joint expanded. Telson deeply cleft. Other characters agreeing with *Pallasea*.

The species included are:—1. *Parapallasea Borowskii* (Dybowsky), 1874; 2. *P. Lagowskii* (Dybowsky), 1874; 3. *P. Puzyllii* (Dybowsky), 1874; all from Lake Baikal.

#### CARINOGAMMARUS, n. g.

Distinguished from *Gammarus* by having carinate segments, the carina medio-dorsal only; relative proportions of the peduncles in the two pairs of antennæ, of the two pairs of gnathopods, and of the inner and outer ramus of the third uropods, variable.

The species included are:—1. *Carinogammarus cinnamomeus* (Dybowsky), 1874; 2. *C. Wagii* (Dybowsky), 1874; 3. *C. pulchellus* (Dybowsky), 1874; 4. *C. Seidlitzii* (Dybowsky), 1874; 5. *C. rhodophthalmus* (Dybowsky), 1874—all these five from Lake

Baikal; 6. *C. caspius* (Pallas), 1771, from the Caspian Sea; 7. *C. atchensis* (Brandt), 1851, from Isle of Atcha and Unalasehka; 8. *C. subcarinatus* (Bate), 1862, from Bering Strait; 9. *C. fluriatilis* (Rösel), 1755, from rivers and ponds of Europe. To these may be added, though with some doubt, *C. macrophthalmus* (Stimpson), 1853, from Grand Manan; and *C. mucronatus* (Say), 1818, from Florida.

#### ACANTHOGAMMARUS, n. g.

Body with median, more or less dentate, carina, and also lateral or marginal carinæ more or less developed. Head with very short rostrum. Fifth side-plates much shallower than fourth. First antennæ the longer; accessory flagellum usually much developed, always with more than one joint. Third and fourth peræopods with second joint narrowed below. Third uropods with rami subequal, not foliaceous. Telson deeply cleft.

The generic name alludes to the dentate carinæ.

The species included are the following six from Lake Baikal, all instituted under the generic name *Gammarus* by Dybowski in 1874:—*Cabanisii*, *Ziçukowiczii*, *Godlewskii*, *Rodoszkowskii*, *armatus*, and *parasiticus*.

#### EXPLANATION OF THE PLATES.

*n.s.*, natural size.

*a.s.*, upper antenna; *a.i.*, lower antenna.

*l.s.*, upper lip; *l.i.*, lower lip.

*m.*, mandible; *mx.* 1, 2, first and second maxillæ; *maxp.*, maxillipeds.

*gn.* 1, 2, first and second gnathopods.

*prp.* 1–5, first to the fifth peræopods.

*plp.* 1, 2, 3, first, second, and third pleopods.

*ur.* 1, 2, 3, first, second, and third uropods.

T., telson.

#### PLATE 30.

##### A. *Talorchestia Deshayesii* (Andouin).

The central figure is a lateral view of a young male specimen. The two gnathopods and second and fifth peræopods are shown separately, magnified to the same scale, with parts of each more highly magnified.

##### B. *Talorchestia tridentata*, n. sp.

The first and second gnathopods, and second and third peræopods, are magnified to the same scale, the inner surface of the hand of the second gnathopods being shown separately; parts of the three other limbs are more highly magnified.

**C.** *Orchestia Sulensoni*, n. sp.

Parts of the first and second gnathopods and of the second peræopod, and the whole of the third uropod, are more highly magnified than the rest of the figures, which are all drawn to the same scale.

## PLATE 31.

**A.** *Talorchestia nova-hollandiæ*, n. sp.

Parts of the first and second gnathopods of both male and female, and of the second peræopod, and the whole of the telson, are more highly magnified than the rest of the figures.

**B.** *Hyale Galatæa*, n. sp.

The first gnathopod, the third uropod, and the telson are more highly magnified, as well as drawn to the same scale as the other figures.

**C.** *Hyale diplodactylus*, n. sp.

Parts of the first and second gnathopods of the male, and the second gnathopod of the female, with the whole of the third uropod and the telson, are shown on a higher scale of magnification than that of the figures in general.

**D.** *Hyale macrodactylus*, n. sp.

Parts of the two gnathopods and the second and fifth peræopods are more highly magnified than the complete figures of the same limbs.

## PLATE 32.

**A.** *Hyalella Warmingi*, n. sp.

The antennæ, limbs, uropods, and telson are drawn to the same scale, while more highly magnified figures are given of the mouth-organs, of parts of the first and second gnathopods of the male, and second gnathopod of the female, of the third uropod and the telson. *pl.segm.* 3 shows the side of the third pleon-segment.

**B.** *Hyalella Meinerti*, n. sp.

Both gnathopods of both sexes, and the telson and third uropods, are shown on a higher scale of magnification.

**C.** *Hyale maroubra*, n. sp.

Parts of the two gnathopods, of the second and fifth peræopods, the second and third uropods, and the telson are more highly magnified, and the apical spines of the sixth joint in the peræopods are shown on a still higher, or third, scale of magnification.

## PLATE 33.

**A.** *Allorchestes malleolus*, n. sp.

Parts of the gnathopods of both sexes, the telson of the male in dorsal view, the third uropod and telson of the female in lateral view, are more highly magnified than the parts represented in the other figures.

**B.** *Allorchestes compressus* Dana.

Parts of the first gnathopod of the male, and the first and second gnathopods of the female, are more highly magnified.

C. *Allorchestes plumicornis* (Heller).

Part of the first gnathopod is more highly magnified than the other appendages here figured.

D. *Allorchestes humilis* Dana.

Parts of the two antennæ, of the two gnathopods, the third uropod and the telson, are shown on the higher scale of magnification, on which also the two maxillæ are drawn.

## PLATE 34.

*Iphiplateia Whiteleggei*, n. sp.

The central figure at the top of the plate is the animal in dorsal view. The separated head, antennæ, and appendages of the peræon and pleon are more highly magnified. The minute mouth-organs and the third uropods are magnified on a still higher scale, and some of the details of the mouth-organs are still more enlarged.

## PLATE 35.

A. *Pereionotus Thomsoni*, n. sp.

D., dorsal view of first five peræon-segments, with the third peræopods.

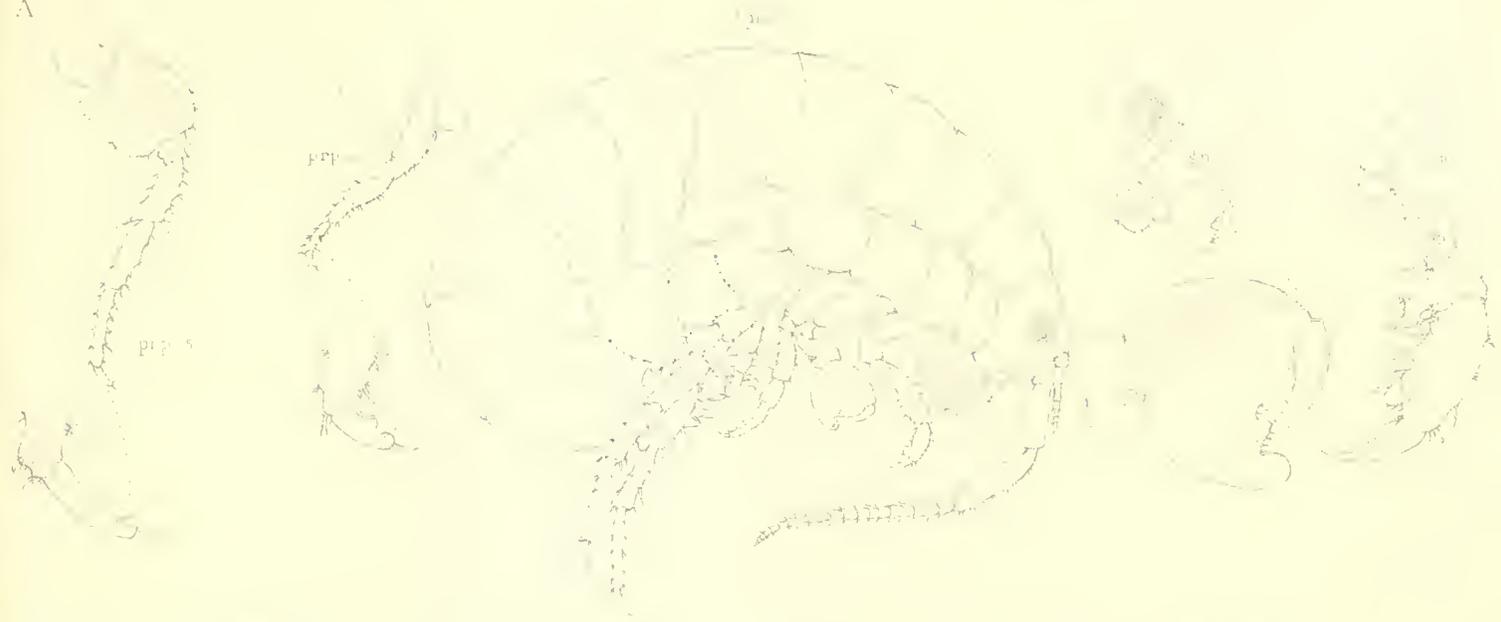
L., lateral view of the same segments.

The separated head and antennæ, the maxillipeds, second maxilla, and appendages of peræon and pleon, are more highly magnified, all on the same scale. Part of the maxillipeds, the second maxilla, the uropods and telson are also given on a higher scale.

B. *Iphinotus Chiltoni*, n. sp.

Part of the maxillipeds is more highly magnified than the other figures. Ur. I', 2', 3', and T', are drawn from a different specimen from that which furnished the other figures.

A



B



C



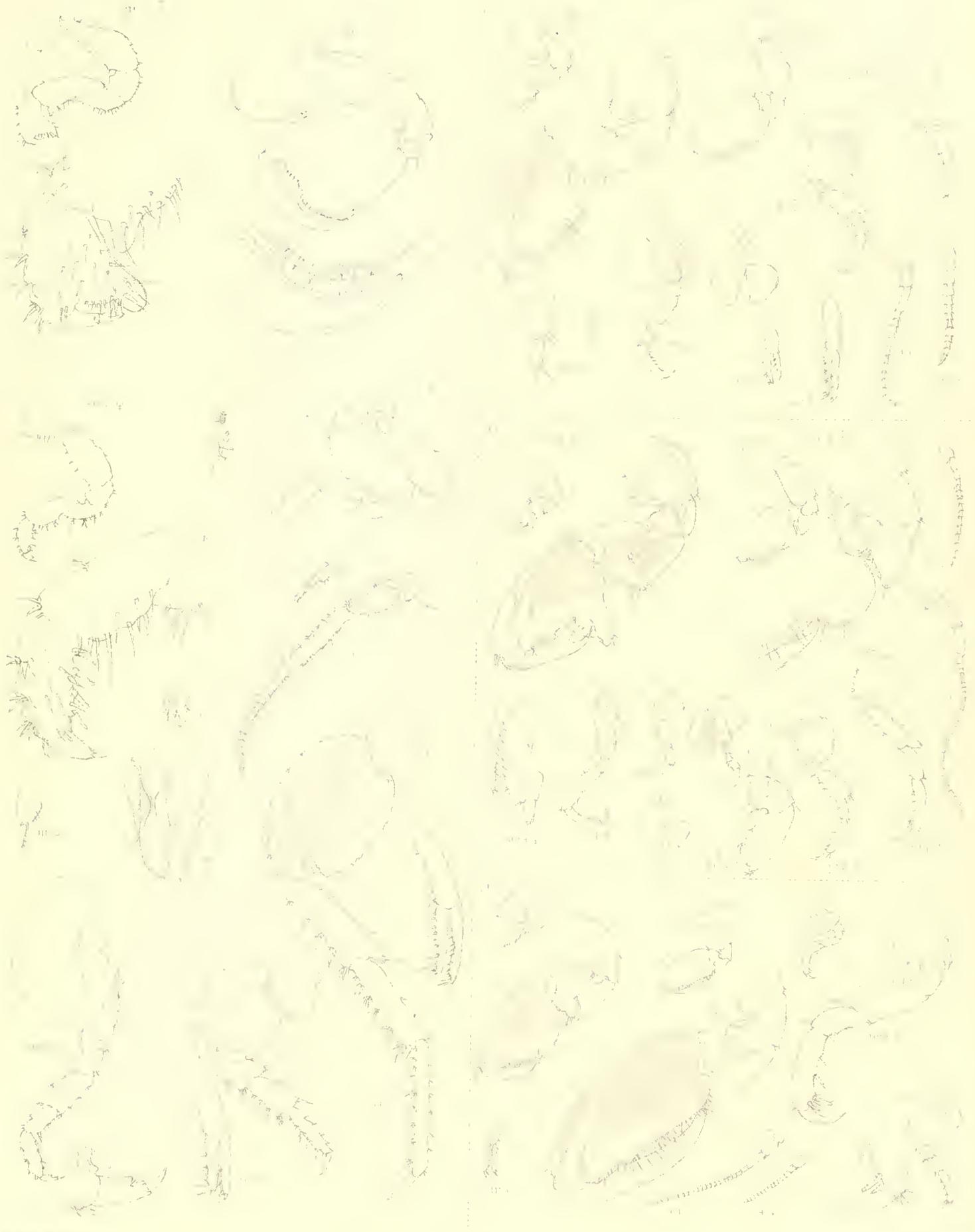
Pl. 30. A. Stebbing

Pl. 30. C. Stebbing

A TALORCHESTIA LEMMINGSI AUSTRIN.  
 B TALORCHESTIA TRIDENTATA n. sp. C TALORCHESTIA SULENSIS n. sp.



A

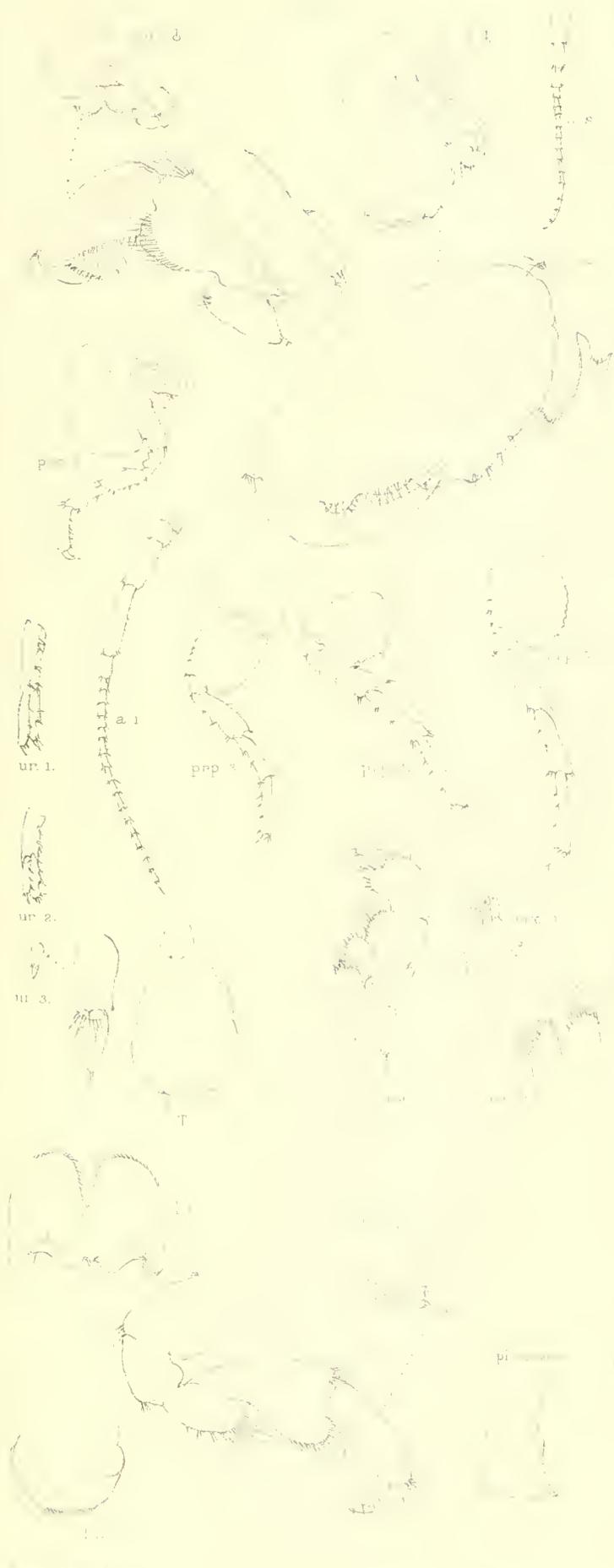


A. TALORGEZIA NOVAE-HOLLANDIAE n. sp.  
 C. HYALE DIPLODASTYLUS n. sp.

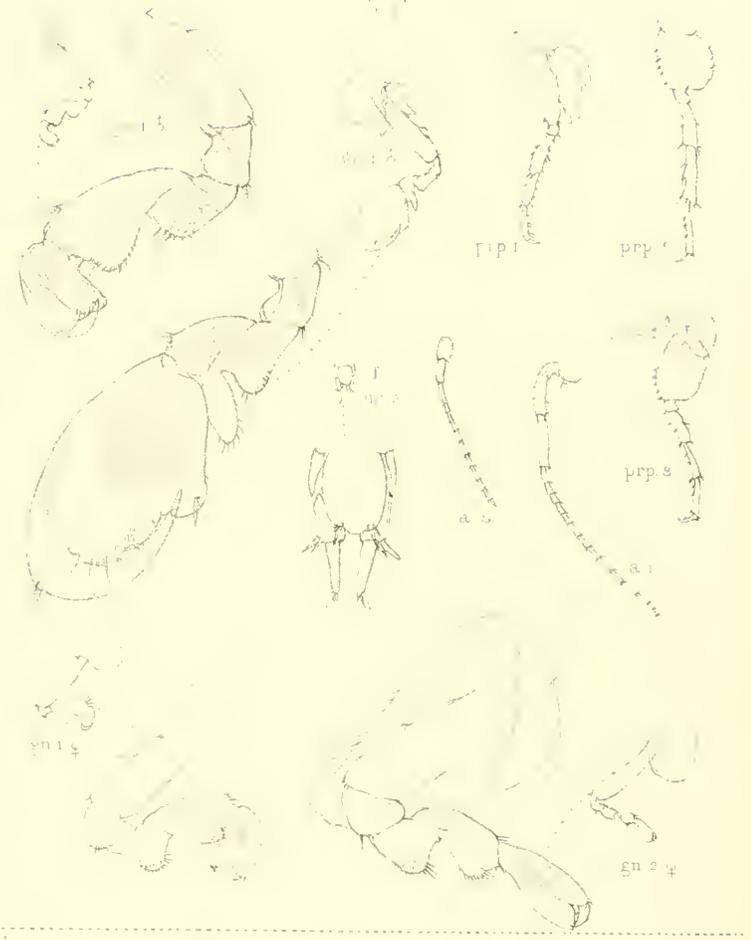
B. HYALE DIPLODASTYLUS n. sp.  
 D. HYALE DIPLODASTYLUS n. sp.



A.



B.



C.

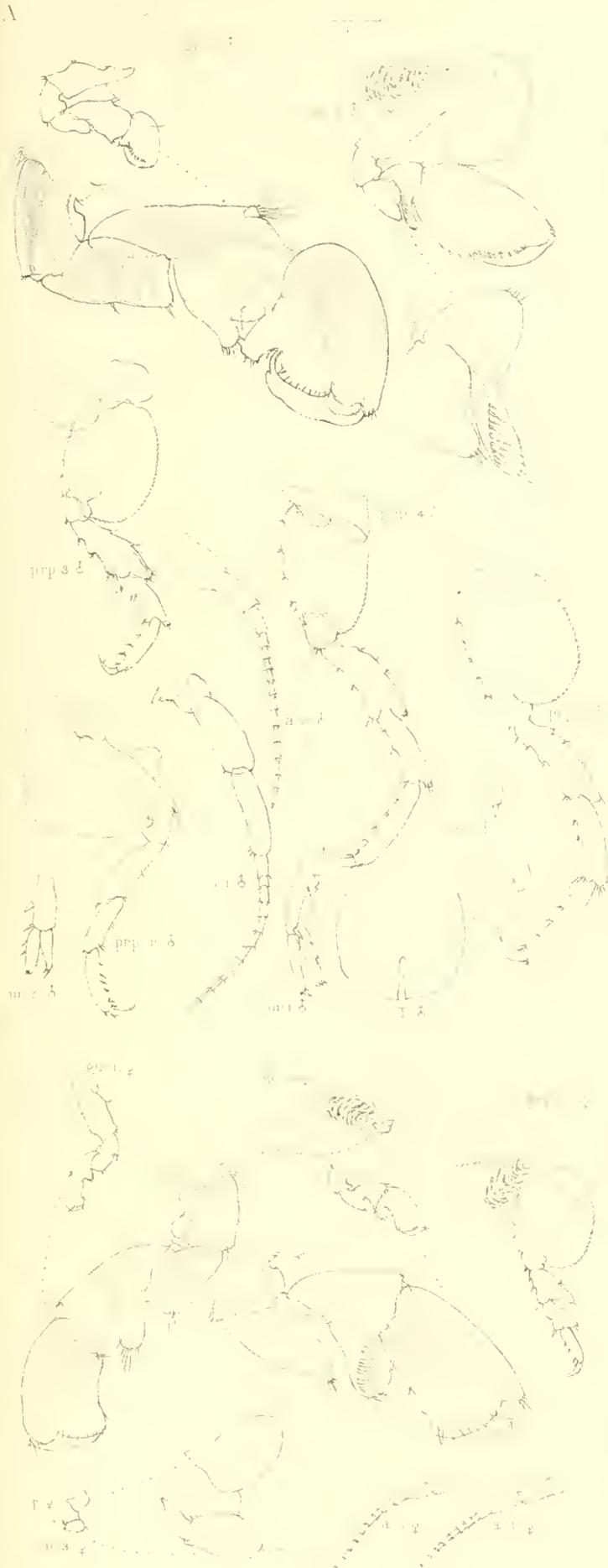


A. HYALELLA (Stebbing) n. sp.

B. HYALELLA (Stebbing) n. sp.

C. HYALELLA (Stebbing) n. sp.

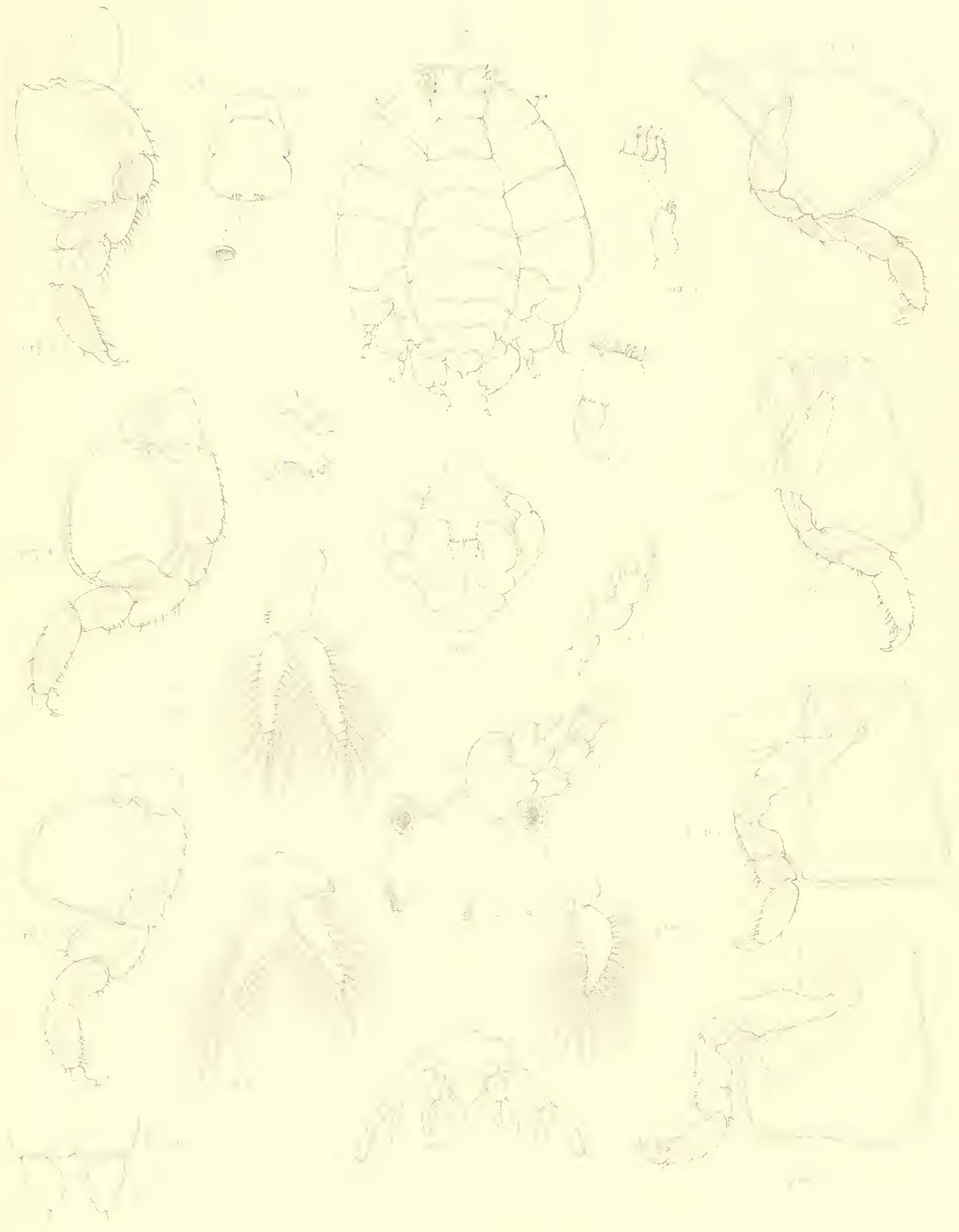




A. *ALLORCHESTES MALLEOLUS* n. sp.  
 C. *ALLORCHESTES PLUMICORNIS* n. sp.

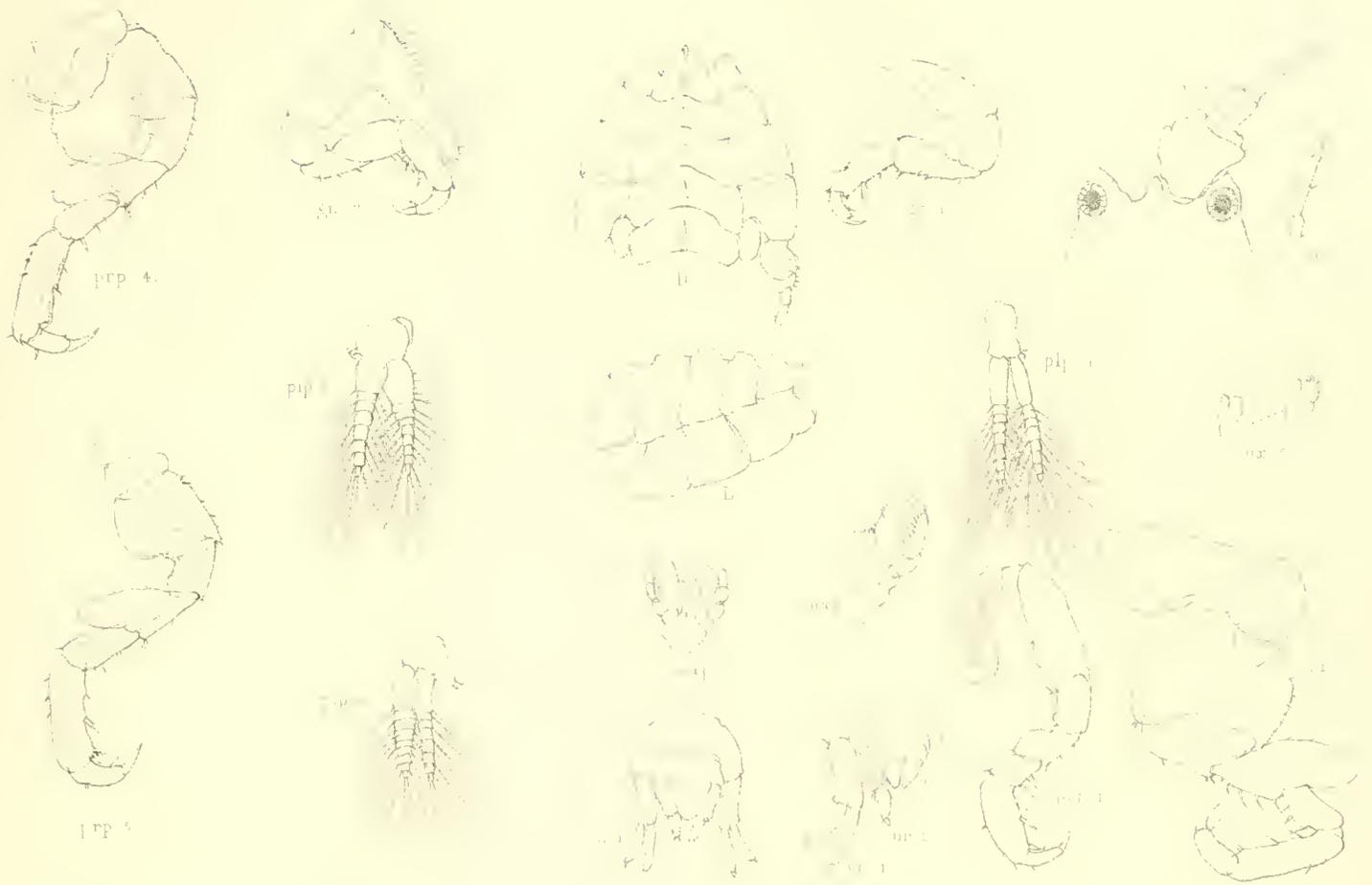
B. *ALLORCHESTES MALLEOLUS* n. sp.  
 D. *ALLORCHESTES PLUMICORNIS* n. sp.



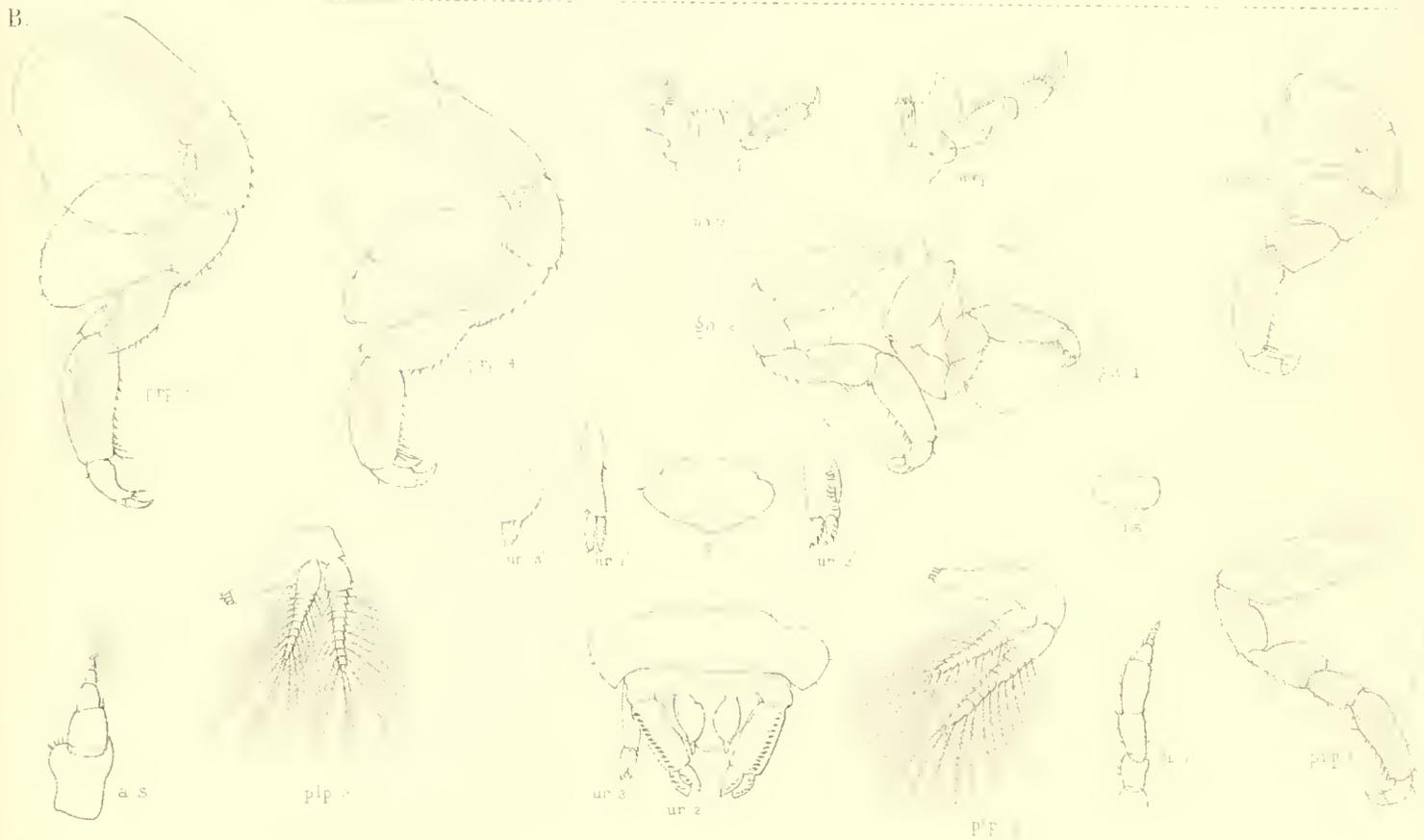




A



B



A FERENCHYTES THOMSONI n. sp. B IPHINETUS CHILTCHI n. sp.





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Part	III. 1882. ....	1	8	0	1	1	0	Part	VIII. 1892. ....	0	8	0	0	6	0
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Part	VI. 1883. ....	1	0	0	0	15	0	Part	XI. 1894. ....	0	2	6	0	2	0
Part	VII. 1883. ....	0	5	0	0	3	9	VI. Part	I. 1894. ....	2	0	0	1	10	0
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Part	XII. 1885. ....	0	6	0	0	4	6	Part	VI. 1896. ....	0	8	0	0	6	0
Part	XIII. 1884. ....	0	6	0	0	4	6	Part	VII. 1896. ....	0	12	0	0	9	0
Part	XIV. 1885. ....	0	6	0	0	4	6	Part	VIII. 1897. ....	0	2	6	0	2	0
Part	XV. 1885. ....	0	4	6	0	3	6	VII. Part	I. 1896. ....	0	10	0	0	7	6
Part	XVI. 1885. ....	0	5	0	0	3	9	Part	II. 1897. ....	0	12	0	0	9	0
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Part	XVIII. 1888. ....	0	2	6	0	2	0	Part	IV. 1898. ....	0	10	0	0	7	6
III. Part	I. 1884. ....	1	14	0	1	5	6	Part	V. 1898. ....	0	18	0	0	13	6
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Part	IV. 1885. ....	0	8	0	0	6	0	Part	VIII. 1899. ....	0	12	0	0	9	0
Part	V. 1887. ....	0	8	0	0	6	0								
Part	VI. 1888. ....	0	6	0	0	4	6								

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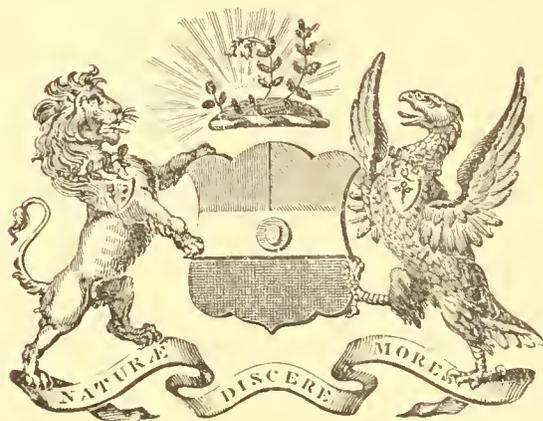
THE  
TRANSACTIONS  
OF  
THE LINNEAN SOCIETY OF LONDON.

ON FOSSIL AND RECENT LAGOMORPHA.

BY

C. I. FORSYTH MAJOR, M.D.

*(Communicated by Prof. G. B. Howes, Sec. Linn. Soc.)*



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IX. *On Fossil and Recent Lagomorpha.* By C. I. FORSYTH MAJOR, M.D.  
(Communicated by Prof. G. B. HOWES, Sec. Linn. Soc.)

(Plates 36-39.)

Read 16th June, 1898.

## TOOTH-CHANGE AND TOOTH-FORMULA IN THE LAGOMYIDÆ.

THE three extinct Lagomyidæ, *Titanomys*, *Prolagus*, and *Lagopsis*, and the surviving *Lagomys*, have five upper cheek-teeth, as against six in Leporidæ (*Palæolagus* and *Lepus* s. l.). From a comparison of the form and relative size of the teeth in *Lepus* and *Lagomys*, the type genera of both groups, Waterhouse\* and Gervais† had rightly argued that the last upper molar of *Lagomys* corresponds to the penultimate upper molar in the Hare. Since *Lepus* changes the three anterior of the upper six, and the two anterior of the lower five cheek-teeth, the formula being therefore  $P. \frac{3}{2}, M. \frac{3}{3}$ , it might have been further inferred that the number of premolars in Lagomyidæ is the same as in the Leporidæ.

Curiously enough, in recent species of *Lagomys* the tooth-change has never been examined. In 1870 ‡, O. Fraas described and figured the milk-dentition of *Prolagus*, with  $\frac{5}{4}$  cheek-teeth, there being three deciduous molars above and two below. The obvious inference is that the premolars are the same in number as the milk-teeth, and therefore in agreement with what is known in *Lepus*.

Fraas, however, proposes quite a novel definition of what we have to consider to be premolars, with the unavoidable result of thus introducing an element of confusion. Finding the three upper posterior and the three lower posterior cheek-teeth of *Prolagus* more in agreement as to general form with each other than with those anterior to them, which are two in the upper and one in the lower jaw, he concludes that these last are to be considered as premolars. According to this theory, which conflicts with the prior statement of the number of deciduous teeth, the tooth-formula would be  $P. \frac{2}{1}, M. \frac{3}{3}$ . But this second statement is again in flagrant contradiction with the following description of the mode in which the tooth-change is supposed to occur. The anterior upper premolar, termed  $P. \frac{2}{2}$  by Fraas, is stated to have no deciduous predecessor, the place of the anterior of the three deciduous teeth being taken by the premolar following behind the first, the so-called  $P. \frac{1}{1}$ ; while the anterior premolar pierces the jaw in front of  $P. \frac{1}{1}$  and comes in place

\* G. R. Waterhouse, 'A Natural History of the Mammalia,' vol. ii. p. 14 (1848).

† Zool. et Pal. Franç., sec. ed. pp. 48, 49 (1859).

‡ Württemb. naturw. Jahresh. xxvi. p. 169 (1870).

through the same lacuna ("Zahnlücke"), produced by the dropping out of the first deciduous. The two posterior deciduous teeth are, according to the writer, situated on the top of molars I. and II. (!) respectively, like so many caps. So that, according to this description, of the five upper cheek-teeth of *Prolagus*, the first and the last have no deciduous predecessors, but the three intermediate have. In the lower jaw Fraas finds two deciduous cheek-teeth: "Neben dem ersten zweiwurzeligen Deciduum, der über dem einzigen Praemolaren sitzt, ist noch ein zweiter zweiwurzeliger Deciduum, der von dem ersten Molaren verdrängt wird." According to this, in the lower jaw the supposed unique premolar and what he believes to be the first true molar would have deciduous predecessors.

Those astounding views necessarily created a distrust in Fraas' description of  $\frac{3}{2}$  deciduous molars (in *Prolagus*); and as a consequence most of the subsequent authors on the subject, up to this day, have, with regard to the Lagomyidæ, preferred to adhere to the old Cuvierian dictum, viz., that in all the Rodents with more than three molars, only the one (or more) anterior to the three are replaced, and that the latter alone are to be considered true molars.

Filhol has observed the two anterior lower cheek-teeth to change in *Titanomys*, and he apparently extends this observation to the maxillary teeth as well: "Chez le *Titanomys*, les deux premières dents étaient sujettes au remplacement" \*.

The one author who first rightly interpreted the tooth-formula of Lagomyidæ is Winge, although he has not seen the tooth-change. Of Fraas' statements he says that they are not clear, partly due to some of the premolars being called molars; and he continues to say that *Lagomys*—which, according to him, includes the fossil "*Myolagus*" and its allies— "has  $\frac{5}{5}$  or  $\frac{5}{4}$  cheek-teeth; these are the  $\begin{smallmatrix} 2 & 3 & 4 & 5 & 6 \\ 3 & 4 & 5 & 6 & 7 \end{smallmatrix}$  or  $\begin{smallmatrix} 2 & 3 & 4 & 5 & 6 \\ 3 & 4 & 5 & 6 \end{smallmatrix}$  of the typical  $\frac{7}{7}$ , as is seen from a comparison with *Lepus*; in the maxillary the three anterior teeth, in the mandible the two anterior are changed" †.

In the first part of his memoir on Tertiary Rodentia, Schlosser speaks invariably of only one inferior premolar and of a fourth inferior true molar (m. 4) in fossil Lagomyidæ ‡; but later on he gradually § arrives at the true statement of things as given in the supplement to the above memoir, in the following words:—"In this group (*i. e.* the Lagomorpha) at least the first two anterior teeth in each jaw are changed, so that we must speak of two, respectively three premolars" ¶.

My own observations are to the following effect:—

1. *Titanomys*.—This genus has five cheek-teeth in the upper jaw. The deciduous teeth are three in the maxillary and two in the mandible, as is seen in the Rott skeleton described below. The two deciduous inferior teeth, as mentioned above, have already been figured by Filhol ¶¶.

\* Ann. Sc. Géol. x. p. 29 (1879).

† "Om Pattedyrenes Tandskifte" (Vidensk. Meddel. Naturh. Forening i Kjöbenhavn f. 1882), p. 48 (1883). See also H. Winge, in 'E Museo Lundii,' i. pp. 108, 111 (1888).

‡ 'Palæontographica,' xxxi. p. 10 &c. (1884).

§ *Op. cit.* p. 110, Ann. 2.

¶ Palæontogr. xxxi. p. 327 (1885).

¶¶ *Op. cit.* p. 29, pl. 3, fig. 3.

As to the number of lower cheek-teeth, I find, as a rule, five in one of the species, *Titanomys Fontanesi*; but in two out of seventeen mandibular rami there are only four teeth, there being no trace of an alveolus for the last small tooth, which probably will be found constantly present in young specimens.

In the other species, *T. risenoriensis*, the fifth lower molar is supposed to be oftener missing than not. Pomel called *Amphilagus*—regarded by him as a subgenus of *Lagomys*—those specimens of *T. risenoriensis* in which five mandibular cheek-teeth were present; those with only four teeth he placed in his genus *Lagodus* (*Lagodus picoides*, Pomel, = *Titanomys risenoriensis*, H. v. Mey.). Filhol has based a fusion theory on the presence or absence of the small molar in question\*. He assumes that at a certain given moment there prevails a tendency to simplification in the Lagomyine dentition—firstly by the fusion of the last (fifth) tooth with the penultimate, and secondly by the tendency of the fused elements to disappear.

This theory is at once disposed of by the fact that in the mandibles of *Titanomys Fontanesi* before me both the fifth tooth and the posterior colonnette of the fourth—which colonnette Filhol considers to be the fifth tooth fused to the fourth—are present together. I think that for *T. risenoriensis* the same explanation holds good as with regard to *T. Fontanesi*, viz. the fifth tooth has sometimes been lost in the young animal and its alveolus obliterated; its frequent absence is simply explained by the fact that it has dropped out in the fossils.

Anyhow, the formula of *Titanomys* will have to be written as follows:—

$$P. \frac{3}{2}, M. \frac{2}{2-3}, \text{ or } \frac{p. 3, p. 2, p. 1; m. 1, m. 2}{p. 2, p. 1; m. 1, m. 2 (m. 3)}$$

2. *Prolagus*.—I have at my disposal the deciduous molars of two species of *Prolagus* [*P. aeningensis* (Kön.) and *P. sardus* (Wagn.)]; there are three in the upper and two in the lower jaw, as seen already by Fraas in the first-named species. In the skull of a young *P. sardus*, where the deciduous teeth are *in situ*, the following may be seen:—The anterior of the three deciduous teeth is not situated directly above the anterior premolar, but slightly backward, closely appressed to the second deciduous, so that with its anterior moiety it covers only the posterior part of the premolar; besides it could not possibly cover the latter completely, being much smaller. It is needless to say that neither of the true molars, both of which are already protruded in the skull under observation, supports a milk-tooth; as a matter of fact, the tooth called molar I. by Fraas, which in reality is the posterior of the three premolars, is situated under the posterior of the three deciduous molars, as is the middle premolar under the middle deciduous.

In the lower jaw of both species the two anterior of the four lower cheek-teeth replace the two deciduous teeth.

Therefore, since *Prolagus* has in the full-grown animal five cheek-teeth above and four below, its tooth-formula will be:—

$$P. \frac{3}{2}, M. \frac{2}{2}, \text{ or } \frac{p. 3, p. 2, p. 1; m. 1, m. 2}{p. 2, p. 1; m. 1, m. 2}$$

\* Ann. Sc. Géol. x. p. 28 (1879).

3 & 4. *Lagopsis* and *Lagomys*.—Since these genera have five cheek-teeth in both jaws, there being a small fifth inferior tooth, their tooth-formula will be:—

$$P. \frac{3}{2}, M. \frac{2}{3}, \text{ or } \frac{p. 3, p. 2, p. 1; m. 1, m. 2}{p. 2, p. 1; m. 1, m. 2, m. 3}$$

*To sum up.* The number of premolars is constant in all the genera of Lagomyidæ, and the same as in *Lepus*; whereas that of the true molars varies in the different genera; not *vice versa*, as has been supposed by Lydekker\*, Flower†, and Zittel‡.

The upper m. 3, always present in *Lepus*, is always absent in the Lagomyidæ. Of the lower true molars, m. 3 is always present in *Lagopsis* and *Lagomys*, when not lost in the fossil: it is always absent in *Prolagus*; while in *Titanomys* this tooth is rarely absent in one species, *T. Fontannesi*, more frequently in the other, *T. visenoviensis*, but presumably always present in young specimens of both.

### 1. Genus TITANOMYS.

*Titanomys*, H. v. Meyer, Neues Jahrb. 1843, p. 390.

*Lagodus*, Pomel, Cat. méth. Vert. foss. Loire et Allier, p. 41 (1853); Depéret, Arch. Mus. Lyon, iv. p. 126 (1887).

*Lagomys* (subg. *Amphilagus*), Pomel, op. cit. p. 42.

*Lagomys*, Lydekker, Cat. Foss. Mamm. Br. Mus. i. p. 255 (1885).

*Lagomys* (*Lagopsis*), Schlosser, Pal. Oestr.-Ung. viii. p. 86, foot-n. 4 (1890), p.p.; Depéret?, Arch. Mus. Lyon, v. p. 58 (1892).

#### TITANOMYS VISENOVIENSIS.

*Titanomys visenoviensis*, H. v. Meyer, Neues Jahrb. 1843, p. 390; Gervais, Zool. et Pal. fr., prem. éd., Expl. No. 46, pl. xlvi. fig. 2 (1848-52); Bronn, Leth. Geogn. iii. p. 103 (1853-56); Gervais, Zool. et Pal. fr., deux. éd., p. 50, pl. xlvi. figs. 1, 2 (1859); H. v. Meyer, Palæontogr. xvii. p. 225, pl. xlii. (1870); Filhol, Ann. Sc. Géol. x. p. 26, pl. ii. figs. 25, 26, pl. iii. figs. 1-18 (1879); Schlosser, Palæontogr. xxxi. p. 29, pl. xii. figs. 36, 38, 39, 41, 43, 45, 47, 48 (1884); Zittel, Handb. d. Palæont. i., iv. p. 552 (1891-93).

*Titanomys trilobus*, Gervais, Zool. et Pal. fr., prem. éd., Expl. No. 46, pl. xlvi. fig. 1 (1848-52).

*Lagodus picoides*, Pomel, Cat. méth. p. 41 (1853).

*Lagomys* (subg. *Amphilagus*) *antiquus*, Pomel, op. cit. p. 43.

*Amphilagus antiquus*, Schlosser, op. cit. p. 30.

*Lagomys visenoviensis*, Lydekker, Cat. Foss. Mamm. Brit. Mus. i. p. 258 (1885).

#### *Historical Sketch.*

In announcing his new genus *Titanomys* (type species *T. visenoviensis*), from the Lower Miocene of Weisenau near Mayence, H. v. Meyer characterizes it as having prismatic cheek-teeth, agreeing in size and number and resembling in form those of *Lagomys*, with the difference, however, that the lower molars of the fossil present a distinct

\* Cat. Foss. Mamm. Br. Mus. i. p. 255 (1885); Nicholson & Lydekker, Manual of Palæont. ii. p. 1412 (1889).

† Flower & Lydekker, 'Introduct. to the Study of Mammalia,' p. 491 (1891).

‡ Zittel, Handb. d. Palæont. i., iv. p. 551 (1891-93); id. Grundz. d. Palæont. p. 825 (1895).

posterior appendage ("Hinteransatz") not known to exist in *Lagomys*, while the Weisenau Rodent lacks the distinctly developed tooth-particle ("Zahntheil") in the last lower molar of existing *Lagomys* and of those of the "ossiferous breccia"; by which is apparently meant the *Prolagus* of Corsica and Sardinia.

We meet here at the outset with several incorrect statements. The upper molars are not, as we shall see later, prismatic, and the lower are only incompletely so. By the alleged agreement in number of the molars of both *Titanomys* and *Lagomys* we are to understand that both genera have four lower cheek-teeth, the author believing at that time that the existing *Lagomys* has four mandibular cheek-teeth, while in reality there are five. H. v. Meyer considered the fifth small cylindric tooth of *Lagomys* to be a third prismatic particle connected with the anterior molar, as is the case in *Prolagus*. The author further makes a distinction—which is repeated two years later in his 'Fossil Mammals of Eningen,' where incidentally the genus *Titanomys* is mentioned\*—between a distinct "Hinteransatz" in the posterior molars of *Titanomys*, and the "distinctly developed" posterior or third "Zahntheil" of the last molar in some Lagomyidæ, without being aware that the two are one and the same thing and homologous.

The characteristics given of the upper molars are not incorrect, but rather vague, showing that the author did not succeed in making out the pattern of the triturating surface, as is confirmed also by his manuscript drawings subsequently published by Schlosser.

In the first edition of his 'Zoologie et Paléontologie françaises,' Gervais figures, without description, two mandibular rami from the Lower Miocene of Saint-Gérard-le-Puy (Allier); the fig. 1 of pl. 16 is named *Titanomys trilobus*, the fig. 2 *T. visenoriensis*. In the explanation of the plate it is stated that the identification with *T. visenoriensis* rests on a comparison with a mandible of this species from Germany in the British Museum (this is under No. 21495, from Weisenau). Gervais had no upper molars from the French deposit, but says that those from Germany, which are in London, "sont assez semblables à celles des Lapins, mais beaucoup plus courtes et plus arquées," adding that they are of the same form as those from the Miocene of the Limagne, called *Marcuinomys* by Croizet and *Platyodon* by Bravard. These are two manuscript names.

In 1853 Pomel issued a small work of a high standard on the fossil vertebrates of the Loire and Allier basins, pretending to be nothing more than a catalogue †. The descriptions are in consequence very short, and as there are no figures, the utility of this excellent publication has been rather limited. The Leporidae family opens ‡ with a new genus, *Lagodus*, from the Tertiary of Langy; the only species, *L. picoides*, scarcely larger than *Lagomys pusillus*, is based mainly on the upper and lower cheek-dentition, the description of which I transcribe at length for future reference. From this it will be seen that the author assigns to his genus *Lagodus* five upper and four

\* 'Zur Fauna d. Vorwelt.—Foss. Säugethiere etc. von Eningen,' p. 10 (1845).

† Catal. méthod. et descr. des Vert. foss. découverts dans le Bassin hydrogr. sup. de la Loire, et surtout dans la Vallée de . . . l'Allier (1853).

‡ *Op. cit.* p. 41.

lower cheek-teeth; the first superior was missing, and from the form of the alveolus it is declared to have been very small. "En haut il paraît y avoir eu cinq molaires; la seconde est plus étroite que chez les *Lagomys* et pour ainsi dire réduite à une seule lame marquée en travers de deux plis d'émail, de manière à figurer presque trois croissants concentriques; les trois autres ont deux lames dont la première est simple, et la seconde pourvue des deux replis d'émail de la dent qui précède, excepté à la cinquième dent, où elle est plus petite." The lower teeth are said to be four in number, "par absence de la dernière. Première tétragone divisée par deux sillons en deux cylindres comprimés, dont l'antérieure plus saillante est aussi un peu plus large et la seconde a en arrière un petit pli d'émail partant de l'angle interne surtout évident à la dernière molaire et s'effaçant assez tard par la détritition. Ces cylindres sont moins comprimés d'avant en arrière que chez les *Lagomys*, et leur disque de détritition est ovale oblong, brusquement atténué en angle du côté externe, arrondi vers l'interne."

From the later descriptions of *Titanomys* and from examination of originals, we are enabled to refer Pomel's *Lagodus* to the former genus, and at the same time to appreciate the accuracy of his description. But without this help and in the absence of figures, it becomes difficult to form an exact conception of the complicated pattern of the upper teeth, from their necessarily too short characteristics by Pomel. Hensel, when describing the teeth of *Prolagus* (his *Myolagus*), was on the look-out for allied forms; he gives in full Pomel's description of *Lagodus* \*, but fails to see the curious relationship existing between the upper premolars of the former and all the upper cheek-teeth of the latter.

The small enamel fold described by Pomel as starting from the internal angle of the posterior lamina in the three mandibular teeth behind the first is the "Hinteransatz" of H. v. Meyer's *Titanomys*. The relations of the latter to his *Lagodus* are not discussed by Pomel; he suggests the former to be probably the same as *Prolagus sansaniensis* (Lartet's *Lagomys sansaniensis*).

Pomel's *Amphilagus* rests on lower jaws; he considers it to be a subgenus of *Lagomys*, apparently because in both there are five lower cheek-teeth: "la dernière molaire" (in *Amphilagus*) "très petite est cylindrique et caduque, en sorte qu'il ne reste souvent que quatre dents à la mâchoire." The form of the anterior lower premolar is the same as in "*Lagodus*" and *Titanomys*, and very different from the premolar of *Lagomys*, a character which at once suggests that "*Lagodus*" and *Amphilagus* may be identical, and that the absence of the small posterior appendage in the lower molars attributed to *Amphilagus* is due to the specimens being from older individuals than those assigned to "*Lagodus*."

In Bronn's 'Lethæa Geognostica,' Pomel's *Lagodus* is given as a synonym of *Titanomys risenoriensis* on the authority of H. v. Meyer ("fide Meyer in litt.").

The second edition of the Zool. et Pal. franç. (1859) gives good reasons for considering *Titanomys trilobus* as the young of *T. risenoriensis*. Of the last lower molar in particular Gervais says:—"la dernière montre encore avec assez d'évidence un troisième lobe, qui

\* Zeitschr. d. deutsch. geol. Ges. viii. p. 699 (1856).

est d'ailleurs petit et qui, à un âge plus avancé, eût été confondu avec le second lobe de la même dent, comme cela se voit chez le sujet de la figure 2" (*T. risenoviensis*); and he goes on stating, as Pomel had done for his *Lagodus*, that this little posterior column is gradually worn away. It is mentioned by Gervais only in the last molar, and his figures show no trace of it in the anterior molars.

Referring to Pomel's *Lagodus* and *Amphilagus*, Gervais launches an ungenerous and unfounded accusation against this author, alleging that the former genus is "du moins en partie" based on his, Gervais', figure of *Titan. trilobus*, and that *Amphilagus* rests on fig. 2, representing *Titan. risenoriensis*. No mention is made of Pomel's description of the upper dentition of "*Lagodus*." If the latter writer failed to recognize in his *Lagodus* and *Amphilagus* H. v. Meyer's *Titanomys risenoviensis*, it was perfectly excusable at the time he wrote, when this species had been so very imperfectly diagnosed both by H. v. Meyer and by Gervais, who both failed to make out the pattern of the upper teeth. Up to this day we have not been better off with regard to the upper cheek-teeth from the type-locality Weisenau.

It would have been fairer on the part of Gervais to acknowledge that Pomel's description of the inferior molars of "*Lagodus*" had gone far in enabling him (Gervais) to recognize the non-validity of his species *T. trilobus*, and that Pomel had besides described more accurately than himself the lower teeth, in demonstrating the presence of the "petit pli d'émail" in *all* the posterior teeth of younger specimens. He certainly could not have based this statement on Gervais' fig. 1 of the young specimen, where only the last molar shows a posterior appendage. The accusation with regard to *Amphilagus* is quite as unfounded as the first one. Pomel assigns five teeth to the lower jaw of his genus, Gervais' figure shows only four; the description of the first tooth of *Amphilagus* does not exactly agree with the tooth in Gervais' figure, from which last, moreover, it could not be made out that the two cylinders of each of the posterior teeth are united by cement, as stated by Pomel to be the case in his *Amphilagus*. Other particulars occur in the description of *Amphilagus*, which might at once have convinced an impartial critic that Pomel based his description on originals. These were, many years later (1879), handed by M. Pomel himself to Prof. Filhol\*.

In his posthumous paper (1870) on the skeleton of a young *Titanomys risenoriensis* from the Lignite of Rott near Bonn, now in the British Museum (No. 41085), H. v. Meyer mentions rooted cheek-teeth in *Titanomys*, and he has been understood to state that only the deciduous teeth of this genus are provided with roots. However, when reading attentively H. v. Meyer's paper—I might almost say, in reading between the lines as well—one necessarily comes to the conclusion that in adult specimens the permanent molars were also rooted, and that the author himself had suspected this fact, but hesitated to proclaim it. Two kinds of rooted *Titanomys*-teeth are mentioned in the paper. With regard to those of the Rott skeleton, the author states that their triturating surfaces are concealed in the matrix, so that their opposite ends only could be examined; but this does not hide the fact, he continues, that the two posterior upper

\* Ann. Sc. Géol. x. pp. 27, 28 (1879).

teeth were formed as in *Lagomys*. This evidently implies that they have no roots; for the writer proceeds to state that in the teeth anterior to those just mentioned lengthened roots can be seen. In the two anterior cheek-teeth of the lower jaw, H. v. Meyer describes a short crown and a long root, composed of two strongly converging parts; and these two teeth seem to be situated somewhat higher than the two posterior, which suggests that they had not yet emerged above the alveolar margin. Contrary to the anterior rooted teeth, these two posterior ones are described as "prismatic"; the whole of their crown has an enamel coating, and is not completely closed below. The author concludes that the teeth seem to indicate that the animal was of immature age, a supposition which would explain the differences of the anterior teeth from those of *Lagomys*.

As a matter of course, in the lagomorphous Rodentia with permanent cheek-teeth growing by persistent pulps, the deciduous teeth are rooted too as in the Rott skeleton. But the author proceeds to state (p. 128) that he has examined detached teeth of the *Titanomys* from Weisenau of two kinds: on the one hand, small teeth corresponding to the anterior teeth of the Rott specimen; on the other, lower teeth differing from the last by a lengthened prismatic crown and quite insignificant roots; and upper teeth as well, of larger size than those corresponding to the upper anterior teeth from Rott, supposed by H. v. Meyer to be possibly deciduous. In the larger teeth the roots are said to disappear almost completely; "die flach prismatische, gekrümmte Krone vertritt zugleich die Hauptwurzel, und es wird nur aussen oben ein kleines Würzelehen wahrgenommen, das auch in einer entsprechenden Stelle des Kiefers eingreift, während das an der Innenseite mit einer Rinne versehene Zahnprisma die eigentliche Alveole ausfüllt."

From what will be seen later on, these larger teeth, upper and lower, are in fact the permanent teeth of *Titanomys*, as H. v. Meyer hesitatingly suggests. Therefore there is no foundation in the distinction—such as is drawn by Depéret—of two genera, founded on the presence or absence of roots in the permanent teeth, viz.:—

- (1) *Titanomys*, with roots in the deciduous set only.
- (2) *Lagodus*, with roots in the permanent teeth as well (premolars and true molars).

Proceeding with our historical sketch in chronological order, we next have to consider Filhol's description of *Titanomys risenoriensis* from Saint-Gérard-le-Puy (Allier) \*, which has already been quoted more than once in the preceding pages. Among the synonyms of this species are given *Amphitagus antiquus*, Pom., and *Lagodus picoides*, Pom.: the identification of the former rests on one of the type specimens of Pomel; the latter is not discussed in the paper. An important character noted by Filhol is the relatively considerable longitudinal extension of the bony palate in *Titanomys*. The shortness of the bony palate in lagomorphous Rodents is doubtless a specialization; but by its greater extension *Titanomys* approaches more the condition of other Rodentia and Mammalia generally. The same is true of *Palaeolagus*, from the Miocene of North America, which presents curious resemblances with *Titanomys* in its dentition also. Moreover, we meet with a lengthened bony

\* Ann. Sc. Géol. x. p. 26 (1879).

palate in *Lepus valdarnensis*, Weith. \*, from the Upper Pliocene of Tuscany, and in three existing Leporines, *Lepus hispidus*, Pears., from the foot of the Himalayas, *L. Netscheri*, Schleg. & Jent., from Sumatra †, and *Romerolagus Nelsoni*, Merr., from the Popocatepetl (Mexico) ‡, all three of which have other generalized characters in common with each other and partly with *Palæolagus*.

*Description of Original Specimens.*

1. *The Rott Skeleton*.—In its present condition, of the two anterior lower cheek-teeth described and figured by H. v. Meyer, only the imprint is preserved, with the exception of the anterior half of the front tooth, which is still in place. From what can still be seen, and with the help of H. v. Meyer's description and figures, there remains not the slightest doubt that these two anterior teeth belong to the deciduous set, since they bear the characters of milk-teeth, viz., a short crown and (two) long roots, much diverging from each other downward. The number of teeth in front of the two posterior in the upper jaw is left uncertain in the figures and text of the original memoir. A close examination shows that there are three of them: the first apparently is provided with a stouter internal and a somewhat weaker external root; the two following with one internal and two smaller external roots, the latter strongly diverging from the shaft in opposite directions. Here, too, we have the characteristic features of milk-teeth, of which there are consequently three upper in *Titanomys*, as might have been anticipated by analogy to *Prolagus*. The immature condition of the specimen can be further inferred from the fact that the two posterior teeth, viz., the fourth and fifth in the series, are not yet on the same level with the three in front of them. As these two posterior teeth are broken at their lower ends, nothing can be stated as to their roots.

Still less—and this applies to all the teeth of the Rott specimen—can be made out about the pattern of their triturating surface, which, as noticed already by H. v. Meyer, is concealed in the matrix. This deficiency is partly supplied by some teeth from the type-locality of Weisenau, in the British Museum.

2. *Titanomys risenoriensis from Weisenau*.—A fragment of the right upper jaw from the Lower Miocene of Weisenau, in the Geological Department of the British Museum (21495), Pl. 36, fig. 19, shows the two posterior premolars, p.1, p.2, and part of the alveolus of the anterior premolar, p.3. These upper teeth were seen by Gervais, who alludes to them §, contenting himself with the above-reported general remarks. The first of the two premolars preserved, p.2, at once calls to mind by its general form the anterior upper premolar, p.3, of *Lepus*, and to it therefore may be justly applied Gervais' remark referring to all the upper teeth in London, viz., that they are "assez semblables à celles des Lapins." The general outline of this tooth is somewhat triangular, the broader basis being on the inner side, which is imperfectly divided by a slight notch into two abraded

\* Jahrb. k.-k. geol. Reichsanst. vol. xxxix. p. 80 (1889).

† 'Notes from the Leyden Museum,' vol. ii. note xii. p. 59 (1880).

‡ Proc. Biol. Soc. Washington, x. pp. 169–174 (1896).

§ Zool. et Pal. Franç. 1st ed. t. ii. expl. no. 46 (1848–52); 2nd ed. p. 50 (1859).

cusps (8 & 9). Proceeding outward, we meet with two enamel folds starting from the anterior side of the tooth. The one placed more internally (*b*) is by far the larger of the two; it opens freely on the anterior side, and thence proceeds first internally, and then, gradually attenuating, postero-externally, thus assuming approximately the form of a crescent, whose anterior horn is much shorter than the posterior. Both horns are delimited externally by a cusp (6), having its long axis almost parallel to the long axis of the skull, and protruding with its internal convex border into the enamel fold just described, while its shorter and almost longitudinal external border forms the inner margin of the much smaller second enamel fold (*c*). On the outer side of the tooth we meet with a large bulging enamel tubercle (5), worn by attrition on its inner side only, and showing thus that the outer side in this otherwise much-worn tooth is only partially affected by trituration.

The second tooth, p. 1, presents the general contour of the crown of lagomorphous Rodents, the transverse diameter largely predominating over the longitudinal; the anterior border is slightly more convex than the posterior. The minute pattern of the triturating surface, however, is very different from that which we are accustomed to consider characteristic of upper leporine molars. The main difference from p. 2 consists in the two enamel folds being shut out from the anterior border by a transverse anterior lobe, which in p. 2 is apparent only in a much reduced condition, its outer portion being entirely wanting. In p. 1 the anterior lobe or "wall" delimits the anterior horn of the enamel fold (*b*) on its front side, so that in this tooth the anterior horn is much more lengthened transversely than the posterior. As compared with p. 2, p. 1 has undergone, as it were, a lateral pressure, by which the various parts of the surface have been forced into a more transverse direction. This is apparent, especially in the strong cusp (6) separating enamel folds *b* and *c*, which is no more longitudinally directed as in p. 2 but has likewise assumed the form of a crescent with its convexity projecting inward into enamel fold *b*, and forming externally the inner margin of enamel fold *c*. The latter has in its turn assumed a more transverse direction, and is only incompletely shut out from the outer border of the tooth by a blunt enamel tubercle (5), occupying mainly the postero-external part of the tooth. The summit only of this tubercle is slightly worn.

The inner border of p. 1 is more distinctly divided than in p. 2 into two abraded cusps by a vertical groove, manifesting itself on the triturating surface in the shape of a short enamel fold, or notch (*a*).

The levelling effect of trituration—favoured by the enamel folds in both teeth being more or less completely filled with cement,—together with the more transverse direction assumed by the folds and cusps of p. 1, tends to produce a lophodont character of its triturating surface; or rather, we have a selenodont type leaning towards lophodonty.

3. *Titanomys risenoviensis*, from the Allier (France). Br. Mus. 31094 (Bravard Collection).—A detached tooth (Pl. 36, fig. 12) is more worn still than that just described, as revealed by its triturating surface being more flattened and the enamel folds more narrowed. It can only be either p. 1 or m. 1. P. 3 is quite out of the question, as, to judge from its alveolus, it was a very small tooth; p. 2 is reduced in its antero-external,

m. 2 in its postero-external portion (compare fig. 19, Pl. 36, with fig. 6); so that the choice remains only between p. 1 and m. 1. It resembles closely the p. 1 described; only it is narrower, and the anterior lobe of the latter is more developed in its internal portion, although the inverse was to be expected, the p. 1 described being less worn. For these reasons I think it more likely to be m. 1. This tooth shows two small roots on the outer side; on the inner side the crown gradually thins out downward into a single large root. It cannot be a milk-tooth, because the two small external roots do not diverge downwards, but run parallel with each other. We have here another proof, if one were needed, that in *Titanomys visenoriensis* the upper teeth are provided with roots; although this fact has been denied with regard to this species of the Lower Miocene.

*Mandibular teeth of Titanomys visenoriensis.*—As a characteristic feature of the lower cheek-teeth of *T. visenoriensis*, H. v. Meyer makes mention of a small posterior lobe, calling it a distinct posterior appendage (“ein deutlicher Hinteransatz”)\*. About the occurrence of this small particle much uncertainty prevails. When establishing the genus, in the paper just quoted, H. v. Meyer mentioned it in a general way as present in the lower cheek-teeth, seemingly implying that all of them were provided with this appendage. In his posthumous memoir, however, speaking again of the Weisenau specimens, he says that it occurs on the *posterior* cheek-teeth and would have disappeared by effect of attrition †. Pomel assigns it to the three posterior cheek-teeth of “*Lagodus picoides*,” adding that it takes its origin from the internal angle, that it is more evident especially in the last molar and disappears rather late by attrition ‡.

According to Gervais § it would occur only on the fourth tooth (m. 2), and as a character of young specimens; the same is stated by Filhol ||, who had at his disposal a considerable number of lower jaws. Schlosser ¶ styles it a third lobe occurring as an anomaly (“abnorm vorkommend”) in “m. 3” (meaning m. 2) of *Titanomys visenoriensis*; although in the same memoir he figures manuscript drawings by H. v. Meyer, where it is shown in two molars. This same small lobe occurs in *Palæolagus* also; it is transitional in one species, *P. Haydeni*, as described by Cope \*\*, apparently persisting in another species, *P. triplex* ††. On a former occasion I incidentally pointed out the interest attached to it from both a phylo- and ontogenetic point of view ‡‡.

As to the occurrence of this small lobe or cusp in *T. visenoriensis*, my own observations tend to show that it is constantly present in young specimens, not only of the posterior, but also of the anterior lower teeth, including p. 2. In a fragment of a right mandibular ramus of *T. visenoriensis* from the Allier (Bravard Collection, Br. Mus. 31094–104), Pl. 37, fig. 25, exhibiting the two anterior cheek-teeth, p. 1 and p. 2, in a moderate stage of wear, traces of this lobe are visible in both these premolars, very distinctly in the posterior (p. 1).

\* Neues Jahrb. 1843, p. 390.

‡ Cat. méth. p. 41 (1853).

|| Ann. Se. Géol. x. p. 27 (1879).

\*\* ‘The Vertebrata of the Tertiary Formations of the West,’ p. 876 (1883).

†† *Op. cit.* p. 881.

† Palæontogr. xvii. p. 226 (1870).

§ Zool. et Pal. Franç. sec. ed. p. 50 (1859).

¶ Palæontograph. xxxi. p. 32 (1884).

‡‡ Proc. Zool. Soc. London, p. 203 (1893).

It has been found convenient to give the detailed descriptions of the lower molars of this and all the other genera in a separate chapter (p. 473).

#### TITANOMYS FONTANNESI.

*Lagodus Fontannesi*, Depéret, Arch. Mus. Lyon, iv. p. 127, pl. xiii. figs. 19–19 c (1887).

*Lagomys (Lagopsis) verus*, Schlosser, Pal. Oestr.-Ung. viii. p. 86 (1890); Depéret (?), Arch. Mus. Lyon, v. p. 57 (1892).

Under the name of *Lagodus Fontannesi*, Depéret described a fragment of an upper jaw, from the Middle Miocene of La Grive-Saint-Alban (Isère), as related to *Titanomys visenoriensis*, H. v. Meyer; but, in addition to its larger size, he distinguished it by other more important characters.

Schlosser has supposed, without assigning reasons, that *Lagodus Fontannesi*, Dep., is synonymous with *Lagomys (Lagopsis) verus*, Hens. (= *Lagomys awingensis*, H. v. Mey.), and Depéret, in his second publication on the Fauna of La Grive, is disposed to accept Schlosser's views. It may be asked at once, what then becomes of the left palate, figured and described by Depéret in his first memoir\*, where he considers it, rightly in my opinion, to belong to the *Lagomys verus*. As this question will be discussed under the head of *Lagopsis verus*, when it will be shown that Depéret's original view in distinguishing between "*Lagodus Fontannesi*" and *Lagomys verus* is the correct one, we have for the present only to deal with Depéret's first memoir, in which "*Lagodus Fontannesi*" is described, and where he asserts that it is distinct as a genus from *Titanomys visenoriensis* of the Lower Miocene.

For this Depéret gives two reasons. In the first line he maintains that his *Lagodus* preserves in its adult dentition part of the characters of the deciduous dentition of *Titanomys visenoriensis*, meaning that in the latter the milk-teeth alone are rooted, while in the former the permanent cheek-teeth are rooted as well. I have already disposed of this supposed difference, by showing that the permanent teeth of *Titanomys visenoriensis* are likewise rooted.

Depéret's second reason is given in the following words:—"Le *Lagodus Fontannesi* se distingue d'ailleurs facilement du *Titanomys visenoriensis* . . . par quelques différences dans les dessins d'émail qui ornent la surface de la couronne" (*i. e.* of the upper molars). "D'après M. Filhol, le lobe postérieur des molaires supérieures du *Titanomys* d'Auvergne est orné d'un double pli en chevron entourant une pointe externe; dans le *Lagodus* de La Grive il y a trois plis en chevron concentriques et pas de pointe extérieure bien manifeste" †.

The enlarged figures of the triturating surface in the teeth of "*Lagodus Fontannesi*" and *Titanomys visenoriensis* do not help us, as they are sadly inaccurate. The artist who drew the former ‡ completely failed to understand the pattern; while in Filhol's enlarged drawings § the artist has not even made an attempt at accuracy, contenting himself with drawing the outlines of the teeth, and leaving out almost completely the details of the

\* Arch. Mus. Lyon, iv. p. 164, pl. xiii. fig. 17 (1887).

† *Op. cit.* p. 128.

‡ *Op. cit.* pl. xiii. fig. 19 b.

§ *Op. cit.* pl. iii. fig. 15.

crown's surface. In the figures which I give of the teeth of both forms\*, no essential difference is to be seen in the pattern. The disagreement in the description of the two writers finds its explanation in the somewhat loose way of describing the triturating surface, *i. e.* by the failure to distinguish between a dentine surface bordered by two enamel ridges which alternates with an enamel fold filled with cement, so that only the two enamel borders of the fold appear on the surface. As an outcome of this alternation we find, when proceeding from the inner side of the tooth to its outer side, the following succession in the middle line of the tooth: enamel ridge; dentine; enamel ridge; cement; enamel ridge; dentine; enamel ridge; cement; enamel tubercle of the outer side.

Apparently the two writers do not always apply the term "chevron" to the same thing. Filhol, speaking of the "deuxième élément" of the tooth, by which he means the part of the crown backward from the anterior lobe, his "premier élément," says: "Chez les *Titanomys*, on peut le considérer comme constitué par un chevron à sommet interne, dont les deux extrémités circonscrivent une pointe externe. Ce premier chevron est borné en dedans par un deuxième chevron dont le sommet correspond au bord interne de la dent. Ce mode de structure est surtout bien marqué sur la troisième molaire" †. This description, which is quite correct as far as it goes, applies equally well to the species of the Lower and to that of the Middle Miocene, as may be seen by a comparison of the figures (Pls. 36, 37, 39); by consulting the figures it may be further seen that what the author calls chevrons are the spaces of dentine bordered by enamel ridges, which spaces mark the position of enamel cusps before wear set in.

Depéret, in describing the same "troisième molaire," *i. e.* the posterior of the three premolars, of *Lagodus Fontannesii*, says:—"Cette couronne se compose de deux prismes d'émail étroitement accolés, un peu mieux distincts en dehors que du côté interne, qui est de forme arrondie. Le prisme antérieur [Filhol's premier élément] est composé d'un seul pli d'émail transverse; le prisme postérieur au contraire, à surface triturante coupée obliquement en arrière, présente deux plis d'émail en chevron à pointe interne, ce qui dessine sur la couronne trois petits croissants concentriques, si l'on compte la lamelle d'émail qui limite le bord interne de la couronne" ‡.

It is certainly not accurate to describe the single cylinder of which these upper teeth consist as composed of two enamel prisms "étroitement accolés." Apart from this, Depéret's description, like Filhol's, applies to both *Lagodus Fontannesii* and *Titanomys visenoriensis*. By "deux plis d'émail en chevron à pointe interne," the author evidently has in view, firstly, the larger, internal, of the two enamel folds; secondly, the crescent-shaped cusp (6) external to it, which by the effect of wear presents a dentinal surface bordered by an outer and an inner enamel ridge. By counting, moreover, the enamel border of the internal side of the crown, Depéret arrives at the number of three "petits croissants concentriques," which on the following page are called "trois plis en chevron concentriques." Filhol leaves out of account the enamel fold by which his two chevrons are separated.

\* Pl. 36. figs. 18, 19; Pl. 37. fig. 11; Pl. 39. fig. 16 (*Titanomys visenoriensis*). Pl. 36. figs. 6-8, 12-15 (*T. Fontannesii*).

† *Op. cit.* p. 30.

‡ *Op. cit.* p. 127.

As a result of this minute analysis we find that there exists no essential difference in the tooth-pattern of the two supposed genera.

The roots of the *Titanomys*-molars have next to be described. I have elsewhere dealt incidentally with the conditions in *Titanomys (Lagodus)*\*. I was impressed by the fact that the chief points of wear are on the inner side in the upper, on the outer in the lower molars, and that these parts are the first to appear lengthened (vertically) in teeth in a condition intermediate between brachyodonty and hypselodonty, while the outer sides of upper, and the inner sides of lower molars remain, as it were, in a passive condition (for upper molars of *Titanomys* see Pl. 39, figs. 1, 2, 5, 13, 14, 19). It then appeared to me that the upper teeth of *Titanomys* showed the hypselodonty—which, as above demonstrated, is here in fact “accompanied by a gradual and essential change of the pattern of the crown”†—to extend gradually towards the outer side. In the description of the pattern of the *Protagus*-molars (pp. 452, 453) I have reconsidered my former view, and have been able to show that the obliteration of the original pattern is chiefly the consequence of an atrophy on the outer side; whereas the secondary pattern is brought about by a new addition, starting from the inner side and directed chiefly *inward*. It remains none the less true “that the vertical elevation of the crown, the first stage towards hypselodonty, always has its starting-point from the *inner* side of upper molars”‡. I added at the same time that “the inner root (of the upper molars) which ultimately will remain open, gradually extends outward, increasing in size, and receives a coating of enamel”§. It is against this latter assertion especially that the Rév. Père Hende has directed a criticism, couched in energetic terms ||. When he begins by saying that I had not demonstrated my assertion, he is perfectly right; but I had at the time no other intention than to assert, reserving full demonstration for a work on the Lagomorpha under preparation, as intimated on p. 208.

The Rév. Père's arguments are to the effect that the roots of teeth cannot be imagined to receive a coating of enamel, because brachyodonty “est un arrêt de développement, une fixation par cessation de mouvement, une détérioration du fût transformé en racine. Conséquemment la dent ne peut revenir à son mouvement initial.” In order to demonstrate that “*logiquement*” hypselodonty is more primitive (“plus ancien”) than brachyodonty, and that “*réellement* ces deux faits sont phylogéniquement indépendants,” the Rév. Père adduces the incisors of Rodentia. “D'autre part toutes les incisives des Rongeurs étant essentiellement hypselodontes et à toutes les époques, au point qu'elles emportent la définition de l'ordre, il faut admettre qu'elles n'ont pas varié, qu'elles ont un caractère commun fixé, et qu'à ce titre l'hypselodontisme est plus général que le brachyodontisme.”

It is not hypselodonty, as such, which is the more primitive condition, but the growing of a tooth by a persistent pulp. And, since hypselodont teeth continue to grow by persistent pulps during the greater part or the whole of the animal's life,

\* Proc. Zool. Soc. London, 1893, p. 206.

† *Id.*

‡ *Id.*

§ *L. c.*

|| ‘Mémoires concernant l'Hist. naturelle de l'Empire Chinois, par des Pères de la Compagnie de Jésus,’ t. iv, p. 75 (1898).

they may, in a sense, be termed primitive; but, as a matter of course, brachyodont and semihypselodont teeth, before they are perfectly developed, have the cavities at their bases open as well as hypselodont teeth; and when they are in this condition, their brachyodonty is not yet "un arrêt de développement." Ontogenetically and "logiquement," every hypselodont tooth passes through a brachyodont condition, the shaft only gradually increasing in length. Phylogenetically, brachyodonty is also more primitive than hypselodonty, as is known to all scientific morphologists who have a knowledge of palaeontology.

On Pl. 39, figs. 19 and 20, I have delineated side by side in the anterior view a posterior upper right premolar, p. 1, of *Titanomys Fontannesi*—the same specimen of which the upper view is figured on Pl. 36, fig. 8—and an upper right molar of a young *Pteromys*, in which the roots are not yet closed. Fig. 14 represents the anterior view of a right upper molar of *Tit. visenoviensis*, figured in upper view on Pl. 36, fig. 18. Now, if we are entitled to call roots, even though they be imperfectly developed, the three prolongations of the crown in *Pteromys* (fig. 20), I think we are justified in applying the same term to the evidently homologous parts in the figured teeth of *Titanomys* (cf. figs. 14 and 19, and figs. 1, 4, 5, and 13), and in repeating what I have said formerly\*, that the inner root of *Titanomys*, which ultimately will remain open, increases in size and receives a coating of enamel.

Even perfectly adult brachyodont teeth preserve at their extremity a minute opening for the passage of nerves and vessels, so that it may be left to individual judgment at which phase in the ontogeny or phylogeny of a tooth we may begin to use the term "root." Having no desire to juggle with words I would, be quite ready to desist using this term for the part of the tooth of *Titanomys* which is the homologue of the inner root of *Pteromys*; but thereby nothing would be altered. The question at issue is, whether or not a coating of enamel has extended to that part; and that this has been the case is shown plainly enough by the figures.

It is interesting to compare the tooth of *Tit. visenoviensis* (fig. 14) with those of *Tit. Fontannesi* (figs. 1, 13, 19). The small outer roots are perfectly closed in the former and more detached from the shaft than in the latter. The tooth of the former, as shown by the upper view (Pl. 36, fig. 18), is from an old individual; but in none of the numerous upper premolars or molars of *Tit. Fontannesi* have I met with closed outer roots. The coating of the enamel does not extend so far downward on the inner side in *Tit. visenoviensis* as in *Tit. Fontannesi*.

A further difference between the Lower and the Middle Miocene species is also characteristic. In the former (Pl. 39, fig. 14) the external part of the crown extends more outward than in *Tit. Fontannesi*, beyond the small roots; this character has been already noticed and explained in the description of the triturating surface, as due to the atrophy of the outer region being less advanced in *Tit. visenoviensis* than in the more recent species.

To proceed now to a closer examination of the small outer roots of the upper molars and premolars of *Titanomys*. In a passage, quoted above, p. 440, from II. v.

\* Proc. Zool. Soc. London, 1893, p. 206.

Meyer's posthumous description of the Rott skeleton, mention is made of upper molars of *Titanomys* found isolated, but only one small outer root is ascribed to them. I likewise find that the anterior milk-tooth, d. 3, of the Rott skeleton has one small outer root. Almost all the isolated teeth at my disposal, of both species, exhibit two symmetrical outer rootlets, which represent the lower free terminations of two prominent ridges on the upper outer region of the tooth, as in the figured deciduous tooth of *Lepus* Pl. 39. fig. 9, *b*), with the difference that in the latter the posterior part of the first appears higher, and the ridges, therefore, more lengthened than in *Titanomys*. The ridges, of which the outer rootlets are the lower terminations, are present also in molars and premolars of all Lagomorpha growing from persistent pulps. Figs. 7 and 8 (Pl. 39), representing germs of the first upper true molar of a rabbit, show them in side view (at the right side of the figures).

In a left upper jaw of *Titanomys Fontannesi* the roots of the cheek-teeth are described in the following manner by Depéret:—"La disposition des racines est aussi très particulière, et diffère de ce que l'on voit chez les Léporidés pour se rapprocher d'autres groupes de Rongeurs tels que les Spermophiles. Chacune des quatre dernières molaires porte trois racines, dont une interne grosse, ovulaire transversalement, et deux externes relativement très petites et arrondies. L'alvéole de la première molaire est petit et rond: il annonce une molaire uniradiulée et à couronne assez petite"\* . The figure of the specimen † shows the empty alveoli of p. 2 and m. 1, so that the mode of disposition of the roots in the jaw can be seen. Depéret's description is confirmed and supplemented by the figure which I give (Pl. 36. fig. 23) of a left maxillary from which the teeth have dropped out.

P. 2 of *Til. visenoviensis*, the anterior lobe of which we have seen to be somewhat reduced antero-externally (Pl. 36. fig. 19), as compared with the posterior teeth, has only one outer rootlet (Pl. 39. fig. 5*a*); in the place of the antero-external rootlet it displays a curious conformation, which gives at once a clue to that of the rootless molars of the other lagomorphous genera, and explains why the upper teeth described by H. v. Meyer have one outer rootlet only. There is no free antero-external radicle to this tooth; but, as seen in the side-view (fig. 5*a*, Pl. 39), a raised ridge runs along its antero-external side down to the bottom, where, as shown in the lower view of the tooth (fig. 5, *b*), it is confluent with the lower opening of the large inner root, the homologue of the widely open cavity in the genera (*Lagopsis*, *Prolagus*, *Lagomys*, *Lepus*) with rootless teeth.

To judge from its alveolus, p. 2 of *Titanomys Fontannesi* was more like p. 1 and the true molars, than p. 2 of *Til. visenoviensis*.

Fig. 2, Pl. 39. represents (*a*) the anterior, and (*b*) the outer view, of the last upper molar, right side, of *Til. Fontannesi*, the upper view of which has been figured in Pl. 36. fig. 6. Both outer rootlets are broken off, but they seem to have had a free

\* Charles Depéret, "Rech. sur la Succession des Faunes de Vert. Miocènes, etc.," Arch. Mus. Hist. Nat. Lyon, t. iv. p. 171 (1887).

† *Op. cit.* pl. xiii. fig. 19.

termination like the teeth anterior to them (figs. 1, 13, 19). The outer view (*b*) shows the whole of the outer side devoid of enamel.

The levelling effect of trituration tends to produce a more lophodont character of the crown. In an unworn condition, however, these teeth present a much more bunodont appearance, and it requires a very small effort of imagination to trace them back—conspicuously so the intermediate in the series, which are more typical—to a more brachyodont as well as bunodont form, in which the predominant feature is that the cusps, while the intervening enamel folds would appear as shallow valleys, are not yet filled with cement. We meet with such brachyodont types in the Eocene (classed as Creodonts and Lemuroids); more than any other, the Eocene "*Pelycodus helveticus* Rüt.," and *Plesiadapis*, both so-called Lemuroids, show teeth in close agreement with *Titanomys*. Let, *vice versú*, a brachyodont molar of the shape of "*Pelycodus helveticus*" (Pl. 36, fig. 3) or *Plesiadapis* (Pl. 36, fig. 2) become somewhat more hypselodont by the heightening of its shaft, and let the valleys between the cusps be filled with cement, and the result will be a *Titanomys*-tooth. This I had in view when, on a former occasion\*, I stated that the structure of the lagomorphine molar can be traced back to a "pelycodoid type."

## 2. Genus PROLAGUS.

*Lagomys*, G. Cuvier, Oss. foss. iv. pp. 21, 22 (1812), sec. ed. iv. pp. 200, 203 (1823); Rud. Wagner, Kastner's Arch. f. d. ges. Naturlehre, xv. pp. 14, 18 (1828); id. Oken's Isis, p. 1136 (1829); p. p. H. v. Meyer, Neues Jahrb. 1836, p. 58; p. p. id. Foss. Säugeth. etc. von Öeningen, p. 6 (1845); Waterhouse, Nat. Hist. Mammalia, ii. p. 32 (1848); Lartet, Not. Colline de Sansan, p. 21 (1851); p. p. Fraas, Württ. naturw. Jahresh. xxvi. p. 171 (1870); Lydekker, Cat. Foss. Mamm. Brit. Mus. i. pp. 256, 257 (1885), v. p. 325 (1887).

*Anoema*, König, Icones Foss. Sectiles, pl. x. fig. 126 (1825).

*Prolagus*, Pomel, Cat. méth. p. 43 (1853).

*Myolagus*, Hensel, Zeitschr. deutsch. geol. Ges. viii. p. 695 (1856).

*Archæomys*, Fraas, Württ. naturw. Jahresh. xviii. p. 130 (1862).

G. Cuvier was first to recognize that some fossil remains, which belong to the above genus, are those of a lagomorphine Rodent; he figured and described them from an ossiferous breccia of Corsica, and later from a breccia of Sardinia, considering them to be a species of *Lagomys*.

In 1825 König figured, in his 'Icones Foss. Sectiles,' a skeleton from Öeningen.

H. v. Meyer (1836) notes among the Mammals of Öeningen the genus *Lagomys*; the same, according to Murchison, had been previously suggested by Laurillard †. H. v. Meyer further supposes that König's *Anoema* might belong as well to the former genus.

From the Miocene of Sansan (Gers) and Venerque (Haute-Garonne), Lartet mentions a lagomorphine Rodent of the size of a large rat, which he proposes to unite with

\* P. Z. S. 1893, p. 208.

† R. J. Murchison, "On a Fossil Fox found at Öeningen, near Constance," Trans. Geol. Soc. London, iii. 2, p. 285 (1832).

*Lagomys*, on account of its having one superior molar less than the genus *Lepus*; adding, however, that the Sansan fossil has one inferior molar less than the existing *Lagomys*.

For this same Rodent from Sansan, Pomel proposed to create the sub-genus *Prolagus*, on the ground of its differing from *Lagomys* "par la dernière molaire inférieure, qui a trois prismes par réunion de la cinquième molaire à la quatrième. Du reste, la première est aussi triangulaire. On pourrait nommer l'espèce *Prolagus sansaniensis*." The hypothetical fusion of two molars, stated here as an undoubted fact, does not stand close investigation, any more than in the case of *Titanomys*. But to this I shall return in the sequel.

An excellent description of the remains of the lagomorphine Rodent from the ossiferous breccia of Sardinia is given by Hensel. He founds on them his new genus *Myolagus*, and points out that one of the two Lagomyidæ from Eningen, *Lagomys Meyeri*, v. Tschudi, is closely related to the Sardinian fossil, and therefore likewise to be placed in the genus *Myolagus*. (It is a pity that the perfectly well-characterized *Myolagus* has, for priority's sake, to give way to Pomel's "*Prolagus*," just as it is to be regretted that Pomel's amply-described *Lagodus* has to stand back before H. v. Meyer's imperfectly characterized *Titanomys*.) Hensel refers to Pomel's *Prolagus*\*, and rightly observes that the characters mentioned by the latter writer recall to mind the genus *Myolagus*; he considers them, however, to be insufficient for a decision. This was quite true at the time when Hensel wrote. It is incorrect to say, as has been done by H. v. Meyer †, that Hensel based his genus uniquely on the form and number of the lower cheek-teeth and the position of a foramen mentale. Hensel had laid great stress also on the pattern of the upper teeth ‡, a character which H. v. Meyer, as in the case of *Titanomys*, studiously avoids discussing.

A step backward is made by Fraas, when he figures and describes a well-preserved mandibular ramus from Steinheim under the name of *Archæomys steinheimensis*. He was set right by H. v. Meyer §, who referred the supposed *Archæomys* from Steinheim to "*Lagomys (Myolagus) Meyeri*, Tschudi," and in 1870 he atoned for his mistake by giving a full description of the Steinheim Rodent in question.

#### PROLAGUS ENINGENSIS.

*Anozma eningensis*, König, Icones Foss. Sect. pl. x. fig. 126 (1825).

*Lagomys eningensis*, p. p. H. v. Meyer, Neu. Jahrb. p. 58 (1836).

*Lagomys eningensis*, Waterhouse, Nat. Hist. Mammalia, ii. p. 32 (1848).

*Lagomys Meyeri*, v. Tschudi, in H. v. Meyer, Zur Fauna d. Vorwelt. Foss. Säugeth. etc. von Eningen, p. 6, pl. ii. figs. 2, 3, pl. iii. fig. 2 (1845); Lydekker, Cat. Foss. Mamm. Brit. Mus. i. p. 257 (1885).

*Lagomys sansaniensis*, Lartet, Not. Coll. de Sansan, p. 21 (1851).

*Prolagus sansaniensis*, Pomel, Cat. méth. p. 43 (1853).

\* *Op. cit.* p. 702.

‡ *Op. cit.* p. 895.

† Palæontogr. xvii. p. 228 (1870).

§ Neu. Jahrb. 1864, p. 197; 1865, p. 843.

- Myolagus Meyeri*, Hensel, Zeitschr. deutsch. geol. Ges. viii. p. 699 (1856); Fraas, Württ. naturw. Jahresh. xxvi. p. 171, pl. v. figs. 2-16 (1870); Schlosser, Palæontogr. xxxi. p. 28, pl. xii. fig. 44 (1884).  
*Archæomys steinheimensis*, Fraas, Württ. Naturw. Jahresh. xviii. p. 130, pl. ii. fig. 19 (1862).  
*Lagomys (Myolagus) Meyeri*, H. v. Meyer, Neu. Jahrb. p. 197 (1864), p. 843 (1865).  
*Lagomys verus*, p. p. Fraas, Württ. Naturw. Jahresh. xxvi. p. 171 (1870).  
*Prolagus Meyeri*, Depéret, Arch. Mus. Lyon, iv. p. 123, pl. xiii. figs. 18-18c (1887).  
*Myolagus sansaniensis*, Filhol, Ann. Scienc. géol. xxi. p. 46, pl. i. fig. 8 (1891).  
*Lagomys (Prolagus) Meyeri*, Depéret, Arch. Mus. Lyon, v. p. 55, pl. i. figs. 30, 31 (1892).

When publishing his first note on *Lagomys*-like Rodents from Ceningen (1836), H. v. Meyer was not aware that two rather different forms occur there; he comprises them both under the name of *Lagomys ceningensis*. Later on, in his Monograph of the fossil Vertebrata from Ceningen, he arbitrarily sets aside König's specific name for the smaller form, for which he adopts a manuscript name by v. Tschudi, *Lagomys Meyeri*, found on one of the labels, while he reserves the name *Lagomys ceningensis* for the larger form. As stated before, the same author identified the lagomorphine Rodent from Steinheim with the smaller form from Ceningen; and in the sequel equally those from several other Miocene deposits in Germany.

On the ground of Pomel's description of the Sansan species, Schlosser adds *Lagomys (Prolagus) sansaniensis*, Pomel, to the synonyms of *Myolagus Meyeri*; and likewise the *Lagomyidæ* from the Spitzberg in the Ries, near Nördlingen (Bavaria), referred to *Lagomys verus*, Hens., by Fraas (1870). Filhol has figured as *Myolagus sansaniensis* (E. Lartet) the type-specimen, a mandibular ramus, of Lartet's *Lagomys sansaniensis*, and is satisfied that "cette espèce, comme on le verra par l'examen de la figure grossie que nous en donnons, était très différente de toutes celles qui ont été décrites"\*. It is precisely this enlarged figure of the lower cheek-teeth which shows conclusively that the Sansan fossil is one and the same with the *Prolagus* species from Ceningen and Steinheim, as conjectured by Schlosser and confirmed by Depéret †, who has added La Grive-Saint-Alban (Isère) ‡, Mont-Ceindre, and Gray § to the localities of this widespread Middle Miocene species.

The following descriptions are based on specimens collected at La Grive-Saint-Alban by myself.

In the genus *Prolagus* the molars are no longer rooted, and, with the exception of the deciduous teeth, all the cheek-teeth grow from persistent pulps. It does not, however, follow that the triturating surface preserves throughout the animal's life the same pattern. This is the usually accepted belief ||; but although the proofs to the contrary

\* Ann. Sc. Géol. xxi. p. 47, pl. i. fig. 8 (1891).

† Arch. Mus. Lyon, v. p. 57 (1892).

‡ *Op. cit.* iv. p. 167 (1887), v. p. 56 (1894).

§ *Op. cit.* v. p. 57.

|| See, e. g., Giebel, in Bronn's 'Klassen und Ordnungen des Thierreichs,' vi. v. p. 152 (1875), where he treats of the Rodentia with laminated teeth ("Blätterzähne"), including the Lagomorpha. He says of them: "Die Kauflächen dieser Zähne ändern ihre Zeichnung durch Abnutzung nicht." He might have known better, at least as regards the Hares, from what Hilgendorf had said ten years before (Monatsber. K. Preuss. Akad. d. Wissensch. Berlin, 14 Dez. 1865, p. 673) respecting the upper grinding-teeth of young Hares.

are not in all cases so evident, and so surprising at the same time, as in the group under consideration, or as in Geomyidæ \*, or *Haplodontia* †, it is nevertheless a fact that neither in Rodents nor in Mammalia generally is the surface of the crown absolutely identical throughout its length; although in many of them we may speak of a *relative* constancy of pattern.

Hensel, in the description of the upper teeth of *Prolagus*, has overlooked this circumstance, and as a result has in one case wrongly interpreted the tooth-structure. This occurs in the description of "*Myolagus sardus*;" ‡ but, since Fraas has endorsed Hensel's error in his description of *Prolagus aeningensis* (Kön.) ("*Myolagus Meyeri*") §, which differs very little from the former, we shall have to deal with the argument in the present description as well. How little both Hensel and Fraas were aware of the change of pattern depending on the age of the animal is shown by the way in which, for convenience sake, they studied the tooth-crown. Hensel does not figure the natural surface of attrition, but gives transverse sections of it ||; while Fraas declares ¶ that it is more convenient to examine the teeth from the inferior side, meaning the open alveolar end of the shaft!

Fig. 21, Pl. 36, represents the four upper grinding-teeth of *Prolagus aeningensis* in a rather worn condition. Both the upper true molars, the fourth and fifth in the series, those teeth which in *Titanomys* exhibit a beginning of reduction on the postero-external side, have undergone in *Prolagus aeningensis* a considerable change as compared with the same teeth in the former genus. Of the two more or less crescentic enamel folds of *Titanomys*, only one, apparently the inner, persists, in the form of a very small enamel islet in the posterior part of the triturating surface (*b*). The notch of the internal side (*a*) has been transformed into a transverse enamel fold, which, as we shall find to be likewise the case in *Lagomys* and *Lepus*, approaches the outer side of the tooth. The enamel lining of the outer side, partially interrupted in the postero-external corner of m. 2 of *Titanomys*, is almost entirely missing in the external border of both the molars of *Prolagus* (and of its posterior premolar as well). In other words, the outer parts of the crown, those which are the least affected by trituration, have degenerated in consequence of disuse; and we might be inclined to assume that compensation has been effected by the transverse fold penetrating towards the outer part. But this is not, to all appearance, the exact explanation of the phenomenon. The triturating surface in the tooth of the young animal—in the part of the shaft which is the earliest formed—is more square than in the adult; in the latter, it presents the well-known narrow transverse shape of the lagomorphine upper molar. If we remove one of these teeth from its socket and examine it from the anterior or posterior side, it can be seen that,

\* C. Hart Merriam, 'Monographic Revision of the Pocket Gophers. Family Geomyidæ' (North American Fauna, no. 8), pl. 16 (1895).

† Proc. Zool. Soc. London, p. 706 (1897).

‡ Zeitschr. deutsch. geol. Ges. viii, pp. 690, 691 (1856).

§ Württ. naturw. Jahresh., xxvi, pp. 174, 175 (1870).

|| "Die Backenzähne sind stets senkrecht zu ihrer Axe angeschliffen worden, daher sind die Abbildungen eigentlich eine Aneinanderreihung der einzelnen Querschnitte" (*l. c.* p. 703).

¶ *Op. cit.* p. 173.

while its outer border maintains throughout its height almost a vertical direction, or is even concave, the inner part of the tooth slopes down medially, from below to above (taking into account its natural position in the maxillary). The tooth, therefore, as it continues to grow, extends persistently in a transverse direction; but this growth takes place chiefly, if not exclusively, towards the internal side; so that the transformation of the internal notch of the *Titanomys*-tooth into the transverse fold of the true molars of *Prolagus* is not the result of its extension outward but inward. In other words, new formation takes place in that part of the tooth where there is increased work, while the outer part—that which is scarcely or not at all affected by trituration—not only remains stationary, but even becomes atrophic.

On the other hand, since in the more specialized forms, beginning with *Prolagus sardus* (Pl. 36. fig. 24), the transverse enamel fold reaches almost the outer side in the true molars, it is very possible, and even likely, that secondarily a slight extension *outward* of this transverse fold takes place; although the outer border of the tooth is nearly functionless, its condition, almost devoid of enamel, would nevertheless effect a too rapid wear of the dentine if some compensation were not ensured.

The posterior of the three premolars, p. 1, situated between the first molar and the second premolar, is intermediate in shape as in position. Both the crescentic enamel folds of *Titanomys* are preserved in this tooth in the shape of central enamel islets, a much larger internal one (*b*), with an elongate anterior horn, and a smaller outer one (*c*) (fig. 21). The transverse fold (*a*) which opens on the inner side is much shorter than in the molars; it is scarcely more than an elongate notch. To put it otherwise, as compared with the molars, p. 1 presents less *reduction* in its external part, and less new formation in regard to the transverse fold starting from the inner side. Exactly the inverse is apparent when we compare p. 1 with the tooth in front of it.

This latter (p. 2) has triangular contours, with the apex internally, a shorter, slightly convex anterior, and a longer posterior side; as a consequence, its outer border runs obliquely. In its pattern, this premolar strongly resembles the *Titanomys*-teeth; instead of a transverse enamel fold we find in it a short notch (*a*) on the inner side, as in *Titanomys*; while almost the whole of the crown-surface is occupied by the two crescentic enamel folds (*b* and *c*), with an indication of a minute third one—equally marked in *Titanomys*—on the antero-external corner. The latter is more distinct in younger specimens of *Prolagus awningensis* (Pl. 36. fig. 10, p. 2). The enamel folds alternate with crescent-shaped, pointed cusps.

On comparison of p. 2 with p. 1 it becomes at once clear that the main difference between the two consists in the circumstance that the crescentic enamel folds in the former have become reduced to the condition of enamel islets, their communication with the antero-external margin of the tooth having ceased. When describing p. 1 of *Prolagus sardus*, in which, as a comparison of our figures shows, this tooth (fig. 24, p. 1) is almost identical with its homologue in *P. awningensis*, Hensel labours under a strange misconception. He says:—“Das Merkwürdigste aber an dem Zahn sind zwei isolierte Schmelzcyliner. Sie befinden sich in dem äusseren und hinteren Viertel des Zahnes.”\*

\* *Op. cit.*, p. 690.

After describing these enamel cylinders accurately, he continues:—"Der Inhalt dieser beiden kleinen Cylinder ist ganz gewiss Zahnbein, obgleich eine mikroskopische Untersuchung nicht angestellt werden konnte. Man sieht aber an dem Wurzelende des Zahnes die beiden Cylinder, sowie den ganzen Zahncylinder, hohl, daher sie auch wie dieser sich später wohl mit Zahnbein füllen werden. Wir haben hier ein Beispiel einer Zahnbildung, die bisher noch nicht beobachtet wurde. Denn hier ist nicht eine Vereinigung einzelner Cylinder zu einem Ganzen wie bei den sogenannten zusammengesetzten Zähnen, sondern eine Einschachtelung "[inclusion]" zweier einzelner Zähnchen in einen grossen."\*

It seems strange that so accurate an observer should not have perceived at once that the islets ("isolierte Schmelzcyliuder") of p. 1 are the homologues of the two enamel folds which, on the preceding page, he had described in the anterior tooth (p. 2); and that an enamel fold whose central part dips vertically, and deeper in the shaft of the tooth than the peripheral, generally becomes by attrition reduced to a central islet. This is a phenomenon of the most common occurrence in teeth of all Mammalian orders. Hensel's misconception is intelligible only from his apparently not being aware that teeth growing from a persistent pulp, like the brachyodont teeth, though only to a certain extent, are liable to changes in the pattern of their triturating surface.

As a matter of course the enamel islets of p. 1 are filled with cement, as are the enamel folds of the anterior tooth. The argument adduced by Hensel goes for nothing, as not only the dentine, but also the cement is always missing in the root-ends of these teeth, both substances being not yet developed in these younger stages.

As mentioned on a preceding page, Fraas has endorsed Hensel's statements, when describing the similar-fashioned p. 1 of *P. unguensis*. He is, besides, of opinion that the deciduous teeth furnish the explanation of the conformation of p. 1:—"Die Betrachtung der Milchzähne wirft auf diese in der That von allen bekannten Zähnen abweichende Bildungsweise ein Licht." † A supposed extraordinary phenomenon calls for an extraordinary explanation, and this he gives when describing the deciduous teeth ‡. He means to say that there is a connection between the roots and the enamel folds, inasmuch as the cylindrical roots are included in (or by) the tube composing the whole tooth, as it were, nested in it ("eingeschachtelt")—just as we should speak of willow-boxes nested one into the other—the folds appearing on the surface of attrition, according to this theory, being but the upper ends of the cylindrical roots! The only thing which the author thinks remarkable is the fact that the central folds, which are in connection with the roots, are present as well in the permanent teeth which are devoid of roots. At the bottom of this singular theory lies, first, the author's initial statement, to the

\* *Op. cit.* p. 691.

† *Op. cit.* p. 175.

‡ *Op. cit.* pp. 177, 178. "Die Falten . . . die auf der Kaufläche des Zahns zu Tage treten sind nichts anderes, als die oberen Enden der in die Zahnbüchse eingeschachtelten Wurzelcylinder. Sehen wir somit an den Milchbackenzähnen auf deren Oberfläche Schmelzfalten zu Tage treten, wo die Wurzeln sich vereinigen, so begreift sich dieser Faltenschlag leicht. Das Eigenthümliche ist nur, dass sich die inneren, mit den Wurzeln zusammenhängenden Falten auch an den permanenten Zähnen zeigen, die über ihre ganze Dauer wurzellos sind. Es ist diess, so zu sagen, die Uebertragung eines Jugendzustandes auf das Alter. . . ." etc.

effect that the roots of the deciduous teeth of *Prolagus* have a coating of enamel: "sie bestehen genau aus derselben Schmelzmasse, wie die Zahnbüchse selbst, die das Zahnbein umgiebt" \*; and secondly the fact that in some instances he seems to have mistaken for roots what in reality are the tube-like lower terminations of the enamel folds.

In the first tooth of the upper series (p. 3, Pl. 36. fig. 21) the two enamel folds are also present; they penetrate into the surface of the crown from its anterior side and run in a longitudinal direction. The anterior border ("wall") of the triturating surface, already slightly shortened in p. 2, is still more shortened in p. 3, being reduced to a short longitudinal stump on the antero-internal corner.

From what has previously been stated, we are prepared to find, in different stages of attrition of these upper teeth, some difference in the pattern; this is, in fact, what takes place. The enamel islet of m. 2 has disappeared in old specimens; and such is the case in the specimen figured by Fraas †. The enamel islet of m. 1 varies in size according to age, being larger in younger specimens. The same holds good with regard to the two enamel islets of p. 1. We anticipated that in young stages of this tooth the enamel islets would have the shape of enamel folds opening freely on the margin of the tooth, as is the case in p. 2. This is, in fact, what happens in young specimens of the following species (*P. sardus*). Of *P. æningensis* I have no very young examples.

P. 2 varies little with age; the notch on the inner side is more distinct in comparatively young individuals, and there is shown in this stage (fig. 10) a third very small enamel fold in the postero-external corner of the tooth, which soon disappears by attrition.

*Deciduous upper teeth of P. æningensis.*—Fraas has figured the three deciduous upper cheek-teeth *in situ* ‡; he scarcely describes their pattern, contenting himself with the statement that the anterior one is well provided with folds ("faltenreich"), and that it presents much resemblance to the *second* of the permanent dentition §.

I have only detached upper deciduous teeth, five in number. Two of these are in the British Museum, under M5237, from my collections. The anterior milk-tooth (d. 3) is not represented among these five detached teeth; according to the figure of Fraas, and to what I know of the same tooth of *P. sardus*, it has triangular contours; while the detached teeth at my disposal are squarish oblong, almost tetragonous, their transverse diameter slightly exceeding the longitudinal. They show (Pl. 36. fig. 29) an internal notch and two enamel folds, the latter opening freely on the outer side. The internal of the two folds (*b*) has the form of a crescent and is the larger of the two. The roots are three in number; the outer two very minute, the inner single one considerably larger; the former run parallel with each other, but not with the odd inner root, which strongly diverges from them inward, while they diverge outward (Pl. 39. figs. 21, 22).

#### PROLAGUS SARDUS.

*Lagomys sardus fossilis*, Rud. Wagner, Oken's Isis, p. 1136 (1829).

*Lagomys fossilis*, Id. op. cit. p. 1139.

\* In this there is some truth; see above, pp. 446, 447.

† *Op. cit.* pl. ii. fig. 6.

‡ *Op. cit.* pl. ii. fig. 14.

§ P. 177.

- Lagomys corsicanus*, Rud. Wagner, op. cit. p. 1139; Giebel, Fauna d. Vorwelt, i. p. 99 (1847); Gervais, Zool. et Pal. franç., first ed. p. 32 (1848), second ed. p. 50 (1859); Lortet, Arch. Mus. Lyon, i. p. 53, pl. 8 (1873).
- Myolagus sardus*, Hensel, Zeitschr. deutsch. geol. Ges. viii. p. 695, pl. xvi. figs. 7, 8, 11 (1856); Forsyth Major, Atti Soc. Ital. Milano, xv. p. 390 (1873); id. Kosmos, vii. (vol. xiii.) pp. 6, 7 (1883).
- Lagomys (Myolagus) sardus*, Schlosser, Palæontogr. xxxi. p. 29 (1884).
- Lagomys sardus*, Lydekker, Cat. Foss. Mamm. Brit. Mus. i. p. 256 (1885), v. p. 325 (1887); Schlosser, Pal. Oestr.-Ung. viii. p. 86 (1890).

This Pleistocene species, which is somewhat larger than its Middle Miocene forerunner, closely resembles the latter in its upper molars, as the comparison of the figure shows. However, the specialization of the true molars has progressed, for in the teeth of the adult no trace remains of the two crescentic enamel folds (Pl. 36, fig. 24). P. 1 agrees in the two species. P. 2 is scarcely different in either; the enamel folds in p. 2 of the adult *Prolagus sardus* are slightly reduced in size, and the larger inner fold (*b*) is, in old specimens, sometimes shut out from the outer border by intervening dentine (fig. 24, p. 2). P. 3 has its anterior "wall" somewhat more developed than in *Prolagus aenigensis*.

Of this species I have collected a good number of young specimens. The examination of younger stages of the teeth is of considerable interest, as they recall, more than the adult teeth, the primitive features of the *Titanomys*-type.

Firstly as to p. 2. This tooth, being the most conservative, shows, as might have been anticipated, the least change from young to old. The diminutive postero-external enamel fold, however, which we met with in a moderately young specimen of *P. aenigensis*, is visible only in very young individuals of *Prolagus sardus*.

P. 1, as has been intimated above, exhibits in the young stage a close approach to p. 2; the two enamel folds are not yet reduced to the shape of islets, but open freely on the outer side of the tooth (Pl. 36, fig. 11); the only appreciable difference, apart from its square outline, consisting in this, that the crescentic cusp (*g*) which divides the two enamel folds has its anterior horn less produced outward, so that the folds unite in a common delta on the outer side. The next stage of the still young p. 1 (fig. 16) is the pattern we met with in old p. 2; the small external enamel fold (*c*) alone opens on the outer side, while the larger internal fold has been reduced to the shape of a crescentic islet (*b*). The third stage is that of the adult, the external fold likewise having become an islet (fig. 24).

It might be expected that very old specimens of p. 1 would show the complete disappearance of the islets, as is the case in the true molars; this condition I have never found in *Prolagus sardus*, although I have had the opportunity of examining more than a hundred upper jaws. But it occurs in a Pliocene form of Continental France (Roussillon), of which more will be said hereafter.

In the youngest stages of the anterior true molar (fig. 4, in jaws which still preserve the deciduous dentition, remains of the two enamel folds are still visible; they are very imperfectly divided by the last trace of the once powerful intermediate cusp. In a slightly more advanced stage (Pl. 36, fig. 16 (m. 1), one or two diminutive enamel islets, situated postero-externally to the internal end of the transverse fold, are the last vestiges

of the enamel folds of m. 1. In rare cases, very young m. 2 likewise show at the same place a diminutive circular enamel islet, fig. 16 (m. 2).

The deciduous teeth (Pl. 36, fig. 4) are scarcely different from those of the preceding species; but in these teeth also the crescentic cusp "6" does not completely divide the two enamel folds. D. 3 is triangular; d. 2 in younger stages somewhat approaches to a triangular contour.

#### PROLAGUS LOXODUS (Gerv.).

*Lepus* sp., Gervais, Zool. et Pal. Fr. 1<sup>e</sup> éd. i. p. 32 (1848).

*Lepus loxodus*, Gervais, ib. ii. explic. pl. xxii., pl. xxii. fig. 9 (1848-52).

*Lagomys loxodus*, Gervais, Zool. et Pal. Fr. 2<sup>e</sup> éd. p. 50 (1859); id. Zool. et Pal. gén. p. 148 (1867-69).

? *Lagomys (Prolagus) corsicanus*, Depéret, Mém. Soc. Géol. France, i. p. 56 (1890), iii. p. 122, pl. xii. figs. 1, 1 a (1892).

? *Myolagus elsanus*, Forsyth Major, Atti Soc. Tosc. Sc. Nat. i. p. 229, 238 (1875), &c. (*vide infra*).

Gervais' *Lagomys loxodus* has been a stumbling-block for fifty years, owing, as I think, to the circumstance that the pattern of the four posterior right upper cheek-teeth preserved had not been grasped and was incorrectly represented. An inspection of the original specimen would at once settle the question; but since I am not acquainted with the original, I must deal, as best I can, with the published figure and Gervais' incomplete description.

The figure is four times natural size. Gervais' description runs as follows:—"Diffère des *Lagomys* actuels et diluviens par la forme ovulaire et sublosangique des doubles lobes de ses seconde à quatrième molaires supérieures; la molaire antérieure est en même temps plus forte, et elle a ses replis plus compliqués;—taille sensiblement inférieure à celle du Lapin de Garenne"\*. It was found in the town of Montpellier, in the fluviatile Pliocene marls †. At the same locality, under the Palais de Justice, was found the *Semnopithecus mouspessulanus*; and this circumstance is of importance, as proving that these fossils belong to the older of the two faunas, mixed together under the designation Montpellier. *Semnopithecus* occurs also in the Lower Pliocene of Casino (Tuscany).

The reason for which Gervais considered the teeth to be the first, second, third, and fourth is obvious; the last in the series is equal in shape to the penultimate, while in *Lagomys* the last molar has a postero-internal appendage. I believe them to be the second, third, fourth, and fifth (p. 2, p. 1, m. 1, m. 2) of a species of *Prolagus*, because the anterior tooth has the characteristic triangular outline of p. 2 of *Prolagus*, with the apex turned inward (*cf.* pl. 36, figs. 10, 21, 24, p. 2). In further agreement with *Prolagus*, Gervais' figure of this tooth exhibits on the outer side two enamel loops; on the inner, one. The more minute features of this tooth, as well as of those following behind, were not recognized, and therefore the latter have been represented in the manner in which lagomorphous upper teeth generally were and still are, founded on the belief that they are composed of two distinct lamellæ closely connected.

In my opinion there is not the slightest doubt left that we have to do with a species

\* Zool. et Pal. Fr. 2<sup>e</sup> éd. p. 50.

† *L. c.*

of *Prolagus*, and I feel sure that a close examination of the fossil, if it still exists in the Museum of Montpellier or elsewhere, will confirm my view.

It remains to enquire whether there is some reason for identifying it with one of the species of *Prolagus* found in deposits contemporaneous, or approximately so, with the strata of Montpellier in question. Of these there are two: (1) *Prolagus (Myolagus) elsanus*, which I have mentioned from the lignites of Casino, in the Val d'Elsa, Tuscany; and (2) "*Lagomys (Prolagus) corsicanus*," described under this name from Roussillon by Depéret\*. The little I have to say of the former will be stated in a separate paragraph hereafter.

As to the latter, Depéret declares that it agrees in size as well as in all other characters with the *Prolagus* from Corsica and Sardinia, and he therefore describes it under the above name. This proceeding is as it should be; so long as no differences are traceable between both there is no reason for two specific names. But, so far as my own experience goes, the circumstance of a mammalian species surviving unaltered from the Lower Pliocene to the present era (I have found calcified remains of *Prolagus sardus*, var. *corsicanus*, in an "abri sous roche" of the Neolithic period in Corsica) would be quite unique, and it is *a priori* highly improbable, even taking into consideration that insular species may become, up to a certain extent, conservative in their character. I therefore incline towards the belief that hereafter characters distinguishing the Roussillon from the island form will be shown to exist.

The presence of a third lower molar, supposed by Depéret to appear occasionally in the Roussillon fossil, would be such a distinctive character, since it has never been observed in the Pleistocene species; but I give further on (pp. 482, 483) what I hold to be the real explanation of the fact noticed by Depéret, viz. that the supposed m. 3 in certain jaws from Roussillon is simply a portion of m. 2, which has been accidentally detached.

Another character noticed by Depéret in the Roussillon species deserves mention here. In the specimen from this locality first described † it was stated that the three posterior upper cheek-teeth are similar to each other, being "construites sur le type ordinaire des Léporidés." In the third volume of the 'Mémoires' a second specimen is described ‡; in this the "première arrière-molaire" (p. 1) differs from the same tooth of the first specimen by "exhibiting on the surface of its posterior lobe a double chevron-shaped enamel fold, recalling the molars of *Titanomys*. These folds must disappear rather rapidly by effect of trituration, thus explaining their absence on the specimen previously figured, which apparently was more adult." Depéret adds that these chevron-like folds exist equally in the corresponding tooth in the specimens of "*Lagomys corsicanus*" from Bastia (Corsica), although this character is not represented in the figure of the latter published by Lortet §, and he concludes that the above is a complete confirmation

\* Ch. Depéret, "Animaux pliocènes du Roussillon," Mém. Soc. Géol. France, i. p. 56, pl. iv. figs. 27-35 (1890); iii. p. 122, pl. xii. figs. 1, 1 a (1892).

† Mém. Soc. Géol. France, i. p. 57 (1890).

‡ *Op. cit.* iii. p. 122, pl. xii. figs. 1, 1 a (1892).

§ Arch. Mus. Lyon, i. pl. viii.

of the identity of the Corsican and Sardinian fossil with the Pliocene animal from Roussillon.

I venture to suggest that the inverse conclusion may be drawn from these statements. The character in question has been figured and exhaustively described in the preceding pages. Of *Prolagus sardus*, I have represented on Pl. 36. three stages. Fig. 11 shows p. 1 of a young individual in which the two enamel foldings (*b* and *c*) are large and confluent on the outer margin. In fig. 24 (p. 1 from an adult and rather old individual), they are seen to be separated from each other and reduced to the shape of central enamel islets. Fig. 16 exhibits an intermediate condition (see p. 456). If these chevrons are not represented in Lortet's figure quoted by Depéret, this is due to an inadvertence of the artist; for an examination of the figure quoted shows that the artist had seen something of the kind, but omitted to represent it accurately. In the vast number of maxillaries of *Prolagus sardus* from Bastia and various Sardinian localities which have passed through my hands, I have never missed the presence in p. 1 of the two enamel folds; but it is possible that they may disappear in very old individuals. The fact that, of the only two specimens from Roussillon examined, this character was absent in one, proves in my opinion that the Roussillon species, although geologically older, has exceeded the island species in the transformation of the cheek-teeth, thus representing the last stage of *Prolagus*; *i. e.* that which approaches closest to the condition shown by p. 1 of *Lagopsis* and *Lagomys*.

The peculiarity which I am about to mention in the anterior lower premolar of the *Prolagus* from Casino is not recorded by Depéret in the lower p. 2 from Roussillon; but it would be worth while to re-examine this tooth in the specimens from the latter place; for the two *Prolagi* from Roussillon and Casino may be identical, if we judge from the association of other identical species in the two localities. The same may be said of the fossils from Roussillon and Montpellier; but the information concerning the *Prolagus* from the latter locality at present at our disposal is insufficient for close comparison with other fossil forms.

#### PROLAGUS ELSANUS, Maj.

*Myolagus elsanus*, Forsyth Major, Atti Soc. Tosc. Sc. Nat. i. pp. 229, 238 (1875); *id.* in L. Rüttimeyer, Ueber Pliocen und Eisperiode auf beiden Seiten der Alpen, p. 15 (1876); *id.* Atti Soc. Tosc. Sc. Nat. Proc. Verb. p. xc, 11 Maggio 1879.

A few fragmentary mandibular rami from the Lower Pliocene lignites of Casino, Val d'Elsa (Tuscany), preserved in the Pisa Paleontological Museum, have been long ago noticed by me, and I have on various occasions stated that, by the conformation of their lower anterior premolar (p. 2), their reference to Hensel's genus *Myolagus* (*Prolagus*) is beyond doubt. As at the time no species of *Prolagus* had been recorded from the Lower Pliocene, I felt justified in assigning a new specific name to the Casino fossil.

Of some importance, not only as distinctive for the species, is the following character not previously recorded by me, but of which I was perfectly aware at the time, for it is shown in two sketches which I made of the lower anterior premolar, right and left, presumably of the same specimen. At the postero-internal margin of this p. 2 is a

narrow enamel fold—more distinct in the left-hand tooth—corresponding to a shallower and wider fold in *Titanomys*, which forms the anterior boundary of a minute terminal cusp, marked “*t*” in the figures (*Titanomys*, Pl. 37. figs. 2, 3, 7, 25). More about the significance and the homologies of this terminal cusp will be said in the chapter treating of the lower cheek-teeth. I mention it here, since in no other species of *Prolagus* have I met with it in p. 2, and it may therefore be characteristic of *Prolagus elsanus*.

The only teeth known from Casino are mandibular; and as those from Montpellier are maxillary, no direct comparison can be made between them. Both deposits are contemporaneous, and bear other species in common; wherefore there are good grounds for assuming the specific identity of the remains of *Prolagus* from the Italian with those of the French deposit. If this can be satisfactorily shown in the sequel, Gervais' specific name will have to replace mine on grounds of priority.

### 3. Genus LAGOPSIS, Schloss.

#### LAGOPSIS VERUS (Hensel).

*Lagomys æningensis*, H. v. Meyer, Neu. Jahrb. 1836, p. 58, p. p.; id. Foss. Säugethiere &c. von Öeningen, p. 6, pl. iii. fig. 1 (1845); Biedermann, Petrefacten aus d. Umgeg. v. Winterthur: II. Die Braunkohlen von Elgg, p. 13, pl. iii. figs. 1, 2, 3 (1863); Lydekker, Cat. Foss. Mamm. Brit. Mus. i. p. 256 (Specim. Br. Mus. nos. 42815, 42816 (?), 42820 (?)) (1885).

*Lagomys verus*, Hensel, Zeitschr. deutsch. geol. Ges. viii. p. 688, pl. xvi. figs. 12, 13 (1856); Depéret, Arch. Mus. Lyon, iv. p. 161, pl. xiii. figs. 16, 17 (1887).

*Titanomys æningensis*, H. v. Meyer, Palæontogr. xvii. p. 228 (1870), p. p.

*Lagomys (Lagopsis) æningensis*, Schlosser, Palæontogr. xxxi. p. 31 (1884), p. p.

*Lagomys (Lagopsis) verus*, Schlosser, op. cit. p. 31, pl. xii. figs. 40, 46, 49 (1884); Depéret, Arch. Mus. Lyon, v. p. 57 (1892), p. p.

Hensel's type-specimen is a mandibular ramus, and will therefore be more fully discussed in a later chapter. He was impressed by its approaching much nearer the recent *Lagomys* than the remains of *Prolagus* (“*Myolagus*”) described in the same paper. “Ich nenne die Art *Lagomys verus*, weil sie sich durch die Zahl ihrer fünf Backenzähne, durch die Stellung des Foramen mentale und durch den ersten unteren Backenzahn, der nur aus einem Cylinder besteht, als ein ächter *Lagomys* ausweist” \*.

It is perfectly true that this fossil is closely related to *Lagomys*. However, Schlosser proposed to raise “*Lagomys æningensis*, H. v. Mey.,” and “*Lagomys verus*, Hens.,” to the rank of a genus, *Lagopsis*, a position with which I in general agree, while I disagree in part with the reasons assigned for it. There is no doubt that some of the larger Lagomyidæ of Öeningen, which were comprised by H. v. Meyer under the above name, are identical with Hensel's *Lagomys verus*; but with regard to other specimens this has not yet been demonstrated. We cannot therefore throughout regard “*Lagomys æningensis*, H. v. Mey.,” as synonymous with “*Lagomys verus*, Hens.,” as Schlosser has hesitatingly assumed in his ‘Næger des europ. Tertiärs’ (p. 32) and more positively asserted later †, followed by Lydekker ‡.

\* *Op. cit.*, pp. 688, 689.

† Beitr. Pal. Oestr.-Ung. viii. p. 86 (table) (1890).

‡ Cat. Foss. Mamm. Brit. Mus. i. p. 256 (1885).

Schlosser bases his new genus *Lagopsis* on the differences (from *Lagomys*) in the shape of the anterior lower premolar (p. 2), "und das, wie es scheint, häufige Fehlen des vierten Molaren," thereby meaning the lower m. 3. I agree with the first proposition; as to the latter, it will be shown later on that in all the specimens of *Lagomys verus*, in which m. 3 is missing, it has simply dropped out, for its alveolus is present.

The upper teeth of *Lagopsis*, which are here described for the first time, although more closely resembling *Lagomys* than *Prolagus*, present, however, characters which strengthen the conclusion based on the lower teeth, viz. the establishment of a separate genus. *Lagopsis* realizes the penultimate stage in the evolution of the cheek-teeth of Lagomyidæ, *Lagomys* the last.

The description of the upper cheek-teeth of *Lagopsis* may be appropriately preceded by that of *Lagomys*\*. The numerous existing species of *Lagomys* show a considerable constancy in the pattern of their cheek-teeth. Young individuals were not available to me. In the adult we find a further step away from the *Titanomys* type; not only the two true molars, but the posterior premolar (p. 1) likewise, have lost every trace of the crescentic enamel folds, so that p. 1 has become very similar to the true molars, all three showing the transverse fold proceeding far outward. P. 2 exhibits, in a very interesting manner, a reduction of the *Titanomys* type. There is no transverse fold, the original internal notch being maintained; of the two crescentic enamel folds (*b*) and (*c*) only the former, the internal, remains, and it bears on its outer side a strong cusp (*6*) and opens on the antero-external margin of the tooth. P. 3 shows a further reduction as compared with *Prolagus*. Of the internal notch only a feeble vestige is visible, and of the two typical enamel folds only the internal one, which runs obliquely from the middle of the anterior margin in a postero-external direction.

Depéret has figured from La Grive a left palate devoid of teeth, but exhibiting very distinctly the alveoli of the five cheek-teeth; he assigns this fossil, quite rightly in my opinion, to *Lagopsis verus* †.

Among the fossils collected by myself at La Grive are two rooted upper cheek-teeth (Brit. Mus., G. D., No. 5264), which in size agree with the lower teeth of *Lagopsis verus* from the same deposit. *Lagopsis* being the one Tertiary genus which, by the form of its lower teeth, comes nearest to *Lagomys*, it could be anticipated that the upper teeth of the fossil would likewise show a near approach to the recent genus, and this is, in fact, the case. Additional evidence is furnished by a specimen from Ceningen, to be described later on.

One of the isolated teeth just mentioned, from La Grive (Pl. 36, fig. 31), exhibits the same somewhat triangular outline—the apex being turned outward—and about the same characteristic enamel folding (*b*) as the upper p. 2 of *Lagomys*. In the p. 2 of *Lagomys* the outer enamel border of the crescent (*b*) is raised into a strong triangular cusp, with its convexity turned inward; in the fossil tooth the inner border of the crescent is raised in the same manner. From p. 2 of *Prolagus æningensis* (Kön.) (Pl. 36, fig. 21) the tooth

\* Enlarged horizontal sections of the upper cheek-teeth of *Lagomys alpinus* and *L. nepalensis* are given by Hensel. *op. cit.* pl. xvi. figs. 1 & 5.

† *Op. cit.* p. 164, pl. xiii. fig. 17.

figured in fig. 31 can at once be distinguished; the former is much smaller, has a triangular outline with the apex turned inward, and a smaller enamel crescent (*c*), smaller than, and external to (*b*). The upper teeth of *Titanomys Fontannesii*, which in size come nearer to the original of fig. 31, though slightly smaller, are provided with roots, and they present other differences which have already been described. From its resemblance to *Lagomys* this tooth (fig. 31) can therefore with certainty be determined as belonging to *Lagopsis verus*. The second of the isolated teeth before mentioned, from La Grive (Pl. 36. fig. 32), agrees in size with the first; and for this reason alone *Prolagus aeningensis* can be excluded. It is either p. 1 or m. 1, if we judge from its agreement with the corresponding teeth in *Lagomys*.

In the Palæontological Collection of the British Museum (No. 42815) is preserved a slab from Eningen, showing the skeleton, "in a much crushed and imperfect condition," of a lagomyid Rodent, which Lydekker has determined as *Lagomys aeningensis*, H. v. Mey., because it agrees very closely in size with that figured by H. v. Meyer on pl. iii. fig. 1 of his 'Fossile Säugethiere von Eningen'\*. On examination of this specimen (No. 42815) several cheek-teeth are seen in a fragment of the cranium, presenting their inner sides, the bone being here broken away. The lower parts of these teeth, in the neighbourhood of the crowns, as well as these, were hidden in the matrix when the specimen came into my hands. By carefully removing the matrix, the triturating surfaces of the three anterior cheek-teeth (the three premolars) were laid bare, and it became at once apparent that this fossil is a *Lagopsis*.

It was too late to have the teeth figured in the present memoir, so that I must content myself with their description. I give figures of them elsewhere †. The posterior of the three teeth (p. 1) exhibits the pattern, which is shown by the homonymous premolar of *Lagomys* and by the latter's two true molars. On the outer side of this tooth is a shallow and open groove, which, so far as can be made out under a strong lens, has no enamel border. From the middle of the inner margin a lozenge-shaped narrow enamel fold (*a* of my figures in Pl. 36) runs transversely across two-thirds of the breadth of the triturating surface towards the outer side; the posterior enamel border of this fold is raised into a strong crest, running parallel with the anterior enamel border of the tooth, both presenting a slight convexity turned anteriorly. The enamel fold is filled with cement in its outer narrower portion, its wider internal opening being devoid of this substance.

The pattern of the middle premolar, p. 2, proves that the isolated tooth from La Grive (Pl. 36. fig. 31) has been rightly determined as p. 2. As in the latter and in *Lagomys*, there is only a comparatively shallow internal enamel fold (*a*) present in the tooth from Eningen, the greater part of the triturating surface being occupied by the enamel crescent (*b*) before described in the tooth from La Grive. Outside the crescent (*b*) appears a small enamel ring filled, like the latter, with cement; this ring is doubtless the vanishing homologue of the outer enamel crescent (*c*) of *Titanomys* and *Prolagus*, described in the preceding pages and figured in Pl. 36. In the La Grive specimen (fig. 31) there is

\* Catalogue of the Fossil Mammalia in the British Museum (Natural History), i. p. 256, No. 42815 (1885).

† Geol. Mag., dec. iv. vol. vi. p. 370, figs. 1 & 2 (1899).

a mere vestige of some such element in the same place, the tooth being presumably more worn than that in the Eningen specimen. As in the La Grive tooth, that from Eningen has both enamel margins of crescent (*b*) raised into triangular cusps, with the convexity turned inward.

The anterior premolar, p. 3, of the Eningen fossil is not dissimilar to the same tooth of *Prolagus aenigensis* (Kön.). Whereas in recent *Lagomys* the triturating surface of p. 3 exhibits only one enamel fold—starting from about the middle of the anterior margin and running backward obliquely, *i. e.* postero-externally—the same tooth in *Lagopsis* shows two enamel folds, as in *Prolagus aenigensis*, opening on the anterior margin, and thence running almost straight backward.

These differences from *Lagomys* strengthen, therefore, Schlosser's opinion, that the Miocene fossil is to be considered as a genus (*Lagopsis*) distinct from *Lagomys*. At the same time they present a further link in the gradual transformation of the tooth-pattern (*Titanomys*—*Prolagus*—*Lagopsis*—*Lagomys*—*Lepus*), which begins in the hindmost molar of Lagomyidae and, gradually proceeding forward, stops at p. 1 in *Lagopsis* and *Lagomys*, and at p. 2 in *Lepus*.

#### Genus LEPUS s. l.

It would seem more rational to treat of the Miocene *Palæolagus* before *Lepus*, since there are strong reasons for the assumption that the former is the ancestor of the latter. On practical grounds, however, I think it more advisable to give the description of *Lepus* first, because we can fully understand the dentition of *Palæolagus* only after having dealt with the dentition of the young of the existing genus; and because, on the other hand, the latter exhibits a further development of the modernization initiated by *Titanomys*.

Hensel, writing in 1856, stated that, contrary to the usual descriptions of authors, the upper molars of *Lepus* consist each of a single cylinder, which in the second, third, and fourth teeth is provided with a deep enamel fold, filled with cement and penetrating from the inner side\*. When contending that all the previous writers on the subject had incorrectly interpreted the conformation of the leporine molar, Hensel could hardly have guessed that 13 years later he might have made an almost similar complaint. We continually meet with descriptions and figures of lagomorphous animals in which the upper molars are represented as formed by two cylinders closely united or soldered together, presenting three transverse enamel ridges!

As compared with the *Lagomyidae*, by the presence of m. 3 in the maxillary, *Lepus* exhibits a more primitive condition. In the characters under consideration, however, *Lepus* is undoubtedly the extreme member of the series. While in *Lagomys* the posterior premolar (p. 1) has alone acquired the transverse fold of the true molars, in *Lepus* (Pl. 36, fig. 33) p. 2 has been transformed as well. P. 3 alone retains what we may fairly consider to be the ancestral enamel folds, as well as the ancestral internal notch. There is no anterior "wall"; wherefore the enamel folds open freely on the anterior side.

\* Zeitschr. deutsch. geol. Ges. p. 681 (1856).

In a skull of *L. nigricollis* from Ceylon (B. M. Z.D. No. 81.4.29.7) (Pl. 36. fig. 34) I find that the modernization has begun to invade p. 3 also; in the tooth of the right side the internal notch (*a*) has assumed the shape of a lengthened fold, stretching half-way across the crown and provided with plications as in the other molars.

M. 3 of *Lepus* is a small, vanishing cylindrical tooth; in rare cases, however, of *L. europæus* a transverse fold has been observed in this\*.

Now as to the condition of the teeth in the young of *Lepus*. Hilgendorf stated long ago † “that the upper cheek-teeth of young Hares are provided with a crescentic enamel tube, which forms a transition to the fossil *Myolagus*.” This is perfectly true, but it is not all.

In the Rabbit *Oryctolagus cuniculus*, the two posterior upper deciduous teeth when worn, and the permanent molars when slightly abraded (Pl. 36. fig. 5), exhibit a pattern identical to that presented by the two anterior true molars of *Palæolagus*, as figured in Pl. 36. fig. 36, viz., an internal notch and a central crescentic enamel fold. Before attrition has set in, they exhibit besides a strong crescentic cusp (*6*), which delimits the outer side of the enamel fold (fig. 1). On the outer side of the cusp is seen a minute and shallow enamel fold, incompletely divided into an anterior and a posterior part by a ridge descending from the middle of the outer slope of the cusp (*c*, figs. 1, 5). In d. 2 the anterior horn of the larger crescentic enamel fold stretches further outward than in d. 1, and almost reaches the outer border of the tooth. When attrition is going on, the shallower outer fold may be seen for a short while on the triturating surface, under the form of one or two minute enamel islets, which are soon completely worn away. The deeper inner crescentic fold (*b*), apparently that mentioned by Hilgendorf, persists longer.

Here then we still meet with, in an ephemeral condition, the elements constituting the *Titanomys*-tooth: two enamel folds (*b* and *c*) separated by a strong cusp (*6*) and an internal notch (*a*). The deciduous teeth of *Lepus* s. l. are cast off without presenting any other change except that produced by further wear (fig. 26). In the permanent teeth (Pl. 36. fig. 17) the internal notch begins to extend. That this growth takes place, in these initial stages at least, wholly in an inward direction—by a prolongation of the two internal cusps, which have gradually been transformed into transverse lobes ‡—becomes evident when we compare these teeth before attrition and in a moderately worn condition. In the former stage the crescentic fold is separated from the internal

\* Hilgendorf, in Monatsber. K. preuss. Akad. der Wiss. Berlin. 14 Dec. 1865, p. 673.

† *Ibid.*

‡ “8” and “9” in the figures of all the upper cheek-teeth on Pls. 36, 37, 39. The scarcity of my material prevents me from entering into particulars with regard to the young stages of other recent Leporidae. In a slightly abraded p. 2 of *Caprolagus hispidus* (Pl. 36. fig. 27), *b* and *c* surround almost completely the well-developed cusp (*6*) and unite together to form a common outlet on the antero-external side of the tooth. The enamel exhibits numerous secondary plications characteristic of the teeth of this Hare. In the deciduous teeth of *Sylvilagus brasiliensis* (Pl. 35. fig. 20), *a* and *b* are united and present the pattern of a branched fork, visible also in young stages of permanent teeth; in the latter (*b*), represented by the two branches of the fork, soon disappears from the triturating surface. In the true Hares, *Lepus* s. str. (Pl. 36. figs. 22, 25, 28), the primitive pattern is more ephemeral still than in the Rabbit; the enamel crescent (*b*) is quite superficial. As is generally the case in disappearing structures, these vanishing elements present a considerable amount of variation in different specimens of the same species.

notch only by a longitudinal enamel ridge; in the latter it is still in its place, while the internal notch has grown into a transverse fold stretching across half the transverse diameter of the triturating surface\*.

*Upper Incisors of Leporidae.*

The upper incisors of several Leporidae present some little-known peculiarities.

In his description of *Lepus nigricollis*, G. R. Waterhouse says:—"The upper incisor teeth have each two longitudinal grooves, placed very closely together, and not very distinct" †. About the same statement is made with regard to *Lepus yarkandensis*, Günth., by Büchner, who believes this to be a special character of the species:—"Sehr charakteristisch für *Lepus yarkandensis* ist der Bau der oberen Nagezähne, durch welchen diese Art sich, wie es scheint, von allen Gattungsgenossen unterscheidet. Die Vorderfläche des oberen Backzahnes weist nämlich zwei flache, schwach markirte Rinnen auf; dieselben verlaufen dicht neben einander auf der inneren Hälfte der Vorderfläche" ‡.

I have before me the type-specimen of *L. yarkandensis*, Günth. (Br. Mus. Z. D. No. 75. 3.30.10); an examination of the outer surface of its upper incisors shows but one groove, as in other Leporidae; the groove is filled with cement, but only incompletely, so that the outer and inner border of the zone of that substance is marked by two longitudinal striæ which somewhat simulate grooves. There is besides a median superficial depression of the cement layer, so that the appearance of three longitudinal grooves is produced. (In *Caprolagus hispidus* the median hollowing of the cement is more accentuated.)

In *L. nigricollis*, as a rule, the appearance of two grooves is produced by the same cause as in *L. yarkandensis*. Sometimes, however, there is in the former species a very shallow longitudinal groove in the enamel, to the outside of the principal groove filled with cement; the former is somewhat more distinct in the unique skull of a specimen from Ceylon in the Br. Mus. (Z. D. No. 81.4.29.7).

The fact of the presence of cement in the groove having been overlooked has given rise to another misunderstanding. Waterhouse says that in *Lepus ruficaudatus* the

\* According to Père Heude, the anterior upper premolar, p. 3, of *Lepus* is composed of p. 3 and a more anterior premolar, which latter is said to be represented by the median of the three anterior lobes ("6" of my figures) of p. 3. (*op. cit.* pp. 63, 64, pl. xiii. figs. 4, 5, 7, 1898). As I believe to have satisfactorily demonstrated—although not, perhaps, to the Rév. Père's satisfaction—that this "6" of p. 3 is the homologue of "6" in the posterior premolars and true molars of all Lagomorpha, I think we can, for this reason alone, dismiss the fusion theory, since each of these posterior teeth would have to be considered also as a compound of two. (Similar remarks apply to p. 2 of the lower jaw of *Lepus*, which, according to Père Heude, is = p. 2 + p. 3.) I may add here that I have never observed in the upper molars or premolars of *Lepus* a longitudinal enamel ridge closing the opening of the internal enamel-inflection (*a* of my figures), as figured and described by Père Heude ("fissure qui se ferme avec une lamelle d'émail chez l'adulte," *op. cit.* p. 65, pl. xiii. fig. 4), and would gladly learn in which species this occurs.

† G. R. Waterhouse, 'A Natural History of the Mammalia,' ii. p. 73 (1848).

‡ Eug. Büchner, 'Wiss. Resultate der von N. M. Przewalski nach Central-Asien unternommenen Reisen,' i. 5, p. 193 (1894).

superior incisor "has the external groove less deep, and placed nearer to the inner edge of the tooth," than in the Common Hare \*; and W. T. Blanford states of *Lepus dayanus*, Blf., that "the upper incisors appear very indistinctly grooved" †. The species mentioned are precisely among those in which the groove of the upper incisors is very deep; but they present the appearance of being shallow, owing to the cement which incompletely fills them. In fact, the cement appears in all species in which the groove penetrates further backward than in the commonly accessible species (*L. europæus*, *Oryctolagus cuniculus*), and it is in that case very often associated with other complications which we have now to consider.

Hodgson gives as one of the distinctive characters of *Caprolagus hispidus* the following:—"the groove in front of the upper incisors is continued to their cutting-edge so as to notch it" ‡. Strictly speaking, the cutting-edge of the upper leporine incisors is always notched—even in *Lepus europæus*; only, in *C. hispidus* (text-fig. VIII), the groove, filled with cement, is much broader and penetrates further backward, so that the natural section presented when the incisor is viewed from its lower side (same fig.) shows the groove under the form of a very elongated triangle, with the apex at its posterior end. A more complicated form has been noticed by Hilgendorf, as stated in the following brief sentence:—"Die oberen Schneidezähne von *Lepus callotis* aus Mexico und *Lepus nigricollis* aus Indien sind gabelig schmelzfaltig (dentes complicati); die entsprechenden Zähne der afrikanischen Hasen bilden durch eine einfachere Einbuchtung des Schmelzes einen Uebergang von jenen zu den anderen Hasenarten" §. In a later note by the same writer further particulars are given ||. In the text-figures I-XXIV are shown, enlarged (about 4×1), the principal modifications of the enamel-folding of upper leporine incisors viewed from below and with the anterior border directed downward. Some slight differences between the few descriptions given by Hilgendorf and my figures of the supposed same species are apparently due to different causes: in the first place, because Hilgendorf describes tooth-sections. Moreover, specimens of the same species may vary slightly (cf. figs. XVI & XVII), owing partly to individual variation. But the shape of the enamel-fold varies equally at different stages in the age of the animal; species whose incisors show the most complicated pattern in the adult have as yet no trace of this in very young animals; and, *vice versâ*, in very old specimens complication tends to disappear again. As shown by several of the text-figures, slight variations between the right and left incisor of the same individual also occur. These circumstances will, of course, have to be taken into account for systematic purposes.

The most complicated folding in Hilgendorf's material was presented by a *L. callotis*, Wagn. (= *L. mexicanus*, Lichtenst.), from Mexico ¶, in the shape of a **T**, whose transverse

\* *Op. cit.* p. 77.—R. Swinhoe (Proc. Zool. Soc. Lond. 1870, p. 234) makes a similar remark with regard to *L. hainanus*.

† W. T. Blanford, "On New Mammals from Sind," P. Z. S. London (1874), p. 663.

‡ Journ. As. Soc. Bengal, xvi. 1, p. 576 (1846).

§ Sitzungsber. Berl. Ak. Wiss., Sitzg. 14 Dec. 1865 (1866).

|| Sitzungsber. Ges. naturf. Freunde Berlin, Sitzg. 15 Jan. 1884, pp. 18-21.

¶ *Op. cit.* pp. 18, 19.

part, turning backward, runs approximately parallel with the anterior border of the tooth, and is slightly folded from behind, so that it may be compared with an outspread fork. Figs. XVI and XVII, representing the left incisors of two specimens from Mexico in the Nat. Hist. Museum, labelled *Lepus callotis*, show this same form, with a slight complication of the transverse part in one of them (XVII). *L. melanotis*, Mearns (fig. XV), from Clapham, New Mexico, belonging to the same group (*Macrotolagus*), exhibits in the right incisor the T pattern in a much reduced form, and in the left a condition approximating to that of the African *L. savatilis*, of which more hereafter.

The nearest approach to *L. callotis* is seen, according to Hilgendorf, in *L. dayanus*, Blf., to which species he refers also the *L. nigricollis* of the first note. I have figured (fig. XVIII) the right incisor of the co-type of *L. dayanus*, from Sukkur, Sind (Br. Mus. Z. D. No. 90.4.9.2), which corresponds almost exactly to Hilgendorf's description. A nearly similar form I find to be exhibited by *L. hainanus*, from Hainan (fig. XIX); the folding, however, is considerably shorter, and the opening broader. In *L. nigricollis* from Ceylon (fig. XXI) the branches of the fork are more elongate, and the anterior opening is considerably more constricted, than in *L. hainanus*.

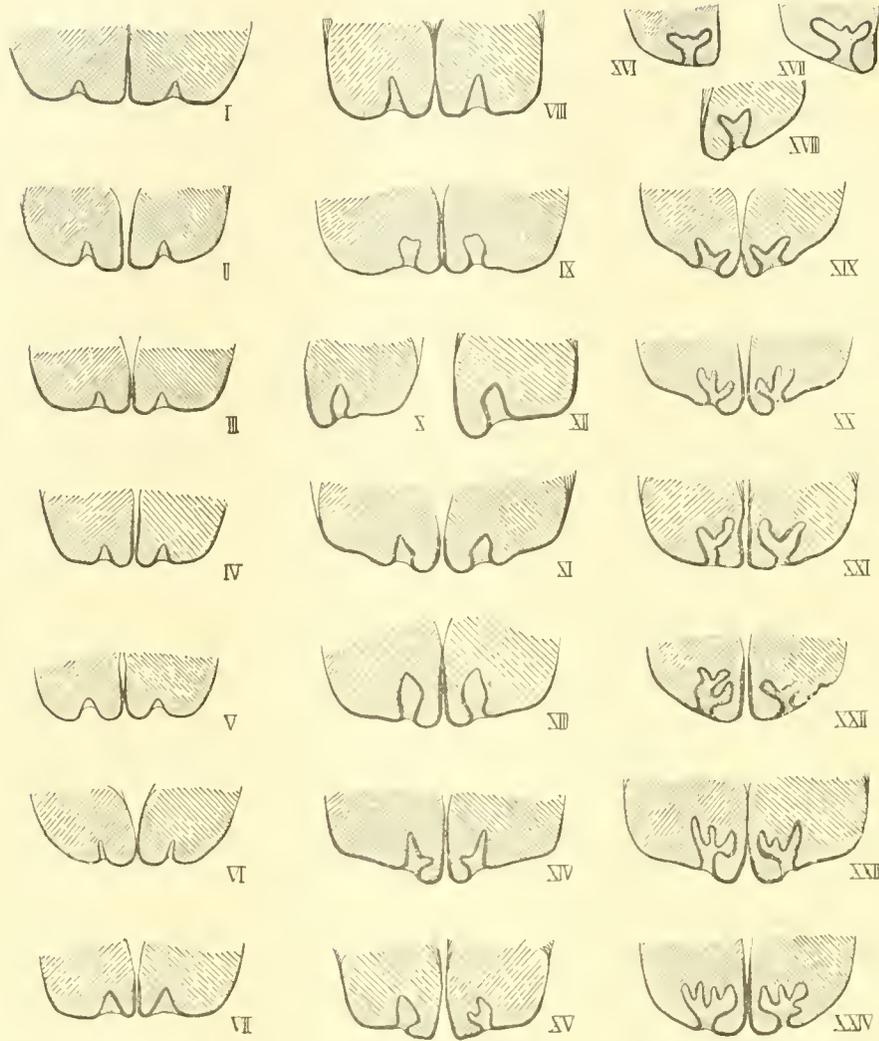
*L. peguensis*, Blyth, from Pegu (fig. XX), shows a further complication, already foreshadowed by one of the *callotis* specimens (fig. XVII), there being three branches of the fork. Not much different is the left incisor—the right one is damaged—of a *L. nigricollis* from the Nilghiris (fig. XXII), and both incisors of *L. ruficaudatus* (*L. kurgosa*, Gray) from the Punjab (fig. XXIII). The maximum of complication known to me is exhibited by a *L. ruficaudatus* from Rajputana (fig. XXIV), where the left incisor exhibits a four-branched fork, the right being a slight modification of the same pattern.

Following the description of the incisors of *L. dayanus*, Hilgendorf gives that of an undetermined skull brought home from Africa by the Von der Decken Expedition. In this the T with a narrow opening is still strongly marked, but the median moiety of the transverse part is reduced. The whole of the enamel-fold occupies less space than in *L. dayanus*, not being so much extended either backward or laterally\*. This description applies fairly well to my fig. XIV, *L. Victorie*, Thos., from Nassa, Victoria Nyanza, except that the opening of the fold is not narrowed.

Figs. IX, X, and XII represent *L. savatilis*, F. Cuv., from Pirie Bush, King William's Town (Cape), Transvaal, and "Cape of Good Hope" respectively, in none of which is there a bifurcation at the posterior end; the folding penetrates far backward and the opening is wide, as described by Hilgendorf † in *L. savatilis*. Fig. XI, "*Lepus* sp.", from Sena, Zambesi, is of the same pattern; and so is *L. Whytei*, Thos., type-specimen, from Pacombi River, Nyasa (fig. XIII); in the latter, however, the fold penetrates further back than in figs. IX–XII, and the opening is comparatively more restricted. To this form seems to approach Hilgendorf's specimen of "*Lepus capensis*,"

\* *Op. cit.* p. 20.

† *Op. cit.* p. 21.



Anterior end of upper Leporine incisors, from below. Enlarged.

No. I.	<i>Lepus variabilis (altaicus)</i> .	Russia.	Brit. Mus. Z. D.	535 a.	49.5.13.4.
II.	<i>L. variabilis</i> . ♀.	Altye, Moraysbire.	"	—	94.2.15.2.
III.	<i>L. sinaiticus</i> .	Midian, N.W. Arabia.	"	—	78.8.9.1.
IV.	<i>L. Judææ</i> , Gray, ♀, type.	Palestine.	"	—	64.8.17.5.
V.	<i>L. sinensis</i> , Gray, type.	China.	"	—	38.10.29.23.
VI.	<i>L. cumanicus</i> , Thos., type.	Venezuela,	"	—	94.9.25.18.
VII.	" <i>L. yarkandensis</i> ?"	Koko Nor.	"	—	94.2.2.12.
VIII.	<i>Caprolagus hispidus</i> , Pears.	(Ind. Mus. Coll.—B. H. Hodgson.)	"	—	79.11.21.204.
IX.	<i>Lepus saxatilis</i> .	Pirie Bush, King William's Town (Cape).	"	—	98.10.8.1.
X.	<i>L. saxatilis</i> , ♂.	Transvaal.	"	—	93.11.26.2.
XI.	<i>Lepus</i> sp.	Seua, Zambesi.	"	—	83.2.6.3.
XII.	<i>L. saxatilis</i> .	C. G. Cope.	"	525 a.	42.12.6.5.
XIII.	<i>L. Whytei</i> , Thos., ♀, type.	Pacombi River, Nyasa.	"	—	94.1.25.14.
XIV.	<i>L. Victoriae</i> , Thos.	Nassa, Victoria Nyanza.	"	—	95.3.7.2.
XV.	<i>L. (Macrotolagus) melanotis</i> , Mearns, ♂.	Clapham, New Mexico.	"	—	94.5.9.29.
XVI.	<i>L. ( " ) callotis</i> .	Mexico.	"	—	58.9.22.2.
XVII.	<i>L. ( " ) callotis</i> .	Mexico.	"	—	53.8.29.37.
XVIII.	<i>Lepus dayanus</i> , eo-type.	Sukkur, Sind.	"	—	90.4.9.2.
XIX.	<i>L. hainanus</i> .	Hainan	"	—	70.7.18.18.
XX.	<i>L. peguensis</i> , Bf., ♀.	Pegu.	"	—	91.5.12.1.
XXI.	<i>L. nigricollis</i> , F. Cuv.	Ceylon.	"	—	81.4.29.7.
XXII.	<i>L. nigricollis</i> .	Kotagiri, Nilgiris.	"	—	91.10.7.154.
XXIII.	<i>L. ruficaudatus (kuryosa)</i> , Gray.	Punjab.	"	1176 a.	—
XXIV.	<i>L. ruficaudatus</i> .	Rajputana.	"	—	91.10.7.151.

from Mozambique\*, collected by Peters, which, however, is certainly not a *Lepus capensis*. The latter differs scarcely from *L. europæus*, Pall., s. l. (including *L. occidentalis*, de Wint.), by its minute enamel-folding, not filled with cement.

The forms which remain to be described (figs. I-VII) are all approximately of the same type, viz. a triangular fold with the apex turned backward; the fold in none of them stretching so far back as in *Caprolagus hispidus* (fig. VIII), mentioned above. The pattern of the latter is approached somewhat by that of fig. VII, from a specimen labelled "*Lepus yarkandensis?*," from Koko Nor (Br. Mus. Z. D. No. 94.2.2.12), exhibiting an enamel-fold with thick borders, but shorter than in *C. hispidus*, and with a much wider opening. It is decidedly not *L. yarkandensis*, Günth. The type of the latter, which is not figured, approaches in the form of the folding *L. sinensis*, Gray, the type of which (Br. Mus. Z. D. No. 38.10.29.23) is represented in fig. V. Both are imperfectly filled with cement, in *L. sinensis* still less so than in *L. yarkandensis*. The latter differs also from the former by the opening and the whole fold being narrower.

*L. tibetanus*, Waterh., has no trace of cement; in the shape of its fold it is intermediate between the former two; the opening is slightly broader than in *L. yarkandensis*.

The conformation of the type of Gray's "*L. Judææ*" (fig. IV), from Palestine, and of "*L. sinaiticus*" (fig. III), from Midian, N.W. Arabia, almost identical in both, is shown by the figures.

*L. timidus*, Linn. (*L. variabilis*, Pall.) (figs. I & II) hardly differs, but still the two figures of this species show that there are slight differences between a specimen from Russia (fig. I) and one from Scotland (fig. II). In this species I have always found the enamel-fold with a filling of cement, though very often incomplete. In *L. europæus*, Pall., I have never met with a trace of cement. This difference would seem to be a good character for distinguishing isolated fossil incisors of the two species; but it is probable that much-weathered specimens of *L. timidus* may have lost their cement.

*Lepus cumanicus*, Thos., from Venezuela (Br. Mus. Z. D. No. 94.9.25.18), the type of which is represented in fig. VI, stands somewhat apart by its very narrow and comparatively elongate enamel fold.

Hilgendorf holds these complications of the enamel in the upper incisors to be a specialization, the only reason given being that in the fossil *Prolagus* (*Myolagus*) nothing of the kind is seen. "Phylogenetisch betrachtet, ist die bedeutende Schmelzentwicklung des *Lepus mexicanus* gleichfalls ein Extrem; denn die Einbiegung der Schmelzplatte an der Vorderfläche tritt bei den fossilen Leporiden-Gattungen (*Myolagus*) als eine seichte Einknickung auf, deren Seitentheile fast die ganze Vorderfläche einnehmen" †. This argument would be of some weight if *Prolagus* could be considered ancestral to *Lepus*; but this is certainly not the case, although the molars of the former are of a more primitive type than those of the latter. As insisted upon in the present memoir, the Lagomyidæ, of which *Prolagus* is a member, run parallel with the

\* *Op. cit.*, p. 21.

† *Op. cit.*, p. 20.

Leporidae from the Lower Miocene (or it may be from the Oligocene) to the present time.

The incisors provided with enamel-folds point back towards cuspidate incisors, for the enamel-folds of lophodont and laminated teeth are obviously the derivatives and homologues of the "valleys" separating the cusps or tubercles. Now it is very suggestive that we meet with cuspidate incisors in *Plesiadapis*, a genus from the lowest Eocene of Rheims, classed among the Lemuroidea by Lemoine and other writers, considered by Schlosser and me to be a very primitive Rodent. In the jaws of *Plesiadapis* the teeth are greatly reduced in number. In the lower jaw we have only one powerful elongated incisor, directed obliquely forward and upward, and separated from the five cheek-teeth—the premolars being already reduced to two—by a considerable diastema. On its posterior face the lower incisor has a cingulum supporting a small cusp. The upper incisors, too, are separated by a long interval from the five cheek-teeth, and appear to have been three in number (Lemoine considers the very small outer one to be the canine). The two outer pairs are very small and unicuspidate; the inner pair robust, generally tricuspidate, there being an anterior pair of cusps, and backwardly an additional cusp, which starts from a kind of cingulum\*.

If we imagine the cusps of these upper incisors of *Plesiadapis* to have become lengthened in accordance with a general change of the more brachyodont incisors into a hypselodont one, and their interstices filled with cement, so that by trituration a level surface can be produced, the result would be a pattern somewhat similar to that of several of the figured Leporidae. The posterior cusp of *Plesiadapis*, projecting from behind into the cavity †, would produce a posterior ramification like that of the Leporidae.

The test will lie in the search for Tertiary Leporidae exhibiting an intermediate stage between the condition of the upper incisors of *Plesiadapis* and that of recent Leporidae. An examination of the incisors of *Palaolagus* might decide the question.

#### GENUS PALEOLAGUS.

*Palaolagus*, from the Tertiary of North America, is represented by Leidy ‡ and by Cope § as showing in the teeth only one character distinctive from the genus *Lepus*, viz. the more simple conformation of the anterior inferior premolar of the extinct genus, and of this character more hereafter. When, however, we go over the descriptions, accompanied by numerous figures, and an examination of originals, several of which are in the British Museum, we cannot but be struck at once by some very essential differences in the triturating surfaces of the two genera. When do we ever meet with molars in any species of *Lepus* showing the complete absence of all traces of enamel, with the exception of part of the marginal border? This is the case in old

\* Lemoine, in Bull. Soc. Géol. France, xix. 1, p. 278, pl. x. fig. 50, a, b, c (1891).

† Lemoine, *l. c.* pl. x. fig. 50, b, c.

‡ Proc. Acad. Philadelphia, p. 89 (1856); id. 'Extinct Mammalia of Dakota and Nebraska,' p. 332, pl. xxvi. figs. 14-20 (1869).

§ 'The Vertebrata of the Tertiary Formations of the West,' i. p. 870, pls. lxvi., lxvii. (1883).

specimens of *Palæolagus*. The pattern of less worn teeth, too, is rather different from what occurs in *Lepus*. In none of the numerous triturating surfaces of *Palæolagus*-teeth figured do we meet with a transverse fold penetrating so far outward as in the four intermediate teeth of *Lepus*, and in the true molars and posterior premolar of *Lagomys*. This is confirmed by Cope's description:—"The inner side of the four intermediate molars is deeply grooved *for a short distance*" (italics mine; cf. Cope's figures), "which gives a fissure-like notch on attrition. This disappears after use, as does also a less profound crescentic fossa in the middle of the crown, whose concavity is directed outward" \*.

This statement, in my opinion, does not fully describe the pattern in young specimens, which seems to be very ephemeral in *Palæolagus*. In a fragment of the right upper jaw of *P. Haydeni* in the Brit. Mus. (5727), of which I give an enlarged figure (Pl. 36, fig. 36), the alveolus of the second premolar (p. 2) is shown, and the three teeth p. 1, m. 1, m. 2 are seen in place. The empty alveolus of the premolar suggests that in its contour this tooth very much approached the corresponding tooth of *Prolagus æningensis* (Pl. 36, fig. 21), and to judge from what we find in the following tooth (p. 1) there is a strong assumption that the pattern of p. 2 of *Palæolagus* also resembled that of *Prolagus æningensis*. P. 1 of *Palæolagus* exhibits the internal notch (a) with which we are acquainted in *Titanomys* and in the deciduous teeth of *Prolagus*, *Lagomys*, and *Lepus*, and which moreover persists as such in the premolars of *Prolagus*, in the second premolar of *Lagomys*, and in the anterior premolar of *Lepus*. In the premolar of *Palæolagus* we find, on proceeding inward, a crescentic central enamel islet in the centre of the crown, known already from the descriptions and figures of Leidy and Cope. It is, too, an old acquaintance of ours; for to all appearance it is the homologue of the large internal enamel-fold (b) of *Titanomys*, whose further history we have followed up in the other genera. But this is not all. From the antero-external corner of p. 1 of *Palæolagus* starts an enamel-fold in a postero-internal direction, terminating near the outer end of the crescentic fold's posterior horn. No mention is made of this outer fold in Leidy's and Cope's descriptions; it is, however, visible in one p. 2 of Cope's figures (pl. lxxvii, fig. 16 a); but I have not seen it delineated for the same tooth together with the crescentic fold, as in the figure which I publish. The outer fold just described is undoubtedly the homologue of the outer enamel-fold (c) of *Titanomys*, and I do not doubt that still younger stages of *Palæolagus*—which have been figured by Cope, but in an unsatisfactory manner—will show a greater development of both the enamel-folds, and therewith a stronger resemblance to the pattern of the *Titanomys*-teeth and the posterior premolars of *Prolagus*.

The true molars of *Palæolagus* in the specimen figured exhibit only the crescentic central islet (b) and the internal notch. As stated by Cope in the passage quoted above, and as shown likewise by the illustrations of both the American writers, the internal notch and the crescentic islet are worn away by attrition, without any other change taking place. In this consists the great difference between the American fossil and all the forms

\* *Op. cit.*, p. 876.

previously described in this paper. While in all the upper grinding-teeth of *Titanomys* the initial condition, two crescent folds and an internal notch, is retained throughout life, and this is more or less so in the premolars of *Prolagus*, in the molars of the latter the crescentic folds are worn away and the internal notch is enlarged to a transverse fold, s in the molars and p. 1 of *Lagopsis* and *Lagomys*, and in the molars and posterior premolars of *Lepus* s. l. Milk-teeth and very young permanent molars of *Lepus* show, with slight variations, the pattern before described as characteristic of moderately-worn teeth of *Palæolagus*. No modernization takes place in the latter; the only change we perceive, by the further progress of wear, is the complete obliteration of the crescentic folds and of the notch on the inner side. In *Lepus*, the large crescentic fold of the deciduous teeth, and a small islet external to it—present in some of the species, and representing the *external* crescentic fold of *Lagomyidæ*—disappear at a very early stage of the two posterior premolars and of the two anterior true molars, and are replaced in the permanent teeth by the transverse fold already described.

The permanent teeth of *Palæolagus*, therefore, can only be compared with the deciduous teeth of *Lepus*; like these (Pl. 36. fig. 26), they exhaust their primitive pattern, without evolving a secondary one\*.

*Palæolagus* cannot find a place in our phylogenetic series (*Titanomys*—*Prolagus*—*Lagopsis*—*Lagomys*). With regard to the condition of their upper cheek-teeth, the species of *Palæolagus* in which these teeth are known would follow after *Titanomys*. But they are certainly not the forerunners of *Prolagus*, except in the form of the true molars; while *Prolagus* is more conservative than *Palæolagus* in the conformation of its two posterior premolars. On the other hand, *Palæolagus* is certainly the forerunner of *Lepus*, and presumably its ancestor; and this cannot be said of the *Lagomyidæ*, in all of which the upper m. 3 has been lost.

*To resume.*—We have in the preceding pages followed the transformation in the pattern of the upper cheek-teeth on three lines:—(1) From genus to genus; (2) from behind forward in the dental series; (3) from young to old.

(1). *From genus to genus*, we might almost say from species to species, the series is as follows:—*Pelycodoid* type (*Pelycodus*, *Plesiadapis*)—*Titanomys visenoviensis*—*T. Fontanuesi*—*Palæolagus*—*Prolagus auningensis*—*P. sardus*—*Lagopsis*—*Lagomys*—*Lepus*.

*Pelycodus* and *Plesiadapis* are genera of the Lower Eocene.

*Titanomys* appears in the Lower Miocene, and vanishes in the Middle Miocene.

*Prolagus* appears in the Middle Miocene and lingers on, protected by an insular habitat, until the Neolithic period.

*Lagopsis* is at present known only from the Middle Miocene.

*Lagomys* makes its appearance in the Pleistocene and survives to the present day.

*Lepus*, preceded by the Oligocene and Miocene *Palæolagus*, appears with many of its present generic characters in the Lower Pliocene, and survives to the present day.

\* The remarkable Hare from Sumatra, *Nesolagus Netscheri*, approaches *Palæolagus* more than other recent Leporidae, inasmuch as, by the feeble development of the transverse enamel-fold (Pl. 37. fig. 17), it represents a first stage in the evolution of the secondary pattern. The same form exhibits other primitive features, to be described later on.

(2) *From behind forward in the dental series.*—The true molars are the first to be transformed, and successively one after the other of the premolars, the anterior premolar (p. 3) being the most conservative.

(3) *From young to old.*—The cheek-teeth of the genera under consideration exhibit, in the first developed parts of their shaft, more or less evident traces of the ancestral pattern; *mostly so* the deciduous teeth, which are cast off when the primitive pattern has almost vanished, and without showing a beginning of transformation; *least so* the true molars, which in the first stages observable of the calcified tooth, and before trituration has set in, show the primitive pattern already reduced and the secondary in process of evolution.

#### LOWER MOLARS OF LAGOMORPHOUS RODENTIA.

To state it in a general way, the lower molars of the Lagomorpha present the same characters as their upper antagonists: viz. anteriorly in the series we meet with complication, posteriorly with a simple transverse pattern. On closer examination, however, it may be seen that in the mandibular teeth the process which we have followed through its various stages in the upper set is accelerated. Although it must be taken into account that we have one premolar less below than above, none the less—leaving for the present out of consideration the reduction which takes place at the posterior end (m. 3)—there is in the adult mandible only one tooth, the anterior, which differs materially from the others, by being more complicated. In *Titanomys*, the oldest member of the group, this tooth (p. 2) as generally described and figured, presents a more simple structure than in later genera, and even than do the other teeth of *Titanomys*, by being composed of only one column, divided into two lobes by an inner and an outer enamel-inflection; whereas in the teeth situated posteriorly there are two columns, the division between them being complete; they are held together by cement.

We meet here with a phenomenon which is pretty general among Rodents, whether the number of their cheek-teeth be three, four, five, or six. To state it more fully:—

1. The mandibular cheek-teeth precede those of the maxilla in the reduction of their number; we have instances of  $\frac{6}{5}$ , of  $\frac{5}{4}$ , and of  $\frac{4}{3}$  cheek-teeth, but never of  $\frac{5}{6}$ , or  $\frac{4}{5}$ , or  $\frac{3}{4}$ .

2. Very frequently the anterior tooth in the lower series, whether it be p. 2, or p. 1, or m. 1, is more complicated than those behind; which circumstance suggests that the complication has some connection with the anterior position of the tooth in question.

3. When the anterior lower tooth is nearly or actually equal in pattern to those behind, this is generally so in older forms. Thus we find that in Winge's Anomaluridae—including mostly Tertiary genera—provided with four lower teeth, the anterior one (p. 1) is equal or subequal in size and pattern with the others, and sometimes even of smaller size. Again, in Muridae, with three inferior cheek-teeth, the geologically older forms have the anterior one (m. 1) equal or subequal in size with the two following, whereas the complication of the first molar appears only in more recent forms. The same is true with regard to the lagomorphous Rodentia, where the anterior tooth is p. 2, and in the oldest known genera (*Titanomys*, *Palæolagus*) of a rather simple pattern.

The explanation which I suggest for these curious occurrences is as follows:—When an anterior tooth drops out from the mandible—generally through an apparent interference of the incisor with its pulp—some compensation for its loss is necessary, as the corresponding maxillary tooth is generally still in its place; this compensation is brought about by a complication on the anterior side of the tooth which has become the first in the series by the loss of the originally anterior one. Those genera which are nearer in date to the epoch when the anterior tooth was lost will still present a less complicated form of that which has succeeded to this position, while in the later genera the foremost tooth will have acquired the complication. When p. 2 is dropped, p. 1 will become the foremost tooth, and the same cycle will recommence, and so on.

I next proceed to a closer examination of the lower cheek-teeth, starting from those of *Titanomys*. A superficial comparison of the anterior tooth, p. 2, of this genus, with that of the other Lagomyidæ, shows that in the former it is more simple than in the latter, and presents an approximately tetragonal outline at its triturating surface; in *Prolagus*, *Lagopsis*, and *Lagomys* this is triangular (apex in front). Thus it is that we find the tooth generally described; but on closer examination the matter is somewhat more complex. I have figured five specimens of p. 2 of *Titanomys Fontannesii*, from La Grive-Saint-Alban, in different stages of wear; four are isolated teeth (Pl. 37. figs. 1–4); the fifth is in its place in a left ramus, presenting the complete series of two premolars and three molars (Pl. 37. fig. 7). Of *T. visenoriensis* I have one specimen, in a fragment of the right ramus, containing the two premolars (Pl. 37. fig. 25). This species is from the Allier (Bravard Collection, Br. Mus. Geol. Dep. No. 31095). The first stage in *T. Fontannesii* (fig. 1) represents a tooth which has not yet come into wear. In the main it is composed of two lobes; the anterior is subconical, the posterior is much more extended transversely, and composed of a tapering outer and a thicker, rounded inner cusp; moreover, on the middle of its posterior surface appears a small cusp (*t*); the anterior surface of this lobe is wrinkled. Even in this early stage the separation of the two lobes is incomplete; a ridge, running almost longitudinally backward, from the middle of the posterior side of the anterior lobe towards the posterior, shows that trituration would very soon have connected the two by a narrow isthmus of dentine, thus separating from each other an outer and an inner enamel-inflection. This we see, in fact, brought about in the second stage (fig. 2). Towards the middle of the anterior margin of the anterior lobe, a feeble cusp is visible in the first stage (1, fig. 1); the same is more distinct in the second stage (1, fig. 2), where it is nearer to the inner side. This cusp, to all appearance, is Winge's 1, Osborn's *paraconid*. Whether it contains potentially some other element I must leave undecided; as a matter of fact, in the two teeth described, it does not occupy exactly the same position; and in *T. visenoriensis* (1, fig. 25) it is more approximated to the outer side. What is called the *paraconid* is, however, somewhat inconstant in its position\*. In p. 2 of *T. vise-*

\* See, *et.*, the text-figures in W. D. Matthew, "A Revision of the Puerco Fauna," Bull. Am. Mus. Nat. Hist. ix. (1897).

*noricensis* (fig. 25) it is evident as a small vertical pillar, lying far below the triturating surface of the moderately worn tooth.

To return to the second stage in *Titanomys Fontannesii*. The inner of the two principal enamel-inflections resembles somewhat in outline its homologue in *Lagopsis verus* (Pl. 37. fig. 26, p. 2). It is seen to be composed of two parts: a posterior, which communicates by a narrowed opening with the internal margin of the tooth, and thence runs straight towards the middle of the tooth, and an anterior circular one; the two communicating with each other by a narrow channel. The terminal cusp (*t*) is situated much nearer the inner side than in the first stage. I have dealt with this terminal cusp of the lagomorphous Rodentia on a former occasion, and homologized it with Osborn's *hypoconulid*\*; a view from which I see no reason to depart. In the third stage (fig. 3) this hypoconulid is still apparent; but the "paraconid" has disappeared, and so has the circular part of the inner enamel-inflection. The transverse posterior part of the latter is on its way to be shut off from the inner margin, and to assume the form of a circular enamel islet. "*t*" is visible on the posterior internal edge of the tooth. In the fourth stage (p. 2 of fig. 7), the circular enamel islet is quite separated from the inner margin, and has become confluent with the outer enamel-inflection, so that the triturating surface of the tooth presents—if we except a small enamel fold limiting anteriorly the still extant *t*—only one enamel-inflection, penetrating from the middle of the outer margin and approaching the inner. In the fifth stage (fig. 4) we find only the latter inflection, *t* also having disappeared. This tooth in its general outline again approaches the first stage.

No lower deciduous teeth of *Titanomys* are at my disposal. Filhol has figured  $\bar{d}_1$  and  $\bar{d}_2$  of *T. vissenoiensis* from Saint-Gérard-le-Puy (Allier); from this figure nothing more can be made out than that in *d.* 2 the anterior part seems to be more produced anteriorly than in *p.* 2. No description is given of the triturating surface †.

The anterior lower premolar of *T. vissenoiensis* is distinguished from the same tooth in *T. Fontannesii* by the persistence of the enamel-inflection of the inner side in the adult (Pl. 37. fig. 25); in the immature specimen figured by Gervais, and originally described as a separate species, *T. trilobus*, the two enamel-folds are confluent in the middle of the triturating surface, thus completely separating an anterior and a posterior lobe ‡. The terminal cusp (*t*) present in the specimen figured (Pl. 37. fig. 25) must certainly be expected to be visible likewise in younger specimens; Gervais makes no mention of it in this tooth; in the profile view of the tooth, however §, there are two vertical grooves on the inner side. A small anterior pillar ("paraconid") on the anterior side (1), below the triturating surface, has already been mentioned as present in the British Museum specimen.

\* Proc. Zool. Soc. London, 1893, p. 203.

† H. Filhol, "Études des Mammif. foss. de Saint-Gérard-le-Puy, Allier." Ann. Sc. Géol. x. p. 29, pl. iii. fig. 3 (1879).

‡ Zool. et Pal. Fr. p. 51: "les deux lobes de la première [molaire] n'y sont point encore réunis l'un à l'autre par un petit isthme d'ivoire"; pl. 46, fig. 1 (1859).

§ *Op. cit.* pl. 46, fig. 1 c.

We have to follow up this same tooth,  $\overline{p. 2}$ , in the other genera of Lagomyidæ. In *Lagopsis verus* (Pl. 37, fig. 26), from the Middle Miocene of La Grive-Saint-Alban, the posterior transverse lobe of  $p. 2$  is undivided, with no trace of  $l$ . The next anterior lobe is separated from the former by a T-shaped enamel-inflection on the inner side—which has already been mentioned as approaching in form its homologue in *Titanomys Fontannesi* (fig. 2)—and by an outer one. We have, therefore, here the two enamel-inflections of *T. risenoriensis* and of the young of *T. Fontannesi*. However, in *Lagopsis* the lobe is more distinctly divided than even in fig. 2 (*T. Fontannesi*), into an outer and an inner cusp; for in the former the T-shaped inflection extends more anteriorly, and the lobe is delimited in front by two smaller enamel-folds. These latter delimit on their anterior side two further cusps, an outer and an inner; the latter corresponds to 1 (paraconid), as seen by comparison with fig. 2; the former may correspond to the pillar which in *T. risenoriensis* (fig. 25) is nearer the outer than the inner side. In any case, in *Lagopsis* the anterior part of  $p. 2$  is much more developed than in *Titanomys*; for we have, in the former, two comparatively stout cusps against one feeble cusp in each of the two species of the latter. Besides, there is in *Lagopsis* a small odd cuspidule, situated in front of the anterior pair, and in the middle line of the tooth, to which it gives a triangular form.

The principal difference in *Lagomys*, to which *Lagopsis* is nearly related, consists in the fact that the characteristic T-shaped inflection of the *Lagopsis*  $p. 2$  is either absent or replaced by a slight indentation of enamel. The latter is the case, *e.g.*, in *Lagomys rutilus*\*, the former in *L. alpinus* and *L. nepalensis*†. Moreover, the odd anterior cuspidule has vanished in *Lagomys*.

In *Prolagus* also the anterior part of  $d. 2$  is much more complicated than in  $\overline{p. 2}$  of *Titanomys*. Fig. 5, Pl. 37, shows this tooth of *Prolagus sardus*, var. *corsicanus*, from the ossiferous breccia of Toga, near Bastia (Br. Mus. Geol. Dep. No. M3486); fig. 6, the same tooth of the Miocene *Prolagus awingensis* from La Grive-Saint-Alban; both from the left side. I have still younger stages than those figured of this deciduous molar, showing the posterior lobe completely separated from the middle one. The anterior lobe of  $d. 2$  of *P. awingensis* (fig. 6) is tripartite, as in *Lagopsis*, but the odd anterior cuspidule is less distinctly divided from the inner than in the latter genus. In the tooth of *P. awingensis* the whole tripartite lobe is connected only by cement with the rest of the tooth; in younger stages it is still more divided into a smaller external cusp—which is isolated, also, in the  $d. 2$  of *P. sardus* figured (fig. 5)—and a larger internal one comprising both the "paraconid," 1, and the odd anterior cuspidule. The isolated small external cusp of *P. sardus* is situated far below the triturating surface; the inner larger one, showing no separated odd cuspidule, is connected on its inner side with the rest of the tooth, as happens likewise, though very rarely, in the corresponding permanent tooth,  $p. 2$ , of the same genus. In still more advanced stages

\* For a figured specimen of this tooth see E. Schäff, "Ueber *Lagomys rutilus*, Severtzoff," Sep.-Abdr. aus Zool. Jahrb. ii. p. 69, fig. 5 b.

† R. Hensel, "Beiträge z. Kenntn. fossiler Säugethiere," Zeitschr. deutsch. geol. Ges. viii. pl. xxvi, figs. 2 & 6 (1856).

of wear of the deciduous tooth of *Prolagus*, the whole of the anterior tripartite lobe appears invariably connected with the posterior part of the tooth by a dentinal isthmus, thus giving the whole tooth some resemblance to m. 1 inf. of a vole; and it has, in fact, been mistaken for a molar of *Microtus*.

A characteristic feature of the anterior lower premolar,  $\overline{p. 2}$ , of *Prolagus*, is an odd isolated cusp or pillar, connected only by cement with the rest of the tooth, and situated on its anterior side, thus giving to the whole tooth a triangular outline, as in *Lagopsis*. In *Prolagus æningensis* (Pl. 37. fig. 9) this cusp is situated near or close to the middle line; in *P. sardus*\*, of which I have examined hundreds of specimens, its position is nearer the inner side. As before mentioned, in very rare cases of *P. sardus*, this usually isolated cusp is united with the tooth near the inner side, as in d. 2 of fig. 5. In other cases of *P. æningensis* (fig. 12, Pl. 37.) and *P. sardus*, it may be united with the tooth near its outer side. This latter fusion I found to have taken place in 19 specimens of  $\overline{p. 2}$  out of 575 examined, from the ossiferous breccia of Monte San Giovanni (Sardinia) (*P. sardus*), and in two cases out of 84 examined from Toga, near Bastia (*P. sardus*, var. *corsicanus*). The cusp was united with the tooth near the inner side in two of the 575 examples from Monte San Giovanni. Cusp "t" I have met with only in  $\overline{p. 2}$  of *Prolagus elsanus* (page 460).

A comparison with the specimens before described shows the usually odd isolated cusp to be the homologue of the "paraconid" combined with the anterior odd cuspidule of *Lagopsis*, while the outer cusp of the tripartite anterior lobe is present, also, in  $\overline{p. 2}$ ; in *P. æningensis* it is generally stouter than the outer cusp (6) of the median lobe, whereas in *P. sardus* the inverse is the rule. In exceptional cases of *P. sardus* I find this outer cusp of the anterior lobe completely isolated, as it is in the deciduous tooth of fig. 5.

A second characteristic feature of the  $\overline{p. 2}$  of *Prolagus* (figs. 9, 12) is a longitudinal enamel-fold, filled with cement, which, beginning from behind the isolated anterior cusp, proceeds backward to near the hinder margin of the tooth, thus completely dividing the middle lobe into an outer and an inner cusp, and incompletely so the posterior one, on which it also encroaches. The longitudinal arrangement of the elements of this  $\overline{p. 2}$  of *Prolagus*, in opposition to the transverse arrangement of the posterior teeth, is very striking.

I now proceed to a consideration of the same tooth in the Leporidae. With reference to  $\overline{p. 2}$  of *Palæolagus*, Leidy states:—"The anterior four inferior molars [of *Palæolagus*] bear a near resemblance in form and constitution with the corresponding series of *Titanomys eisenociensis*, as represented in pl. 46 of Gervais' Zool. et Pal. Fr." †. Comparing it with the same tooth in *Lepus*, Leidy further says in the original description of *Palæolagus*:—"The first inferior molar is bilobed, and not trilobed as in the latter (*Lepus*)" ‡. In his second memoir the first inferior molar of *Palæolagus* is said to be composed of a double column as in the others, the same tooth in the Hare of a triple column §. Cope

\* R. Hensel, l. c. pl. xvi. fig. 8.

† 'Extinct Mammalian Fauna of Dakota and Nebraska,' p. 333, pl. xxvi. (1869).

‡ Proc. Ac. Philad. p. 89 (1856).

§ Extinct Mamm. Fauna, &c., p. 331.

supplements this description by the following information based upon a great number of remains:—"I am able to show that it is only in the immature state of the first molar that it exhibits a double column, and that in the fully adult animal it consists of a single column with a groove on its external face"\* . A more complete description is given on p. 878:—"There is the merest trace of a posterior lobe"—corresponding to the terminal lobe (*t*) of *Titanomys*—"at this time, and that speedily disappears. The anterior lobe is subconical, and is entirely surrounded with enamel. By attrition, the two lobes are speedily joined by an isthmus, and for a time the tooth presents an 8-shaped section, which was supposed to be characteristic of the genus. Further protrusion brings to the surface the bottom of the groove of the inner side of the shaft, so that its section remains in adult age something like a **B**." From this description it appears that p. 2 of *Palæolagus Haydeni* is almost exactly like the same tooth in *Titanomys Fontannesii*.

The difference between the p. 2 of *Palæolagus* and *Lepus* is stated by Cope to be as follows:—"In the extinct genus the first tooth "consists of one column more or less divided. In *Lepus* this tooth consists of two columns, the anterior of which is grooved again on the external side in the known species." Leidy's description of the Leporine p. 2, as being composed of three lobes or columns, is more accurate. It is quite true that in the adult p. 2 of many Leporidae appears to be composed of two columns, with an additional antero-external enamel-inflection (see Pl. 37, figs. 13 & 19); but by no means universally so, and, so far as my experience goes, it is never so in the young (Pl. 37, figs. 8, 18, 22, 23).

In the immature p. 2 of *Lepus* s.l. (Pl. 37, figs. 8, 22), as well as in the immature stage of all the other inferior molars of the same, the posterior and the middle-lobe column are completely divided; only in later stages a very narrow isthmus of dentine connects them on the inner side (Pl. 37, figs. 13, 20, 23). The fact of a primary separation into two lobes of the inferior molars of *Lepus* was first announced by Hilgendorf ‡.

The unworn lower p. 2 of the Wild Rabbit (Pl. 37, fig. 8) displays anteriorly the anterior of the three columns completely divided into a smaller outer and a larger inner subconical cusp; this division is brought about by a longitudinal enamel-inflection, which invades part of the middle lobe as well, so that the latter is also divided, though incompletely, into an outer and an inner cusp. (Compare the homologous enamel-inflection of *Prolagus*, fig. 9.)

Passing on to the lower cheek-teeth backward from p. 2, the various stages which I have represented in Pl. 37 show in the lower molars the simple transverse pattern of the two lobes of p. 1; m. 2 is a secondary one, as in the upper teeth, though in the inferior molars the original pattern is much more ephemeral, least so in p. 1, which forms a transition between p. 2 and the true molars.

\* 'The Vertebrata of the Tertiary Formations of the West,' p. 874, pls. 56 & 57 (1883). † *Op. cit.* p. 870.

‡ "Bestehen die unteren Backzähne anfangs aus zwei getrennten Schmelzlamellen, welche erst später mit einander verwachsen, so dass ein wesentlicher Unterschied zwischen zusammengesetzten und schmelzfaltigen Zähnen der hasenartigen Thiere nicht zu machen ist." Monatsber. d. K. preuss. Akad. d. Wiss. zu Berlin. Sitzg. v. 14. Dec. 1865, p. 673 (1866).

These teeth, as a whole, exhibit in younger stages a greater longitudinal diameter than in the adult; this is notably the case in *Titanomys* (Pl. 37, figs. 7, 10, 24), and is chiefly due to the greater development and independence of the terminal cusp (*t*).

The youngest mandible of *Titanomys* which I possess is a left ramus of *T. Fontannesii* (Br. Mus. Geol. Dep. M5267 *b*), figured Pl. 37, fig. 10. P. 2 and m. 3 have dropped out. Flanking the three corners of the alveolus for p. 2 are visible the small alveoli for the roots of deciduous teeth; the anterior and the postero-external seem to belong to d. 2; the postero-internal was presumably occupied by the anterior root of d. 1. P. 1 is still in the socket and had not yet come into use. Both the principal lobes composing this tooth are surrounded by enamel; but the wrinkled central surfaces of the lobes are composed of dentine, with the exception, perhaps, of the summits of some of the wrinkles, which, to judge from their shining appearance, may bear a very slight coating of enamel\*. In p. 1 and the true molars of *adult Titanomys Fontannesii*, the enamel bordering appears interrupted in the middle of the anterior margin (Pl. 39, fig. 6 *a*). Hilgendorf has recorded a similar instance of the absence of the enamel bordering on the inner half of the anterior border in the lower cheek-teeth, p. 2 excepted, of *Lepus*†. The anterior transverse lobe of p. 1 (fig. 10) still shows traces of having been divided originally into an outer and an inner cusp and of the "paraconid" on its anterior border; vestiges of the latter are visible also on p. 1 of a slightly older individual (fig. 16, of the right side), and on m. 2 of the same right ramus. The terminal cusp *t* ("hypocoonulid") is present in both p. 1 and m. 1 of the younger specimen (fig. 10), as well as in p. 1, m. 1, and m. 2 of the second individual (fig. 16), and in p. 1 of a third (fig. 21, right side). In the left ramus, exhibiting the complete series of five cheek-teeth (fig. 7), *t* is present in all of them. In p. 1 of *T. visenoviensis* (fig. 25) it is remarkably large, although partly fused with the posterior lobe; and it is equally present on the posterior border of m. 1 and m. 2 of the second specimen of *T. visenoviensis* (fig. 24); so that, contrary to what has been stated by former writers, the cuspidule in question may be present in all the four anterior cheek-teeth of this species.

Passing on to the recent representatives of the family, it may be seen from fig. 22 (Pl. 37.), of an immature *Caprolagus hispidus*, that p. 1 nearly approaches p. 2 in its anterior complication. The two principal lobes are not yet connected on the inner side by a dentinal isthmus, but are merely held together by cement; the anterior lobe is distinctly composed of an outer and an inner cusp, the latter being more pointed and slightly higher than the former. The anterior border of the tooth presents two minor cusps, an outer and an inner, the median odd cusp of p. 2 being absent. Both the lobes show a very marked wrinkling of their surface. As in p. 2, *t* is apparent on the posterior margin of the second lobe.

Two very distinct minor cusps are likewise visible on the anterior border of p. 1 of the

\* We have here an instance similar to that recorded by Hensel in *Mus decumanus, rattus, musculus, sylvaticus, agrarius*, and *minutus*, where in perfectly unworn molars "überzieht der Schmelz die Höcker der Zahnkrone niemals vollständig, sondern lässt an den Spitzen das Zahnbein frei hervortreten." Zeitschr. d. deutsch. geol. Ges. viii. pp. 283, 284, pl. xiii. figs. 2, 3 (1856.)

† Sitzungsber. Ges. naturf. Freunde zu Berlin, 14 Jan. 1884, p. 23.

Rabbit (fig. 8); the first lobe of the same is mainly composed of an outer and an inner cusp, separated by a median hollow; the second lobe is wrinkled as in p. 2 of the same species. The minor cusps, though less distinct, are visible also in m. 1 and m. 2 of the Rabbit, in m. 2 almost vanishing. I have noted their presence in the true molars of young specimens of other species as well (*Lepus europæus*, *Lepus* sp. from China, *Sylvilagus brasiliensis*): *t* is generally present in unworn deciduous teeth, in premolars, and in molars of several Leporidae.

To sum up the above as regards the lower cheek-teeth, p. 2--m. 2. An original arrangement into outer and inner cusps, separated by a median longitudinal valley, is traceable in the lower molars of Lagomorpha generally. It is more distinct in the anterior cheek-teeth, and persists throughout life in p. 2 of most genera in both families; it is less distinct, though perfectly perceptible, in true molars, in which it very soon disappears by wear, being replaced by the transverse arrangement. In p. 2 we have to distinguish between an older complication and secondary additions; the increase in the plication alone is present in the posterior cheek-teeth, the anterior cusp not. On comparing adult stages of p. 2 of *Titanomys* with the corresponding tooth of all other Lagomorpha which, on the whole, are more recent forms, the latter appear to be more complicated; but in young stages p. 2 of *Titanomys Fontannesii* presents also a complicated appearance. This cannot be an incipient complication, for that part of the shaft of the tooth which is situated on the opposite end of the pulp-cavity is, as a matter of course, always the oldest. Hilgendorf has found the interruption of the enamel border on the inner side also of lower molars of *Lepus*\*, a fact which points towards a degeneration of this part of the tooth, and would seem to call for a compensatory increase on its outer side. However, I am not aware of a perceptible additional increase on the outer side of lower molars of more recent forms, as compared with older ones †.

Upper molars are more progressive than lower as concerning occasional additions. An ingenious explanation of this general occurrence is given by Winge in the following remark:—"The explanation of the maxillary teeth making a larger increase than those of the lower jaw is in all likelihood the following: they are placed in an unmovable bone, where the conditions for nourishment are more favourable than in the comparatively slender and movable mandible" ‡. In our special case an increase of the lower molars in the transverse direction can be the more dispensed with, since in the Leporidae the movement of the jaws is chiefly lateral. This will not be denied by any one who has ever examined the shape of their glenoid cavity or watched a Rabbit or Hare chewing. Moreover, the dentine of both upper and lower cheek-teeth shows unmistakable signs of this movement, in the presence of transverse striae, due to the action of the transverse enamel crest of the opposite tooth.

It remains to discuss in some detail the last molar, m. 3, about which very divergent views have been put forward.

\* *Op. cit.* p. 23.

† Neither am I aware of lacunæ on the *internal* enamel bordering of any Lagomyidae; but I must add that no sections were made.

‡ Vidensk. Meddelelser naturhist. Forening i Kjøbenhavn f. Aar. 1882, p. 17 (1883).

Fig. 7, Pl. 37, shows this tooth in place in a left mandibular ramus of *Titanomys Fontannesii*. It is not a simple cylinder, as in *Lagopsis* and *Lagomys*, but is composed of two lobes, a larger anterior one and a small posterior, attached to the former in the same manner as in the anterior molars the terminal cusp (*t*) is attached to the lobe preceding it, viz. separated from it by cement, only in the upper part. For this reason, and because the anterior lobe of m. 3 shows traces of greater complication, I homologize the posterior lobe of this tooth with *t* of the anterior molars; the anterior lobe of m. 3 would then represent *both* the principal lobes of the anterior molars.

When discussing the tooth-formula of *Titanomys*, allusion was made to Filhol's suggestion that the terminal cusp of m. 2 of *T. visenociensis* might be the representative of m. 3 of the recent *Lagomys*, in the specimens of the former where this is missing. "Si cette opinion est juste, on pourrait en tirer comme conclusion qu'à un certain moment, sur les animaux voisins des *Lagomys*, il y a une tendance à la simplification du système dentaire, d'abord par la fusion de la dernière dent avec l'avant-dernière, et ensuite par la tendance à la disparition de cet élément soudé"\*. Filhol here ignores the circumstance that all the anterior teeth have this "troisième lobe" as well, while in their case we have not at our disposal an occasional small isolated tooth to suggest a fusion theory. Besides, as was said before, this theory may be at once disposed of by a glance at our fig. 7, showing m. 2 with a well-developed terminal cusp (*t*), m. 3, the supposed homologue of this latter, being likewise present. Other figures also (figs. 10, 16) show m. 2 with the terminal cusp, together with the alveolus of m. 3.

As will be seen further on, Schlosser seems to incline to the opinion that the presence of a terminal cusp in m. 2 of *T. visenociensis* is an indication of m. 3 having become fused to m. 2; for he says that m. 3 of *Lagopsis verus* may be the analogue of the terminal cusp (*t*) in m. 2 of *Titanomys* †. It is, however, difficult to make out what meaning he wishes to attach to this vague term "Analogon".

*Lagopsis*.—The type-specimen, Hensel's *Lagomys verus* ‡, has five lower cheek-teeth, the last being a small cylindrical tooth, precisely as in the recent *Lagomys*, to which *Lagopsis* is closely related. The tooth in question was not complete in Hensel's specimen, but a fragment seems to have remained inside the alveolus; else he would have presumably used the term "ausgefallen," whereas he says, speaking of the condition of this tooth, that it is broken away ("weggebrochen").

Three more or less complete mandibular rami, from Deggenhausen, Elgg, and Hohenhöven respectively, are mentioned by H. v. Meyer, and drawings of their teeth, found among H. v. Meyer's MSS. have been reproduced by Schlosser §. They show an agreement in their p. 2 with Hensel's *Lagomys verus*, and Schlosser therefore concludes ||, rightly, I think, that they are of the same species. He further deems it not improbable ¶ that *Lagomys æningensis*, H. v. Mey., from Æningen may be identical with *Lagomys*

\* Ann. Sc. Géol. x. p. 28 (1879).

† 'Nager des europ. Tertiars.' p. 32 (1884).

‡ Zeitschr. d. deutsch. geol. Ges. 1856, p. 688, pl. xvi.  
figs. 12, 13.

§ *Op. cit.* p. 31, pl. viii. figs. 40, 46, 49.

|| *Op. cit.* pp. 31, 32.

¶ *Op. cit.* p. 32.

*verus*, Hens." That this is true with regard to the Eningen specimen in the British Museum has been shown on p. 462. I can affirm the same for the Seyfried specimen \* at present in the Constance Gymnasium, where I examined it and found it to have the characteristic  $\overline{p.2}$  of *Lagopsis verus*. With regard to the Karlsruhe specimen †, since the shape of its  $\overline{p.2}$  cannot be clearly made out from H. v. Meyer's figures and description, the true position of this "*L. eningensis*, H. v. Mey.," cannot be satisfactorily determined for the present. It might quite as well be a *Titanomys Fontannesii*. In the former, as well as in the specimens from Deggenhausen, Elgg, and Hohenhöven, no last molar ( $\overline{m.3}$ ) could be seen; as, however, this tooth is very caducous, its absence in the fossils is not in the least conclusive; it may have dropped out and the alveolus been filled with matrix. Nor does Schlosser attach any great weight to the absence of this small tooth in the three specimens drawn in H. v. Meyer's MSS.; this, however, for reasons with which I completely disagree. "Auf das Fehlen des letzten einfachen Backzahnes bei den drei von H. v. Meyer gezeichneten Exemplaren darf wohl nicht allzuviel Gewicht gelegt werden. Es ist nicht unmöglich, dass auch hier, wie bei *Titanomys visenoviensis*, im normalen Kiefer nur 3 zweilobige Molaren vorhanden sind, und dass daher der stiftförmige m. 4" (meaning m. 3) "des Hensel'schen Originales als Analogon des bei *T. visenoviensis* abnorm vorkommenden Lobus des m. 3" (meaning m. 2) "betrachtet werden muss." ‡

This whole statement is somewhat vague; the author seems to assume (1) that in *T. visenoviensis* both the m. 3 and the third lobe (*t* in my figures) of  $\overline{m.2}$  occur only abnormally; (2) that in "*Lagomys verus*" the presence of  $\overline{m.3}$  is equally an abnormal occurrence. From these two assumptions the inference is drawn that m. 3 in the type of *Lagomys verus* is the analogue of the equally abnormal third lobe in m. 2 of *T. visenoviensis*. Schlosser concludes by saying that he is almost inclined to consider the presence of  $\overline{m.3}$  as a juvenile character, and that this tooth is caducous (hinfällig). This is very probably true with regard to *T. visenoviensis*, and I have myself suggested it in the preceding pages. But it is decidedly erroneous with regard to  $\overline{m.3}$  of *Lagopsis verus*, as are all the other suggestions tentatively put forward in the passage quoted. With regard to *T. visenoviensis*, the matter has been fully discussed above. As to the  $\overline{m.3}$  of *Lagopsis verus*, in all my specimens from La Grive-Saint-Alban, either the tooth itself or its very distinct alveolus is present (Pl. 37, figs. 14, 26). Depéret, too, has before figured a mandibular ramus of *Lagopsis verus* from the same locality, showing the  $\overline{m.3}$  §; and Biedermann has described this same tooth in specimens from Elgg.

*Prolagus*.—There is no third inferior true molar,  $\overline{m.3}$ , in this genus; m. 2 is composed of three lobes, the posterior connected with the middle one by cement, in the same way as the latter is with the anterior one. From this circumstance Pomel concluded—just as Filhol has in the case of *Titanomys*—that in *Prolagus* m. 3 had become fused with  $\overline{m.2}$ . Of the *Prolagus oeningensis* of Sansan, he says:—"Ceux de Sansan différent

\* H. v. Meyer, "Fossile Säugethiere, etc., von Eningen," Fauna d. Vorwelt, p. 6, pl. iii. fig. 1 (1845).

† *Ib.* pl. ii. fig. 1.

‡ *Op. cit.* p. 32.

§ Arch. Mus. Lyon, iv. p. 164, pl. xiii. figs. 16, 16 a (1887).

encore, comme sous-genre, par la dernière molaire inférieure, qui a trois prismes par réunion de la cinquième molaire à la quatrième”\*. Fraas holds the same opinion †.

This theory would at first sight seem to be supported by what Depéret has found in the *Prolagus* of Roussillon. He figures two mandibular rami ‡, in one § of which he records five cheek-teeth, in the other || only four; and he goes on to say:—“ Cette différence est moins importante qu’elle ne peut sembler au premier abord; elle tient simplement à ce que le dernier prisme d’émail de la série dentaire est soudé au prisme précédent de la quatrième molaire dans l’une de ces mandibules, tandis que ce même prisme libre constitue une cinquième molaire dans la fig. 29. Cette soudure, qui se fait d’ailleurs uniquement par l’intermédiaire d’une certaine quantité de ciment, ne me paraît pas avoir l’importance qu’on lui a attribuée pour la distinction des deux genres *Lagomys* et *Prolagus*, puisqu’elle est variable suivant les sujets dans le petit Léporidé de Roussillon”¶.

I agree with Prof. Depéret that this difference has no great importance in the Roussillon jaws, though not for the reasons adduced, for I apprehend he is mistaken when he institutes comparisons with *Lagomys*, and considers that the isolated prism of his fig. 29 “constitue une cinquième molaire.” H. v. Meyer met with similar occurrences among twenty mandibular rami of *Prolagus oeningensis* (Kön.) from Steinheim, and refers to them in the following words:—“ In some instances one might be induced to believe that the posterior of the three prisms constituting the last molar is separated, so that the creature would have the character of *Lagomys*”; but he judiciously adds:—“ On closer examination, however, it can be seen that the posterior prism is included in the alveolus of the rest of the tooth, so that it evidently is part of the latter” (“ dass das hinterste Prisma nicht durch die Alveole von dem übrigen Zahn abgeschlossen ist, zu dem es daher offenbar noch gehört”)\*\*. Numerous mandibular rami of the *Prolagus oeningensis* from La Grive have passed through my hands, as well as from 600 to 700 of *P. sardus* from the Corsican and Sardinian ossiferous breccias and caves. Not unfrequently I found the third prism of  $\overline{m. 2}$  separated from the rest of the tooth; but by the criterion established by H. v. Meyer there could never be a doubt as to the interpretation, which invariably was that, either by fracture or by the weathered condition of the cement, the last prism had been separated from  $\overline{m. 2}$ ; as are likewise, though more rarely, separated from each other the two prisms of the anterior teeth. I do not doubt for a moment that the same explanation will hold good in the case of the Roussillon specimens. In *Prolagus* each of the prisms has its alveolar niche formed by two partial septa starting from the outer and inner alveolar border; but these must not be confused with the complete septum separating one alveolus from the other.

I consider the third prism of  $\overline{m. 2}$  of *Prolagus* to be the homologue of *t* of the

\* Cat. méth. et descr. Vert. foss. du Bassin de la Loire et de l’Allier, p. 43 (1853).

† Württemb. naturw. Jahresh. xxvi. p. 170 (1870).

‡ “ Anim. plioc. du Roussillon,” Mém. Soc. Géol. France, i. p. 57, pl. iv. (1890).

§ *Op. cit.* pl. iv. figs. 29, 29 a.

|| *Op. cit.* pl. iv. figs. 28, 28 a.

¶ *Op. cit.* p. 57.

\*\* Neues Jahrb. 1865. p. 843.

*Titanomys*-teeth; and that  $\overline{m. 3}$  having been lost in the former genus by some means or other, the terminal cusp of  $\overline{m. 2}$  has become enlarged in compensation. We have numerous analogies for similar occurrences, but we have none for the ever-recurring theories of fusion between tooth and tooth, which on closer examination always break down. This notwithstanding, we shall still hear of them, since they yield the explanation which lies nearest at hand.

Again, although *Prolagus* presents in its molars, at least in the upper ones, more primitive characters than *Lagopsis* and *Lagomys*, it cannot be considered to be the direct ancestor of these; for it cannot be surmised that a tooth— $\overline{m. 3}$ —after having been lost, reappears in a later genus. Hilgendorf regards  $\overline{m. 3}$  of *Lepus* as a recent acquisition, for he terms it “phylogenetisch der jüngste (Zahn)”\*; presumably for the same reason for which he considers the maximum of enamel-plication observed by him in upper incisors (of “*Lepus mexicanus*”) to be “phylogenetisch ein Extrem” †, because there is no trace of it “bei den fossilen Leporiden-Gattungen (*Myolagus*).” There is no good reason for considering the Miocene *Prolagus* (*Myolagus*) in the ancestral line of *Lepus*, simply because no true Leporidae have been found in the European Miocene; nor in inferring from the various primitive characters of *Prolagus* that the absence of  $\overline{m. 3}$  is a primitive character as well. Besides, Hilgendorf does not take into consideration the fact that *Lagopsis* and *Titanomys*, both of which are contemporaneous with and even partly (*T. risenoviensis*) older than *Prolagus*, possess a  $\overline{m. 3}$ . I presume that, for similar reasons, Hilgendorf would consider the  $\overline{m. 3}$  of *Lepus* a recent acquisition also; and here we must remember that the Oligocene *Palaeolagus* has both  $\overline{m. 3}$  and  $\overline{m. 3}$ .

Noack describes the last lower molar of young *Lepus saxatilis* as composed of two antero-posteriorly placed cusps, which seem (“scheinbar”) to be separate, but at any rate (“jedenfalls”) are only loosely connected, which makes it doubtful whether they ever coalesce to form a compact tooth. This conformation of  $\overline{m. 3}$  is in the author’s opinion a sufficient justification for the following generalization: “Jedenfalls ist im Unterkiefer von *L. saxatilis* noch die Tendenz zu 6 Backenzähnen vorhanden.” ‡ Why not, while we are at it, towards eight?—since it is stated immediately afterwards that the same partitioning of the two lobes is also visible in two of the anterior molars. The

\* Sitzungsber. d. Ges. naturf. Freunde Berlin, Sitzung v. 15. Januar 1884, p. 23.

† *Op. cit.* p. 20.

‡ Th. Noack, “Neue Beiträge zur Kenntniss d. Säugethier-Fauna von Ostafrika,” Zool. Jahrb. Abth. f. Syst. etc. vii. p. 545 (1893). The writer of this pamphlet has examined numerous dentitions of foetal and young Rabbits, and “*L. vulgaris*” (meaning *L. europaeus*), and finds among other things in their cheek-teeth cusps which are absent in the adult. So far, good. Apart from this, his descriptions and generalizations show on almost every line that he has approached this difficult subject without sufficient scientific training. Hilgendorf’s short sentence of 1865: “Die oberen Backzähne junger Hasen sind mit einer halbmondförmigen Schmelzröhre versehen, wodurch ein Übergang zu dem fossilen *Myolagus* gebildet wird,”—is of infinitely higher scientific value than the pages filled with laborious descriptions in the paper quoted. If the author had taken Hilgendorf’s words as a starting-point and a guide in the investigation of upper leporine cheek-teeth, he might have been able to do some useful work. He knows about tritubercular teeth; he also seems to be aware that on one occasion the molars of lagomorphous Rodents have been compared with those of diprotodont Marsupials, and that

numerous juvenile dentitions which were at the author's disposal might have shown him that the separation of the two lobes is characteristic of young stages in the inferior cheek-teeth of *Lepus* generally.

#### THE BONY PALATE IN THE LAGOMORPHINE SKULL.

The greatly reduced bony palate is considered to be one of the characteristic features in the skull of Lagomorpha. At first sight the only difference in this respect between Leporidae and Lagomyidae appears to be that in the latter family the palatal bridge is shorter than in Leporidae. On investigating the matter more closely, however, it may be seen that in Leporidae the bony palate is shortest in the genus *Lepus* s. str., viz. in those forms which are most specialized for running and leaping; and that the shortness is principally due to a reduction in length of the os palatinum. In Lagomyidae, on the contrary (Pl. 39, figs. 34, 36, "p"), the latter bone is comparatively elongate, while the part of the bony palate formed by the maxillaries (*m*) is greatly reduced, so that in some cases the latter do not even join in the middle line anteriorly, the middle of the anterior margin of the palatal bridge being formed by the palatine bones. As seen from the figures, *Prolagus* (fig. 36) is in this respect scarcely different from *Lagomys* (fig. 34).

It might, *a priori*, be expected that this specialization of the Lagomorpha will be reduced to a minimum, in other words that the bony palate will be longest, in the oldest members of the group, and this is in fact so. Cope describes this part of the skull of *Palaeolagus* as follows:—"The palatine bones are flat and occupy more than half the palate between the molars. Their common suture is at least as long as that of the maxillaries, and extends as far forward as the posterior border of the second molar. From this point the anterior suture extends to the posterior border of the third molar. The palatal notch is rectangular, and is not wider than the palatine bone on each side of it."\*

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some phylogenetic speculation has been based thereon. The author avails himself of these two types, the tritubercular and the diprotodont, in tracing *two* primitive types in the teeth of *one* species, *Lepus saxatilis*; the anterior upper cheek-tooth is referred to the tritubercular type; the conformation of the two anterior lower teeth, on the other hand, "decidedly suggests the molars of Kangaroos and Wombats, and makes it probable that the ancestors of the Lagomorpha were Marsupials, holding about the middle between *Phascolomys* and *Lagorchestes*" (p. 545). By the cheek-teeth of its ripe embryo, the Wild Rabbit is far removed from *Lepus europaeus* (p. 553); and the cheek-teeth of the latter were evolved from the tritubercular type (p. 551). The rabbit's skull approaches the Marsupial type (p. 551). The author seems to be unaware of the existence of deciduous cheek-teeth in the Leporidae. On p. 549, the anterior of the upper cheek-teeth is twice termed p. 1. Supposing that we have really to do with a premolar, the anterior premolar in the upper series would be p. 3, according to Hensel's mode of writing, adopted by the present writer, or p. 2, according to the usual custom, but under no circumstances p. 1. Considering, however, that the two teeth referred to by Prof. Noack belong, the one to a mature, the other to an unripe embryo of *L. europaeus*, in which species the tooth-change takes place only some time after birth, the alleged p. 1 is in reality a d. 3 (d. 2 of authors). On pp. 544 and 545 the remarkable circumstance is noted that in the half-grown *L. saxatilis* the second and third anterior upper cheek-teeth are more retarded in their development than the same teeth in embryos of *L. europaeus*. The very obvious explanation is that those of the former species are premolars, those of the latter deciduous teeth.

\* E. D. Cope, 'The Vertebrata of the Tertiary Formations of the West,' i. p. 875 (1876) pl. lxvi, figs. 1, 4 (1883).

The only known palate of *Titanomys* is that figured by Filhol\*, which too is elongate. According to him †, the length of the palatal bridge in *Lagomys* and *Titanomys* respectively is as follows:—

	millim.
<i>Lagomys tibetanus</i> .....	0.002.
<i>Lagomys ogotona</i> .....	0.0015.
<i>Titanomys risenoviensis</i> ...	0.0015.

The suture between the palatines and maxillaries is not shown in the figure of *Titanomys*. Thanks to the kindness of Mons. M. Boule, I have been able to examine the original in the Paris Museum, and can state that in this oldest member of the Lagomyidæ the family character is already very evident in the reduction of the maxillaries, inasmuch as the palatines occupy the anterior margin of the bridge in the middle line, the two maxillaries not joining each other. The difference in the length of the palatal bridge between *Titanomys* on the one side, and *Lagomys* (with *Prolagus*) on the other, is therefore wholly due to the greater elongation of the former's palatine. In *Palæolagus* ‡ both bones are lengthened, as compared with other Leporidae, and especially with the most modernized species of the family. The anterior palatal notch formed by the maxillaries extends forward slightly beyond the anterior margin of p. 3, as it does in *Nesolagus Netscheri* (Pl. 39. fig. 38), which is one of the most primitive of recent Leporidae. The posterior palatal notch of *Palæolagus* reaches as far backward as a line uniting the middle of the alveoli of m. 1. Besides, the horizontal portion of the ossa palatina is also transversally much less reduced than in most of the recent Leporidae, the breadth of the posterior palatal notch being approximately equal to half the breadth of the space between it and the alveoli. While in this latter character *Palæolagus* converges towards the Lagomyidæ, or rather goes beyond them—for, to judge from the figures, the palatal notch of *Palæolagus* is considerably narrower than even in *Titanomys*—it is thoroughly leporine with regard to the part which the maxillaries take in the formation of the bony palate.

Those among recent Leporidae which, on account of their several primitive characters, may be placed in a separate section (*Caprolagus*-group), as opposed to *Lepus* s. str., are more primitive also in the character of the greater antero-posterior length of the palatal plates of the palatine and maxillary bones, as may be judged from various instances figured in Pl. 39. Fig. 32 represents the palate of *Caprolagus hispidus* (Pears.); fig. 33, of *Sylvylagus (Romerolagus) Nelsoni*; fig. 37, the same part of *Oryctolagus crassicaudatus* (Geoffr.); fig. 38 that, already mentioned, of *Nesolagus Netscheri* of Sumatra. It is well known that the bony palate of the Rabbit, of which a figure is not given here §, has a greater longitudinal extension than in the Common Hare and that its palatal notch is narrower; both these characters are much more pronounced in the young. Fig. 35

\* H. Filhol, "Étude des Mammifères fossiles de Saint-Gérard-le-Puy (Allier)," Ann. Sc. Géol. x, pl. 3, fig. 16 (1879).

† *Op. cit.* p. 31.

‡ Cope, *op. cit.* pl. lxvi, figs. 1, 4.

§ Excellent lower views of skulls of the Rabbit, side by side with those of *Lepus europæus*, have been figured by H. v. Nathusius ('Über die sogenannten Leporiden,' pl. ii. 1876).

(Pl. 39) represents these parts of a young *Sylvilagus brasiliensis* (Linn.), which closely resembles *Palæolagus* in the great antero-posterior extension of both the palatine and the maxillary bones and in the very narrow palatal notch, both coming near to the normal condition of Mammals.

As might have been expected, the Pliocene *Lepus valdarnensis*, Weith., also presents a more normal palatal region than the various specialized species of *Lepus*, and may for this reason alone be assigned to the *Caprolagus* section. The anterior and posterior palatal notches are much narrower than in *L. europæus*, and the whole of the bony palatal bridge is considerably longer; this being especially due to the elongation of the maxillaries\*.

The greater reduction of the palatal plate of the maxillary bone in Lagomyidæ, as compared with Leporidæ, might seem to be due to the greater backward prolongation of the foramina incisiva in the first-named family. On closer examination, however, it becomes evident that in reality we have to do with a fusion of two originally separated vacuities, viz. the true foramina incisiva, and a sort of palatal fontanelle behind them. In *Lagomys*, the premaxillæ generally, though not in all the species, join in the middle line between the foramina incisiva and the fontanelle behind them; in Leporidæ, the confluence of the two fissures has generally, but not always, become complete. An approach to Lagomyidæ (fig. 36) is given by the bottle-shaped appearance of the "foramina incisiva" which Bangs considers to be characteristic of "*Lepus sylvaticus transitionalis*"†—the same occurs also in other American Leporidæ—and which is but the remnant of the original separation of the true foramina incisiva from the palatal fontanelle. I therefore do not think that Winge is right, when he assumes that the separation of the two openings is a secondary character in *Lagomys*, brought about by the new formation of a bony plate‡. Judging from Cope's figure §, the fusion of both openings seems to have already taken place in *Palæolagus*. But if we judge from recent forms, in which the premaxillæ are very thin in this region, it appears probable that the apparent fusion in the figured palate of *Palæolagus* is due to the defective preservation of the premaxillæ in the figured specimen.

#### ON THE LIMB-SKELETON OF LAGOMORPHA.

There is a great difference between the Lagomyidæ and Leporidæ, and between the various members of the latter, in the absolute length of the fore and hind limbs, and in their relative length, compared with each other. The differences, moreover, are not only in size; and it is the antibrachium which in the first place presents notable divergences in the different groups. Even for systematic purposes it will be necessary henceforth to take into consideration these, as well as other, parts of the skeleton; and we cannot content ourselves with such general statements as "hind limbs longer than the fore limbs," and "hind limbs and fore limbs subequal."

\* A. Weithofer, in Jahrb. k.-k. geol. Reichsanstalt, Bd. xxxix. p. 80 (1889).

† Proc. Bost. Soc. Nat. Hist. xxvi. p. 407 (1895).

‡ H. Winge, 'Jordfundne og nulevende Gnavere,' &c., l. c. p. 113: "Forskjellen fra Haren er kun, at det egenlige *F. incisivum* er afskilt ved en nyopstaaet, ikke altid fuldstændig Benbro."

§ *Op. cit.*, pl. lxvi. fig. 1.

In comparing the characters of the common Hare (*L. europæus*) with those of the domesticated Rabbit, Nathusius enters into full particulars of the differences presented by the antebrachium, summing them up in the following statements:—

<i>Hare.</i>	<i>Rabbit.</i>
Ulna weaker than the radius, situated behind the latter.	Ulna stronger than the radius, situated laterally.

In relation to the basilar length of the skull and the length of the vertebral column, the anterior and posterior limbs are in their totality, as well as in their different parts, *longer* in the Hare, *shorter* in the Rabbit.

<i>Hare.</i>	<i>Rabbit.</i>
Humerus longer than antebrachium.	Humerus and antebrachium subequal in length.

Length of the antebrachium as compared with the tibia:—

<i>Hare.</i>	<i>Rabbit.</i>
Antebrachium shorter than the tibia by about one-fourth its length.	Antebrachium shorter than the tibia by one-half its length*.

With regard to the remarkable differences in the antebrachium of the two animals, the writer concludes that they are doubtless associated with their different habits, the Rabbit burrowing and the Hare living above-ground †. Put in this general way, the conclusion is undoubtedly true. Nathusius, however, does not seem to have been aware that the difference is chiefly due to the specialization of the *Hare's* fore-leg, which specialization is nothing else than the beginning of the process carried much further in the modern swift-footed Ungulates. It therefore remains to be seen how far, if at all, the structure of the Rabbit's antebrachium is a consequence of its burrowing propensities,—an adaptation to them. For neither from what we know of its habits, nor from the structure of its fore-limb, can the Rabbit be considered to be a truly fossorial Mammal, as is, *e. g.*, the Mole, or, among Rodentia, the genera *Geomys*, *Spalax*, and *Siphneus*.

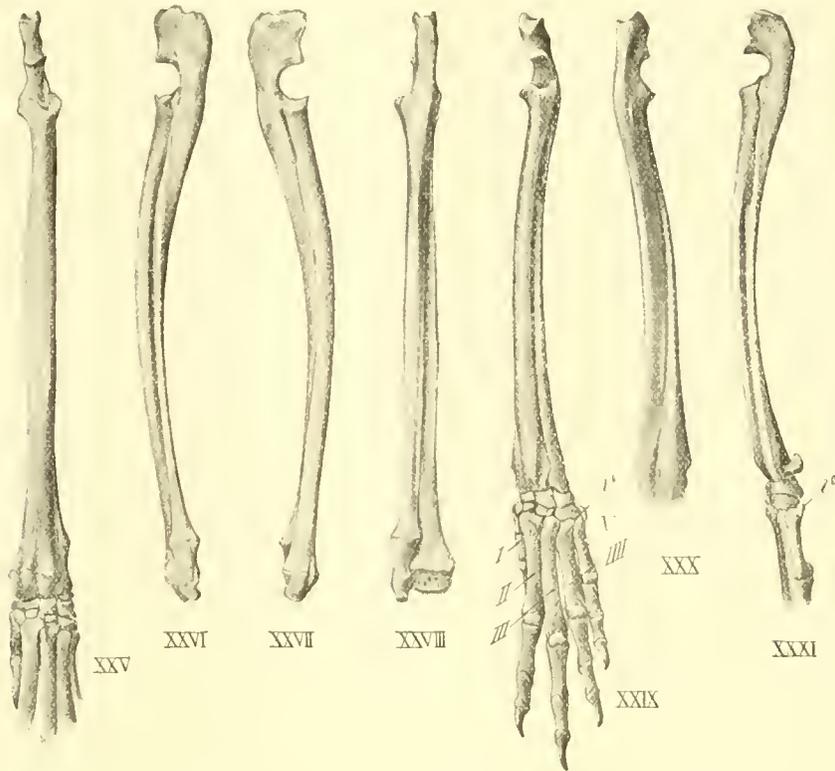
In districts where the Rabbit finds burrowing in the ground too hard a task, it manages to do without it ‡; as it sometimes does, perhaps, for other unknown reasons.

\* H. v. Nathusius, 'Über die sogenannten Leporiden,' pp. 17, 31-33, 67, figs. 2-5 (p. 32) 1876.

† *Op. cit.* p. 33.

‡ W. Thompson states (Proc. Zool. Sec. London, part v. p. 52, 1837) that in the North of Ireland persons who take Rabbits make a distinction between the *Burrow-Rabbit* and the *Bush-Rabbit*, and that the latter is so designated in consequence of having a "form like the Hare, and which is generally placed in bushes or underwood." The Rev. G. T. Dawson, speaking of the Wild Rabbit, says:—"There is a variety . . . which never burrows in the ground, but lies beneath bushes, or among the herbage of hedges or woods, and is called by the common people of that part of Hertfordshire which borders upon Bedfordshire the *Bush-Rabbit*, and in the northern parts of the same county the *Stub-Rabbit* . . . A non-burrowing Rabbit may, in its distress, scramble into a hole, or burrow, if there happens to be one in its way, in which to die in secrecy; but, as far as my own observation extends, I never remember one

One of my principal reasons for separating a certain number of Leporidæ, under the designation of *Caprolagus*, from the swift-footed *Lepus* (figs. XXV-XXVIII), is the



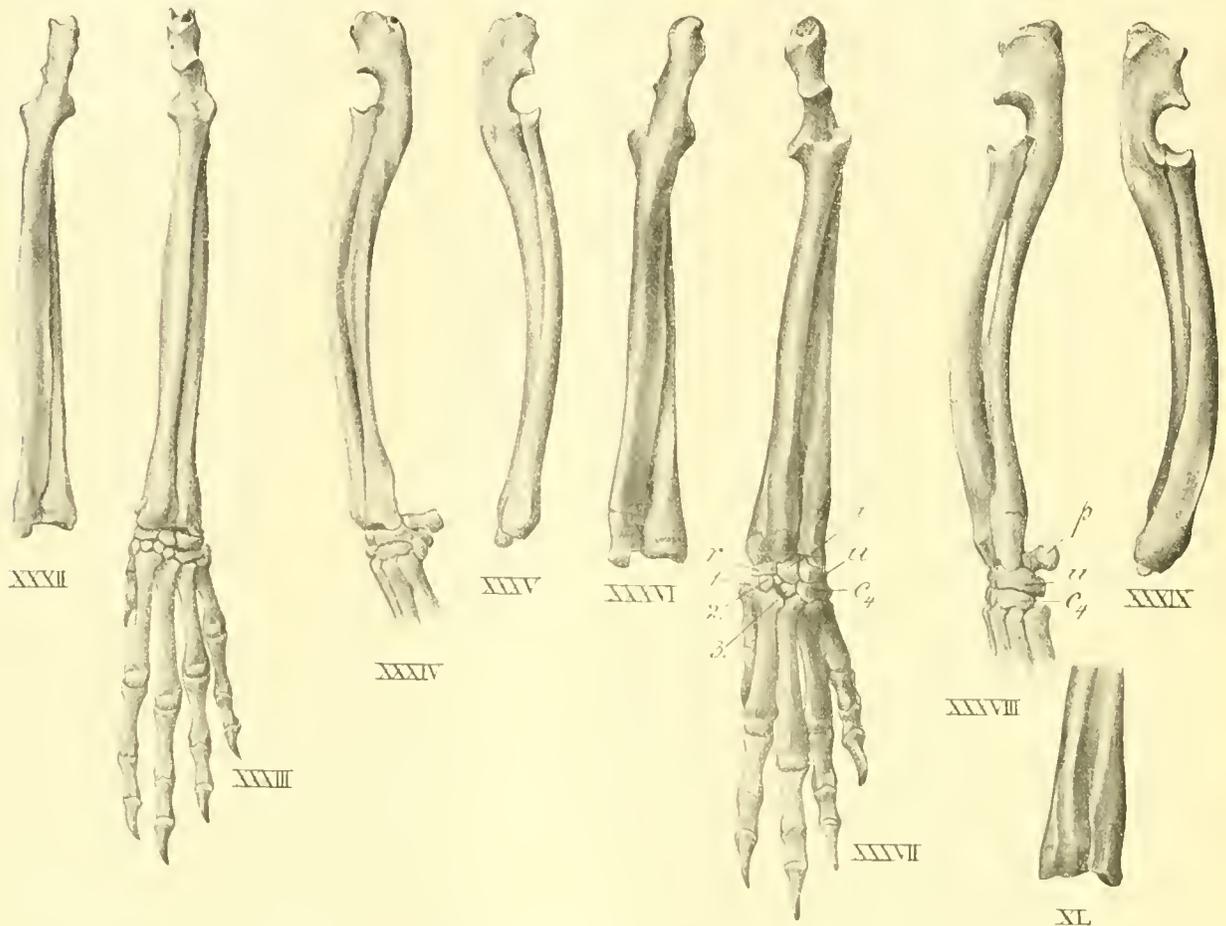
Figs. XXV-XXVIII. Left antibrachium of *Lepus timidus*, Linn. (*L. variabilis*, Pall.),  $\frac{1}{3}$  reduced. XXV, front view; XXVI, ulnar (external) view; XXVII, radial view; XXVIII, posterior view.

Figs. XXIX-XXXI. Left fore-limb of *Sylvilagus brasiliensis* (Linn.), nat. size. XXIX, front view. I-V = first to fifth metacarpals, v = carpal 5 (vesalianum); XXX, radial view; XXXI, ulnar view.

structure of the antibrachium; but of several of the former it is expressly stated that they do not burrow at all, or at least that they are not habitual burrowers. I have thought it would be instructive for my present purpose to record the observed facts of the physiology of the organs of locomotion of various Lagomorpha, by collecting as much information as is available to me.

of the *bush-rabbits* running to ground, even when wounded, and certainly it is contrary to its habits to do so under different circumstances" ('Zoologist,' iii. p. 903, 1845). In W. Thompson's 'Natural History of Ireland' (vol. iv. p. 30, 1856), his former statement is repeated, and strengthened on the authority of Dr. R. Ball, "who has long been aware of the difference of habit and appearance between burrow- and bush-rabbits in the County of Cork." In Bell's 'History of British Quadrupeds' (2nd ed. pp. 344, 345, 1874) it is reported that "on moors, where the soil is wet, Rabbits often refrain from burrowing, and content themselves with runs and galleries formed in the long and matted heather and herbage. In more than one instance we have known a family to take possession of a hollow tree and ascend its inclined and decayed trunk for some distance." In comment on this, Prof. Howes has drawn my attention to the fact that the Oriental Black-necked Hare (*L. nigricollis*) habitually resorts to the hollows in trees when pursued, and that while the European Rabbit may bring forth its young above-ground ('Zoologist,' ser. 3, vol. i. p. 18) the Hare may do so in a burrow.

Of *Oryctolagus crassicaudatus*, which, in the conformation of its antibrachium (text-figs. XXXII–XXXV), is almost identical with *O. cuniculus* (Pl. 38. fig. 30), Smith says in a general way that it inhabits “rocky situations” in South Africa, and that “its manners connect it closely with the Rabbit.”\* Alexander Whyte describes the same species in his journey through the high-lying country in the North Nyasa district, and he



Figs. XXXII–XXXV. *Oryctolagus crassicaudatus* (Geoffr.).—Left fore-limb, nat. size. XXXII, posterior view; XXXIII, front view; XXXIV, ulnar view; XXXV, radial view.

Figs. XXXVI–XL. *Caprolagus hispidus* (Pears.).—Left fore-limb, nat. size. XXXVI, posterior view; XXXVII, front view: *r*=radiale, *i*=intermedium (lunar), *u*=ulnare. 1–3=carpalia 1–3. *C*<sub>4</sub>=carpale 4 (hamatum). XXXVIII, ulnar view: *p*=pisiform; XXXIX, radial view; XL, front view of antibrachium, proximal end.

too compares it with the Rabbit †. But nowhere have I found it expressly stated that this species is burrowing; the rocky “situations” and “places” to which, according to both observers, it is confined, certainly would not favour burrowing propensities.

\* A. Smith, in *S. Afr. Quart. Journ.* vol. ii. p. 87 (1833) (sub “*Lepus rupestris*”).

† “Perhaps the most interesting mammal we secured was the hare of the plateau, and which might well be termed a ‘rock-rabbit.’ . . . It is very local and peculiar in its habits, confining itself to the highest and most rocky places on the plateau. On this account we found it most difficult to procure good specimens. It kept dodging about the granite boulders, and we seldom got a shot until it was quite close on to us. . . . It was never found out in the open . . . .” (*British Central Africa Gazette*, 15th Oct. 1895 to 1st Feb. 1896, p. 22.)

Of the "*Lepus brasiliensis*" of Paraguay, whose fore-limbs (text-figs. XXIX–XXXI) much resemble those of the Rabbit, D'Azara states expressly that it is not a burrowing animal\*, and the same is confirmed by Rengger †.

About the habits of *Sylvilagus sylvaticus*, the "Grey Rabbit" of the United States, we know from Bachman that "though it digs no burrows in a state of nature, yet when confined it is capable of digging to the depth of a foot or more under a wall in order to effect its escape" ‡. *S. artemisiae*, closely related to *S. sylvaticus*, is described by Clark as burrowing §.

Special recognition is due to the following graphic description by Coles of the locomotion of three different groups of Hares, viz. the Marsh-Hare (*S. palustris*), the "Wood-Rabbit" (*S. sylvaticus*), and the "Jackass Hares" (*L. callotis*). Comparing in the first place the two former, he says:—"The Marsh-Rabbit . . . looks smaller, although actual measurement does not show any very decided difference in size. This deceptive appearance is owing to the different gait . . . The animal's gait . . . is a direct consequence of the comparative shortness of its legs—of the hinder ones particularly . . . The animal's general configuration is more squat and bunched; it seems to run with its body nearer the ground ||, scuttles along with shorter, quicker steps, more constrained and spasmodic, moving by jerks, as it were; and has little or nothing of the free bouncing movements that mark the progress of the Wood-Rabbit. In these respects the last-named species is exactly intermediate between the Marsh-Rabbit and the large "Jackass" Hares (*Lepus callotis*) of the West, in which length of stride, height of bound, and general freedom of swinging gait reach an extreme. These Western Hares are the swiftest of their tribe in this country, and the Marsh-Rabbit is just the opposite. As attested by all observers, the speed of the latter is appreciably less than that of even

\* "Il ne fouille point de terriers, quoiqu'on dise, qu'étant poursuivi, il se cache sous des troncs pourris et entre les débris des végétaux." ('Essais sur l'Hist. nat. des Quadrupèdes de la Province du Paraguay,' ii. p. 58, 1801).

† J. R. Rengger, 'Naturgeschichte der Säugethiere von Paraguay,' 1830.—"Höhlen oder unterirdische Gänge gräbt es keine" (p. 248). "Sein erster Lauf ist schnell; er halt aber nicht lange aus und wird bald von den Hunden eingeholt" (p. 250).

‡ Journ. Acad. Nat. Sci. Philad. vol. vii. p. 335 (1837). The following statement as to the feeble endurance in running of *S. sylvaticus* is almost identical with what Rengger says of *S. brasiliensis*:—"Although it runs with considerable swiftness for a short distance, yet it soon becomes wearied, and an active dog would overtake it, did it not retreat into some hole of the earth, into heaps of logs or stones, or into a tree with a hole near its roots. . . . In the Northern States, where the burrows of the Maryland marmot and skunk are numerous, this hare retreats to their holes" (*op. cit.* p. 328).

§ "Wherever the thorny clumps of chapparal and the loose sandy soil afford protection to this smallest of rabbits, it may be found in great numbers. No matter when or where one of these may be seen, a clump of chapparal or its burrow seem always at hand; thus it does not travel far, and a few jumps bring it to a place of safety. . . . The burrows usually run into sand hillocks formed around bushes: sometimes, however, they are dug into the bare compact surface." (J. H. Clark, in Spencer F. Baird, 'Mammals of N. America.—Part ii. Special Report upon the Mammals of the Mexican Boundary,' p. 48, 1859.)

|| Cf. also Bachman on *Sylvilagus palustris*: "Instead of leaping like the common Hare, it runs low to the ground, darting through the marsh in the manner of the Rat." (J. Bachman, "Deser. of a new Species of Hare found in South Carolina," Journ. Acad. Nat. Sci. Philad. vii. p. 196. Read May 10th, 1836.)

the Wood-Rabbit, though it certainly appears to get over the ground quite cleverly, particularly to one who has just missed, by under-shooting, a running shot" \*.

The most remarkable member of the family, as to its habits, is the "*Romerolagus Nelsoni*, Merr.," from Mount Popocatepetl, Mexico, of which it is stated:—"This singular animal has exceedingly short hind legs, and instead of moving by a series of leaps, like ordinary rabbits, runs along on all fours, and lives in runways in the grass like the meadow-mice" †. Mr. E. W. Nelson, the discoverer of this creature, has furnished the following further particulars:—"A search under the overhanging masses of long grass-blades showed a perfect network of large arvicola-like runways tunneling through the bases of the tussocks, and passing from one to another under the shelter of the outcurving masses of leaves. It was evident that the rabbits were very numerous here . . . So far as observed, these animals are strictly limited to the heavy growth of saccatan grass, between about 3050 and 3650 meters . . . They make their forms within the matted bases of the huge grass tussocks, by tunneling passage-ways along the surface of the ground through the mass of old grass leaves and stems, and then hollowing out snug retreats within the weather-proof shelter thus obtained" ‡.

I am unfortunately unacquainted with the limb-skeleton of this interesting animal. Although from the foregoing description it results that it cannot be considered a burrowing animal, I venture to anticipate that its ulna will be found at least as little reduced as in the common Rabbit, and not placed behind the radius.

Hodgson § gives the following information on the habits of *Caprolagus hispidus* (Pears.):—"The Hispid Hare is a habitual burrower, like the Rabbit; but, unlike that species, it is not gregarious, and affects deep cover, the pair dwelling together, but apart from their fellows, in subterranean abodes of their own excavation . . . Less highly endowed with the senses of seeing and hearing than the Common Hare or Rabbit, and gifted with speed far inferior to that of the former or even of the latter species, the Hispid Hare is dependent for safety upon the double concealment afforded by the heavy undergrowth of the forest || and by its own burrow, and accordingly it never quits the former shelter, and seldom wanders far from the latter, whilst the harsh hair of its coat affords it an appropriate and unique protection against continual necessary contact with the huge and serrated grasses, reeds, and shrubs in the midst of which it dwells, and

\* Elliott Coues, "Observations on the Marsh-Hare," Proc. Boston Soc. of Natural History, xiii. pp. 87, 88, 89 (1869).

† C. Hart Merriam, "*Romerolagus Nelsoni*, a new Genus and Species of Rabbit from Mount Popocatepetl, Mexico," Proc. Biol. Soc. Washington, x. p. 169 (1896).

‡ *Op. cit.* pp. 169, 170.

§ B. H. Hodgson, "On the Hispid Hare of the Saul Forest," J. A. S. Bengal, xvi. 1, pp. 573, 574 (1847).

|| By later writers it is denied that *C. hispidus* is an inhabitant of the forest. Blanford ('Fauna of British India,' Mammalia, ii. p. 454. 1891) says:—"According to Hodgson the Hispid Hare inhabits the *Sâl* forest, whilst Jerdon states with more probability that it is found in the Terai (that is, of course, the marshy tract usually thus called), frequenting long grass and bamboos &c." Jerdon's words are:—"It frequents jungly places, long grass, and bamboos, and, from its retired habits, is very difficult to observe and obtain" (T. C. Jerdon, 'Mammals of India,' p. 226, 1867).

dwells so securely that it is seldom or never seen even by the natives, save for a short period after the great annual clearance of the Tarai by fire; and they tell me that it feeds chiefly on roots and the bark of trees, a circumstance as remarkably in harmony with the extraordinary rodent power of its structure as are its small eyes and ears, weighty body, and short strong legs, with what has been just stated relative to the rest of its habits. The whole forms a beautiful instance of adaptation without the slightest change of organism"\*. Even if it had not been expressly stated, I would have concluded from the structure of the fore limbs (text-figs. XXXVI-XL) that the Hispid Hare is a burrowing animal: in fact, the only member of the family whose organization betrays fossorial propensities.

Nothing is known about the habits of the Sumatra Hare, *Caprolagus* (*Nesolagus*) *Netscheri* †. From the structure of its fore limbs, Pl. 38, fig. 28, it may be safely inferred that it is a bad runner, and it may be an occasional burrower; but it is certainly much less fossorial than *C. hispidus*.

The mode of locomotion of *Lagomys* (*L. pusillus*) is thus described by Pallas:—"Incedunt *L. pusilli* elumbi et subsultante gressu, sed propter brevitatem pedum, maxime posteriorum, neque celeriter currunt, nec nisi inepte exsiliunt. In posticos pedes raro eriguntur" ‡. Winge concludes from this that "the mode of locomotion is therefore the same as in *Lepus*." Besides, he thinks it probable that the ancestors of *Lagomys* have been better runners than the recent species; this, on account of the resemblance of the rump- and limb-skeleton between *Lagomys* and *Lepus*. Also, according to the same writer, some features in the skull of *Lagomys*, showing that the organs of smell and sight are less developed, point nevertheless towards a former different condition §. As seen from the figures (Pl. 38, fig. 20), *Lagomys* resembles ordinary Rodents and Insectivores in the lateral position and non-reduction of the ulna, and also in its comparatively short hind legs. This is the primitive condition. Are we, then, to assume that the ancestors of *Lagomys*, starting from this condition, reduced their ulna and shortened their hind legs, only to revert again to the former primitive condition presented by the living species? Equally far-fetched seems to me the supposition that the choanæ had formerly been wider and the eyes larger. Neither *Prolagus* (Pl. 39, fig. 36) nor *Titanomys* supports the former assumption, and there is no indication of larger orbits in *Prolagus*, nor of supraorbital processes in either of the two fossil genera. The statement, "incedunt *L. pusilli* elumbi et subsultante gressu," which recalls Coen's description of *S. palustris* ("scuttles along with shorter, quicker steps, more constrained and spasmodic, moving by jerks, as it were"), proves, in my opinion, an *incipient* stage of the leporine locomotion.

\* The view expressed in the latter part of the last sentence is not correct.

† H. Schlegel, "On an anomalous Species of Hare discovered in the Isle of Sumatra: *Lepus Netscheri*" ('Notes from the Leyden Museum,' vol. ii. note xii. p. 59, 1880).

‡ 'Nova Species Quadrup. e Glirium Ordine,' p. 35 (1778).

§ H. Winge, 'Jordfundne og nulevende Gnavere (Rodentia),' p. 113.

## FIFTH CARPAL RAY.

*The Pisiform.*

Krause describes the pisiform of the domestic Rabbit as articulating with the ulnare on its volar side\* ; in the description of the ulna †, it is stated that the distal termination of this bone has a condyle for the facet of the ulnare. These two statements imply that the pisiform of the domestic Rabbit articulates—as in Man—with the ulnare only. If they are correct, the German domestic Rabbits are different from those of this country; for in the English domestic and wild Rabbits I find the bone called pisiform articulating with the ulna as well as with the ulnare; this is the case moreover in all Leporidae (Pl. 38, fig. 2, text-figures XXXI, XXXIV, XXXVIII), in all Lagomyidae (Pl. 38, fig. 4), and in the great majority of Mammalia. In the Leporidae the pisiform, the proximal part of which extends considerably in a transverse direction on the volar side of the carpus, shows even two facets for the volar side of the ulna.

From the following statements it appears that the so-called pisiform of Mammalia is a compound bone.

Daubenton mentions three accessory bones in the carpus of *Hyllobates* and *Inuus caudatus*; one of them is, in *Hyllobates*, situated as follows: “il se trouve placé sur le joint qui est entre le troisième et le quatrième os du premier rang;” situated, therefore, on the articulation between the ulnare and pisiforme ‡. The carpal bones of *Inuus* are said to have the same position as in *Hyllobates*, only differing in their form §. In *Papio* the accessory bone in question is said to be wanting ||.

Cuvier's description is almost identical. Speaking of the “ossified nodules in the muscle tendons” of the carpus, he says:—“Il y en a deux par exemple, dans le gibbon et le magot: l'un dans le tendon du cubital externe, sur le joint du pisiforme avec le cunéiforme . . . manque dans les sapajous” ¶.

Leboucq describes and figures \*\*\* a case in the Gibbon:—“Chez un Gibbon (*Hyllobates leuciscus*) de la collection de l'Université de Gand, il existe entre le cubitus et le cubital du carpe un nodule osseux articulé latéralement avec le pisiforme (p'. fig. 28). Ce nodule me semble représenter le cartilage qui disparaît chez l'homme.” (Reference is here made to the previous description of a cartilaginous nodule which is constantly met with in human embryos of the third and fourth month.) “En même temps que le crochet terminal du cubitus s'accuse nettement, il se développe dans le ménisque embryonnaire un nodule cartilagineux elliptique, faisant suite d'une part à la pointe du crochet et de l'autre se dirigeant vers l'extrémité proximale de l'intermédiaire.” It disappears

\* W. Krause, ‘Die Anatomie des Kaninchens in topogr. und operativer Rücksicht,’ 2te Auflage, p. 120 (1884).

† *L. c.* p. 119.

‡ Buffon et Daubenton, *Hist. nat. gén. et partie.* xiv, p. 105 (1766).

§ *L. c.* p. 127.

|| *L. c.* p. 151.

¶ *Leçons d'Anat. Comp.* 2<sup>e</sup> ed. i. p. 425 (1835).

\*\*\* H. Leboucq, “Rech. sur la Morphologie du Carpe chez les Mammifères,” *Arch. de Biologie*, publ. par Van Beneden et Van Bambeke, v. p. 83, pl. iv, fig. 28 (1884).

constantly after the fourth month \*. Leboucq considers this cartilaginous nodule of the human fœtus the homologue of the ossicle in *Hylobates*; both are parts of the pisiform, the pisiform of human anatomy being, in his opinion, but the distal epiphysis of the complete pisiform †. In a later paper the cartilaginous nodule is homologized with the os trigonum (tarsi): “je crois donc pouvoir considérer ce nodule et l’os trigonum comme homologues” ‡, whence it would follow that the ossicle of *Hylobates* is equally the homologue of the trigonum.

The ephemeral cartilage of the human embryo has since been discovered in an ossified condition in a carpus of an adult, and received the name triquetrum secundarium §. Both this cartilage in the fœtus and the triquetrum secundarium occupy a more radiad position than the ossicle of the Gibbon, wherefore it would appear that they are not, after all, the homologues of the latter, and this is proved to be the case by the discovery by Kohlbrügge of *two* accessory ossicles in the Gibbon. In three specimens of the three species *Hylobates leuciscus*, *H. agilis*, and *H. Mülleri*, an ossicle is situated between the styloid process of the ulna, the pisiform, and the ulnare. It rests on the processus styloideus and articulates with it and the ulnare. The pisiform joins the carpus at the point of junction between the ossicle and the ulnare. Kohlbrügge recalls the description of Daubenton, in whose honour the ossicle is named (*ossiculum Daubentonii*); and he adds that Camper had seen it in the *Inuus* ||. In the carpus of a *Hylobates syndactylus* the following condition is described:—“Situated between the radius and the ulnare is an ossicle, which is joined to the radius and to the ossiculum Daubentonii by a fibrous ligament; between both is cartilaginous tissue.” The ossicle which, to all appearance, is that described by Camper in the Mandrill—and which has hence received the name *ossiculum Camperii*—was present in both hands of the Gibbon; in the left manus the ossiculum Daubentonii was reduced to a small osseous nucleus ¶. From its position, the ossiculum Camperii corresponds to the cartilaginous nodule discovered by Leboucq in the human fœtus, and is therefore the homologue of the triquetrum secundarium (triangulare) of Man \*\*. There can be no doubt that the ossiculum Daubentonii is the element which Leboucq has described in an adult *H. leuciscus*, since they occupy the same position. In Leboucq’s figure—dorsal aspect of the carpus—the pisiform (*p.*) has been removed backward, in order to bring it into evidence ††.

\* *Op. cit.* p. 81, pl. iii. fig. 17.

† *Op. cit.* p. 83.

‡ H. Leboucq, “Sur la Morphologie du carpe et du tarse,” *Anat. Anz.* i. p. 20 (1886).

§ Pfitzner, “Bemerkungen zum Aufbau des menschl. Carpus,” *Verh. Anat. Ges.* 7. Vers. in Göttingen 1893 (*Ergänzungsheft Anat. Anz.* viii. p. 191 (1893)).—See also *Morph. Arb.* iv. p. 508 (1895).

|| J. H. F. Kohlbrügge, “Versuch einer Anatomie d. Genus *Hylobates*” (*M. Weber, Zool. Ergebn. einer Reise in Niederländisch Ost-Indien*, i. pp. 338, 339, pl. xvii. fig. 9 (1890–91)).

¶ *Op. cit.* p. 339, pl. xvii. fig. 10.

\*\* The ossiculum Camperii (triquetrum secundarium, triangulare) or, as Thilenius terms it, os intermedium antebrachii, has been found in *Homo*, *Hylobates*, and *Inuus*, as mentioned in the text, and, by Pfitzner, in a carpus of *Phascotomyx*. Pfitzner’s specimen is figured and described by Thilenius (*Morph. Arb.* v. p. 9, pl. i. fig. 12 (1865)). I find what I take to be the same bone in Lemurs, Insectivora, and Rodentia, whereon more will be said in another place. (See *P. Z. S. London*, 1899, pp. 428–437.)

†† *Op. cit.* p. 101 (explan. of fig. 28).

Leboucq's view that the human pisiform is the homologue of the mammalian pisiform *minus* the ossicle he figures in the Gibbon receives confirmation by a discovery of Pfitzner's in the human adult carpus. He found in five cases a proximal process of the pisiform\*. To this "*pisiforme secundarium*" would correspond the "*ulnare antebrachii*" of Thilenius, met with in ten manus of five embryos, where it is situated volad and ulnad of the proc. styl. ulnæ, and proximally from the pisiform †. Both German authors take this element to belong to the same category as the os Camperii, viz. to be a carpal of a "preproximal series." We have, however, seen that Leboucq shows that the os Daubentonii, which in *Hylobates* is not unfrequently an independent ossicle, is contained in the mammalian pisiform. For my part, I see no stringent reason to assign this os Daubentonii to a "preproximal" series; from its position I consider it to be the first, proximal, carpal of the fifth ray, and it might therefore appropriately be designated as V. 1; it corresponds to the I. 1 on the radial side, the radiale marginale, which in *Echidna* actually articulates with the radius (Owen). In Reptilia, especially in Emydidæ, we frequently find an ossicle or a cartilage occupying the position of a V. 1. Its absence in the Urodela is easily explained by the reduction of the ulnar part of the urodele carpus, even the fifth digit being lost. The reduction of the ulna and the ulnad extension of the ulnare may account for its being, in Mammalia, generally situated on the volar face.

What, then, is the distal part of the mammalian pisiform? One might suggest, as the easiest expedient for getting rid of this embarrassing element, that it is V. 2, viz. the second carpal of the fifth ray.

But, besides there being, as we shall see hereafter, another competitor for this distinction, there is not the slightest evidence of the distal pisiform having at any time occupied a similar position. On the other hand, it shows evidence of a former greater complexity. In most, if not in all Mammalia, except Man and the Anthropoids, the pisiform is provided with a distal epiphysis; and in some there is more than that. In the Rodent *Bathyergus maritimus*, as described by Von Bardeleben, "... the præpollex and the postminimus are both very well developed. The latter consists of two bones, of which the proximal (*pi.p.*) is the true pisiform, and measures 5 millim. in length, while the distal is 7.5 millim. in length. We must therefore in the future distinguish a proximal from a distal 'pisiform,' and I regard the former as, in all probability, the carpal, and the latter as the metacarpal segment of the postminimus" ‡.

Two skeletons of *Bathyergus maritimus* are in the Natural History Museum, neither of them quite adult. In the older one, which is the original of Von Bardeleben's figure 3, the distal part of the pisiform is incompletely ossified, as shown in the figure; it is still completely cartilaginous in the younger specimen. A similar, more or less ossified distal

\* Morph. Arb. iv. p. 508 (1895). "Dieser Fortsatz war (in vier Fällen) proximal, und zugleich eher etwas dorsal als volar gerichtet. Seine plane Fläche stellt eine kontinuierliche Fortsetzung der Gelenkfläche des Hauptstücks dar; im Übrigen war der Fortsatz ringsherum durch eine tiefe Einziehung abgesetzt."

† Morph. Arb. v. p. 470 (1896).

‡ "On the Præpollex and Præhallux, with observations on the Carpus of *Theriodonmus phylarchus*," Proc. Zool. Soc. London, 1889, p. 260, pl. xxx. fig. 3, *pi.p.*, *pi.d.*; id. Verh. Anat. Ges. 3te Vers. Berlin (Ergänzungsheft) Anat. Anz. iv. p. 108 (1889).

pisiform I find in the hystriicine *Ctenomys* and in *Mus*, and it will probably be met with in many other fossorial and climbing Rodents.

What seems to be a remarkable adaptation of the distal pisiform to a special function is exhibited by the strong cartilage, which in *Pteromys* is prolonged to support the lateral membrane serving as a parachute. Thilenius makes of it an element of an antebrachial series, his "ulnare antibrachii" \*; but he is misled by Owen's much reduced figure of the skeleton of a "*Pteromys volucella*" †, in which the detached cartilage has been drawn proximally to the pisiform and separated from it by a small interspace. The true connection of this cartilage was already known to Buffon ‡. He described it as a bone; but in the only skeleton (*Pteromys magnificus*) at the Natural History Museum in which this element is preserved it is perfectly cartilaginous, and as such it is described by Owen in *Sciuropterus volucella* §. In *Pteromys magnificus* it is chiefly attached to the distal end of the pisiform, and, by a much smaller process, to the tuberosity of the fifth metacarpal. Its direction is in the beginning right backward, in the prolongation of the long axis of the osseous pisiform; but gradually it turns upward, forming in its entirety a semicircle. It might be maintained that the patagial cartilage of Sciuropterini is in origin quite extraneous to the pisiform, and that it has only secondarily become supported by this widely projecting bone. With the scanty material at my disposal, I am not in a position to follow up the matter closer, nor is this the place to do so. A clue might be obtained from young specimens of *Iteromys*; and if they should show both the usual pisiform epiphysis and the patagial cartilage, they would support the view of an extraneous origin of the latter.

The lengthened subcylindrical bone which in the insectivore *Chrysochloris* extends from the carpus to the humerus, "simulating a third antebrachial bone," was considered, by Meckel ||, followed by Carus ¶, Peters \*\*, Giebel ††, and Dobson ‡‡ as an ossification of a tendon; regarded by the latter three as that of the m. flexor digitorum profundus. Cuvier §§, A. Wagner |||, Gervais ¶¶, and Owen \*\*\* homologize this bone with the pisiform.

\* Morph. Arb. (Schwalbe) v. p. 508 (1895).

† 'Anatomy of Vertebrates,' ii. p. 385, fig. 154 (1866).

‡ "Il y a de plus dans le polatouche un os (AA) long de 5 lignes, en forme d'arête ou d'éperon, qui tient au quatrième os du premier rang du carpe, et qui s'étend obliquement en arrière et en haut le long du bord de la membrane qui forme les ailes de cet animal." (Hist. Nat. gén. et partie. x. p. 113, pl. xxiv. 1763.)

§ *L. c.*

|| System d. vergl. Anat. ii. (2) p. 374 (1825). He calls the element "ein vom Streckknorren des Oberarmbeins zum Speichenende [it is, however, on the ulnar side] der Handwurzel gehendes, starkes, verknöchertes Band."

¶ " . . . ein dritter Knochen des Untergliedes, welcher jedoch nur als eine verknöcherte Sehne, oder vielmehr ganz verknöchert Muskel (*flexor carpi ulnaris*), anzusehen ist."—C. G. Carus, Erläuterungstafeln zur vergleichenden Anatomie. ii. p. 31. Taf. 9, fig. 19, b' (1827).

\*\* W. Peters, Naturw. Reise nach Mossambique, Zoologie, i. p. 72 (1852).

†† Giebel, in Bronn's Klassen u. Ordnungen, vi., v. p. 534 (1879).

‡‡ G. E. Dobson, 'A Monograph of the Insectivora,' p. 121 (1882).

§§ G. Cuvier, Leçons d'Anat. Comp. 2<sup>e</sup> éd. i. p. 426 (1835).

||| Schreber's 'Säugethiere,' Suppl. ii. p. 120 (1841).

¶¶ P. Gervais, Hist. Nat. des Mammifères, i. p. 252 (1854).

\*\*\* R. Owen, 'On the Anatomy of Vertebrates,' i. p. 392 (1866).

From the description given by Dobson, it becomes quite evident that from the distal end of this bone there arise tendons for the four digits, so that we have here a bone functioning as the common tendon of the flexor digit. prof. From this, however, it does not necessarily follow that it is an ossified tendon. (The pisiform of Man is imbedded in the tendon of the m. ulnaris internus; but scarcely any anatomist will to-day persist in considering it to be a tenontogenous sesamoid. It has been degraded to play the part of a "sesamoid" \*, and that only in Man and some of the Anthropomorpha.)

Dobson has figured the volar aspect of the carpus of a *Chrysochloris Trereelyani* †, in which the alleged ossification of the m. flexor prof. tendon has been removed. Here we see, ulnad from the lunar, the flattened face of a bone (*us.*), which is not referred to in the text; in the explanation of pl. xiii. fig. 5 it is termed the "ulnar sesamoid." Carus ‡ has seen and described this ossicle, and so have D'Alton sen. & jun. § The first-named states that the "ossified tendon" starts ("ausgeht") from it; both Carus and the D'Altons call it a pisiform ("Erbsenbein"); but, so far as I am aware, later authors, with the exception of Dobson, have overlooked it.

In a skeleton of *Chrysochloris aurea*, this so-called sesamoid articulates dorsad with the ulnare, dorsad and radiad with the lunar, proximally with the ulna, volad and distally with the "flexor dig. prof. ossification." The latter shows at the dorsal side of its distal base two facets, the larger ulnad one for the "ulnar sesamoid," the smaller radiad for a volar and distal projection of the lunar.

I take this "ulnar sesamoid" to be the ossiculum Daubentonii, viz. the basal part of the pisiform; but, owing to the distorted condition of the *Chrysochloris* carpus—the lunar articulates with both radius and ulna—and from my insufficient material, which consists in a single skeleton of one of the smallest species, I cannot state my case with greater certainty. If my view is correct, then the "tendon ossification" is in all likelihood the homologue of the distal part of the pisiform of other Mammalia, where it very often starts backward at right angles from the long axis of the limb, sometimes, as in *Hyllobates* ||, directly downward, and sometimes more or less upward, viz. in a proximal direction (*Talpa*). Which is the primitive direction I cannot for the present decide. The Chrysochloridae vary so much from one species to the other that Cope has divided them into three genera ¶; and we may hope that it will be possible to settle the question of the homology of this curious bone when the skeletons of these different forms shall have become available for comparison.

It appears to me that the distal part of the pisiform will prove to be a remnant of a lateral ray, which only secondarily entered into connection with the ulnare and the ulna. Of this lateral ray the other accessory distal elements of *Bathyergus*, *Ctenomys*, *Mus*, and

\* "Das Pisiforme spielt . . . die Rolle eines in der Sehne des Muskels (*flexor carpi ulnaris*) befindlichen Sesambeins," Gegenbaur, Lehrbuch d. Anatomie des Menschen, 6te Aufl. i. p. 422 (1895).

† 'A Monograph of the Insectivora,' pl. xiii. fig. 5 (1882).

‡ *L. c.*

§ E. D'Alton d. Ac. und E. D'Alton d. J., 'Die Skelete der Chiropteren und Insectivoren,' p. 22 (1831).

|| Kohlbrugge, *l. c.* fig. 10.

¶ 'American Naturalist,' xxvi. p. 126, footnote 1 (1892).

even the cartilage of Sciuropterini, possibly were parts. There is not the slightest evidence that the lateral ray has ever been a digit of the manus of the Tetrapoda.

*Carpale 5 (V. 3).*

The question whether there is some ground for assuming a central carpale (V. 2) in the fifth ray is closely connected with the present subject, so that it will be dealt with in this place.

I have known for a long time a comparatively large facet on the proximal ulnar side of Metac. V in two species of the fossil *Prolagus*, *P. oeningensis* (Kön.), and *P. sardus* (Wagn.) (Pl. 38, fig. 19, *v*), for which I could not account, the metacarpals of *Lepus*, which were at my disposal at the time, showing nothing of the kind. This same facet I have of late found to be present in *Lagomys* (*L. rufescens*), where it articulates with a small ossicle, which also presents a facet to the ulnare (Pl. 38, fig. 4, *v*). The ossicle is likewise present and has the same connections in *Sylvilagus brasiliensis* (text-figures XXIX & XXXI), *S.* sp. from Bogotá (Pl. 38, figs. 1, 2, *v*), and *Oryzolagus crassicaudatus* (text-figures XXXIII & XXXIV). In two other species (*Nesolagus Netscheri* and *Caprolagus hispidus*) the facets are visible, but the ossicle has been lost.

What is the ossicle in question?

As is well known, Gegenbaur was the first to express the opinion that the mammalian hamatum is a compound of carpalia 4 and 5, on the ground that in lower forms we find the fourth and fifth digits provided each with a separate carpale\*. Leboucq sees in the mammalian hamatum the homologue of carpale 4 only. "Le carpien 4+5 de Gegenbaur ne correspond exactement dans les premiers stades de développement qu'au métacarpien IV seul; le métacarpien V est placé latéralement par rapport à ce carpien. Le carpien 4+5 se sépare de l'axe au niveau de l'intermédiaire; quant au V<sup>e</sup> métacarpien, tout fait supposer que son rapport avec le dernier os de la rangée distale est secondaire chez les mammifères; primitivement c'est toujours avec le IV<sup>e</sup> métacarpien seul que ce carpien est en continuité. On ne voit à aucun stade de développement ce carpien formé de deux parties, ou présentant le moindre vestige de sa double origine. Où serait alors le carpien 5? En examinant les premiers stades de développement, non-seulement chez l'homme, mais chez les divers mammifères que j'ai pu étudier, on voit que le métacarpien V est placé en face de l'os cubital, mais séparé de lui par un interstice plus grand que celui qui sépare les autres métacarpiens de leur carpien correspondant. On peut admettre que c'est au niveau de cet espace que doit se trouver le carpien 5. Quant à déterminer ce qui doit représenter ce carpien, on peut admettre son absence complète, ou bien le considérer comme non différencié, et contenu virtuellement dans un des éléments squelettiques du voisinage: soit l'os cubital, soit le métacarpien V. L'hypothèse la plus probable serait de considérer le carpien 5 comme ne s'étant pas différencié à l'extrémité proximale du métacarpien V" †.

\* Untersuchungen z. vergl. Anatomie d. Wirbelthiere, i. pp. 45, 53, 121 (1864).

† "Rech. sur la Morphologie du Carpe chez les Mammifères," Arch. de Biologie, publ. par E. van Beneden et Ch. van Bambeke, pp. 92, 93 (1884).

In the following year Turner described and figured five distinct distal carpal bones in a Whale. After having mentioned that in *Mesoplodon bidens* "carpalia 4+5 formed a single bone . . . which was grooved on its dorsal surface opposite the interval between metacarpals IV and V," he proceeds to describe the carpus of an adult *Hyperoodon rostratus*. "The distal carpalia are five distinct bones, not so regularly faceted as those in the proximal row, and with a larger proportion of cartilage between them. These bones pass from the radial to the ulnar border in regular order, as C 1 to C 5, and each is associated with the metacarpal bone of its corresponding digit. A similar arrangement exists in both limbs, and the carpus possesses also an elongated pisiform cartilage, which in one is partially ossified" \*.

Von Bardeleben had previously made the following statement:—"Deutliche Anzeichen einer früheren Trennung in zwei Elemente zeigt das Hamatum bei den Beuteltieren, weniger auffallend bei den Nagern, sowie bei *Ziphius* (*Hyperoodon*). In zwei Stücke getrennt, aber, auf der einen Seite wenigstens, schon im Verwachsen begriffen, ist es an dem Skelete eines jungen Bären in Berlin." †.

To these assertions Baur replied that he had never in any mammalian embryo observed the hamatum to be the outcome of a fusion of two elements, and he adds:—"Wenn es bei älteren Thieren den Anschein hat, als wäre eine Theilung vorhanden, so ist dies eben etwas secundäres und ist morphologisch nicht verwendbar" ‡. In his latest utterances on the subject §, Von Bardeleben mentions only the separation of the hamatum in "*Ziphius* (*Hyperoodon*)," thus tacitly withdrawing the statements regarding other Mammalia, made at the meeting of the Jenaische Gesellschaft of May 15, 1885, above quoted, as well as in a subsequent meeting of October 30 ||.

The manus of the Jena specimen of *Ziphius cavirostris*, to which Von Bardeleben refers, has been described and figured by Kükenthal. It contains altogether three distal carpalia: the one resting on Metac. IV and V shows on its dorsal surface a delicate furrow, "eine zarte Furche als Andeutung einer früheren Trennung zweier Carpalia" ¶. This is what Von Bardeleben, in his "Referat," calls having found in *Ziphius* "eine natürliche Zerlegung des 'Hamatum' in das Carpale IV und Carpale V" \*\*, and further on: "Dass Ref. im Mai 1885 die primitive (vielleicht secundäre—jedenfalls dem Verhalten bei Urodelen entsprechende) Trennung des 'Hamatum' oder Carpale 4+5 (Gegenbaur) in Carpale 4 und Carpale 5 bei *Ziphius cavirostris* auf land (an der Hand des Jenaer Exemplars)." ††.

In his subsequently-published researches, Kükenthal describes fresh facts and sums up those previously recorded ‡‡. In embryos of *Beluga* and *Monodon* there sometimes

\* Journ. Anat. Physiol. xii. pp. 180, 183 (1886).

† Jenaische Zeitschr. f. Naturw. xix. (xii.), Suppl. ii. p. 87, Sitzung am 15. Mai 1885.

‡ Zool. Anz. 1885, p. 487.

§ Proc. Zool. Soc. London, 1894, p. 375; "Hand und Fuss," Verh. d. Anat. Ges. viii. pp. 263, 301 (1894).

|| Jen. Zeitschr. xix. (xii.), Suppl. iii. Sep.-Abdr. p. 78 (1885).

¶ Denkschr. d. med.-naturw. Ges. zu Jena, iii. pp. 38, 46, pl. iii. fig. 18 (1889). See also E. Rosenberg, *op. cit.* p. 2, footnote 4; Kükenthal, in *Morph. Jahrb.* xiv. p. 56 (1893).

\*\* *Op. cit.* p. 263.

†† *Op. cit.* p. 301.

‡‡ Denkschr. med.-naturw. Ges. Jena, iii. pp. 268-280 (1893).

occur five carpalia. An additional instance of five carpalia in an adult *Hyperoodon* is adduced from a specimen in the Royal College of Surgeons\*, and two examples in embryos of the same genus †. The reduction in the number of carpalia is explained by fusion or vanishing ("Schwund"); the fusion is brought about in two different ways:—"Bei den *Ziphioiden* verschmilzt das Carpale distale 5 mit dem C. dist. 4, es kommt also zur Bildung eines Hamatums; bei den *Delphiniden* verschmilzt das Carpale distale 5 mit dem Ulnare, oder aber es kommt überhaupt zu einem völligen Schwunde des ersteren, und seine Stelle wird vom Ulnare eingenommen." Transitions between both types of reduction occur in *Beluga* and *Monodon*.

In an embryo of *Emys lutaria*, of 8 mm. length, Rosenberg found in the place of one hamatum two completely-separated cartilages. "Der mehr ulnar gelegene ist etwas kleiner und steht ausser mit dem Ulnare und seinem radialwärts gelegenen Nachbar-element nur mit dem Metc. IV in Beziehung. Der andere der in Rede stehenden Knorpel trägt das Metc. IV; in seinem dorsalen Abschnitt wird er auch von dem Metc. III berührt, welchem übrigens sein eigenes Carpale zukommt. Es ist kein Zweifel, dass diese beiden ovoiden Knorpel die zu postulirenden Carpale 4 und Carpale 5 sind, die in typischem Verhalten zu ihren Metacarpalien vorliegen . . . es stellen daher das Carpale 4 und Carpale 5 in diesem Stadium vollkommen selbständige Elemente dar." In three larger embryos (10 mm.) the same investigator observed three stages of fusion of the carpalia in question. He considers that this result supports Gegenbaur's view with regard to the hamatum of Mammalia ‡.

Pfützner has given the name *Os Vesalianum* to an ossicle in the human carpus, first described by Vesalius, who considered it to be a sesamoid. It is situated on the ulnar side of the hamatum, and its distal facet touches the tuberosity of the fifth metacarpal §. Later on, he mentions two other cases in Man, one found by Gruber || and a third by himself ¶. In Vesalius' case, the ossicle articulated apparently with the hamatum and Metac. V. In Gruber's case "begann es vom Hamatum abzuwandern und sich dem Met. V enger anzuschliessen, mit dem es wahrscheinlich schon coalescierte." In Pfützner's own case finally, the ossicle had no more connection with the hamatum, and had undergone a synostosis with the Metac. V. Pfützner continues: "Als weitere Rückbildungsstufen haben wir wohl anzunehmen, dass es vom Met. V gänzlich assimilirt wird und in dessen Tuberositas aufgeht," a view which is confirmed by what Thilenius, who terms this element "Carpo-metacarpale 8," has found in the human embryo \*\*. Pfützner is of opinion "dass in gewissem Sinne das Os Vesalianum, namentlich in seiner ursprünglichen Lage, einem hypothetischen Carpale V zu entsprechen vermöchte." Like their predecessors, neither Pfützner nor Thilenius have met in the human carpus with a division of the hamatum into a carpale 4 and 5, in Gegenbaur's sense.

Pfützner's os vesalianum carpi occupies about the same position as the ossicle in

\* *Ibid.*, p. 278, text-fig. 11.

† *Ibid.*, text-figs. 12, 13.

‡ *Morph. Jahrb.* xviii. pp. 8, 9 (1892).

§ *Morph. Arb.* i. p. 756 (1892).

|| *Arch. f. Anat. Phys.* pp. 499, 500, Taf. xii. (1870).

¶ *Morph. Arb.* iv. pp. 543, 544 (1895).

\*\* *Ib.* v. pp. 488, 489 (1896).

Lagomyidæ and Leporidæ mentioned above. I am not aware that it has ever been recorded before in lagomorphous Rodentia; while it seems quite a common element in Mammalia provided with a well-developed fifth digit, at any rate in Rodentia, Insectivora, and Edentata, and was known to the older anatomists. Cuvier mentions it in the Great Armadillo (*Priodon giganteus*), and describes and figures it as situated laterad of the ulnare and articulating with the Metac. V\*. In the figure published by Flower †, it would appear to articulate with the ulnare as well. As to its presence in Rodentia, Cuvier remarks: "Enfin il y a très souvent aussi au bord externe du carpe, en dehors du cunéiforme et de l'unciforme, un os surnuméraire, petit et lenticulaire; on le voit dans le *castor*, le *porc-épic*" ‡. It is figured in a carpus of the *Castor* §. In the 'Leçons d'Anatomie comparée,' mention is again made of this "os surnuméraire" in the *Hystrix*: "... il y a un os surnuméraire entre le pisiforme et l'os métacarpien du cinquième doigt; il est attaché sur l'os crochu" ||.

Thilenius ¶, quoting Cuvier's figure of the *Castor* carpus, is inclined to consider this ossicle as his (Thilenius's) "ulnare externum" = the ulnar part of Pfitzner's triquetrum bipartitum of the adult, found in the human embryo \*\*. He adds, however: "Infolge der radialen Verschiebung des Carpale (4+5) erreicht es indessen auch das Metac. V." The question is whether, when an os vesalianum is present, the hamatum is really displaced, or is not rather in its original position; only secondarily either supplanting the vesalianum, or acting in a compensatory manner for it, when the latter is either displaced or has disappeared. When comparing Thilenius's figures 11 and 12 of this "ulnare externum" †† with figures 13 and 14 ‡‡, representing a later stage, the impression is conveyed that in the latter this ulnare externum (*ue*) has been displaced proximally by the ulnar extension of the hamatum. A secondary *proximal* displacement of a carpal (or tarsal) would, however, be quite unusual, and Thilenius has expressed some doubt §§ whether the figures mentioned all represent the same bone. In fig. 11, where *ue* abuts upon Metac. V, the former element might be Pfitzner's vesalianum (carpo-metacarpale 8, Thilenius). The text-figure XXXIV of the present paper seems to exclude the possibility, ventilated by Thilenius |||, that "vesalianum" and "ulnare externum"—which have not yet been found together in the same manus of Man—might represent one and the same bone. The enormous ulnar and volar expansion of the ulnare, as shown for the Lagomorpha in this figure (XXXIV)—which occurs in other Mammals also—leads to the assumption of its being a compound of an ulnare + ulnare externum Thilen. The "ulnare externum" (= ulnar part of triquetrum bipartitum Pfitzn.) would then be the second (central) carpale of the fifth ray (V. 2).

Meekel has described the os vesalianum in *Erinaceus*:—"Der *Igel* hat in der oberen, weit breitem Ordnung vier Knochen. Kahn- und Mondbein sind zwar verwachsen,

\* Oss. foss. v. 1, p. 127 (1823).

† 'An Introduction to the Osteology of Mammalia,' 3rd ed. fig. 110 "a," p. 307 (1885).

‡ Oss. foss. v. 1, p. 48 (1823).

§ *Ib.* pl. ii. fig. 10.

|| Leçons d'Anat. comp. 2de éd. i. p. 427 (1835).

¶ Morph. Arb. (Schwalbe), v. pp. 508, 509 (1896).

\*\* Morph. Arb. v. pp. 473, 474 (1896).

†† Morph. Arb. v. pl. xxi (1896).

‡‡ *Ib.*

§§ *Ib.* pp. 489, 508.

||| *Ib.* p. 489.

allein das grosse dreieckige Bein trägt aussen und vorn einen kleinen, runden Knochen eingelenkt, den man ein zweites Erbsenbein nennen kann. Von den vier vordern ist das Hakenbein weit kleiner als gewöhnlich, und das dreieckige stösst daher aussen beträchtlich weit an den fünften Mittelhandknochen"\*.

Owen mentions the same ossicle in the Hedgehog, but more distally:—"A sesamoid is attached to the outside of the base of the metacarpal of the digitus minimus" †. In a left carpus of *Erinaceus europæus* lying before me, the ossicle articulates with both the ulnare and Metac. V, the facet for the latter being smaller and, as in *Prionou*, situated ulnad from the ulnare. The same bone is mentioned in *Gymnura* by Dobson ‡.

Referring to this ossicle, Leboucq says:—"Ce qu'on appelle 2<sup>e</sup> pisiforme, existant chez quelques mammifères (hérisson, tatou, etc.), n'est qu'un sésamoïde développé dans le tendon de l'extenseur cubital du carpe" §. It may be a matter of surprise that, in the same chapter in which Leboucq insists with strong arguments that the pisiform cannot be classed among "les os sésamoïdes," he casts aside with a few passing words this equally important bone. The explanation is to be found in the words "chez quelques mammifères;" the author being evidently not sufficiently acquainted with the "os vesalianum."

Having placed the facts before the reader, I have now to sum up. All the attempts (Leboucq, Baur, Rosenberg, Pfitzner, Thilenius) to trace ontogenetically the presumed fusion of carpalia 4 and 5 to form the "hamatum" have confessedly failed. Gegenbaur explains this negative result by supposing that the Mammalia inherited the "hamatum," from lower Vertebrates. This leads him to the assumption that the occasional occurrence of two separate carpalia (4 and 5) among Cetacea is secondary; the more so as we find other very considerable changes in the manus of these animals ||.

To this argument might be opposed the daily increasing number of instances brought forward in which we see primitive characters occurring precisely in those species, or in those organs, which in other respects are highly differentiated (specialized), the preservation of old characters being obviously due to the specialization of others. This by no means new truth was, if I am not mistaken, first enunciated by Haeckel.

In support of the foregoing, I wish to refer to a very noteworthy remark by Gegenbaur himself. In defence of certain conclusions arrived at in his well-known "Gliedermaassenskelet der Enaliosaurier" ¶, he states that in Sauropterygia and Ichthyopterygia the

\* System d. vergl. Anat. ii. 2, pp. 393, 394 (1825).

† 'Anatomy of Vertebrates,' ii. p. 390 (1866).

‡ 'A Monograph of the Insectivora,' p. 21 (1882).

§ Arch. de Biologie, v. p. 84 (1884).

|| "Die Einheitlichkeit des *Hamatum* der Säugethiere ist von mir als ein auf dem Wege der Phylogenese erworbener Befund erklärt worden, da in niederen Abtheilungen der vierte und fünfte Finger je ein discretetes Carpalstück besitzen. Da jener Erwerb durch Concreescenz bald auf die Säugethiere überging, möchte ich bezweifeln, dass im Carpus der Cetaceen der niedere Zustand noch zu erweisen ist, selbst wenn auch unter den vielerlei dort bestehenden Befunden ein Carpale 4 und ein Carpale 5 sich darstellt. Denn die übrigen Veränderungen sind in diesem Handabschnitte zu bedeutend, als dass ein *secundär* erfolgtes Zustandekommen eines dem ursprünglichen ähnlichen Verhaltens zweier distaler Carpalia ausgeschlossen wäre." (C. Gegenbaur, Vergl. Anat. der Wirbelthiere, i. p. 542, 1898).

¶ Jen. Zeitschr. v. (1870).

adaptation to a new function does not in any way explain the typical features of their limbs. "*Where we meet with similar adaptations, the original condition has never been completely effaced*" (italics mine)\*.

The undivided condition of the "hamatum" in terrestrial Mammalia can now be explained in a very simple and obvious manner, since by means of the "os vesalianum" we are enabled to show that the presence of a separate carpale 5 is not in the least limited to a few cases among Cetacea, but is a frequent occurrence in other Mammalia likewise, a circumstance which has hitherto either been wrongly interpreted or entirely overlooked. The "hamatum" of Mammalia is not carpale 4+5 of Reptilia, but it is a carpale 4 which, as a rule, has become enlarged, and has, in addition to its own functions, usurped those of carpale 5. Whether a usurpation is *in every instance* to be assumed is another question, which cannot be entered into here; it may, for the present, be sufficient to repeat that the superadded function of carpale 4 may often be not the cause but the consequence of the degradation of carpale 5.

Where carpale 5 is absent in the terrestrial Mammalia, it has, so far as my experience goes, either disappeared by atrophy, or become absorbed by the tuberosity of Metac. V, as in Man. Finally, therefore, since the fusion of carpale 5 with carpale 4 has never been observed in these, its occurrence may be peculiar to the Cetacea.

#### REMARKS ON THE METATARSUS AND TARSUS OF LAGOMORPHOUS RODENTIA.

1. *Metatarsale I and Tarsale 1*.—Krause states † that in adult Rabbits the os tarsale 1 becomes fused with the os Metatarsi I, and for this he refers to his text-figure 64 B. He continues as follows:—"In new-born animals, however (fig. 64 A), the tibial prominence of the proximal extremity of Metat. I is independent, and consists of an os tarsale and a lengthened distally-pointed bone, representing a rudiment of the hallux, at the distal end of which there is inserted the tendon of the m. tibialis autiens. In reality, therefore, the os tarsale 1 of the Rabbit is the o.t. 2 of Man, and the os Metatarsi I of the Rabbit represents the os tarsale 1, the hallux and os Metat. II of Man." So far as the fig. 64 A, "horizontal section of right hallux of a 12-days-old Rabbit," goes, this is correct, assuming that the two outline-figures of the tarsalia (1 and 2) are meant to show them in a cartilaginous condition. But the lettering of fig. 64 B, "right os Metat. I" (meaning Metat. II of comparative anatomists) of an adult

\* "... muss daran festgehalten werden, dass die Anpassung an eine neue Function keineswegs das Typische der Gliedmaassenform zu erklären vermag. Wo wir solchen Anpassungen begegnen, hat sich der ursprüngliche Zustand nie ganz verwischt. In der Flosse der Balacnen ist das Säugethierarmskelet klar zu erkennen, ebenso wie bei den Cheloniern die Schildkrötenextremität. Hier bei den Enaliosauriern ist auch gar nichts auf Reptilien Beziehbares am Flossenskelet vorhanden. Von der schon bei Amphibien vorhandenen Differenzirung von beiderlei Gliedmaassen nicht ein blosser Schein! Es müsste also an der Gliedmaasse ein Rückgang bis zu den ersten Anfängen erfolgt und von diesen her eine selbständige Ausbildung eingetreten sein, wenn Beziehungen zum Reptiliotypus hier einmal an der Gliedmaasse bestanden haben mögen. Jedenfalls gehören diese Bildungen nicht in die Reihe der Reptiliengliedmaassen, sondern unter die Anfänge, wie sie denn gerade in dem schon beregten Mangel des Differentwerdens von Vorder- und Hinterextremität sogar unterhalb der bis jetzt bekannten Reptilien sich stellen. So birgt sich in diesen Fragen ein interessantes Problem." (Vergl. Anat. der Wirbelthiere, p. 531.)

† W. Krause, Anatomie d. Kaninchens, 2<sup>te</sup> Aufl., p. 132 (1884).

Rabbit, from the medial side, is erroneous. The process I, "place of the real Hallux," is the tuberosity of the Metat. II; with this tuberosity neither the tarsale 1 nor the rudiment of the Metat. I come in contact, and therefore they cannot form a connection with it. The proximal process of Metat. II, numbered 1 (=place [*Stelle*] of the real os tarsale primum), represents instead the rudimentary Metat. I (see Pl. 38, figs. 5 and 6 I), which in young *Lepus* is distinct, but afterwards becomes fused with Metat. II. Tarsale 1 is visible in the young Rabbit in a cartilaginous condition\*, but in this species and in a *Sylvilagus* from Bogotá, in both of which I have been able to examine various stages, I have neither observed an ossification of it, nor a fusion with the rudimentary Metat. I, as assumed by Krause and by Leche. It gradually shrinks and apparently is absorbed†. It is quite possible that in some species a fusion may take place as a rule or exceptionally; but I deny it to have been demonstrated in the Rabbit, in which it is said to be the rule. Professor Howes informs me that he too has searched in vain for evidence of this.

2. *Fusion of Tarsale 2 with Metatarsale II.*—A fact hitherto not noticed in Lagomorpha is the fusion of tarsale 2, the mesocuneiform ( $c_2$  of my figures) with Metat. II. This fusion takes place in *Prolagus* (Pl. 38, figs. 17, 27 *a*), in *Lagomys* (Pl. 38, figs. 16, 26 ( $c_2$ )), and in some Leporidae. In *Nesolagus Netscheri* (Pl. 38, fig. 23), the figured specimen of which is not adult, the fusion is not quite complete; in the older specimen at the Leyden Museum I saw it was complete. In a specimen of *Sylvilagus brasiliensis* from Lagoa Santa, the property of the Copenhagen Museum, tarsale 2 is fused in the right limb and distinct in the left; in an incomplete limb of the same species in the Royal College of Science, London, the fusion is complete.

3. *Præcuneiforme.*—As in the case of the vesalianum carpi (see pp. 501–3), my attention was arrested by an accessory bone in *Prolagus sardus* through a small facet on the tibial side of the proximal termination of Metat. II, or rather of Metat. I, since, as shown before, this part is occupied in the young by the rudimentary Metat. I, which later on becomes fused with Metat. II (Pl. 38, fig. 17, *pc*; fig. 27 *a*, facet on the upper left side of Metat. II). This is the region which corresponds to the insertion of the muse. tib. posticus, and therefore the ossicle, indicated by the facet, is the so-called distal præhallux, or Baur's "klauenartiges Gebilde." Winge has denied the existence of this ossicle in *Lepus* and *Lagomys*‡, but I have found it in both families, and, as we shall see later, it has been met with as a rare occurrence even in *Lepus europæus*. In *Lagomys* it articulates (Pl. 38, figs. 15, 16, 26 *pc*) by a smaller facet with the navicular as well, and lies in the distal continuation of a much larger ossicle (fig. 26, *ti*), which articulates with the navicular and the astragalus. The latter is undoubtedly Baur's and Leboucq's "tibiale" (the proximal ossicle of Von Bardeleben's "præhallux").

I find the smaller, distal, ossicle in the following Leporidae, viz. in *Nesolagus*

\* See Leche, in Bronn's Klass. u. Ordn. d. Thier. vi. v. 28<sup>te</sup> Lief. pl. xcvi. fig. 3 (1885).

† Retterer (Comp.-rend. et Mém. Soc. Biol. (10) i. p. 807, 1894) regards the ossicle, which I with others hold to be a rudimentary Metat. I, as tarsale 1, denying all trace of the former. The presence of a cartilaginous tarsale 1 in young Rabbits is easy of observation, but presumably it was not yet chondrified in the stages examined by Retterer.

‡ II. Winge, "Jordfundne og nulevende Gnavere," E Museo Lundii, i. p. 169 (1887).

*Netscheri* (Pl. 38. fig. 23, *pc*); in *Oryctolagus crassicaudatus* (fig. 22, *pc*), where it seems on its way to undergo a synostosis with Metat. II; in *Caprolagus hispidus* (fig. 24, *pc*), where it has shifted its position completely to the volar side of Metat. II; in a specimen of *Sylvilagus brasiliensis*, from the Copenhagen Museum; and lastly in the Wild Rabbit, where the ossicle is very small and situated volad as in *C. hispidus*. I owe this specimen to Mr. Sherrin, Articulator in the Nat. Hist. Mus., who at my request dissected some Rabbits' feet, in search of the ossicle in question.

In his careful researches "Ueber den Säugetier-Prehallux"\*, Tornier met with this ossicle in one case only of all the Rabbits' and Hares' feet examined, and great stress is laid on this isolated occurrence. "Die Lage dieses überzähligen Knöchelchens beweist unwiderleglich, dass es selbst homolog ist dem Knochen welcher bei vielen der bisher untersuchten Tiere der 1-Medialseite gegenüber liegt. Da er an Hasenfüssen individuell auftritt und an jungen Kaninchen- und Hasenfüssen nicht vorhanden ist, so ist es zweifellos, dass er eine sekundäre Bildung ist, und daraus ist mit Sicherheit zu schliessen, dass er auch bei den Tieren, wo er immer vorkommt, eine sekundäre Bildung ist" †. And again: "Der muse. hallucis abductor-Knochen kommt endlich drittens zuweilen bei erwachsenen Vertretern solcher Thierarten vor, bei welchen der Knochen unter normalen Umständen weder im Alter noch während der Ontogenese vorhanden ist (*Lepus timidus*) ‡; bei diesen Individuen ist er—dagegen giebt es keinen Widerspruch—secundär entstanden" §. Therefore, as already stated in the first-quoted passage, he again asserts that the homologous bone in all other Mammals is equally secondary.

Even if the presence of the ossicle in question, as believed by Tornier, were limited to exceptional cases in one species of *Lepus*, the author's arguments would not be valid. It is one of the characteristics of these reduced "accessory" bones to ossify very late (Thilenius); and its exceptional appearance in *L. europæus* could, *a priori*, be interpreted quite as well in the sense of a disappearing element as in Tornier's sense. But the presence of this bone as a constant element in Lagomyidæ and several Leporidæ totally changes the aspect of the question. In the more primitive forms of Lagomorpha, the ossicle seems always to be present and proclaims itself a reduced element by its varying size and position. In those Leporidæ—of which *L. europæus* is the prototype—which are the most specialized for leaping, we must expect it to be of quite exceptional occurrence.

The ossicle has been observed in the "Hare" likewise by Pfitzner ¶, who calls it the *præcuneiforme*. As to whether this and similar accessory bones are to be considered as "secondary" or "sesamoids," Pfitzner has shown us the way how to proceed ¶, viz. that we cannot base our conclusions on the examination of a single specimen or a few species. The "præcuneiforme" has been studied by Pfitzner especially

\* G. Tornier, "Ueber den Säugetier-Prehallux. Ein dritter Beitrag zur Phylogense des Säugetierfusses." Arch. f. Naturgesch. 1891, pp. 115-204.

† *Op. cit.* p. 181.

‡ Meaning *Lepus europæus*, Pall.

§ *Op. cit.* p. 196.

¶ Morph. Arb. (Schwalbe) i. p. 533 (1892); iv. p. 354 (1895). Prof. Pfitzner has kindly informed me that the species is *L. europæus*, Pall.

¶ *Ll. cc.*; and Morph. Arb. vi. p. 394 (1896).

in the Carnivora (where it had been seen by Meckel); and of the Polecat alone he examined seventeen specimens. His conclusions are summed up in the following words:—"Skelet und Musculatur variieren unabhängig von einander, da findet kein Ineinandergreifen beider Processe statt, höchstens, und stets nur in beschränktem Maasse, ein gewisses Nebeneinanderherlaufen. . . Muskeln und Muskelansätze und Skelet variieren ohne innere Korrelation, und deshalb ist es für die Deutung eines bestimmten Skeletstückes ganz irrelevant, ob ein bestimmter Muskel sich daran ansetzt oder nicht. Das Præcuneiforme bleibt das Præcuneiforme, ob sich *M. tib. anticus* oder *M. tib. posticus* ganz, theilweise, oder gar nicht daran ansetzt, und für die Deutung eines Skeletstücks oder selbst seiner Komponenten, also für die etwaige Frage, ob andere Skeletstücke durch Assimilation mit ihm vereinigt sind, bleibt es ganz gleichgiltig und ohne jede Beweiskraft, welcher Muskel an ihm inseriert.—Aber auch mit den Bändern steht es nicht anders; auch sie variieren nach Vorkommen und Ausbildung ohne Rücksicht auf die Skeletstücke"\*. And Thilenius: "Die Beziehungen, welche die accessorischen Elemente der chiropterygialen Wirbelthiere zu Muskeln, Sehnen oder Bändern besitzen, sind nicht primäre Erscheinungen, sondern secundär während der Ontogenese erworben" †.

When the "tibiale" is not a separate bone, as in many Rodents, it is considered to be part of the navicular, the "tuberositas navicularis medialis" (Baur, Leboncq, Emery ‡). It does not seem to me to preclude the assumption of a medial tibiale, which would be a part or the whole of Emery's "paracentrale" §, the first element of the second ray (II, 1). If then the tibiale marginale (or externum) is the first element of the first ray (I, 1), the suggestion lies not far off that, like the distal "præpollex," the distal "præhallux" (præcuneiforme) is the second element (I, 2) of the same ray, but that it has generally been thrust out of the series.

4. "*Accessory ossicles" articulating with Metatarsal V.*—On Pl. 38, fig. 9, I have represented the enlarged figure of a right Metat. V. from La Grive, *a* from the dorsal, *b* from the volar side. This is still another instance of a fossil metapodial, presenting unusual articular facets, for which, for a long time, I was unable to account, for want of material for comparison.

The ossicle is much larger than the Metat. V of *Prolagus ævingensis*, which otherwise resembles it closely, exhibiting the same particulars as do the fifth metatarsals of *Prolagus sardus* and *P. sardus* var. *corsicanus*. I must leave it undecided whether the figured metatarsal belongs to *Titanomys Fontannesii* or to *Lagopsis verus*, which, judged from other parts of their skeletons, were both of about the same size.

On the volar aspect (*b*) is seen a large facet, starting from the proximal end and running obliquely in the direction of the tuberositas lateralis. In Leporidae I find in the

\* Morph. Arb. vi. p. 394 (1896).

† *Ibid.* v. pp. 544, 545 (1895).

‡ C. Emery, "Beitr. z. Entwicklungsgesch. u. Morph. d. Hand- u. Fuss skelets der Marsupialier;" (Semon's 'Forschungsreisen in Australien,' ii. pp. 394, 395 (1897).

§ C. Emery, "Die fossilen Reste von *Archeosaurus* und *Eryops* und ihre Bedeutung für die Morphologie des Gliedmaassenskelets," Anat. Anz. xiv. pp. 206, 207, figs. 3-7 (1898).

corresponding part no facet, but instead, either a convex swelling of the region, or in some cases, on the contrary, a more or less rugose depression. In *Lagomys* (*L. rufescens* and *L. melanostomus*) there is the facet in the same place, and articulating with it a comparatively large orbicular or triangular ossicle. I think it probable that, in those Leporidæ (*Caprolagus hispidus*, *C. Netscheri*, *Sylrilagus brasiliensis*) where the corresponding region of the Metat. V is raised to a convex protuberance, the ossicle in question has become fused with the former bone.

A similar ossicle has been met with by Pfitzner in Carnivora, viz. in *Ursus arctos* and in *Lutra* \*. I find the same ossicle in Cercopitheciidæ, in *Mus*, and, among Insectivora, in *Erinaceus*, *Gymnura*, *Myogale*, *Condylura* and Centetidæ (*Limnogale*, *Oryzoryctes*, *Microgale*). In the latter, and in *Myogale*, it is enlarged transversely and extends also on to the base of Metat. IV.

Pfitzner homologizes the ossicle in Carnivora with a similar one on the fifth metacarpal of Primates (os hamuli), and regards these and similar occurrences in the third tarsal ray (os unci, in *Felis*) as carpalia (or tarsalia) which have become "abortive," and have been secondarily displaced towards the volar side †. The question would then arise whether we have to consider the ossicle of the Metat. V as pertaining to the fifth or to the fourth ray; for from its position—and the same remark applies to the "os hamuli"—on the tibial side of the Metat. V, and sometimes articulating with Metat. IV also, it may belong to either. For the present the question cannot be settled; but since both tarsal and carpal elements in question are of apparently widespread occurrence, we may hope to get better acquainted with them before long. In the marsupial *Perameles obesula*, Metat. IV and Metat. V have each a separate plantar bone, articulating with their proximal capitulum ‡.

On the dorsal side of the tuberosity of Metat. V—on the left in fig. 9 *a*—is seen what appears to be a facet, partially extending to the volar side also. The same facet is present in both species of *Prolagus*. It at once recalls to mind what occurs on the Metat. V of *Prolagus* and *Lagomys*, and some Leporidæ, where carpale 5 (os vesalianum carpi) articulates with the tuberosity.

A distinct os vesalianum tarsi (Pfitzner) is a very rare occurrence in Man, in whom it has been seen by Vesalius, Gruber, and Spronck §. Pfitzner never saw it free; when distinct—one case figured by Vesalius, two described and figured by Gruber, one by Spronck—it is situated on the fibular side of the pes, "in the angle between the cuboid and Metat. V, articulating with both." An epiphysis which may occur on the tuberosity

\* Tageblatt der 60. Vers. deutsch. Naturf. und Aerzte in Wiesbaden, p. 251 (1887).—Speaking of the Bear, the author states that the ossicle occurs on the plantar base of Metacarpal V; from the context it would appear that this is a misprint for Metatarsal V; at any rate, in *Lutra* it is present on both Metacarpal and Metatarsal V, as stated by the same author.

† Morph. Arb. i. pp. 7, 8 (1891); 541, 542, 587 (1892); iv. p. 539-543 (1895).

‡ C. Emery, "Beitr. z. Entwicklungsgesch. u. Morph. d. Hand- u. Fuss skeletts der Marsupialia" (Semon's 'Forschungsreisen in Australien,' &c., ii. p. 381, Taf. xxxv, figs. 45, 46 (1897).

§ Morph. Arb. i. pp. 522, 595, 596, 756, 757 (1892); vi. pp. 472-475 (1896).

of the human fifth metatarsal is considered by Pfitzner\* as one of the terminal stages of its assimilation by the latter bone.

I find an epiphysis on the tuberosity of Metat. V in the Rodent genera *Georychus* and *Ctenomys*. The bone itself I have never seen independent, but, from what I have stated above as to the fossil metatarsal, there can hardly be a doubt that an ossicle articulates with the tuberosity. The cuboid of *Prolagus*, of which I have a number of specimens, shows a facet—absent in Leporidae—on the proximal fibular side; and this, together with the facet on the tuberosity of Metat. V, suggests the presence in these Lagomyidæ of either one ossicle articulating distad with the Metat. V and proximad with the cuboid, or two ossicles, the proximal of the two articulating with the cuboid, the distal with Metat. V; both possibly articulating originally also with each other at their apposed surfaces. Considering the rather considerable distance which must have occurred between the two facets, the latter hypothesis—of two bones—seems the more probable.

The presupposed proximal ossicle would be the homologue of the “os peroneum” (Pfitzner) of Man † and other Primates, which is the so-called sesamoid in the terminal tendon of the peroneus longus muscle. It has in Man, according to Pfitzner, a frequency of about 8-9%, and is situated on the postero-lateral end of the eminentia obliqua cuboidei. “Hier findet sich in den Fällen bester Ausbildung eine scharf abgesetzte Facette, der eine gleiche auf dem Peroneum entspricht” ‡. This os peroneum was seen by Daubenton in *Hylobates*: “Il y a de plus dans le gibbon un huitième os placé au côté externe du tarse, à l'endroit où le calcaneum touche au cuboïde” §. In the skeleton of a *Hylobates lar* in the Natural History Museum, there is to be seen an ossicle articulating with the cuboid; and it is of quite general occurrence among the Cercopithecidae. Gillette mentions it in Monkeys generally as articulating with the cuboid ||. Whether the ossicle mentioned by G. Fischer in the *Tarsius* is a vesalianum or a peroneum I cannot decide for the present. He says: “Auch findet man in den *Tarsern* noch ein überzähliges Beinchen, rund, linsenförmig, doch länglich, welches eigentlich auf dem letzten Mittelfussknochen aufsitzt, der sich immer mit seinem Kopfe weit nach hinten zieht” ¶. I see the “peroneum” in a minute ossicle in *Limnogale* (an aquatic member of the Malagasy Centetidae), adhering to the tendon of the muscle peroneus longus, laterally from the cuboid, and I believe the reason that it has not been more frequently seen in Mammals is that the muscle is generally cut away in preparing the skeleton.

\* Morph. Arb. vi. pp. 262, 263, 474 (1896).

† *Ibid.* i. pp. 530, 531, 594-598, figs. 12, 13 (1892); vi. pp. 456-462 (1896).

‡ *Ibid.* vi. p. 456.

§ Buffon-Daubenton, Hist. nat. gén. et partic. xiv. p. 106 (1766).

|| “Chez les singes, l'os sésamoïde du péronier latéral est très-volumineux, puisque, chez des individus de petite taille, nous l'avons trouvé au moins aussi gros que ceux du pouce de l'homme, constant et ayant la forme d'un trois-quarts d'ovoïde régulier; il possède une face véritablement articulaire, un peu convexe, et qui répond à une facette également encastrée de cartilage de la partie inférieure du cuboïde.” (Journ. de l'Anat. et de la Physiologie, viii. p. 533, 1872.)

¶ Gotthelf Fischer, ‘Anatomie der Maki,’ p. 154 (1804). This ossicle is not mentioned in Burmeister's ‘Beiträge z. näh. Kenntniss der Gattung *Tarsius*’ (1846).

The "peroneum" would then be homodynamous with the ulnare externum Thil. (ulnar part of Pftzner's triquetrum bipartitum), = V 2; and the vesalianum tarsi with the vesalianum carpi, = V 3, or tarsale 5, the cuboid being tarsale 4.

The cuboid of Mammalia is generally considered to be a compound of tarsale 4 + tarsale 5; but where an os vesalianum, or its traces on the tuberosity of Metat. V, are present such a supposition cannot, however, be admitted. Emery found in embryos and pouch specimens of the Marsupial genera *Didelphys*, *Epyprymnus*, and *Phascogaleus* separate tarsalia 4 and 5\*. For the former genus at least he has demonstrated that tarsale 4 and tarsale 5 become fused in later stages. This instance of a compound Mammalian cuboid (tarsale 4 and 5) is the only one in the literature which can be taken seriously; but it is quite possible that in other Mammalia too the vesalianum may be assimilated by the cuboid, instead of by Metat. V, as in Man and some Rodentia.

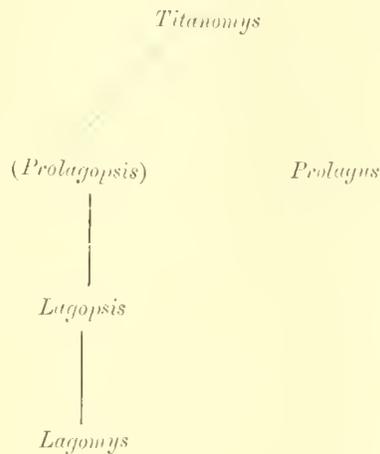
#### CONCLUDING REMARKS AND SUGGESTIONS AS TO CLASSIFICATION.

The oldest known lagomorphine genera, *Titanomys*, and *Palæolagus*, have several important characters in common: still, the differentiation into Lagomyidæ (*Titanomys*) and Leporidæ (*Palæolagus*) had already taken place. In the number of upper molars and in the shape and composition of the bony palatal bridge, *Titanomys* shows itself the precursor of the recent *Lagomys*, *Palæolagus* of the recent *Lepus*; and it is therefore advisable to retain the two groups as families, although they converge back in time. Moreover, in other characters—absence of supraorbital processes, pattern of the cheek-teeth—*Palæolagus* approaches nearer the Lagomyidæ than do the more recent Leporidæ. In the gradual transformation of their cheek-teeth, both groups, as has been amply demonstrated, run parallel from the Lower Miocene down to recent times. The Lagomyidæ, as at present known, start from a more primitive type than the Leporidæ, since in *Titanomys* the cheek-teeth have remnants of roots and the upper ones preserve their original pattern throughout life; whereas in *Palæolagus*, so far as I know, the cheek-teeth are already rootless, and in old age they lose their original pattern, without, however, developing the new one. In the transformation of their tooth-pattern the Leporidæ eventually go a step beyond the point at which the Lagomyidæ stop, the cheek-teeth of *Lepus* being more completely metamorphosed than those of recent *Lagomys*. In this respect, as well as in the specialization of their limbs for swiftness, correlated with the greater perfection of the sense-organs—and, as a consequence, with corresponding modifications of the skull—the Leporidæ are to be considered the more specialized of the two; but there are several members of the Leporidæ which, with regard to the two last-mentioned sets of characters, and the complete or almost complete absence of the tail, preserve considerable similarity to the Lagomyidæ. By the absence of the upper m. 3, and by some peculiarities of the cranium, pointed out by Winge (perforation of the fossa pterygoidea—fusion of the

\* Atti Acc. Lincei, Rend. iv. 2, p. 274 (1895); id. in Semon's 'Forschungsreisen in Australien,' &c., ii. pp. 374, 378, 383; figs. 20, 30, 31, 59 (1897).

spongiose os tympanicum with the petrosum), the Lagomyidæ are more modernized than the Leporidæ.

If we take for a guide the gradual metamorphosis of their upper cheek-teeth, the order of succession in Lagomyidæ is: *Titanomys*, *Prolagus*, *Lagopsis*, *Lagomys*. *Lagomys* is clearly the offspring of *Lagopsis*; but *Lagopsis* cannot be descended from *Prolagus*, the latter having lost the last lower molar (m. 3), which is present in *Lagopsis* (and *Lagomys*). *Lagopsis* must have taken its origin from a form with upper cheek-teeth like or nearly like those of *Prolagus*, but provided with a lower m. 3, a hypothetical "*Prolagopsis*" descended from *Titanomys* or some closely related form with persistent lower m. 3. In *Titanomys* (*T. visenoviensis*) there is already the beginning of the tendency to the loss of this tooth. *Prolagus* equally descends from a *Titanomys*-like form, and has continued without much change from the Middle Miocene to the present era, since it still lingered in Corsica at the Neolithic period.



*Leporidae*.—Apart from attempts to separate the Rabbit as a genus from the rest of the Leporidae, which have not, however, met with common assent, the family has pretty generally been considered to be composed of one recent genus only, *Lepus*. In 1845, Blyth proposed a new genus *Caprolagus*, for Pearson's *Lepus hispidus*\*. The appropriateness of this generic distinction has been contested by Hodgson and by Waterhouse. The former, omitting to take into consideration the remarkable configuration of the skull of the Hispid Hare, pointed out, that "In the Timid and Red-tailed Hares the long ears, the large eyes, the frame as well suited to extreme speed as the eyes and ears to effective vigilance, are certainly in remarkable contrast with the small eyes and ears, heavy frame, and short equal legs of the Forest Hare: but all these distinctions, as well as those of domicile, become less and less tangible in the Variable Hare, the Rabbit, the Tolai and the Tapiti, in which moreover we have variously reproduced, even to the subordinate peculiarities of the Indian Forest Hare, such as its white flesh, its short tail, its subterranean retreat and creeping adhesion thereto, so unlike the dashing career of the

\* E. Blyth, "Description of *Caprolagus*, a new Genus of Leporine Mammalia; with two plates." Journ. As. Soc. Bengal, xiv. i. pp. 247-249 (1845).

red-tailed and English species"\*. Waterhouse's objections are to the following effect:—"Strongly marked . . . as these distinctions are, if the Assam Hare be compared with the Common Hare, they are less so when that animal is compared with the Indian Hare (*Lepus ruficaudatus*), and *much* less so when it is compared with the *Lepus brachyurus* of Japan. This last-mentioned animal has the short ears and tail of the *Lepus hispidus*, and the same large molar and incisor teeth, combined with a powerfully-formed skull, but in this skull the notch which sets free from the fore part of the supraorbital process is not absent, as in *Lepus hispidus*: it agrees in having the patch unusually long, but differs from the skull of *L. hispidus* (as it would appear from Mr. Blyth's figures) in having the zygomatic arches straight and parallel as in other Hares; the Assam species having the zygoma somewhat arched outward. The peculiarities which I have pointed out as distinguishing the lower jaw of the *Lepus ruficaudatus* from that of the *L. timidus* are also found in the lower jaw of *L. hispidus*, but here the angular portion has a still greater transverse diameter"†. The result of these criticisms was the withdrawal of the genus *Caprolagus* by its author‡.

For my part, I am unable to accept these opinions. Some of the remarks of the former writers are undoubtedly just, and two of the examples of other Leporine species, adduced by Hodgson, as resembling the Hispid Hare, are more to the point than Waterhouse's comparisons. But the conclusions I infer from them are very different from those of these authors. The external characters and the conformation of the skull and limbs, in which the Hispid Hare is distinguished from *L. europæus*—taking this latter as the type of the genus *Lepus* s. str.—are very remarkable. The circumstance, which I shall more fully point out hereafter, that there are other Leporines approaching the Hispid, simply shows that the latter—apart from its specialization as the only true fossorial member of the family—does not stand alone, and that several other species equally deserve to be separated from the genus *Lepus*.

The first attempt at a tabular arrangement of the species of *Lepus*, according to their affinities, was made by Baird §, who availed himself of the characters of the skull; limiting himself—with the exception of "*Lepus cuniculus*"—to North American species. The six sections into which the genus is divided show that this excellent observer had on the whole a right conception of the affinities of this group. Not all his sections, however, are of equal value; section B, comprising *L. californicus* and *L. callotis*, is in reality more closely related to A (*L. timidus*, *L. glacialis*, *L. americanus*, *L. campestris*, &c.) than to the other sections; and the same may be said with regard to E (*L. Trowbridgei* and *L. Audubonii*), which, as a matter of fact, is in closer relation with D (*L. sylvaticus* and allies) than with the rest.

With such a good example to follow, a successor, taking up the whole of the known Leporidae, might have been enabled to make a further step forward. This is what J. E.

\* B. H. Hodgson, "On the Hispid Hare of the Saul Forest" (Journ. As. Soc. Bengal, xvi. i. p. 574 (1847).

† G. R. Waterhouse, 'A Natural History of the Mammalia,' ii. p. 80 (1848).

‡ E. Blyth, Catal. Mamm. in Mus. Asiat. Soc. Calcutta, p. 133 (1863).

§ Spencer F. Baird, 'Mammals of North America,' pp. 574, 575 (1859).

Gray attempted to do \*. From the title of the article, "Notes on the Skulls of Hares (Leporidae) and Picas (Lagomyidae) in the British Museum," the actual contents could not be guessed, for the work is an attempt at a complete classification of the Lagomorpha, in which several characters besides cranial are made use of. The characters assigned to the family Leporidae are in part either erroneous (characteristics of the molars), or they do not hold good for all the minor divisions, and are consequently partly in contradiction with the subsequent characteristics of the sections. This family is divided first of all into two sections, one reserved for Blyth's *Caprolagus*, the other for the rest of the Leporidae. This latter is again subdivided into two groups:—A. Hares, B. Rabbits, the latter containing the Rabbit alone, raised to generic rank (*Cuniculus*). In group A are given generic names to some of Baird's divisions. The latter's D (ex *L. sylvaticus*) becomes *Sylvilagus*, his F (*L. aquaticus*, *L. palustris*) *Hydrolagus*; while a genus *Tapeti* is created for the Brazilian Hare, and *Eulagos* for "*L. mediterraneus*" and "*L. Judæa*." In the subdivisions of this A group (Hares), great stress is laid upon a comparatively unimportant cranial character, which had cautiously been made use of by Baird. Thus we get two subdivisions: I. Postorbital process more or less united with the skull (*Hydrolagus*, *Sylvilagus*, *Eulagos*). II. Postorbital process separate from the skull (*Lepus*, *Tapeti*).

The species of the genus "*Lepus*" are classed according to geographical distribution, and thus there are unavoidably thrown together very heterogeneous forms in the African, Asiatic, and American members. Among the latter are *L. Audubonii* and *L. Trowbridgei*, which are thus widely separated from *Sylvilagus*, containing their closest allies.

The fore-mentioned paper was wisely ignored by J. A. Allen, in his Analysis of the species and varieties of North American Leporidae †. Allen on the whole follows Baird, with some improvements in detail, but with one step backward, by widely separating the *Callotis* group from *L. timidus* and its allies.

Some of Gray's generic names have since been used as subgenera, *e. g.* by Mearns, with whose "Analysis of three Subgenera of *Lepus*" ‡, containing some valuable information, I propose to deal elsewhere.

A new genus of Leporidae, *Romerolagus*, from Mount Popocatepetl (3350 metres), was described some years ago by Hart Merriam §. The author's views as to its systematic position are summed up in the following words:—"The skull, singularly enough, does not show the departure from *Lepus* that one would expect from a study of the other bones. It agrees in the main with skulls of the American Cottontails (subgenus *Sylvilagus*), but differs in the postorbital processes, which are small, divergent posteriorly, and altogether wanting anteriorly, and in the jugal, which is greatly elongated posteriorly. The interparietal is distinct, and in old age becomes ankylosed with the supraoccipital. The thoroughly leporine character of the skull shows that the animal can hardly be regarded as ancestral to *Lepus*, as might have been

\* Ann. & Mag. Nat. Hist. xx. 3, p. 219 (1867).

† 'Monographs of North American Rodentia.—II. Leporidae,' by J. A. Allen, p. 283 (1876).

‡ Proc. U. S. Nat. Mus. xviii. p. 551 (1896).

§ Proc. Biol. Soc. of Washington, x. p. 169-174 (1896).

inferred from its short ears, short hind legs, and various skeletal characters, but that it is a specialized offshoot from the genus *Lepus* itself"\*.

My own views as to the significance of the characters of *Romerolagus* are about the same as those with regard to *Caprolagus*. They are certainly of generic value, by comparison with those generally assigned to the genus *Lepus*. But it does not follow that *Romerolagus* can stand as a separate genus, or, to put it in a more general way, that it occupies an isolated position compared with other Leporidae. I feel sure that if the same care had been bestowed on the examination of the skeletons of some other Leporidae near at hand, *e. g.* the aquatic Hares †, Hart Merriam would have arrived at the same conclusion as I have. It will probably be possible to show hereafter that *Romerolagus* is specialized in some respects, as might be anticipated from its habitat. The remarkable shortness of the ears is presumably the combined result of inheritance and specialization. The absence of the tail is certainly an acquired character, as it is in *Lagomys*. The complete clavicle can scarcely be regarded in the same light; but, although I know of no other member of the Leporidae having a "complete" clavicle, *Romerolagus* does not, in this respect either, occupy such an isolated position as the author seems to think. That the skull is "thoroughly leporine" I cannot admit; there are several cranial characters, as will be shown, which are unusual in most Leporidae, but which *Romerolagus* shares with *Palaeolagus*, with some recent Leporidae, and with the Lagomyidae, and which may be regarded as ancestral.

The whole of recent Leporidae may be divided into two groups, probably of higher than generic dignity, which might conveniently be called: A. *Caprolagus* group, and B. *Lepus* group.

A. *Caprolagus* Group:—

1. *Caprolagus*: *C. sivalensis*, Maj.; *C. raldarnensis* (Weith.); *C. hispidus* (Pears.) (type.)
2. *Nesolagus* (nom. nov.): *N. Netscheri* (Schleg. & Jent.).
3. *Oryetolagus*: *O. cuniculus* (Linn.); *O. erassicaudatus* (Geoffr.).
4. *Sylvilagus*, comprising in this term:—
  - a. *Limnolagus* (*S. palustris*, *aquaticus*, &c.).
  - b. *Romerolagus* (*S. Nelsoni*, Merr.).
  - c. *Tapeti* (*S. brasiliensis*, &c.).
  - d. *Sylvilagus* (*S. sylvaticus*, &c.)

The question whether 1–4 are to be considered as genera or subgenera is for the present quite immaterial. *Sylvilagus* s. str. is the least primitive of this group, and *Oryetolagus* stands somewhat apart.

B. *Lepus* Group.—This group contains the one genus *Lepus* s. str., including all the species not contained in group A.

\* *Op. cit.* p. 172.

† This remark refers also to the limbs, although I do not know them from either.

The *Caprolagus* group (A) differs from the *Lepus* group by the following characters, part of which, as said above, it shares with *Palaolagus* and with the Lagomyidæ:—

Lesser specialization for speed, and in correlation with this, lesser development of organs of sense (sight, smell, hearing). Fore and hind feet comparatively short and subequal. Ears short. Eyes smaller. Tail very short or missing.

Cranium, depressed above, anteriorly and posteriorly very little bent downward. Upper contour of frontals and posterior part of nasals almost horizontal (exc. *Oryctolagus*). Inferior border of orbit—formed by malar bone—shorter than in the *Lepus* group; sinus on the lateral face of malar not advancing so far forward (exc. in *Oryctolagus*). Upper border of zygoma bent inward, inferior border arched outward (exc. in *Oryctolagus*). Posterior appendix of zygoma elongate and, in correlation, mandibular condyloid process elongate also (exc. in *Oryctolagus crassicaudatus*).

Infraorbital foramen larger than in *Lepus* and its immediate neighbourhood almost devoid of reticulation. The heavier skull in the A group is in evident correlation with the different mode of locomotion. The following cranial characters of A are apparently in correlation with the less developed organ of smell:—Horizontal portion of os palatinum comparatively well developed; interpterygoid fossa and choanæ comparatively small. Foramina incisiva comparatively narrow and short. Anterior part of nasals less inflated than in *Lepus*. In correspondence with the smaller eyes, the orbits are comparatively small, and the orbital processes more or less reduced.

In conclusion, I wish to express my very special obligations to Prof. Howes for loan of material, valuable suggestions, and the pains he has taken in connection with this memoir.

## EXPLANATION OF THE PLATES.

### PLATE 36.

- Fig. 1. *Caprolagus (Oryctolagus) cuniculus* (Linn.), juv. Right maxillary; d. 3—m. 2.  
 Fig. 2. *Plesiadapis Daubrei*, Lem. Right upper molar. Enlarged copy from Bull. Soc. Géol. France, 3. xix. (1891) pl. x. fig. 62 u.  
 Fig. 3. *Pelycodus helveticus*, Rüt. Right upper molar. Enlarged copy from Abh. Schweiz. Pal. Ges. xv. pl. fig. 12 a (1888).  
 Fig. 4. *Prolagus sardus* (Wagn.). Left maxilla with deciduous teeth (d. 3—d. 1) and first molar. Monte San Giovanni (Sardinia). Br. Mus. G. D. No. M3464.  
 Fig. 5. *Caprolagus (Oryctolagus) cuniculus* (Linn.); slightly older than fig. 1. Right maxilla; d. 3—m. 2; alveolus of m. 3.  
 Fig. 6. *Titanomys Fontannesii* (Dep.). Second (last) right upper molar (m. 2), almost disused. Middle Miocene. La Grive-Saint-Alban (Isère), as all the other specimens of this species\*.  
 Fig. 7. *Titanomys Fontannesii* (Dep.). First right upper molar (m. 1).  
 Fig. 8. *Titanomys Fontannesii* (Dep.). Posterior right upper premolar (p. 1). Br. Mus. G. D. No. 5268  
 Fig. 9. *Titanomys Fontannesii* (Dep.)? Second right upper premolar (p. 2)?\* .  
 Fig. 10. *Prolagus aenigensis* (Kön.). The three left upper premolars (p. 3—p. 1) of young specimen. Middle Miocene. La Grive-Saint-Alban, as all the other specimens of this species. Br. Mus. G. D. No. 5234.

\* The figures marked thus are from specimens in the possession of the author.

- Fig. 11. *Prolagus sardus* (Wagn.). Posterior right upper premolar (p. 1), from a young specimen. Monte San Giovanni (Sardinia). Br. Mus. G. D. No. M3461.
- Fig. 12. *Titanomys Fontannesi* (Dep.). First left upper molar (m. 1), slightly worn.
- Fig. 13. *Titanomys Fontannesi* (Dep.). First left upper molar (m. 1), slightly worn.
- Fig. 14. *Titanomys Fontannesi* (Dep.). Right upper, probably deciduous, molar; much worn\*.
- Fig. 15. *Titanomys Fontannesi* (Dep.). Posterior right upper premolar (p. 1)\*.
- Fig. 16. *Prolagus sardus* (Wagn.). Fragment of right maxillary ramus, with posterior premolar (p. 1), and the two true molars (m. 1, m. 2). Monte San Giovanni. Br. Mus. G. D. No. M3459.
- Fig. 17. *Caprolagus (Oryctolagus) cuniculus* (Linn.). Young individual, slightly older than fig. 5. The two posterior premolars (p. 2, p. 1) and the two anterior molars (m. 1, m. 2) of the right side.
- Fig. 18. *Titanomys visenoviensis*, H. v. Mey. Upper molar, much worn. Bravard Collection. Lower Miocene, Allier. Br. Mus. G. D. No. 31094-104.
- Fig. 19. *Titanomys visenoviensis*, H. v. Mey. The two posterior premolars (p. 2, p. 1), from a fragment of the right maxillary. Lower Miocene of Weisenau (Germany). Br. Mus. G. D. No. 21495.
- Fig. 20. *Caprolagus (Sylrilagus) brasiliensis* (Linn.). Right upper posterior deciduous molar (d. 1), from a skull in the Br. Mus. Z. D. No. 58.4.15.1.
- Fig. 21. *Prolagus æningensis* (Kön.). Complete series of the right upper cheek teeth (p. 3-m. 2)\*.
- Fig. 22. *Lepus timidus*, Linn. (*L. variabilis*, Pall.). Right upper cheek-teeth of young individual; the two posterior deciduous molars have been removed, in order to show the overlying premolars (p. 2, p. 1). Ireland. W. E. de Winton, Esq.
- Fig. 23. *Titanomys Fontannesi* (Dep.). Left upper jaw, showing the empty alveoli of the five cheek-teeth.  $4 \times 1$ \*.
- Fig. 24. *Prolagus sardus* (Wagn.). Complete series of the right upper cheek-teeth, or (p. 3-m. 2). Ossiferous breccia of Monte San Giovanni (Sardinia)\*.
- Fig. 25. *Lepus europæus*, Pall. Unworn right upper median premolar (p. 2) of young individual. From a skull in the Br. Mus. Z. D. No. 523 l.
- Fig. 26. *Lepus timidus*, Linn. Posterior right upper deciduous molar (d. 1), removed from the jaw fig. 22.
- Fig. 27. *Caprolagus hispidus* (Pears.). Median right upper premolar (p. 2), of young individual in the Br. Mus. Z. D.
- Fig. 28. *Lepus* sp. Right upper deciduous molars (d. 3-d. 1). China. Br. Mus. Z. D.
- Fig. 29. *Prolagus æningensis* (Kön.). Right upper deciduous molar (either d. 1 or d. 2)\*.
- Fig. 30. *Lagopsis verus* (Hens.). Right upper deciduous molar (either d. 1 or d. 2). Middle Miocene of La Grive-Saint-Alban\*.
- Fig. 31. *Lagopsis verus* (Hens.). Median right upper premolar (p. 2). La Grive-Saint-Alban. Br. Mus. G. D.
- Fig. 32. *Lagopsis verus* (Hens.). Left upper molar. La Grive-Saint-Alban. Br. Mus. G. D.
- Fig. 33. *Caprolagus hispidus* (Pears.). Complete series of the right upper cheek-teeth. Adult. From a skull in the Br. Mus. Z. D.
- Fig. 34. *Lepus nigricollis*, F. Cuv. Posterior right upper premolar (p. 3). Br. Mus. Z. D. No. 81.4.29.7.
- Fig. 35. *Titanomys Fontannesi* (Dep.). Left upper deciduous molar (either d. 1 or d. 2)\*.
- Fig. 36. *Paleolagus Haydeni*, Leid. Fragment of right maxillary ramus, showing the empty alveolus of the median premolar (p. 2), and the three following cheek-teeth (p. 1, m. 1, m. 2). Br. Mus. G. D. No. M5727.

## PLATE 37.

- Fig. 1. *Titanomys Fontannesi* (Dep.). Isolated lower anterior premolar (p. 2), unworn. Middle Miocene of La Grive-Saint-Alban, like all the other specimens of this species\*.
- Fig. 2. *Titanomys Fontannesi* (Dep.). Another isolated specimen of the same tooth, slightly worn\*.

- Fig. 3. *Titanomys Fontannesi* (Dep.). A third isolated specimen of the same, slightly more worn by attrition than the former\*.
- Fig. 4. *Titanomys Fontannesi* (Dep.). A fourth isolated specimen of the same, much worn\*.
- Fig. 5. *Prolagus sardus* (Wagn.), var. *corsicanus*. The two inferior deciduous molars (d. 2, d. 1) from a left mandibular ramus. The first true molar (m. 1) of the specimen, not figured, shows a vestige of the terminal cusp ("t" = hypoconulid).
- Fig. 6. *Prolagus aëningensis* (Kön.). Left mandibular ramus of young individual, showing the two deciduous (d. 2, d. 1) and the two true molars (m. 1, m. 2). La Grive-Saint-Alban. Br. Mus. G. D. No. M5236.
- Fig. 7. *Titanomys Fontannesi* (Dep.). Complete series of the lower cheek-teeth (p. 2—m. 3) in a left mandibular ramus. Adult. Br. Mus. G. D. No. 5267 a.
- Fig. 8. *Caprolagus (Oryctolagus) cuniculus* (Linn.). The two lower premolars (p. 2, p. 1), in a right mandibular ramus of an immature specimen. Herefordshire. W. E. de Winton, Esq.
- Fig. 9. *Prolagus aëningensis* (Kön.). Complete series of inferior cheek-teeth (p. 2—m. 2), left side. Adult\*.
- Fig. 10. *Titanomys Fontannesi* (Dep.). Posterior premolar (p. 1) and anterior true molars (m. 1, m. 2) in a left mandibular ramus of an immature specimen. p. 1, being still in the socket, has not yet come into attrition. Br. Mus. G. D. No. 5267 b.
- Fig. 11 a. *Titanomys visenoriensis*, H. v. Mey. Isolated upper posterior premolar (p. 1), or anterior molar (m. 1?, right side. Lower Miocene of Weisenau. Br. Mus. G. D. No. 7217 c.
- Fig. 11 b. *Titanomys visenoviensis*, H. v. Mey. Probably posterior premolar (p. 1) or anterior molar (m. 1). Left side. Lower Miocene of Weisenau. Br. Mus. G. D. No. 7217 d.
- Fig. 12. *Prolagus aëningensis* (Kön.). Anterior premolar (p. 2) from a left mandibular ramus.
- Fig. 13. *Caprolagus Lacosti* (Pomel). Anterior premolar (p. 2) from a left mandibular ramus. Upper Pliocene of Perrier (France). Br. Mus. G. D. No. 27618.
- Fig. 14. *Lagopsis verus* (Hens.). The two posterior true molars (m. 2, m. 3) from a right mandibular ramus. La Grive-Saint-Alban. Br. Mus. G. D. No. 5263.
- Fig. 15. *Titanomys Fontannesi* (Dep.). Upper view of left mandibular ramus, exhibiting the empty alveoli of the five cheek-teeth\*.
- Fig. 16. *Titanomys Fontannesi* (Dep.). Posterior premolar (p. 1) and the two anterior true molars (m. 1, m. 2) in a right mandibular ramus. Empty alveoli of p. 2 and m. 3. Br. Mus. G. D. No. M5267 c.
- Fig. 17. *Caprolagus (Nesotagus) Netscheri* (Schleg. & Jent.). Posterior upper premolar (p. 1), right side, from the skull in the Br. Mus. Z. D. No. 92.5.24.1. Sumatra.
- Fig. 18. *Caprolagus sivalensis*, Maj. The two inferior premolars (p. 2, p. 1), from a fragment of the left mandibular ramus. Pliocene, Siwalik Hills, India. Cautley Coll. Br. Mus. G. D. No. 16529. (By an inadvertence of the artist, the anterior side of the teeth is turned to the right—their outer side being directed upwards in the plate—instead of to the left, as in all the other figures of mandibles and teeth of the left side.)
- Fig. 19. *Caprolagus (Romerolagus) Nelsoni* (Merr.). Anterior premolar (p. 2), from a right mandibular ramus. Mount Popocatepetl (Mexico). Br. Mus. Z. D.
- Fig. 20 a, b. *Caprolagus (Sylvilagus) palustris* (Baehm.). Lower anterior premolars (p. 2), right (a) and left (b), from a specimen in the Br. Mus. Z. D.
- Fig. 21. *Titanomys Fontannesi* (Dep.). The posterior premolar (p. 1) and the two anterior true molars (m. 1, m. 2) in a fragment of the right mandibular ramus.
- Fig. 22. *Caprolagus hispidus* (Pears.). The two premolars (p. 2, p. 1) from the right mandibular ramus of an immature specimen in the Br. Mus. Z. D.
- Fig. 23. *Caprolagus hispidus* (Pears.). Complete series of lower cheek-teeth (p. 2—m. 3) from a right mandibular ramus of an adult specimen in the Br. Mus. Z. D.

- Fig. 24. *Titanomys visenoviensis*, H. v. Mey. The two anterior true molars (m. 1, m. 2) from a fragment of the left mandibular ramus. Bravard Coll. Lower Miocene of Allier (France). Br. Mus. G. D. No. 31095.
- Fig. 25. *Titanomys visenoviensis*, H. v. Mey. The two premolars (p. 2, p. 1), from a fragment of the right mandibular ramus. Lower Miocene of Allier. Br. Mus. G. D. No. 31096.
- Fig. 26. *Lagopsis verus* (Hens.). The four anterior cheek-teeth (p. 2, p. 1, m. 1, m. 2) and the empty alveolus of the last (m. 3), in a left mandibular ramus. La Grive-Saint-Alban\*.

## PLATE 38.

- Fig. 1. *Caprolagus (Sylvilagus)*, sp., jun., from Bogotá. Right manus, anterior or upper surface view. Nat. size. *v*—vesalianum (carpale V); *b*—hamatum (carpale IV). Nat. size.
- Fig. 2. The same. External (ulnar) view. Nat. size.
- Fig. 3. *Caprolagus (Oryctolagus) crassicaudatus* (Is. Geoffr.). Br. Mus. Z. D. No. 96.6.6.1. Left manus, ulnar view. Nat. size.
- Fig. 4. *Lagomys rufescens*, Gray. Br. Mus. Z. D. Right manus, anterior view. 2 × 1.
- Fig. 5. *Caprolagus (Oryctolagus) cuniculus* (Linn.), juv. Right tarsus, ulnar view. Nat. size.
- Fig. 6. *Caprolagus (Sylvilagus) brasiliensis* (Linn.), juv. Roy. Coll. Sc., London. Right tarsus, ulnar view. Nat. size.
- Fig. 7. *Caprolagus (Sylvilagus)*, sp. juv. Bogotá. Right tarsus, ulnar view. Nat. size.
- Fig. 8. *Caprolagus (Sylvilagus) brasiliensis* (Linn.), juv. Roy. Coll. Sc., London. Right antebrachium and manus. *a*, anterior, *b*, posterior or volar view. Nat. size.
- Fig. 9. *Lagopsis verus* (Hens.), or *Titanomys Fontannesii* (Dep.). Middle Miocene, La Grive-Saint-Alban. Br. Mus. G. D. No. M5274. Right metatarsus V. *a*, anterior; *b*, posterior view. 2 × 1.
- Fig. 10. *Lagopsis verus* (Hens.), or *Titanomys Fontannesii* (Dep.). Middle Miocene, La Grive-Saint-Alban. Br. Mus. G. D. M 5273. Left ulna. *a*, anterior; *b*, posterior view. Nat. size.
- Fig. 11. *Prolagus sardus* (Wagn.). Left ulna. *a*, anterior; *b*, posterior view. Nat. size. Pleistocene breccia, Monte San Giovanni (Sardinia). Br. Mus. G. D. M 3471.
- Fig. 12. *Prolagus sardus* (Wagn.). Right radius. *a*, anterior; *b*, external (ulnar); *c*, internal (radial); *d*, posterior view. Nat. size. Pleistocene breccia, Monte San Giovanni (Sardinia). Br. Mus. G. D. M3471.
- Fig. 13. *Prolagus sardus* (Wagn.). Left metatarsus II, from behind. 3 × 1. Pleistocene breccia, Monte San Giovanni (Sardinia). Br. Mus. G. D.
- Fig. 14. *Lagomys rufescens*, Gray. Left metatarsus II, external (fibular) view. 3 × 1. Br. Mus. Z. D. No. 74.11.21.17.
- Fig. 15. The same. Posterior view. 3 × 1.
- Fig. 16. The same. Anterior view. 3 × 1.
- Fig. 17. *Prolagus aeningensis* (Kön.). Left metatarsus II, anterior view. 3 × 1. Middle Miocene, La Grive-Saint-Alban. Br. Mus. G. D. No. M5248.
- Fig. 18. The same. External (fibular) view.
- Fig. 19. *Prolagus sardus* (Wagn.). Right metacarpal V, from the outer (ulnar) side, to show the facet for the os vesalianum (carpale V). 5 × 1. Pleistocene breccia, Monte San Giovanni (Sardinia). Br. Mus. No. G. D. No. M3471.
- Fig. 20. *Lagomys rufescens*, Gray jun. Right antebrachium. *a*, front view; *b*, external (ulnar); *c*, internal (radial) view. 2 × 1. Br. Mus. Z. D.
- Fig. 21. *Lagomys rufescens*, ad. Right radius. *a*, internal (radial); *b*, front view. 2 × 1. Khorassan. Col. Yate.
- Fig. 22. *Caprolagus (Oryctolagus) crassicaudatus* (Is. Geoffr.). Left tarsus and metatarsus; internal (tibial) view. Nat. size. From skel. Br. Mus. Z. D. No. 96.6.6.1.

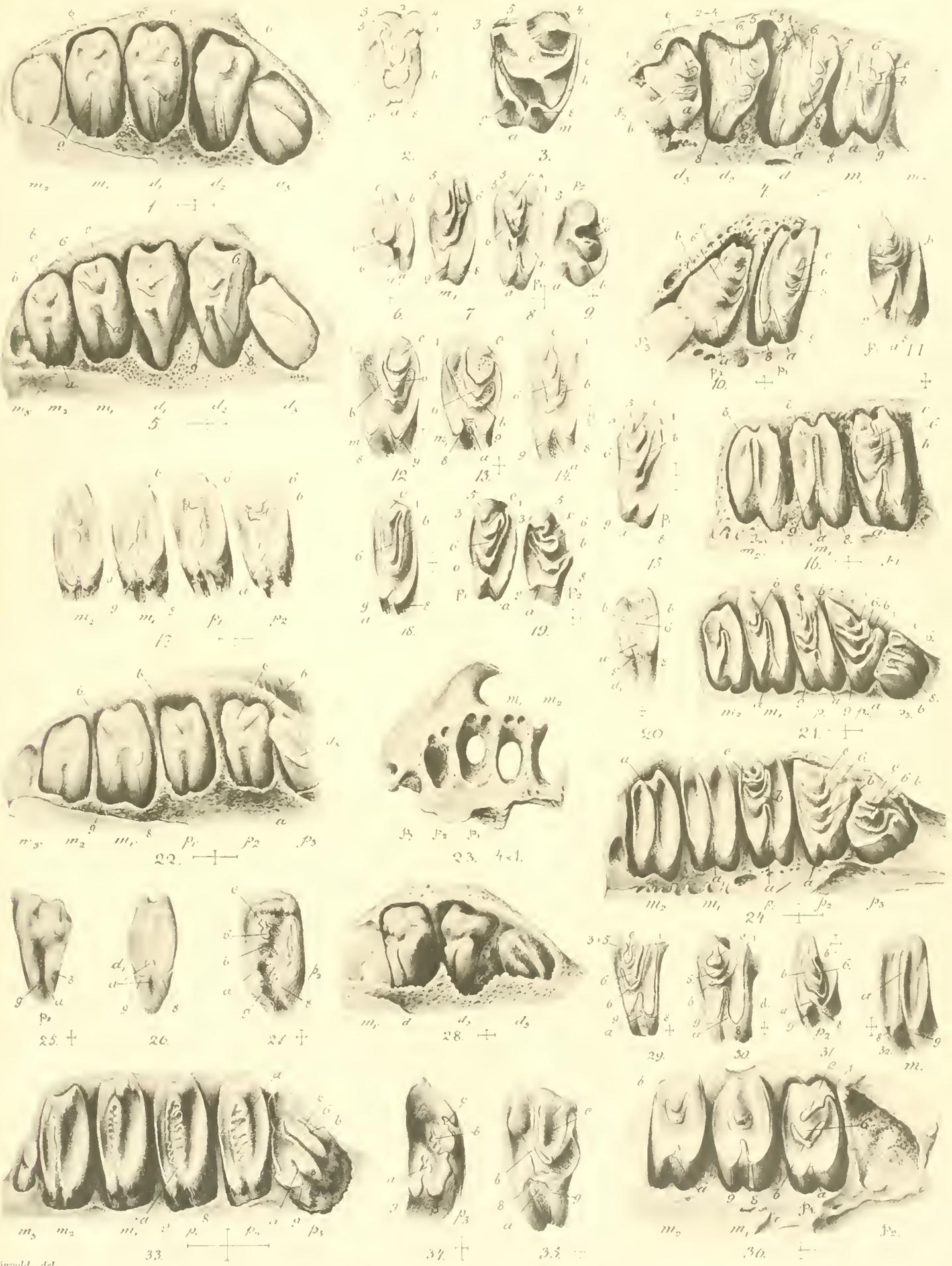
- Fig. 23. *Caprolagus (Nesolagus) Netscheri* (Schleg. & Jent.). Right tarsus and metatarsus; internal (tibial) view. Nat. size. From skel. Br. Mus. Z. D.†
- Fig. 24. *Caprolagus (Caprolagus) hispidus* (Pears.). Right tarsus and metatarsus, internal (tibial) view. Nat. size. Br. Mus. Z. D.
- Fig. 25. *Lepus timidus*, Linn. (*L. variabilis*, Pall.). Right tarsus and metatarsus, internal (tibial) view. Nat. size. Ireland. Br. Mus. Z. D. No. 76.4.10.2.
- Fig. 26. *Lagomys rufescens*, Gray. Right tarsus and metatarsus, internal (tibial view).  $2 \times 1$ .
- Fig. 27. *Prolagus sardus* (Wagn.), var. *corsicanus*. Left metatarsus II. *a*, anterior; *b*, internal; *c*, posterior; *d*, external view. Nat. size. Pleistocene breccia, Toga nr. Bastia (Corsica). Br. Mus. G. No. D. M 3486.
- Fig. 28. *Caprolagus (Nesolagus) Netscheri* (Schleg. & Jent.). Left antebrachium. *a*, front view; *b*, external (ulnar); *c*, internal (radial); *d*, posterior view. Nat. size. Sumatra. Br. Mus. Z. S. Sumatra. Br. Mus. Z. D.
- Fig. 29. *Lagomys rufescens*, Gray. Right ulna. *a*, external (ulnar) view (almost posterior in adult Leporidae); *b*, posterior view (almost internal in adult Leporidae); *c*, front view (almost external in adult Leporidae).  $2 \times 1$ . Khorassan. Col. Yate.
- Fig. 30. *Caprolagus (Oryctolagus) cuniculus* (Linn.). Left antebrachium. *a*, front; *b*, external (ulnar); *c*, internal (radial); *d*, posterior view. Nat. size. Herefordshire.

## PLATE 39

- Fig. 1. *Titanomys Fontanesi* (Dep.). m. 1, sup. dext. Anterior view.  $3 \times 1$ . Middle Miocene. La Grive-Saint-Alban\*.
- Fig. 2. *Titanomys Fontanesi* (Dep.). m. 2, sup. dext. *a*, anterior; *b*, external view.  $3 \times 1$ . La Grive-Saint-Alban\*.
- Fig. 3. *Sciuropterus fuscocapillus*, Blyth. m. 2, sup. dext. Anterior view.  $4 \times 1$ . Br. Mus. Z. D. No. 52.5.9.19.
- Fig. 4. *Titanomys Fontanesi* (Dep.). Upper deciduous molar, much worn. Anterior view.  $3 \times 1$ . Tooth figured Pl. 36. fig. 14.
- Fig. 5. *Titanomys visenoviensis*, H. v. Mey. p. 2, sup. sin. *a*, posterior; *b*, lower view.  $4 \times 1$ . Lower Miocene, Weisenau. Br. Mus. G. D. No. M7217.
- Fig. 6. *Titanomys Fontanesi* (Dep.). Right lower molar. *a*, anterior; *b*, inner; *c*, outer view.  $2\frac{1}{2} \times 1$ . La Grive-Saint-Alban\*.
- Fig. 7. *Caprolagus (Oryctolagus) cuniculus* (Linn.), juv. m. 1, sup. sin., posterior view.  $3 \times 1$ .
- Fig. 8. *Caprolagus (Oryctolagus) cuniculus* (Linn.), juv. m. 1, sup. dext. Anterior view.  $5 \times 1$ . Specimen figured Pl. 36. fig. 1.
- Fig. 9. *Caprolagus (Oryctolagus) cuniculus* (Linn.), juv. dec. 1, sup. dext. *a*, anterior; *b*, outer view.  $5 \times 1$ . Specimen figured Pl. 36. fig. 1.
- Fig. 10. *Pteromys melanotis*, Gray. m. 2, sup. dext. Anterior view.  $3 \times 1$ . Br. Mus. Z. D. No. 48.8.15.2.
- Fig. 11. *Titanomys visenoviensis*, H. v. Mey. Left lower molar. *a*, outer; *b*, inner; *c*, anterior view.  $2\frac{1}{2} \times 1$ . Br. Mus. G. D. No. 21495.
- Fig. 12. *Titanomys Fontanesi* (Dep.)? p. 2 sup. dext. (?) Anterior view.  $4 \times 1$ . La Grive-Saint-Alban. Specimen figured Pl. 36. fig. 9. After renewed examination, the generic affinities of this tooth seem very doubtful.

† *pc.* of this fig. to be read together (= *pc.* præcuneiform).

- Fig. 13. *Titanomys Fontannesii* (Dep.). m. 1 sup. sin. Anterior view.  $3 \times 1$ . La Grive-Saint-Alban. Specimen figured Pl. 36. fig. 12.
- Fig. 14. *Titanomys visnovienseis*, H. v. Mey. m. sup. dext. Anterior view.  $3 \times 1$ . Specimen figured Pl. 36. fig. 18.
- Fig. 15. *Sciuropterus xanthipes* (Milne-Edw.). m. 2, sup. dext. Anterior view.  $3 \times 1$ . Br. Mus. Z. D. No. 95.7.5.1.
- Fig. 16. *Titanomys visnovienseis*, H. v. Mey. m. 2 sup. dext. Lower view.  $10 \times 1$ . Weisenau. Br. Mus. G. D. No. M7217.
- Fig. 17. *Caprolagus (Sylvilagus) brasiliensis* (Linn.), juv. Sternum. Front view. Nat. size. Royal College of Science, London.
- Fig. 18. *Caprolagus (Nesolagus) Netscheri* (Schleg. & Jent.). Sternum. Front view. Nat. size. Br. Mus. Z. D.
- Fig. 19. *Titanomys Fontannesii* (Dep.). p. 1 sup. dext. Anterior view.  $3 \times 1$ . Specimen figured Pl. 36. fig. 8.
- Fig. 20. *Pteromys nitidus*, Desm. Germ of m. 2, sup. dext. Anterior view.  $3 \times 1$ .
- Fig. 21. *Titanomys Fontannesii* (Dep.). dec. sup. sin. Anterior view.  $3 \times 1$ . Specimen figured Pl. 36. fig. 35.
- Fig. 22. *Lagopsis verus* (Hens.). dec. sup. dext. Anterior view.  $4 \times 1$ . Specimen figured Pl. 36. fig. 30.
- Fig. 23. *Prolagus æningensis* (Kön.). dec. sup. dext. Anterior view.  $7 \times 1$ . La Grive-Saint-Alban. Specimen figured Pl. 36. fig. 29.
- Fig. 24. *Prolagus sardus* (Wagn.), var. *corsicanus*. Metatarsus II. Pleistocene breccia of Toga, near Bastia (Corsica).  $3 \times 1$ .
- Fig. 25. *Titanomys Fontannesii* (Dep.). Left mandibular ramus. *a*, inner; *b*, outer view. Nat. size. La Grive-Saint-Alban\*.
- Fig. 26. *Prolagus æningensis* (Kön.). dec. 2 inf.  $4 \times 1$ . La Grive-Saint-Alban\*.
- Fig. 27. *Prolagus sardus* (Wagn.), var. *corsicanus*. Right mandibular ramus. *a*, inner; *b*, outer view. Nat. size. Pleistocene breccia, Toga (Corsica)\*.
- Fig. 28. *Caprolagus (Nesolagus) Netscheri* (Schleg. & Jent.). Right mandibular ramus, outer view. Nat. size. Br. Mus. Z. D. No. 92.5.24.1.
- Fig. 29. *Titanomys Fontannesii* (Dep.). Posterior fragment of right mandibular ramus. *a*, outer; *b*, inner view. Nat. size. La Grive-Saint-Alban\*.
- Fig. 30. *Lagopsis verus* (Hens.). Right mandibular ramus. *a*, outer; *b*, inner view. Nat. size. La Grive-Saint-Alban\*.
- Fig. 31. *Titanomys Fontannesii* (Dep.). Left mandibular ramus. *a*, outer; *b*, inner view. Nat. size. La Grive-Saint-Alban\*.
- Fig. 32. *Caprolagus (Caprolagus) hispidus* (Pears.). Palatal view of skull. Nat. size. Br. Mus. Z. D. No. 48.9.12.11. *m*=maxillary, *p*=palatinum.
- Fig. 33. *Caprolagus (Sylvilagus) Nelsoni* (Merr.) [*Romerolagus Nelsoni*, Merr.]. Palatal view of skull. Nat. size. Popocatepetl, Mexico. Br. Mus. Z. D. No. 97.6.1.5.
- Fig. 34. *Lagomys rufescens*, Gray. Palatal view of skull. Nat. size. Br. Mus. Z. D.
- Fig. 35. *Caprolagus (Sylvilagus) brasiliensis* (Linn.), juv. Palatal view of skull. Nat. size. Royal College of Science, London.
- Fig. 36. *Prolagus sardus* (Wagn.). Palatal view of skull. Nat. size. Pleistocene breccia, Monte San Giovanni (Sardinia). Br. Mus. G. D.
- Fig. 37. *Caprolagus (Oryctolagus) crassicaudatus* (Is. Geoffr.). Palatal view of skull. Nat. size. Br. Mus. Z. D. No. 96.6.6.1.
- Fig. 38. *Caprolagus (Nesolagus) Netscheri* (Schleg. & Jent.). Palatal view of skull. Nat. size. Br. Mus. Z. D.

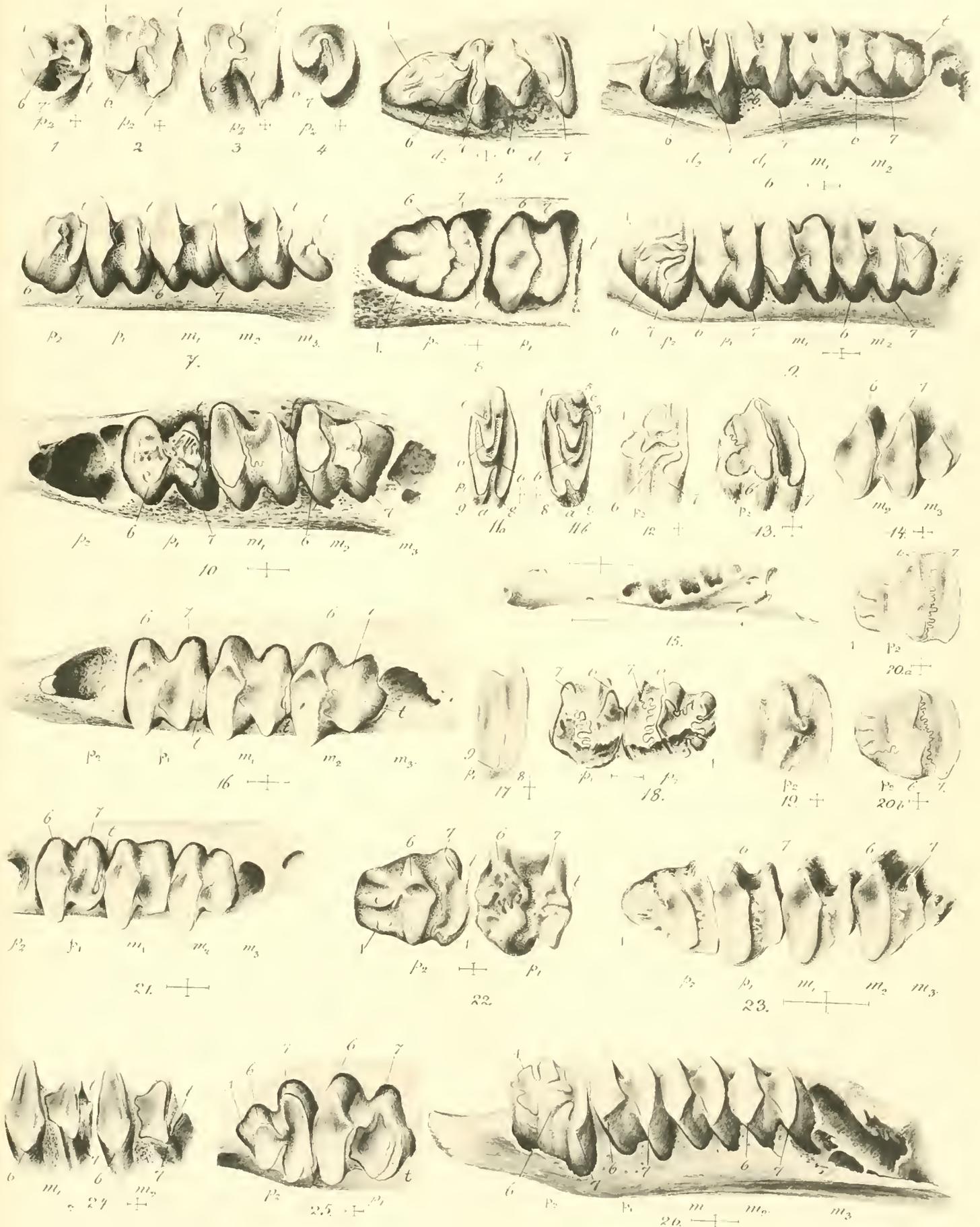


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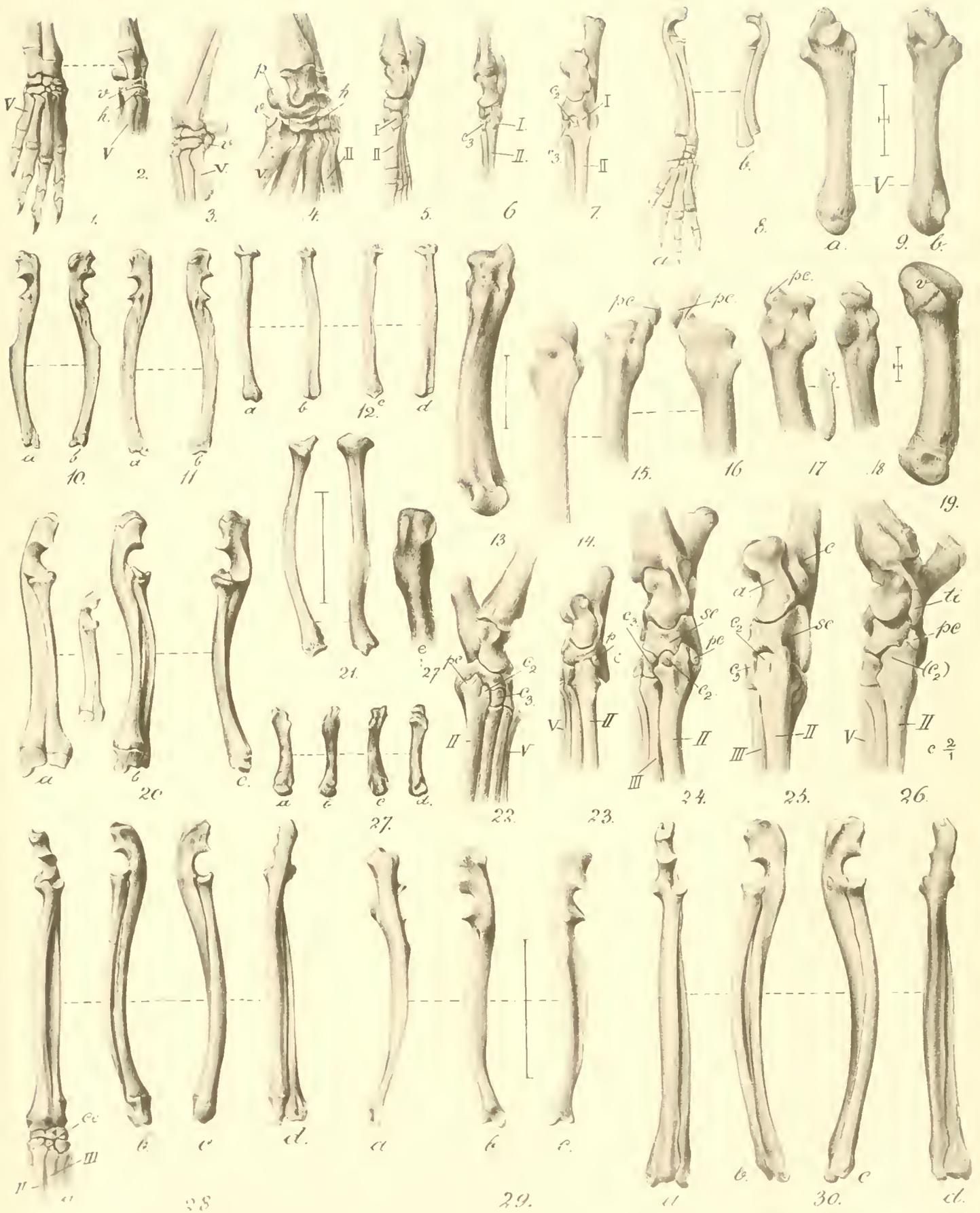


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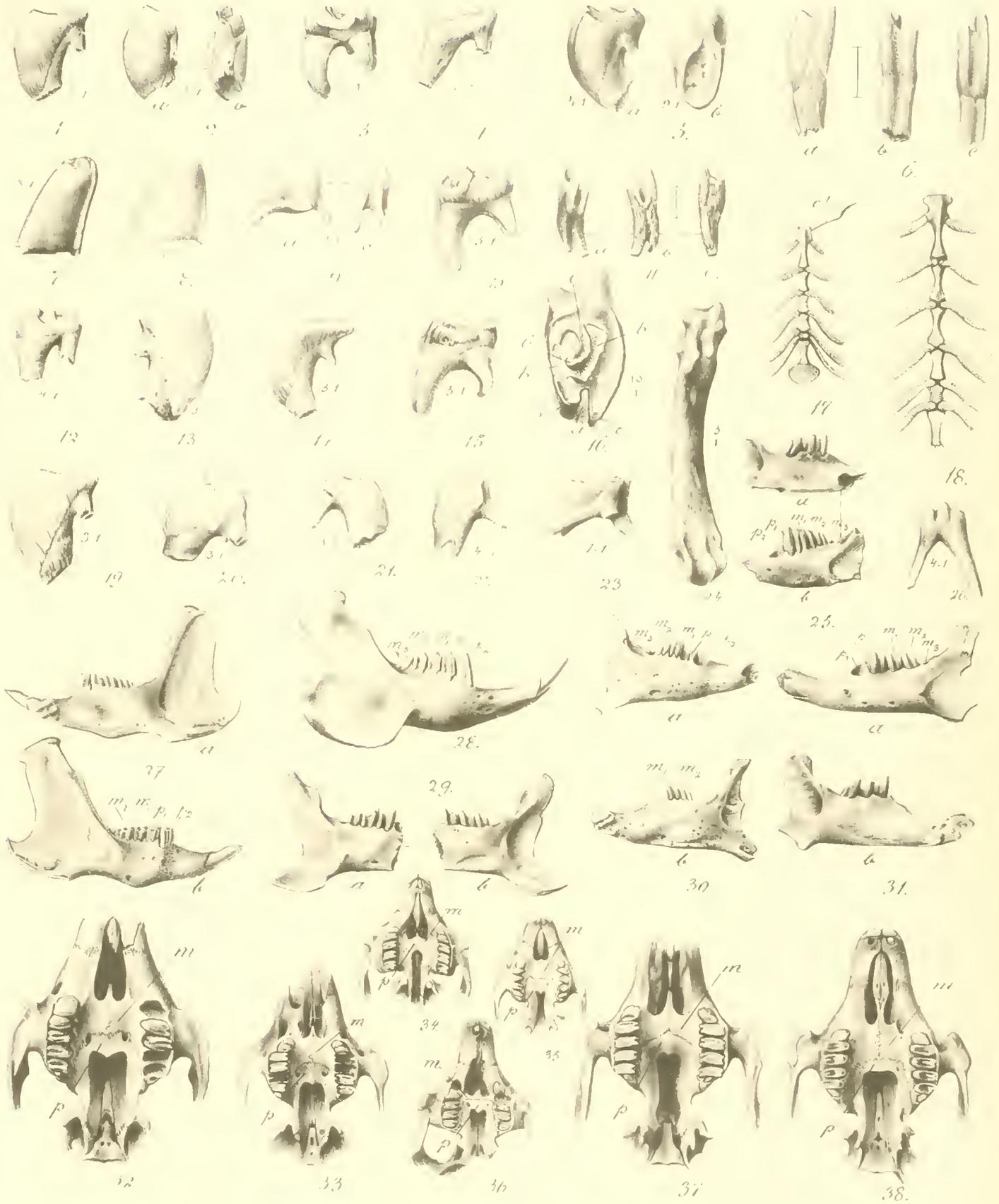
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Part	III. 1885. ....	1	10	0	1	2	6	Part	VII. 1899. ....	0	18	0	0	13	6
Part	IV. 1885. ....	0	8	0	0	6	0	Part	VIII. 1899. ....	0	12	0	0	9	0
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ORDER ALCYONACEA.

BY

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L O N D O N :

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X. *On the Genus Lemnalia, Gray; with an Account of the Branching-systems of the Order Aleyonacea.* By GILBERT C. BOURNE, M.A., F.L.S., Fellow and Tutor of New College, Oxford; University Lecturer in Comparative Anatomy.

(Plates 40-42.)

Read 16th February, 1899.

IN the course of a description of the Anatomy of *Aleyonium digitatum*, Hickson\* has called attention to the unsatisfactory and misleading terms employed in the description of Aleyonarian polyps and colonies. It is the fact that, while Allman and Haeckel have provided us with a set of precise terms descriptive of the component parts of the Hydrozoa, the terminology of the Anthozoa remains in a state of the utmost confusion. For example, the name "polyp" is applied sometimes to the whole Aleyonarian zooid or individual, sometimes only to that part of it, whether retractile or non-retractile, which emerges from the surface of a colony. The name "coenenchyme" is applied to any mass of tissue in which the zooids are imbedded, no distinction being made between the various modes in which zooids may be aggregated together to form a mass or colony. The name "stolon" is used to denote the root-like basal outgrowths by which the *Cornulariidae* are attached to foreign objects, and also the canals lined by endoderm which place the cavities of the zooids composing a colony in communication, and form so large a part of the so-called coenenchyme of colonial Aleyonarians. It is unnecessary to give further examples; these few will suffice as a justification for my burdening zoological literature with a new set of descriptive terms. I do not, however, propose to suggest a complete set of terms for the whole of the Aleyonaria in this paper, but to confine myself to the Order Aleyonacea. Some of the terms proposed are applicable only to the members of this order, others are applicable to all Aleyonarian zooids. In the first place I wish to substitute the name "zooid" for that of "polyp" †. The name zooid is applicable to any asexually-produced individual entering into the composition of a colony, and therefore Kölliker was in error when he restricted it to those arrested and modified individuals whose function it is to drive currents of water through Aleyonarian colonies. These should be called *siphonozooids*. There are, of course, many kinds of zooids, since there are many groups in the animal kingdom in which asexually-produced individuals are united to form colonies, and these may be distinguished as

\* S. J. Hickson, "The Anatomy of *Aleyonium digitatum*," Quart. Journ. Micr. Sci., new ser., vol. xxxviii, p. 354.

† See Moseley, 'Challenger' Reports, Zoology, vol. ii, p. 118, and Milnes-Marshall, Trans. Roy. Soc. Edinburgh, xxxiii, 1888, p. 453.

*hydrozooids, anthozooids, poly- or bryozooids, ascidiozooids*, and so forth. The name zooid is to be preferred to that of polyp, because it is so easily compounded with other names for descriptive purposes.

The Order Aleyonacea comprises those Aleyonarian colonies whose component zooids are elongate and united proximally by fusion of the ectoderm (*Xenia*) or mesogloea (all other Aleyonacea) of their adjacent walls so as to form a bunch. Such a bunch may conveniently be described as an *anthodeté*, from the Greek *δετή*, a fagot. In the simplest forms of the Aleyonacea, the *Xeniida*, the anthodeté may be compared to a bunch of flowers, all simple scapes, the lower moieties of whose peduncles have been fused together, the upper moieties and flowers remaining free. In this case it is obvious that the cavity of every zooid in the bunch extends down to the base of the colony; and the analogy of the bunch of flowers would be complete if it were imagined that all the peduncles were hollow and that their cavities were put into communication, in the region where they are fused together, by numerous short anastomosing canals passing from peduncle to peduncle. As it is obviously convenient to have names which shall

Fig. 1.

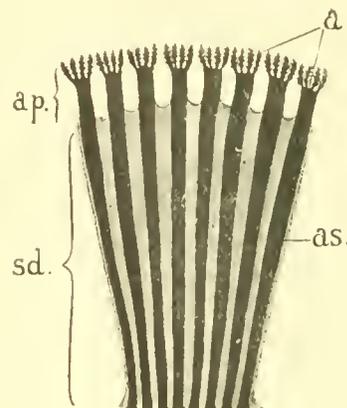


Diagram of a Xeniid colony.—The so-called *cœnenchyme* is represented by shading, the free portions of the zooids and their cavities black. *ap.*, Apodeté; *sd.*, syndeté; *a.*, anthocodia; *as.*, an anthostele. In this and the similar diagrams on the following pages the solenia are omitted.

distinguish that part of the anthodeté where the zooids are fused together from the part where they are separate, I propose to call the former the *syndeté* (*σύν, δετή*), and the latter the *apodeté*. The anastomosing canals lined by endoderm which place the zooid cavities in communication have been variously named “stolons,” “nutritive-canals,” “*cœnenchymal tubes*,” and so on. I propose to call them *solenia*, from the Greek *σωλήμιον*, a little pipe or conduit.

The names *syndeté* and *apodeté* refer to the zooids collectively; but as each zooid consists of a distal free portion, bearing the mouth and tentacles, and a proximal portion fused to its neighbours, it will be convenient to call the former the *anthocodia* (from the Greek *κωδία*, a flower-head), and the latter the *anthostele* (from *στήλη*, a column). In

the *Xeniidae* the anthocodiæ are not retractile, but in the *Alcyonidae* the anthocodia is introversible within the distal part of the anthostele. It should be borne in mind that "retractility" in Alcyonarians properly means the introversion of the anthocodia within the anthostele. The latter is often strengthened at its distal end with spicules arranged *en chevron* to form a crown of eight points, usually called the calyx or verruca. It will be better to call it the *anthoerypt*. The anthocrypts are rudimentary in the *Alcyonidae*, but are well developed in other orders of the Alcyonaria, e. g. the *Gorgonidae*. As will be more particularly described in the latter part of this paper, some Alcyonarian zooids which have been described as "retractile" or "partially retractile" by various authors are not introversible, but simply have the power of folding over or withdrawing the tentacles into the oral disc. In such cases the bases of the tentacles are usually protected by a special development of spicules, which may either be disposed *en chevron* (as in *Siphonogorgia* among the Alcyonacea), or developed into large shield-like plates as in *Primnoa*. Such spicular defences are sometimes called calices, sometimes opercula; it may be useful to give them a special name, *anthopoma*, from  $\pi\acute{\omega}\mu\alpha$ , a lid.

Fig. 2.

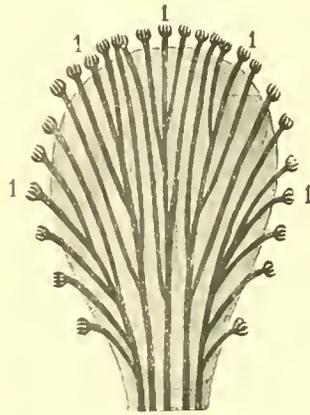


Diagram of an Alcyonid colony in which five chief members are represented as branching in one plane.—The branching-system of each chief member may be described as a corymb; but in the diagram, which is much simplified, the anthocodiæ of the two outside members do not lie in the same plane. They may be said, however, to be corymbs, if the surface of the syndeté is regarded as the plane to which all the branches attain. 1,1. Anthocodiæ of the chief zooids.

The family *Alcyonidae* differs from the *Xeniidae* chiefly in the following respects:—The anthosteles of the zooids are very intimately united by fusion of their mesogloæal walls; only a few of them reach to the base of the colony, the majority ending at various depths in the thickness of the syndeté in solenia which put them into communication with adjacent anthosteles. Returning to the analogy of a bunch of flowers, we may compare the Alcyonid anthodeté to a bunch of corymbs, in which not only the main axes, but also the proximal parts of the secondary, tertiary, and other axes, are fused together; scarcely more than the flowers with very short lengths of peduncle remaining free. If we imagine, as before, that all the axes are hollow and communicate one with

the other by a network of tubular solenia, we have a fairly good idea of the composition of the Alcyonid anthodeté. It must be borne in mind, however, that the anthosteles corresponding to the secondary axes of a corymb do not open directly into the cavity of the primary axis, but into solenia growing out from it. The same is the case with the tertiary and other axes which open into the secondary axes, through the intervention of solenia.

In the *Alcyonidae* the colonies are comparatively simple in shape—mushroom-shaped, as in *Sarcophyton*; lobate or bluntly digitate, as in *Alcyonium*; none of them branch to any great extent. In forms like *Sarcophyton* the apodeté is confined to the distal surface of the anthodeté, the latter being swollen in this region to form the “pileus,” while the syndeté forms a stem. But in *Alcyonium* and its allies the apodeté occupies nearly the whole surface of the anthodeté, being absent only over a very restricted area at its basal end. This is the result of the mode of aggregation and budding of the zooids, the anthocodæ standing out all over the surface of the anthodeté. In the *Nephthyidae*, on the other hand, the anthodeté is variously ramified, and the anthocodæ emerge only on the terminal branches and twigs, where they form clusters. Thus the syndeté may be described as forming a barren stem and branches composed of the adnate anthosteles of a certain number of the zooids forming the colony; the apodeté is confined to the terminal twigs. Wright and Studer \* have described the zooid-cavities, *i. e.* the anthosteles, of the *Nephthyidae* as narrowing below, and ending each in a *cul-de-sac*, but communicating by means of solenia with wide canals, which run in the stem and larger branches; these wide canals they called stem-canals or branch-canals. But Kölliker † long since pointed out that in *Siphonogorgia Godeffroyi* the stem-canals contain prolongations of the mesenteries of the zooids, and are, in fact, the extremely long anthosteles of the primary zooids of the colony; and the case is not different in other members of the *Nephthyidae*. I have examined different species of *Ammonothea*, *Spongodes*, *Lemnalia*, and *Siphonogorgia*, and find that in each the so-called stem-canals are nothing more than the extremely long anthosteles of the primary zooids, and contain prolongations of the asulcar mesenteries, sometimes also of the remaining six mesenteries. It is true that most of the anthosteles in a Nephthyid colony do thin out and end blindly as described by Wright and Studer, but these belong to the secondary, tertiary, and other zooids which spring from the solenia given off by the primary zooids. The continuity of a stem-canal with a zooid-cavity can be determined only by the patient study of long series of sections.

Perhaps the difference between the *Alcyonidae* and the *Nephthyidae* may be best understood if the anthodeté of the latter is regarded as a bundle, not of corymbs, but of compound racemes whose main axes are of very various lengths. Let us imagine a number of racemes *a, b, c, d* (fig. 3), whose secondary and tertiary axes are long, parallel to and fused with the primary axis. The proximal parts of all the racemes are

\* ‘Challenger’ Reports, Zoology, vol. xxxi., Alcyonaria, 1889.

† A. von Kölliker, ‘Festschrift zur Feier des 25-jährigen Bestehens d. phys.-med. Gesellschaft in Würzburg,’ 1874, p. 18.

fused into a single bundle for a considerable length, but eventually first one and then another raceme emerges from the bundle as a branch, and by continued subdivision of their axes and the emergence of bundles of these as secondary and tertiary branches a ramifying system is formed, the ultimate axes finally emerging on the twigs as the anthocodiæ of the zooids.

Fig. 3.

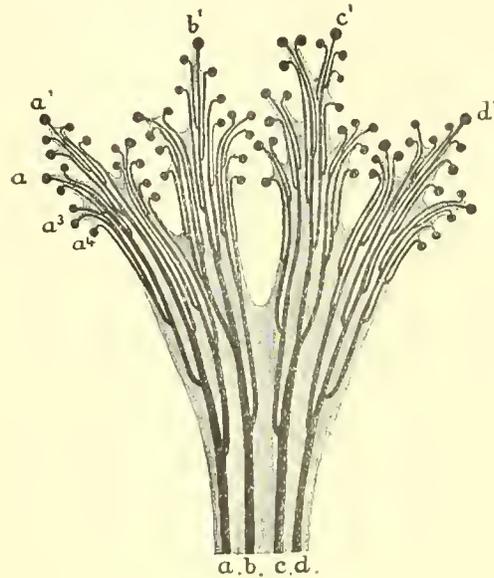


Diagram of the branching-system of a Nephytid.—The anthodetè is represented as consisting of four chief members, *a, b, c, d*, each of which branches in one plane on the racemose system. The anthosteles of the lateral members run parallel to those of the chief members, and are organically fused with them and with each other throughout the greater part of their length. *a', b', c', d'*. Terminal anthocodiæ of the chief members. *a²*. Terminal anthocodia of a lateral member of the second order. *a³, a⁴*. Anthocodiæ of third and fourth orders. It should be noted that the branching-system of the anthodetè as a whole, which in this case is a dichotomy, does not correspond with that of its component members.

In this case the primary axis is represented as growing at a rate equal to the secondary and other axes, but there are cases in which the primary axis is arrested in growth and the other axes grow past it and alone pass into the branches. In other words, the primary zooids may undergo cymose subdivision, and in this case their anthocodiæ degenerate and the apodetè is formed only by the secondary or lower orders of zooids. None the less the longitudinal canals of the stem and large branches are the anthosteles of the primary zooids.

The racemose mode of subdivision of the primary zooids is well illustrated in the genus *Lemnalia*, Gray, a member of the family *Nephytidae* and the subfamily *Siphonogorginae*. The specimen figured in Pl. 40, fig. 4 formed part of a collection of Anthozoa collected by the late Dr. Gulliver at Zanzibar, and presented by him to the Oxford University Museum. It is clearly identical with Verrill's *Ammothea nitida*\*, also from Zanzibar, but it does

\* Bull. Mus. Comp. Zool. Harvard, vol. i. 1864, p. 39.

not belong to the genus *Ammothoa*, for the presence of a close feltwork of spicules in the partitions between the anthosteles of the stem and branches show it to be a member of the subfamily *Siphonogorginæ* as defined by Wright and Studer.

The genus *Lemnalio* was described by Gray in the following terms\* :—

“Coral soft, fleshy, formed of numerous clustered small cylindrical tubes; the outer surface is smooth, destitute of any appearance of spicules, but showing by grooves the union of the different tubes that form the mass, each tube ending in a polype. The base is broad and expanded horizontally, fleshy like the coral, throwing up several stems which are irregularly branched, the lateral branches being somewhat two-rowed, the terminal branches rather clustered, each branchlet ending in a cylindrical polype, the mouth and tentacles of which are completely retractile, only leaving a central knob surrounded by eight slightly depressed radiating grooves, and entirely destitute of any appearance of superficial spicules. The whole coral is flaccid, and the larger branches appear to be more or less compressed, but this may in great part depend on the state of the specimens.” A small woodcut, which faithfully represents the general habit of the type species, accompanies Gray’s description. He included in the genus the type species *Lemnalio Jukesii*, *L. terminalis* = *Alcyonum terminale*, Quoy & Gaimard, and *L. nitida* = *Ammothoa nitida*, Verrill.

Verrill † immediately objected to his species being placed in the genus *Lemnalio* as defined by Gray, pointing out that his *Ammothoa nitida*, though it appeared smooth to the naked eye, was seen under the microscope to be filled with numerous slender closely-interlaced spicules; that similar spicules, .25 to .5 mm. long by .02 to .025 mm. thick, occurred in the interior of the stem, and that the “verrucae” (*i. e.* the anthocodiae) were covered with small stout warty spicules .075 to .125 mm. long by .05 to .075 mm. thick. I can add this further objection, that the tentacles are not retractile in any species of *Lemnalio*, but are simply infolded over the oral disc. In fact, Gray’s diagnosis was utterly wrong in several important particulars, and it was only by chance that I examined the type species in the British Museum and saw that it was closely related to the specimen which I had already identified with Verrill’s *Ammothoa nitida*. But Verrill was equally beside the mark when he compared his species with Savigny’s figures of *Ammothoa virescens* (= *Nephthya Cordieri*, Audouin, Explic. Pl. Sav.). There is no likeness whatever between Savigny’s figures and *Lemnalio nitida*, but there is, on the other hand, a very close resemblance between Quoy & Gaimard’s ‡ figures of *Alcyonum terminale* and Gray’s *Lemnalio*, and the latter author was undoubtedly right in placing this species in his new genus. I have found a specimen in the British Museum which appears to be identical with it. A species described as *Alcyonum ramosum* is figured in the same place by Quoy & Gaimard. In habit it resembles *Ammothoa virescens*, Savigny, but the figures of the anthocodiae, which are pedicelled, with rounded heads and infolded tentacles, recall those of *Lemnalio*. The position of this species must remain doubtful for the present. There are four species of *Lemnalio* in the British Museum—viz., the type

\* Ann. & Mag. Nat. Hist. 1868, ii. p. 442.

† American Journal of Science & Arts, 2nd ser. xlvii. 1869, p. 282.

‡ ‘Voyage de l’Astrolabe,’ Zool. iv. p. 282, pl. xxiii. figs. 15-17.

species *L. Jukesii*; a second seems to be identical with Quoy & Gaimard's *Alcyonum terminale*; the two others are unnamed.

I have been unable to find any reference to Gray's genus subsequent to the paper of Verrill's quoted above. It does not appear in the 'Challenger' report on the Alcyonaria, although one of the species in the British Museum comes from the 'Challenger' collection. The five specimens which I have examined clearly constitute a distinct genus; and I have thought it best to retain Gray's name *Lemnalia*, in spite of the inaccuracy of his diagnosis, and to rewrite the descriptions of the genus and species as follows:—

LEMNALIA, Gray, emend. Bourne.

Colony an upright fixed anthodeté; the syndeté divisible into a stout, barren, smooth stem, from the top of which a few branches, also smooth, are given off; these, after a short course, divide, and the tertiary branches thus formed subdivide into terminal twigs, on which the anthocodiæ emerge. The main stem, branches, and branchlets composed of elongate longitudinally-disposed anthosteles, the more superficial of which appear as longitudinal ribs on the surface. The anthocodiæ may be shortly pedicellate or sessile; their arrangement on a branchlet may be either spicate or racemose. Spicules minute, usually of three kinds:—1. Elongate fusiform, with more or less prominent warty projections; found in all parts of the anthodeté, except at the extremities of the tentacles, and interlaced in an irregular manner to form a feltwork, specially abundant in the partitions between the anthosteles of the stem. 2. Modified double four-rayed stars, confined to the outer wall of the stem, each star sending a prolongation of one ray inward. 3. Scale-like or flattened branched spicules exhibiting a fine sculpture on their surfaces, confined to the distal parts of the tentacles and their pinnules. The anthocodiæ not retractile, but the tentacles can be tightly folded over the wide oral disc, their bases thickly beset with spicula, forming by their apposition a rudimentary anthopoma. The oral disc spacious, cup-like; the mouth, generally narrow, leads into a stomodæum, wide and nearly circular in section in its upper moiety, tapering below to form a narrow, compressed, richly ciliated tube. The zooids so oriented that their sulcar (ventral) aspects are abaxial, their asulcar (dorsal) aspects axial.

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In all the species of *Lemnalia* the stem and branches look smooth to the naked eye, but the feltwork of interlacing spicules becomes apparent on microscopical examination. The partitions between the anthosteles of the stem and main branches are not thick, but are densely packed with spicules of the elongate fusiform kind, thus defining the position of *Lemnalia* among the *Siphonogorginæ*. The genus appears to form a link between *Siphonogorgia* and *Ammothea*, approaching the former in habit and in the development of spicules in the partition-walls of the stem, and the latter in the small size and relative unimportance of its spicules.

The five species which I have examined fall naturally into two groups: (A) those in which the anthocodiæ are sessile and borne in spikes on the branchlets; (B) those

in which the anthocodiæ are pedicelled and borne at irregular intervals on the branchlets so as to form a raceme. They may be described as follows:—

A. *Anthocodiæ sessile, arranged in spikes.*

1. LEMNALIA JUKESII, Gray. (Pl. 40. fig. 1; Pl. 41. figs. 7, 12.)

*Lemnalium Jukesii*, Gray, Ann. & Mag. Nat. Hist. 1868, ii. p. 442.

Anthodeté a broad and short stem fixed by an expanded base; the stem divides into several thick branches, from which the branchlets bearing anthocodiæ are given off. Both stem and main branches devoid of apodetæ, marked by longitudinal ribs representing the superficial anthosteles. Usually a terminal anthocodia on each branchlet, below which the other anthocodiæ are arranged in obscure double rows. Anthocodiæ prominent, of equal diameter to the anthosteles from which they spring. Spicules on the tentacles and pinnules flattened or slightly rounded, scale-like, clavate, or irregular, with finely-sculptured surfaces; measuring from  $\cdot 02$  to  $\cdot 1$  mm. in length (fig. 12). Spicules of the rest of the anthodeté of one kind: elongate, fusiform, with few inconspicuous warty projections, interlaced in an open feltwork on stem and branches, arranged somewhat *en chevron* at the bases of the tentacles, where they form a rudimentary anthopoma, when the tentacles are infolded, approaching the condition in *Siphonogorgia*. Length of fusiform spicules  $\cdot 4$  to  $\cdot 15$  mm.; breadth about  $\cdot 015$  mm. Colour in spirit:—Stem and branches light brown, tentacles deep brown, the colour of the latter partly due to their peculiar spicules. Diameter of anthocodiæ with infolded tentacles about  $\cdot 6$  mm. Habitat unknown.

Gray's figure gives a very fairly accurate representation of the general habit of this species. It is readily distinguished from others by its brown colour deepening to dark brown on the tentacles, and by the fact that the spicules of the stem and branches are all of one kind and more loosely interlaced than in other species.

2. LEMNALIA RHABDOTA, sp. nov. (Pl. 40. fig. 2; Pl. 41. figs. 8, 13.)

Stem of the anthodeté narrowest at the base, widening gradually upward and dividing at about half the height of the whole anthodeté into three stout branches, which almost immediately subdivide into secondary branches bearing a few short branchlets. Anthocodiæ sessile, not projecting far from the surface of the branch, distributed over the secondary branches and their branchlets in somewhat alternate rows, closely approximated at the distal ends of the branches and branchlets, more widely separated in their proximal parts. The branches and branchlets incurved towards the centre of the anthodeté, their tips stout, bluntly digitiform, each ending in a terminal anthocodia larger than the lateral anthocodiæ. Average diameter of the distal ends of the branches  $1\cdot 75$  to  $2\cdot 0$  mm. Average diameter of a terminal anthocodia  $\cdot 75$  mm.; of the lateral anthocodiæ  $\cdot 5$  to  $\cdot 6$  mm. Spicules of the stem of two kinds:—1. Elongate fusiform, varying in length from  $\cdot 25$  to  $\cdot 75$  mm., and in diameter from  $\cdot 035$  to  $\cdot 025$  mm., covered with more or less prominent warty spines, which tend to fuse together towards the middle of the spicule to form two or more collar-like thickenings (fig. 8a). 2. Irregular spicules derived from four-rayed double stars, one ray of each star produced into a long spinous

process pointing towards the axis of the anthodeté. Average length of a double star, measured from the tips of the elongated rays, .13 mm.; average thickness across the centre, .03 to .04 mm. (fig. 13). Spicules of the tentacles irregular, flattened scales of various form, generally elongated and bilobed at the two extremities; their surfaces finely sculptured; length from .09 to .04 mm., width from .03 to .01 mm. Colour in spirit, yellowish white; tentacles brown. Habitat unknown. A single specimen in the British Museum of Natural History, presented by J. B. Jukes, Esq.

This species, though closely allied to, is sufficiently distinct from the following, from which it differs in habit, in the size of the branches and anthocodæ, and in the details of the spicules.

3. *LEMNALIA PERISTYLA*, sp. nov. (Pl. 40. fig. 3; Pl. 41. figs. 9, 14.)

Stem stout, tapering slightly towards the base, dividing at different levels into four or five branches, which pursue a vertical course for some distance before dividing into terminal branches and branchlets bearing anthocodæ. The terminal branches and branchlets lax and more closely crowded than in *L. rhabdota*. Anthocodæ sessile, not projecting far from the surface of the branch, set rather close together on the branchlets, with a tendency to form whorls. A terminal anthocodia to each branchlet, as in *L. rhabdota*. Average diameter of the terminal anthocodæ .75 mm.; of the lateral anthocodæ .5 mm.; diameter of the branchlets about 1.5 mm. Spicules of the stem and branches of two kinds:—1. Elongate fusiform, with scattered, slightly projecting warts; length .5 to .6 mm.; width .02 to .03 mm. 2. Modified double stars of the same general character as in *L. rhabdota*, but smaller, more slender, and with longer projecting rays; average length, measured from the tips of the elongated rays, .12 mm.; average thickness .02 mm. The tentacles have relatively few flat sculptured scales like those of *L. rhabdota*, their place being taken by small fusiform spicules, furnished with two whorls of four rather prominent spinous rays; length of these spicules about .035 mm., breadth about .005 mm., distance from end to end of opposite spines in a whorl .015 mm. Colour in spirit, yellowish white; tentacles light brown. Habitat: Zamboanga, Philippine Islands, 10 fathoms ('Challenger' Collection).

The characters which separate this species from the preceding are the mode of branching, the size of the anthocodæ, and the shape and size of the spicules.

B. *Anthocodæ pedicellate, borne in racemes on the branchlets.*

4. *LEMNALIA NITIDA*, Verrill. (Pl. 40. figs. 4, 5; Pl. 41. figs. 10, 15; Pl. 42. fig. 18.)  
*Ammonothea nitida*, Verrill, Bull. Mus. Comp. Zool. Harvard, vol. i. p. 39.  
*Lemmalia nitida*, Gray, *loc. cit.*

Anthodeté consisting of a stout, smooth stem, some 8 to 9 mm. high by 6 to 7 mm. broad; this, after attaining a height of 10 to 11 mm., again divides, generally dichotomously, and the secondary branches thus formed subdivide two or three times to form terminal branchlets, on which alone the anthocodæ are borne. The branchlets curved inward towards the axis of the anthodeté. Anthocodæ subglobose, shortly pedicelled, borne terminally and laterally on the branchlets at intervals of 1 to 2 mm.; the

tentacles, when at rest, infolded, but not closely pressed against the oral disc. There is usually a group of three to four anthocodiæ at the end of each branchlet, but no distinguishable terminal anthocodia. Spicules of the stem and branches of two kinds:—  
 1. Elongate fusiform, with numerous closely-set, small, warty or spinous projections; average length, .6 mm.; average diameter in the thickest part, .025 mm.; some of the fusiform spicules shorter and thicker, from .35 to .02 mm. in length by .03 mm. in thickness, slightly curved, covered with prominent spiny projections, and presenting every stage intermediate between the ordinary fusiform spicules. 2. Modified double stars with two elongate rays, measuring from .15 to .08 mm. from tip to tip of the elongated rays and from .025 to 0.15 mm. in thickness. Tentacular spicules flat, scale-like, finely sculptured, varying from .075 × .02 mm. to .08 × .01 mm. Colour in spirit, glistening white. Habitat, Zanzibar.

5. LEMNALIA TERMINALIS, Quoy & Gaimard. (Pl. 40. fig. 6; Pl. 41. figs. 11, 16.)  
*Alcyonum terminale*, Q. & G. Voyage de 'l'Astrolabe,' Zool. iv. p. 282, pl. xxiii. figs. 15-17.  
*Lemnalium terminalis*, Gray, *loc. cit.*

Anthodetæ consisting of a short, stout, smooth stem, from the upper end of which several short, stout branches are given off. These form secondary, stoutish, smooth branches from which long, very slender branchlets proceed. Anthocodiæ shortly pedicelled, about .6 mm. in diameter; the tentacles loosely infolded over the oral disc, borne only on the slender branchlets at rather wide intervals. Diameter of a branchlet about .75 mm. Spicules of stem and branches of two kinds:—1. Elongate fusiform, with few but prominent spinous projections, those towards the middle generally considerably larger than the others; length .7 to .3 mm., greatest thickness .04 to .03 mm. 2. Double stars with two elongated rays, the latter rather short and stout; length from tip to tip of the elongated rays about .15 mm., greatest thickness about .03 mm. Tentacular spicules flattened, sculptured, generally X-shaped, sometimes with smooth shaft and bilobed ends covered with warty projections (fig. 16), measuring from .065 × .02 mm. to .035 × .005 mm. Colour in spirit, yellowish white; tentacles light brown. Habitat: Port Molle, Queensland; King George's Sound.

The specimen in the British Museum forms part of the collection made by H.M.S. 'Alert.' There can be little doubt that it is identical with the species described as *Alcyonum terminale* by Quoy & Gaimard from a fragment brought from King George's Sound.

#### *Doubtful Species.*

##### LEMNALIA RAMOSA.

*Alcyonum ramosum*, Quoy & Gaimard, *loc. cit.* pl. xxiii. figs. 8-11.

"*Alcyonum magnum*, molle, multiramosum, stirpe albicante, fulvo striato, polypis fuscis in extremitate ramorum coadunatis; tentaculis brevibus rotundatis."

I think that this form must belong to *Lemnalium* because Quoy & Gaimard's figures of the anthocodiæ closely resemble those of *L. terminalis*. They are further described as follows:—"Les polypes disposés en grappes à l'extrémité des rameaux ne rentrent point dans leur gangue corticale. Il n'y a que les tentacules seuls qui se replient sur eux-mêmes en se fermant comme les pétales d'une fleur . . . . . C'est à l'extrémité des

nombreuses branches que les polypes sont agglomérés en panicules ovoïdes. Chaque individu a un pédicule distinct, court, d'un brun rougeâtre, ou couleur de bistre, de même que les huit tentacules, obtus et arrondis, qui le terminent."

*Anatomy and Histology.*

The description given, in the introductory part of this paper, of the mode of aggregation of the Nephthylidæ applies in every particular to *Lemnalia*. I made several series of sections through branches and a few sections through the stem of *L. nitida*, and I was able to make a series of sections through detached branches of *L. rhabdota* and *L. peristyla*. I was not able to examine the other species microscopically.

Fig. 19 (Pl. 42), which is a section of a tolerably large branch of *L. nitida*, shows that its branches (and the same is the case with the stem) are composed of fused elongate anthosteles. It can be seen that the middle of the branch is occupied by some ten or twelve large anthosteles, whose cavities measure some .75 mm. in diameter, while the cortical portion is occupied by smaller anthosteles whose cavities vary from .25 to .1 mm. in diameter. Nearly all the cavities display ridges or folds which are the prolongations of the mesenteries. The tissues in the centre of the branches and stem were badly preserved, so that I could not make out the details of the mesenterial filaments in all cases; but in some sections, both of the stem and branches, I could distinguish the characteristic grooved and ciliated asular or "dorsal" filaments, and the remaining mesenteries seem to bear filaments down to the very base of the colony. The larger central anthosteles are the chief zooids, the more peripheral anthosteles the secondary and tertiary zooids of the syndeté. The former may be called the chief members, the latter the lateral members of the branch. It can be seen that the chief members do not communicate one with another, but that, as at *m. m.*, they communicate by short and wide solenia with the lateral members, and also that, as at *n. n.*, some of the lateral members of larger size communicate by similar solenia with lateral members of smaller size. It is obvious that there are very few solenia in *Lemnalia nitida*, and that those which exist are almost exclusively confined to the cortical part of the branch. What is true of the branch is also true of the stem.

If lateral members, such as those marked *m* in fig. 19, be traced downward from their solenial connection with a chief member, they are observed to gradually thin out and end in a *cul-de-sac*. If they are traced upward they can be followed through a large number of sections, gradually increasing in diameter, till eventually they emerge on the surface as anthocodiae. In other words, the lateral members do not rise directly from the chief members, but indirectly, through the intervention of solenia, and they grow both aeropetally and basipetally, but their basipetal growth is inconsiderable and may be neglected. Although the lateral members originate indirectly from the chief members in this manner, they may be regarded, for present purposes, as springing directly from them, for by so regarding them we may form a clearer idea of the branching-system of the anthodeté.

The branch of which a section is represented in fig. 19 broke up into a number of branchlets bearing anthocodiae. The group of anthosteles marked A, B, C (chief members)

and  $a, b, c, d, e, f$  (lateral members) were traced into such a branchlet, of which a section is represented in fig. 20 (drawn to a larger scale than fig. 19). It is seen that, whereas the three chief members retain their predominant size and occupy the bulk of the section, the lateral members of the branch have diminished in number. Thus  $a$  is emerging as a small anthocodia;  $b$  and  $c$  have disappeared, having come to the surface in similar fashion lower down on the branchlet;  $e, d,$  and  $f$  have increased in size relatively to the chief members and will emerge as anthocodiæ higher up on the branchlet. The two lateral members marked  $x$  and  $y$  were not present in the branch. They took their origin from solenia growing out of the chief members in the branchlet after its separation from the branch,  $x$  arising from A and  $y$  from B. In the more distal part of the branchlet, fresh solenial outgrowths of the chief members give rise to new lateral members which end in anthocodiæ towards the tip of the branchlet. The three chief members A, B, and C can be traced to the extreme tip of the branchlet, where they emerge to form a terminal group of three anthocodiæ. The larger lateral members  $e$  and  $d$  emerge next below the terminal group, and  $f$  next below these. Now, if the branch represented in section in fig. 19 be traced downward into the stem, it is found that all the lateral members  $a, b, c, d, e, f$  sooner or later make communication with the chief members A and B (in this particular instance C does not give rise to lateral members in the branch and stem), and end blindly below. A, B, and C can be traced down into the stem, where they form lateral members and in turn make communication with a chief member of the stem, thin out, and end blindly below. One or two of the most centrally placed chief members of every branch are continued downward as chief members of the stem. From what precedes, it follows that the growth of the chief members of the branching-system of the anthodeté is not arrested when they give off lateral members, but that they continue to grow in advance of the lateral members derived from, and form the main axes of, the branches and branchlets. Thus, as was explained in the introductory part of this paper, the whole branching-system of any one primary zocid may be compared to a compound raceme of which the lateral members run parallel one to another, and are organically fused together throughout the greater part of their courses. The whole anthodeté is the result of the organic union of several such branching-systems. But the racemose mode of branching is not indefinite in *L. nitida*. Some of the more superficial lateral members of a branchlet are arrested in growth, but continue to branch on the system of a monochasial cyme. Thus, the anthostele  $a$  in fig. 20 ends in an anthocodia at the level of the section, and does not grow further as an individual member. But as the sections are followed upward it is seen that the anthostele sends up a solenium lying in the angle formed by A and  $c$ , and this solenium, some 2 mm. higher up, gives rise to the buds represented under a high magnification in fig. 24. The anthostele marked  $x$  has exactly the same relations. We find therefore in *Lemnalia nitida* a feature common in many plants: namely, that the ultimate lateral members of a composite branching-system adopt a mode of branching different from that of the chief member and its primary branches.

It is to be noticed that in *L. nitida*, and the case appears to be similar in *L. terminalis*, there is not one, but three or four chief members in each branchlet. In *Lemnalia Jukesii*, *rhabdota*, and *peristyla*, the arrangement is simpler, for there is only one chief member in each branchlet, and this emerges at the tip as the terminal anthocodia.

Further, I have not been able to discover that the lateral members of these three species ever branch on the principle of a monochasial cyme, as is the case in *L. nitida*. Sections through branchlets of *L. rhabdota* and *L. peristyla* show that all the lateral members communicate, either directly or indirectly, through the intermediary of lateral members of the first order, with the chief member forming the axis of the branchlet. Thus in these species the mode of branching is that of a compound raceme, without additional complexity. It appears that the more compact arrangement of the anthocodiae on the branchlets of these three species is due to their simpler mode of branching as compared with *L. nitida*.

I have entered into these questions at some length because the mode of aggregation and the system of branching in the Alcyonaria have been insufficiently studied and are imperfectly understood.

Botanists have provided us with a terminology applicable to every conceivable mode of branching, and it is possible, by making use of their system, to throw light on many obscure points in the Alcyonaria.

#### *Anatomy of the Zooids.*

Fig. 18 (Pl. 42), is a drawing of a group of terminal anthocodiae from a branchlet of *L. nitida* which has been decalcified, stained in alum carmine, and made transparent in oil of cloves.

The tentacles are short and broad, provided with a single marginal row of pinnules, their bases confluent so as to encompass a capacious hollow, the oral disc, into which the tentacles can be infolded. The mouth-opening is circular, rather large in *L. nitida*, small in *L. peristyla*; the stomodæum long and pyriform, its smaller end directed downward. The cup-shaped oral disc and the upper wide region of the stomodæum are lined by a tall columnar epithelium containing a few gland-cells, but no nematocysts, so far as I could see. I could not detect any trace of cilia on the epithelium of this region. The uppermost swollen part of the stomodæum is oval or subcircular in section, and is not so much compressed from side to side as is usual in the Alcyonaria. There is no sulcus in its upper part, but towards its narrower end the cells lining its outer or abaxial wall change their character, become attenuated and elongated, and bear each a single very long cilium. This strip of modified epithelium forms a shallow gutter which is undoubtedly a sulcus, but further down, in the narrowest part of the stomodæum, a definite sulcus can no longer be spoken of. In this region the stomodæal tube is compressed laterally, and is lined throughout by a modified ciliated epithelium resembling that of the sulcus. In some cases the sulcar groove disappears entirely, and the cavity of the stomodæum is a simple oval as represented in fig. 21; but more frequently the cells on the long sides of the oval project further into the cavity than those at the two narrower ends, so that the section is keyhole-shaped with a groove at either end. But one cannot speak of a sulcus and sulculus in this case, for the epithelium lining the tube is of the same character throughout. Such an arrangement has not, so far as I am aware, been described in any other Anthozoan \*, and it may be regarded as a

\* Ashworth, Proc. Royal Society, lxiii. (1898) p. 443, describes the stomodæum of *Xenia* as having a well-marked siphonoglyphic (sulcus) in which the cells of the lower third only bear long flagella.

primitive condition from which the single sulcus of the Aleyonarian, or the sulcus and opposite sulculus of the majority of Zoantharian zooids, may have been derived. In *L. rhabdota* and *L. peristyla* the stomodæum is not so long as in *L. nitida*, but it has the same shape and the same arrangement of cilia.

*The Mesenteries.*—In all three species of which I cut sections all the eight mesenteries are continued to the lowest ends of the anthosteles. They are therefore continued into the so-called stem-canals, *i. e.* the anthosteles of the primary zooids. This is also the case in *Siphonogorgia*, but in some other members of the *Nephthyidae*, *e. g.* *Spongodes*, only the asulcar (dorsal) mesenteries are continued into the anthosteles of the stem. At a short distance below the stomodæum the mesenteries are reduced to minute folds or ridges, and it is hard to distinguish a mesenterial filament on the sulcar and lateral pairs. But the asulcar pair bears the characteristic ciliated gutter throughout its extent. My specimens were not sufficiently well preserved to admit of detailed study of the mesenterial filaments. The longitudinal muscles on sulcar aspects of the mesenteries are poorly developed, and, as they are not borne on the longitudinal pleats of the mesogloea, one cannot speak of muscle-banners. In *L. rhabdota*, and particularly in *L. peristyla*, the longitudinal muscles are better developed at the upper ends of the mesenteries, and form a diagonal band passing from the body-wall to the oral disc. In these species also there is a considerable development of ectodermic musculature at the bases and along the inner sides of the tentacles. Slips of muscle-fibres are also given off to the pinnules. These muscles are not nearly so well developed in *L. nitida*; and it will be remembered that in the two first-named species the tentacles can be very tightly infolded into the oral disc, whereas in *L. nitida* they are only lightly folded over. I could find no traces of gonads in any of the species which I examined.

#### *Histology.*

When specimens have lain for many years in spirit, one cannot expect their histological details to be faithfully preserved. My example of *L. rhabdota* was badly macerated; those of *L. peristyla* and *L. nitida* were better, and I was able to make out a few points.

The *ectoderm* of the oral disc and stomodæum has already been described, and its structure is shown in fig. 24, which is a longitudinal section of a very young anthocodiæ. In fully-formed anthocodiæ the tentacles and pinnules are covered with a cubical epithelium, continuous with and generally similar to that of the oral disc. At the bases of the tentacles the superficial ectoderm becomes flatter, and it is reduced to a single flattened layer of cells over the greater part of the anthodeté. In some places, however, and especially where new spicules are being formed and the syndeté is being consolidated by the thickening of the external walls of the anthosteles, groups and patches of columnar ectoderm-cells are found, and these are proliferating rapidly from their lower extremities. In this manner little nests of rounded cells are formed, lying on or in the mesogloea. The mesogloea, as is shown in figs. 22, 23, and 24 (Pl. 42), is honeycombed with irregular spaces, most of which are occupied by spicules. In decalcified specimens, the organic residue of a spicule may generally be seen occupying the centre of a mesogloéal space (*s.sh.* in figs. 22 and 24). Some of the spaces, however, especially those near the

surface of the mesoglœa, are not occupied by spicules, but by groups of rounded or irregular cells which, as may be seen at *scb.* in figs. 22 and 24, are clearly derived from proliferating ectoderm-cells. In sections that have been double-stained with saffranin or picro-carmin and picro-nigrosin the mesoglœa is coloured blue, which takes a deeper or lighter tint according as the structureless matrix is of firmer or softer consistency. Figs. 22 and 24 show that the mesoglœa near the surface is full of spaces and is in most parts soft and lightly stained. Further, that not only are the spaces generally occupied by cells derived from the ectoderm, but that processes of mesoglœa, marked *mg'*, appear to stretch outward between the ectoderm-cells themselves and to isolate individual cells or groups of cells. In fact, we have here the mesoglœa in course of formation as an intercellular substance. The ectoderm-cells proliferate, and while proliferating they secrete the jelly-substance of the mesoglœa. Eventually a honeycomb of mesoglœa is formed, in the cavities of which groups of proliferated cells are enclosed. These enclosed cells are the scleroblasts, and as they become more deeply situated they give rise to spicules in the usual manner. In many cases I have found minute spicule-sheaths, stained deeply by saffranin and with traces of the organic axis of filaments in their interiors, among the proliferating cells just below the surface of the ectoderm, but they are so minute that I have not been able to figure them satisfactorily. It is clear, then, that the mesoglœa increases in thickness during the growth of the anthodeté as a result of the activity of the ectoderm-cells, and that, as it increases, scleroblasts, budded off from the ectoderm, are enclosed in it and give rise to spicules. I have described a similar origin of the mesoglœa and scleroblasts in *Heliopora carulea*\*, but in this case, as no spicules are formed, the subsequent history of the scleroblasts is different.

The *endoderm* in the deeper parts of my specimens was so much macerated that I can say nothing definite about it; but it was generally fairly well preserved in places where new growth was taking place, especially in young buds. In all the superficial parts of the anthodeté zooxanthellæ occur abundantly in the endoderm, and where the latter has undergone extensive maceration they lie loose in the cœlenteron. The best preserved parts of my specimens indicate that the endoderm is much vacuolated, and that the zooxanthellæ are contained in the endoderm-cells. In some cases (see fig. 23, *zæ.*) loose zooxanthellæ are contained in cells which may be wandering cells. Zooxanthellæ are specially abundant in the cavities of the tentacles and their pinnules, and the more one studies Alcyonarians the more one is struck by the accumulation of these organisms in the parts most exposed to the light. One very rarely finds any traces of food in the cœlentera of Alcyonarians; and its absence and the accumulation of symbiotic zooxanthellæ in the nutritive layer, the endoderm, point to the conclusion that the Alcyonaria are, in many cases at least, truly symbiotic organisms depending chiefly, if not exclusively, on the zooxanthellæ for their nutrition. Mr. Stanley Gardiner's † recent and conclusive experiments on the evolution of oxygen by corals living expanded in sunlight gives weighty support to this view.

\* Philosophical Transactions, vol. clxxxvi. (1895).

† Proc. Cambridge Philosophical Society, vol. ix. (1898), pp. 482-484. Mr. Gardiner, however, does not attribute the evolution of oxygen wholly to the zooxanthellæ.

Finally I have a few words to say on the formation of buds in *Lemnalia*. A bud, from which a new zooid grows, is always formed on a solenium which reaches out towards the surface. An early stage is shown in fig. 22. The solenium, *sol.*, expands close to the surface to form a wide cavity, the body-cavity of the future zooid. The endoderm-cells lining the outer wall of this cavity become longer and more columnar than in other parts; their nuclei are more numerous and stain more readily, and numerous zooxanthellæ are accumulated in them. The outer wall of the cavity is only separated from the ectoderm by a very thin sheet of mesogloea, and outside this the ectoderm proliferates rapidly, forming a solid plug, which carries the mesogloea and endoderm before it towards the interior of the cavity. This plug is the beginning of the stomodæum (fig. 23, *st.*). In the next stage the mesogloéal lamina at the bottom of the plug is broken through and the ectoderm becomes continuous with the endoderm; the centre of the plug becomes hollowed out, and the cells arrange themselves as an epithelial lining of the tube thus formed. The mesenteries make their appearance at an earlier stage as folds of the elongate endoderm-cells at the lower end and sides of the still solid plug (fig. 23, *mes.*). Shortly after the stomodæum has become a hollow tube, the cells at its lower end are differentiated to form the elongate columnar ciliated epithelium already described (fig. 24, *st."*). The oral disc and tentacles are developed subsequently, the latter as simple digitiform outgrowths of all three layers in the neighbourhood of the mouth.

I have elsewhere referred to the minute structure of the spicules of *Lemnalia* \*. The elongate fusiform spicules are excellent objects for study, because of their small size and transparency. Fig. 17 shows that each has an axial core, from which offsets radiate outward, nearly at right angles to the core, and every such offset forms the centre of one of the spinous projections. In some of my sections the organic matrix of the spicules was well preserved, and stained deeply with hæmatoxylin. This matrix consists of an external sheath and a central branching axis of organic fibrils which correspond exactly to the axial core and its offsets as shown in figs. 17, 8*a*, and 11*b*. The spicules have, in fact, exactly the same structure as those of *Spongodes*, described in detail in my paper referred to above.

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The more important points dealt with in this paper are:—1. The description of the branching-systems of the Alcyonacea in general and of *Lemnalia* in particular. 2. The restoration and amended description of Gray's genus *Lemnalia*, with an account of some new species. 3. The occurrence of a narrowed, uniformly ciliated tube in the lower part of the stomodæum of *Lemnalia*. 4. The origin of the scleroblasts and the growth of the mesogloea in this genus. 5. The manner in which new zooids are formed from solenial outgrowths. 6. A new set of descriptive terms applicable in particular to the Order Alcyonacea.

Oxford, January 14. 1899.

\* "The Structure and Formation of the Calcareous Skeleton in the Anthozoa," *Quart. Journ. Micr. Science*, vol. xli, (1899), p. 499

## EXPLANATION OF THE PLATES.

## PLATE 40.

- Fig. 1. *Lemnalia Jukesii*. A group of lateral zooids, magnified 15 times.  
 Fig. 2. *Lemnalia rhabdota*. A terminal branchlet,  $\times 15$ . *Zt.*, terminal zooid; *Zl.*, lateral zooid.  
 Fig. 3. *Lemnalia peristyla*. A terminal branchlet,  $\times 15$ . *Zt.* and *Zl.* as in fig. 2.  
 Fig. 4. *Lemnalia nitida*. An anthodeté of natural size.  
 Fig. 5. A terminal branchlet of *Lemnalia nitida*,  $\times 15$ .  
 Fig. 6. Part of a branchlet of *Lemnalia terminalis*,  $\times 15$ .

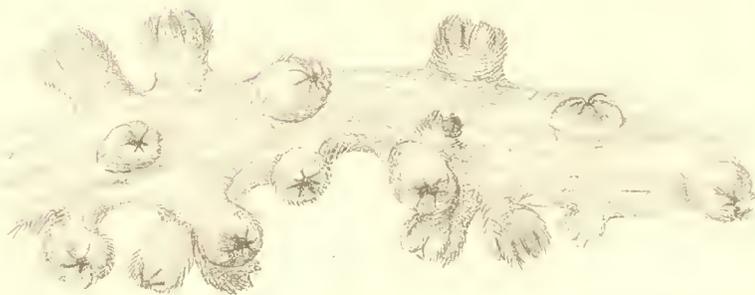
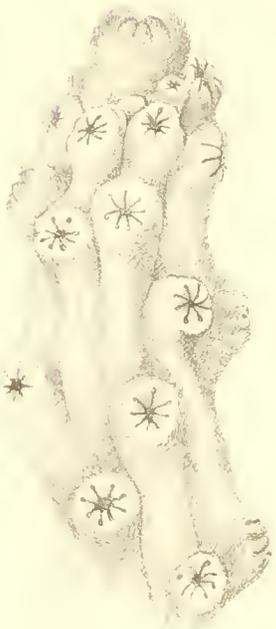
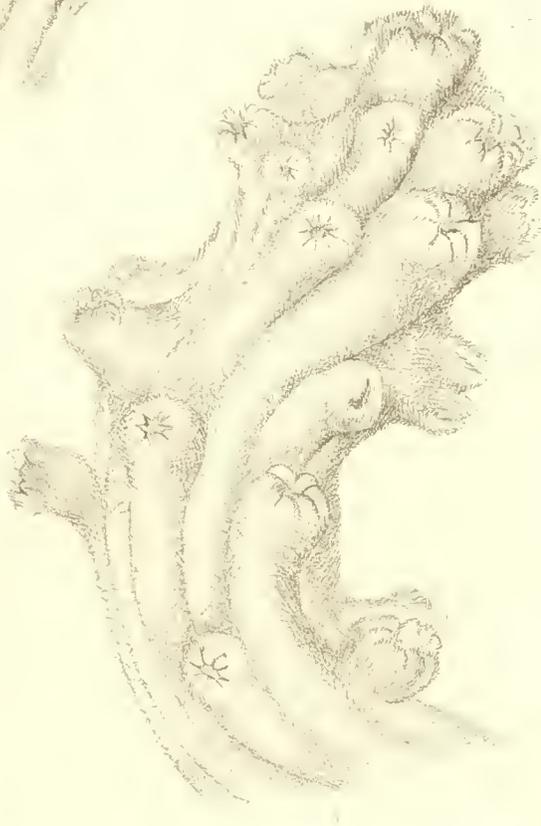
## PLATE 41.

- Figs. 7, 7 a-7 d. Spicules from the stem and anthocodiae of *L. Jukesii*.  
 Fig. 8. *Lemnalia rhabdota*.—8 a and 8 b. Elongate fusiform spicules from the partitions between the anthosteles. 8 c-8 e. Modified double stars from the stem-wall, 8 d being a form intermediate between the spindle and the double star. 8 b magnified 145, the remainder 240 times.  
 Fig. 9. *Lemnalia peristyla*.—9 a-9 c. Fusiform spicules from the stem-partitions and branches. 9 d and 9 e. Double stars from the stem-wall. 9 c and 9 d are intermediate in form between 9 a and 9 e. 9 a and 9 b magnified 145, the remainder 240 times.  
 Fig. 10. *Lemnalia nitida*.—10 a-10 c and 10 f. Fusiform spicules from partitions and branches. 10 d, 10 e, and 10 g-10 l. Irregular spicules and double stars from the stem-wall. Note the intermediate forms 10 d, 10 g, 10 h. 10 a and 10 b magnified 145, the remainder 240 times.  
 Fig. 11. *Lemnalia terminalis*.—11 a-11 c. Fusiform spicules from partition-walls and branches. 11 d and 11 e. Double stars from the stem-wall. Note the axial cord *ax* and the radial cords *ra*, in 11 b. Magnified 240 times.  
 Fig. 12. Scale-like spicules from the tentacles and pinnules of *L. Jukesii*,  $\times 420$ .  
 Fig. 13. Bilobed scales from the tentacles and pinnules of *L. rhabdota*,  $\times 420$ . 13 a is a scale viewed under the polariscope.  
 Fig. 14. Various shaped spicules from the tentacles and pinnules of *L. peristyla*,  $\times 420$ .  
 Fig. 15. Scales from the tentacles of *L. nitida*,  $\times 420$ .  
 Fig. 16. Scales from the tentacles of *L. terminalis*,  $\times 120$ .  
 Fig. 17. A spicule of *L. rhabdota* showing the axial core *ax*, from which cords *ra* radiate outward and emerge on the spines.  $\times 240$ .

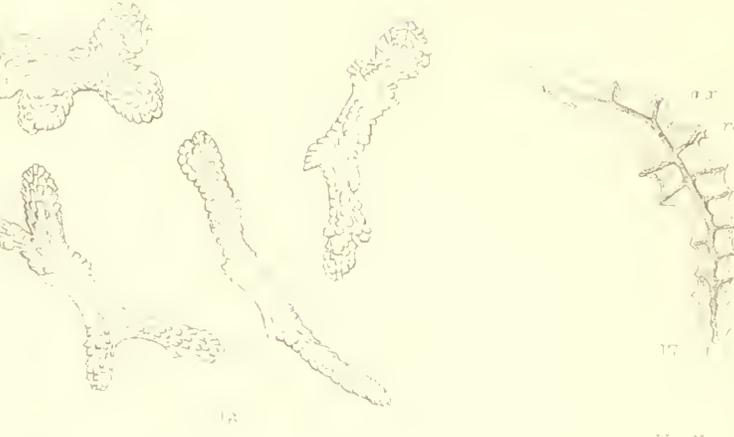
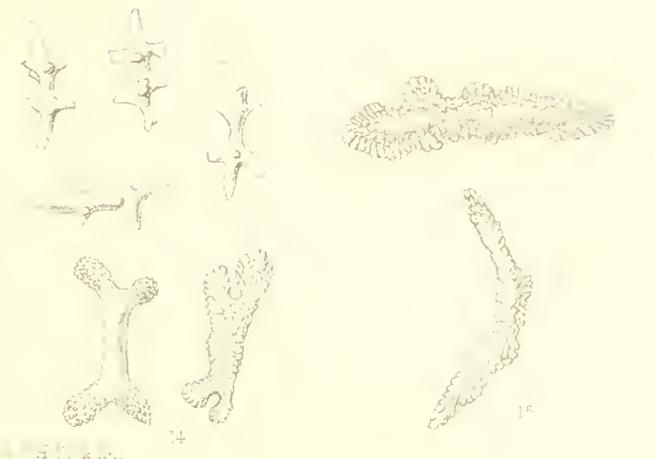
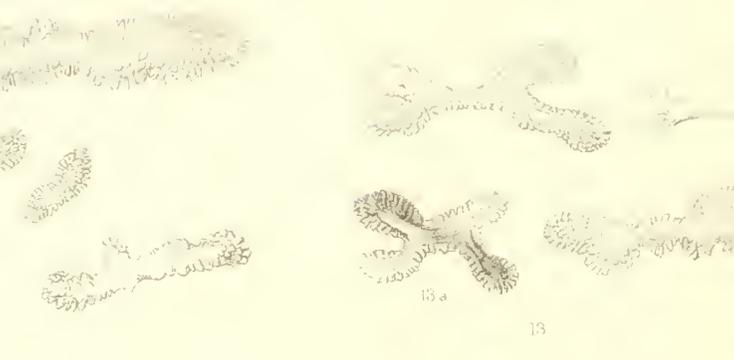
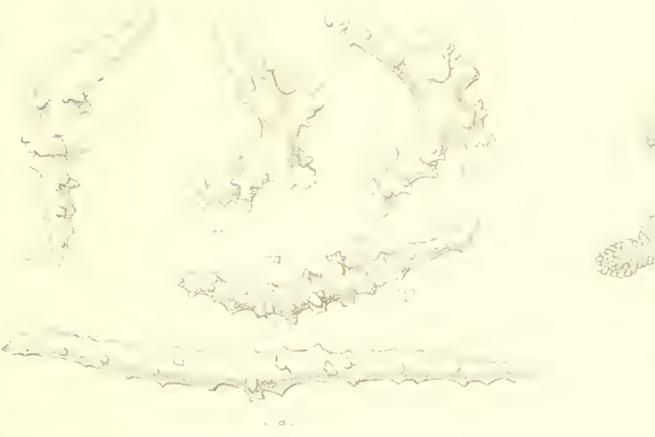
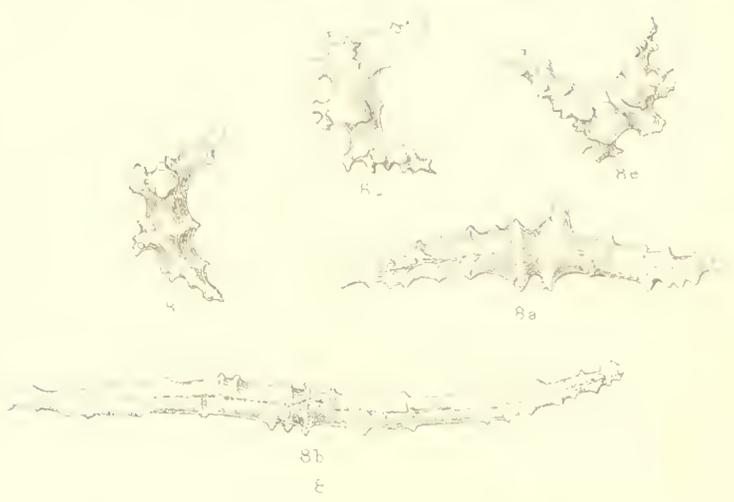
## PLATE 42.

- Fig. 18. *Lemnalia nitida*. Terminal anthocodiae of a branchlet which has been decalcified, stained, and rendered transparent. *T.*, Tentacles; *or.*, oral disc; *M.*, mouth; *st.*', upper non-ciliated wide moiety of the stomodæum; *st.*", its lower tubular ciliated part; *mes.*, mesenteries.  
 Fig. 19. Transverse section of a branch of *L. nitida*,  $\times 35$ . The mesoglæa is represented in grey, and the mesenteries are indicated; all other details are omitted. *mm.*, Solenial connexions between chief anthosteles and lateral anthosteles; *nn.*, lateral anthosteles giving off solenia from which new zooids will be formed. For the remainder of the lettering in this and the next figure see text, pp. 531 & 532.

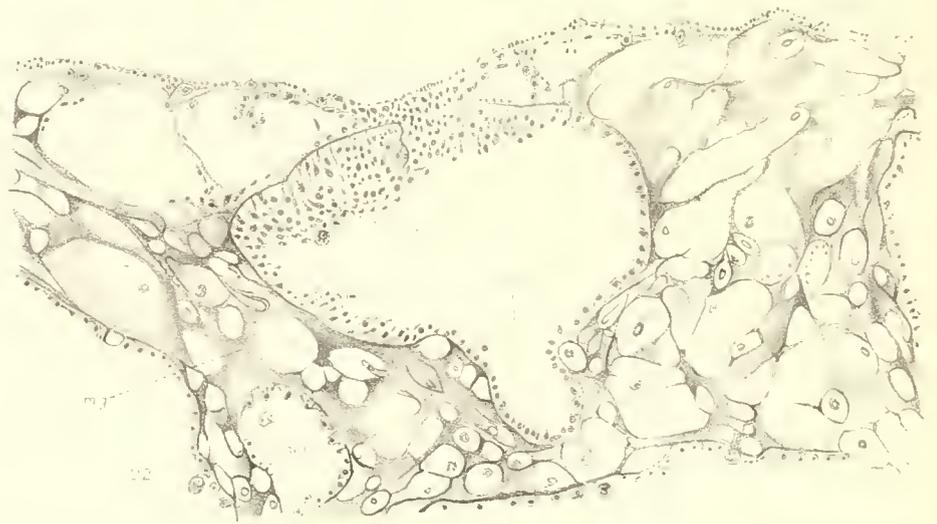
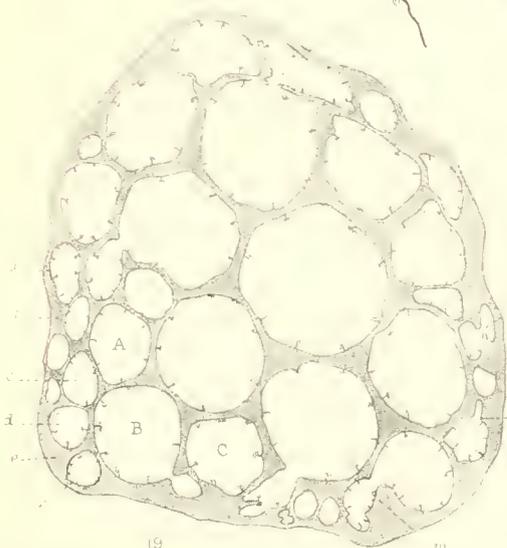
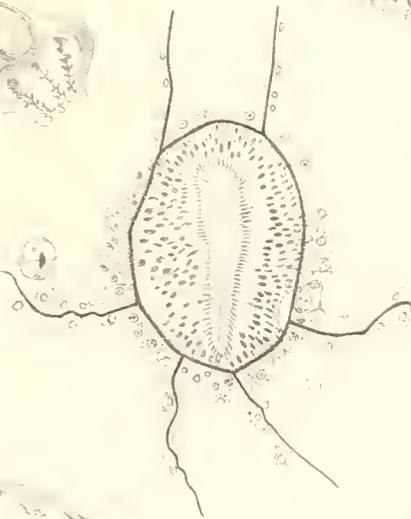
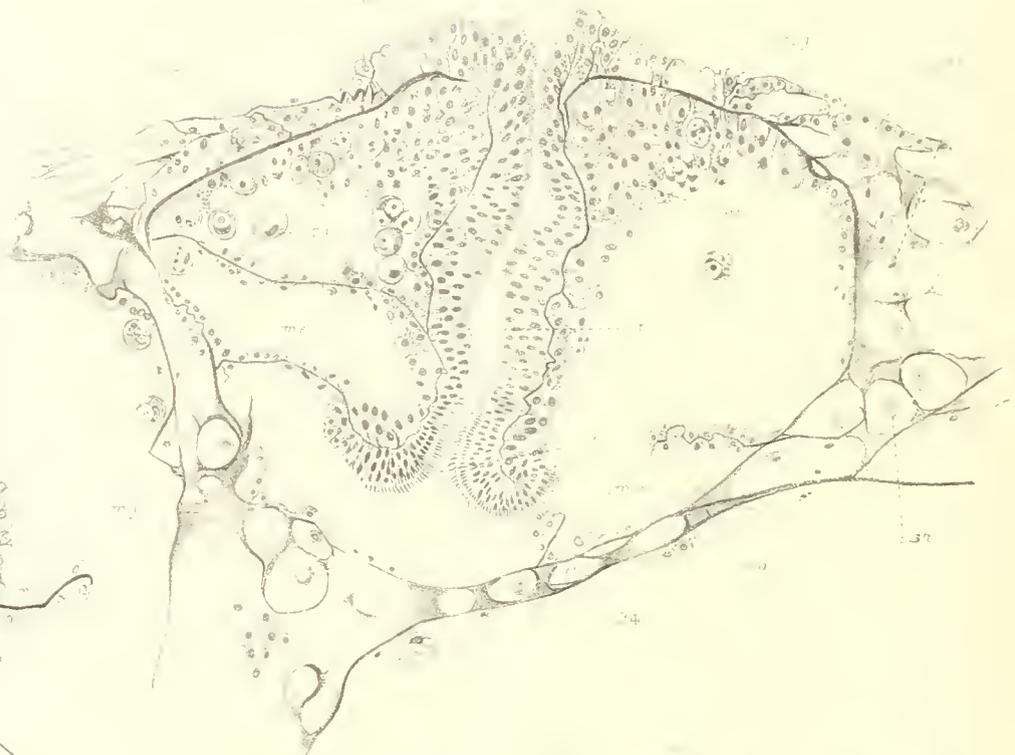
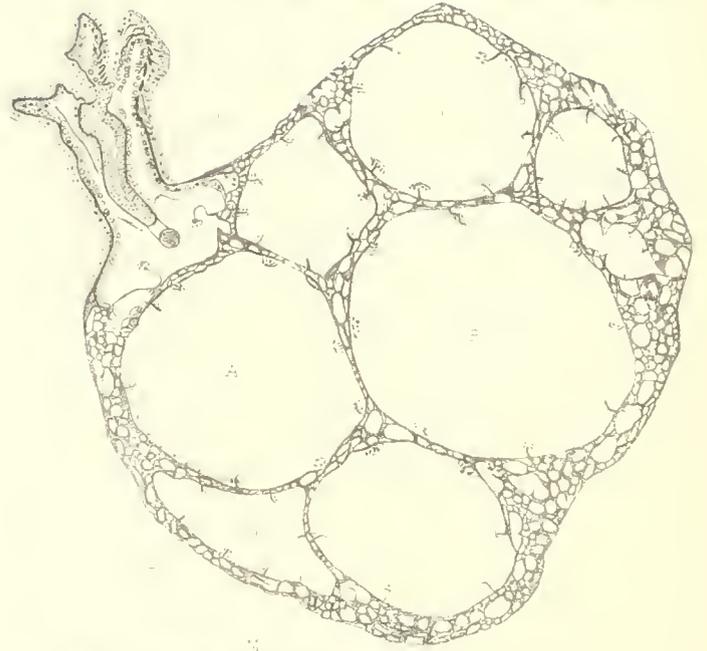
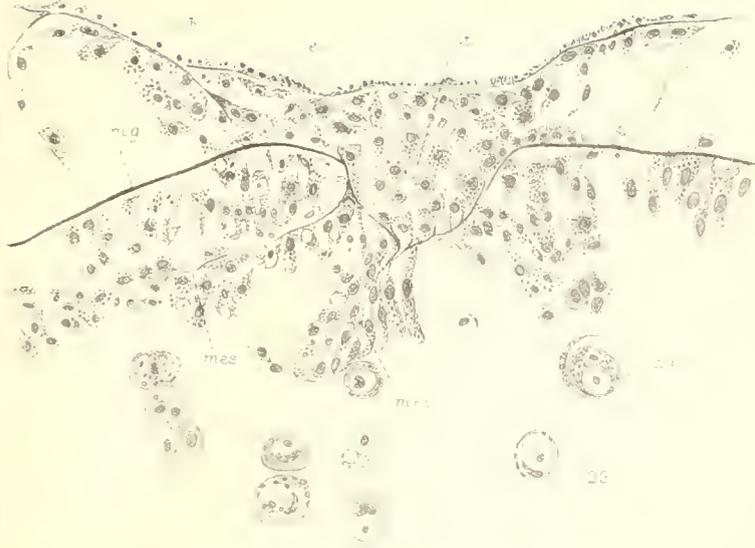
- Fig. 20. Transverse section of a branchlet borne on the branch of which a section is represented in fig. 19.  $\times 60$ . *a.*, A young anthocodia.
- Fig. 21. Transverse section of the lower end of the stomodæum of *L. nitida*, showing the uniform lining of columnar ciliated epithelium. *mes.*, Mesenteries; *en.*, endoderm. Zeiss'  $\frac{1}{2}$  Hom. Imm. Comp. Oc. 4.
- Fig. 22. Transverse section through a solenium of *Lennalia nitida* in which a zooid is beginning to be formed,  $\times 420$ . *ec.*, Ectoderm; *en.*, endoderm; *mg.*, mesoglaea; *sol.*, solenia; *st.*, thickening of ectoderm forming the primordium of the stomodæum; *scb.*, scleroblasts budding off from the ectoderm; *s.sh.*, spicule-sheath.
- Fig. 23. Vertical section through another zooid bud, showing the formation of the mesenteries. *mes.*, Mesenteries; *zx.*, a zooxanthella enclosed in a cell. Other lettering as in fig. 22. Zeiss'  $\frac{1}{2}$  Hom. Imm. Oc. 2.
- Fig. 24. Vertical section through an older zooid bud. *st.'*, Non-ciliated upper, and *st''*, ciliated lower regions of the stomodæum; *mg.'*, mesoglaea in course of formation between ectoderm-cells. Other lettering as before. Zeiss'  $\frac{1}{2}$  Hom. Imm. Oc. 2.















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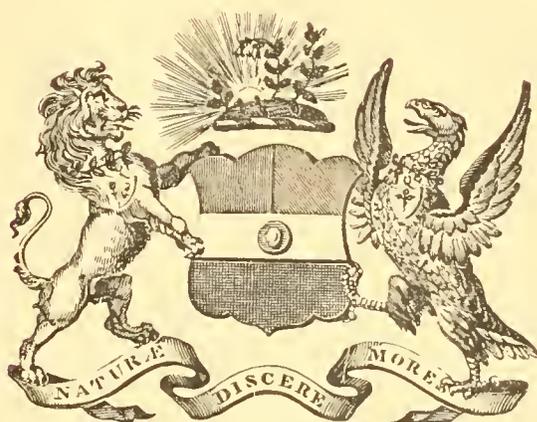
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