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THE DERIVATION AND SIGNIFICANCE OF CERTAIN SUPERNUMERARY MUSCLES OF THE PECTORAL REGION.

By GEO. S. HUNTINGTON, M.D., *Professor of Anatomy, Columbia University, New York.* (PLATES I.–XIV.)

(Read before the 16th Annual Session of the Association of American Anatomists, Washington, D.C., Dec. 30–31, 1902.)

THE primate pectoral region offers peculiar conditions both as regards the ontogeny of the pectoral muscles and the development of the ventral thoracic wall. As the direct result of these conditions a number of supernumerary muscles are encountered in this region, united into a correlated morphological group by their derivation from the plane of the pectoralis major and by the common etiological factors responsible for their production.

These variations present very definite and uniform structural characters, and, while some belong to the rarer muscular anomalies of this region, others, as the sternalis, occur more frequently, and in a remarkably constant percentage of the subjects examined. Abundant records of muscular variations in the pectoral group are scattered through the anatomical periodicals. The sternalis in particular has attracted widespread attention by reason of its peculiar morphological position, and has produced a literature of its own. Modern phylogenetic and embryological investigations have largely enhanced our knowledge of the developmental causes active in the production of departures from the normal myological type of this region, and it hence seems advisable to subject the entire group to a general revision with regard to the mutual relationship of the individual members and their derivation.

The variant muscles here considered are united into a homogenetic group by their common origin from the general muscular plane of the pectoralis. Within the limits of this group, however, certain members appear as muscular integers of reversional significance, in the broader sense presently to be defined, reproducing myological conditions which, while abnormal for the primate type, occur as normal constituents of the pectoral mass in some of the lower mammalian orders. Other variants belonging to this group, on the contrary, do not possess such reversional significance, and appear either as purely fortuitous variations, or as the result of peculiar mechanical and developmental causes, which, by disturbing the normal type of development of the primate pectoral musculature, lead to the production of a series of atypical and supernumerary pectoral muscles.

Thus the *tensor semi-vaginæ articulationis humero-scapularis* (Gruber) reproduces accurately the intermediate pectoralis (*M. sterno-humeralis*) found in certain of the lower mammalia, as in *Cercoleptes* (*cf. infra*, p. 8).

The constant and uniform structural character of this variation in all of the observed instances would alone suggest that it represents a myological type, abnormal as an element of the primate pectoral group, but forming a normal constituent of the pectoralis complex in certain of the specialised types assumed in other mammalian orders.

In the case of certain of the other variants here considered no such homologous muscles are found among the lower mammalian orders.

Both of these morphological subdivisions of the group owe their production primarily to identical etiological factors, resulting in a disturbance of the normal processes of pectoral muscular development.

In the case of the reversional variations this atypical development has occurred along definite channels, leading in other mammalian types to the inclusion in the pectoralis group, as normal constituents of the same, of muscular integers strictly homologous with the human variants. The abnormal human muscle has, so to speak, followed in its development lines of structural stability, which have been adopted in the differentiation from the common antecedent mammalian type of the homologous pectoral segments normally encountered in certain mammalian orders below the primates. These variations may therefore be regarded broadly as reversional, in the sense presently to be more closely defined.

On the other hand, the fortuitous variations belonging to this general group do not represent structures normally found in the musculature of the mammalian series.

Topographically, according to the position occupied by the variant in reference to the plane of the pectoralis major, the entire group may be subdivided as follows:—

A. DEEP SUPERNUMERARY MUSCLES, situated in the interval between the pectoralis major and minor:—

1. *Tensor semi-vaginæ articulationis humero-scapularis* (Gruber).
2. *M. chondro-coracoideus ventralis* (*Pectoralis minimus*).
3. Some forms of the *M. præ-clavicularis.*

B. SUPERNUMERARY MUSCLES, placed superficially to the pectoralis major:—

1. *M. sternalis.*
2. *M. infra-clavicularis.*

In attempting to define the derivation and significance of these variations, and to establish their mutual relationship, the following factors deserve consideration:—

1. The share taken by atypical cleavage of the primitive pectoral mass into the ecto-pectoral (P. major) and ento-pectoral (P. minor and subclavius) in the production of supernumerary intermediate pectoral muscles.

2. The relation between the variant muscles and coexisting deficiencies in the sheet of the pectoralis major, especially conditions indicating that the variant represents a portion of the normal muscle atypically displaced.

3. The peculiar type of development followed by the pectoral group, as determined by Mall[1] and Lewis,[2] together with the

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[1] F. J. Mall, "The Development of the Ventral Abdominal Walls in Man," *Journal of Morphology*, vol. xiv., No. 2, 1898.

[2] W. H. Lewis, "Observations on the Pectoralis major in Man," *Johns Hopkins Hospital Bulletin*, vol. xii., Nos. 121, 122, 123, April, May, June 1901.

development of the sternal bars and their fusion in the formation of the ventral thoracic wall.

4. The occurrence of muscular homologues in mammalian orders other than that of the primates.

5. The possible significance of some supernumerary muscles and superficial pectoral slips as persistent remnants of the thoraco-humeral panniculus, particularly in cases of combination with other aberrant pectoral muscles of undoubted pannicular derivation.

6. The innervation of the variants.

We may consider in the first place the structural details of the individual muscles, and then examine them in reference to the etiological factors above cited.

A. Deep Supernumerary Muscles, occupying the ecto-ento-pectoral interval :—

1. *M. tensor semi-vaginæ articulationis humero-scapularis* (Gruber).

It is necessary, on the ground of priority, to retain this somewhat cumbersome nomenclature, although the definition of the aberrant as M. sterno-humeralis, or sterno-chondro-humeralis, would in many respects be preferable.

In its typical development this supernumerary muscle, situated between pectoralis major and minor, forms a strong, flat fasciculus, arising from the first or second costal cartilage, or from both, and from the lateral margin and ventral surface of the sternum. The muscle traverses the clavi-pectoral space laterad, passing caudad of the subclavius and coracoid process. It lies upon the terminal portion of the pectoralis minor, the fasciculi intersecting the course of those in the latter muscle at an acute angle, and upon the combined origin of the coraco-brachialis and short head of the biceps. It then expands into a strong triangular tendon, which continues beneath the ventral margin of the deltoid and joins the deep layer of the deltoid fascia, thus gaining an indirect attachment to the lateral humeral ridge and tuberosity.

History of the muscle :—

According to Macalister,[1] the muscle was first observed by

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[1] "On Muscular Variations in Human Anatomy," *Trans. Royal Irish Academy*, vol. xxv., pt. i., p. 49, Dublin, 1872.

Gantzer. Wenzel Gruber[1] described it more fully under the name of *M. tensor semi-vaginæ articulationis humero-scapularis* as an elongated triangular or rectangular muscle, 16–19 cm. long, and varying from 3 to 14 mm. in width, occupying the interval between pectoralis major and minor, and included in a special sheath of the coraco-costal fascia. Gruber found the muscle in two male bodies, once bilateral, once confined to the right side. In these cases the muscle arose from the first or second costal cartilages, or from both, and from the adjacent portions of the manubrium and body of the sternum, crossed the pectoralis minor below the coracoid process, and continued over the united coraco-brachialis and biceps, expanding into a membranous tendon which radiated into the deep layer of the deltoid fascia, the cephalic fibres approaching those of the coraco-acromial ligament, while the caudal fibres became lost on the surgical neck of the humerus and the lateral bicipital ridge, after crossing superficially the ascending fibres from the tendon of the pectoralis major. No reference is made in the description to any coexisting deficiency in the sheet of the pectoralis major, and in the accompanying illustration[2] this muscle has been entirely removed.

Subsequently the same observer[3] reported an additional instance of the muscle in a subject with deficient radius.

Testut[4] quotes a case described by Pye-Smith, Howse and Colley in the *Guy's Hospital Reports*, 1870.

Macalister[5] found the muscle on the left side in a female chimpanzee, arising from the cartilages of the first and second ribs.

I am able to report four additional uncomplicated instances of the variation in the human subject, in one of which it occurred on both sides, and a fifth example in which the variant muscle was combined with a M. sterno-chondro-coracoideus ventralis.

The recorded cases of the muscle, described with sufficient

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[1] "Die supernumeraeren Brustmuskeln des Menschen," *Mém. de l'Acad. Imp. de St. Pétersbourg*, 1860, No. 2, tome iii., p. 10.

[2] *Loc., cit.* tab. ii. fig. 2.

[3] *Virchow's Archiv*, Bd. 40, p. 427.

[4] *Les anomalies musculaires chez l'homme*, Paris, 1884, p. 16.

[5] *Loc. cit.*, p. 49.

detail to ensure correct identification, may therefore be tabulated as follows:—

Observer.	Number of Cases.	
W. Gruber,	3 Cases, 1 bilateral,	In man.
Pye-Smith, Howse and Colley,	1 Case,	
Huntington,	4 Cases, 1 bilateral, 1 Case in combination with M. sterno-chondro-coracoideus,	
	In the Chimpanzee.	
Macalister,	1 Case.	
	Total—10 Cases, presenting 12 muscles.	

While this is not a large number of observations, yet the uniform and congruent structural type of the variant in all the recorded cases is very striking, and entitles it to recognition as an established and independent variation. Of the five examples reported at this meeting of the Association, each presents certain features bearing on the derivation and significance of the variant. They are hence described *in extenso*: the first four uncomplicated cases under this heading; the fifth, occurring in combination with the M. sterno-chondro-coracoideus, under the latter muscle.

1st Case (Pl. I.). Subject number 1215, 1902, male, U.S., white, æt. 46.

Left side.—The pectoralis major sheet is complete in the sternocostal division of the muscle, but the interval between this and the clavicular portion is very distinct, and larger than is normally the case. After division and reflection of the clavicular pectoralis a slender muscular belly is exposed, ventrad of the normal subclavius and separated from the same by the clavi-pectoral fascia. The aberrant muscle arises from the cartilage and bone of the first rib, crosses laterad over the pectoralis minor and below the coracoid process, and expands by a broad triangular tendinous leaf into the subdeltoid fascia.

Innervation.—By a filament from the nerve of the clavicular portion entering the muscle along the cephalic border near the origin.

2nd Case (Pl. II.). Subject number 706, 1900, male, Ireland, æt. 37.

Right side.—The sheet of the pectoralis major is deficient in part of the second and third intercostal spaces. This cleft is occupied by a muscular band, arising from the sternum at the mesial extremity of the third interchondral space and from the adjacent margins of the third and fourth cartilages. The aberrant muscle is inclined more obliquely than the cephalic portion of the pectoralis major, beneath which it dips in proceeding laterad. It crosses the pectoralis minor near the insertion and expands into a triangular tendon-plate, which becomes continuous with the subdeltoid fascia.

Innervation.—Branch from nerve of pectoralis major, entering deep surface of muscle.

3RD CASE (Pl. III.). Subject number 1360, 1902, male, Germany, æt. 59.

Bilateral defect of pectoralis major, and corresponding bilateral M. tensor semivaginæ.

A. Left side.—A distinct cleft separates the clavicular from the sterno-costal portion of the pectoralis major, the former leaving the ventral surface of the clavicle bare in its mesial fourth.

The sterno-costal portion is again deficient in its cephalic part. A reduced manubrial segment, arising from the sterno-clavicular capsule, the first costal cartilage and the adjacent portion of the pre-sternum, is separated from a more extensive caudal portion by a distinct interval corresponding to the second chondro-sternal junction and parts of the first and second interchondral spaces. This caudal portion of the pectoralis major arises from the sternum and costal cartilages, from the third to the sixth inclusive. The supernumerary intermediate muscle arises, partly under cover of the manubrial portion of the pectoralis major, from the adjacent borders of the first and second costal cartilages and the corresponding margin of the pre-sternum. Proceeding laterad it expands into a broad tendinous lamina which fuses with the subdeltoid fascia.

B. Right side.—The sheet of the pectoralis major is deficient between the sterno-clavicular articulation and the third chondro-sternal junction. This interval is occupied by the variant intermediate muscle, which arises from the second and third cartilages and the lateral sternal border included between them, and is inserted into the subdeltoid fascia by a broad tendinous expansion. The aberrant muscle is somewhat larger and better developed than the one on the left side, but the two variants correspond closely in all their structural details.

Innervation.—Identical on both sides. A slender branch from the external anterior thoracic nerve enters the muscle near the cephalic border of the deep surface. On the right side a small filament from the same branch passes to the clavicular portion of the pectoralis major.

4TH CASE (Pl. IV.). Subject number 1180, 1902, male, U.S. negro, æt. 29.

Subject of unusual muscular development.

The pectoralis major forms a massive plane, the muscles of the two sides interdigitating by short tendinous fibres across the mid-sternal line.

Right side.—The cleft between the clavicular and sterno-costal divisions is complete and well-developed. On reflecting the pectoralis major a strong flat intermediate muscular band is found crossing the fibres of the pectoralis minor at an acute angle. The variant muscle arises from the ventral surface of the second costal cartilage and the adjacent border of the sternum under cover of the manubrial fibres of the pectoralis major. Laterad its insertion is partly into the ventral lamella of the pectoralis tendon, fusing with the cephalic fibres of the sterno-costal portion, partly by the expansion of the cephalic fibres into a strong tendinous lamina which unites with the subdeltoid fascia.

Innervation.—By two slender twigs, entering the ventral aspect of the muscle and derived from the branch of the external anterior thoracic nerve to the sterno-costal portion of the pectoralis major.

M. sterno–chondro–humeralis, homologous with the above-described human variant, and occurring as a normal constituent of the pectoral complex in other mammalia.

Many of the lower mammalia possess, between the superficial pectoralis and the deeper layer, a well-defined, flat muscular band, which, as M. sterno-chondro-humeralis, extends between the sternum and several of the proximal costal cartilages and the lateral surface of the shaft of the humerus, in some forms expanding broadly toward the insertion. I have met this muscle, which corresponds in all essential features closely to the above-described human variant, especially well developed in many carnivora, although some artiodactyla, as *Dicotyles*, possess the element in its most typical form.

In Pl. V. the pectoral musculature of the mink, *Putorius vison*, is shown, with the deep and intermediate layers exposed on the right side by reflection of the ecto-pectoralis. In Pl. VI. a similar dissection of the pectoral muscles of *Cercoleptes caudivolvulus*, the kinkajou, is shown. In both of these forms the intermediate sterno-humeralis appears completely separate and distinct from both the superficial and deeper layers, as a discrete element of the pectoral musculature.

2. *M. sterno-chondro-coracoideus ventralis* (*Pectoralis minimus*).

Among the numerically large group of the præ-clavicular aberrant muscles, two general divisions may be distinguished, according to the probable derivation of the variant:—

A. Forms which represent primarily and directly traces of the reversional appearance of the sterno-chondro-scapularis, the antecedent type of the human and anthropoid subclavius, and which are hence associated with the latter muscle in the narrower sense.

B. Forms more directly referable to the plane of the pectoralis major, appearing as atypical segments of this muscle.

Of course both of these groups share the common primary derivation from the general pectoral muscular mass, since the subclavius, or its generalized primitive form, the sterno-chondro-scapularis, differentiates from the cephalic part of the deep or ento-pectoral layer, while the pectoralis major appears as the superficial or ecto-pectoral sheet of the pectoral muscular plane.

Still, as a matter of convenience, reference of the variant in any given case to one of the two groups above defined is permissible, thus associating the atypical muscle either with the deeper stratum of the subclavius or with the superficial pectoralis major.

The latter group is so closely related to the variations just described that it can properly be considered in direct connection with them. This becomes especially evident in instances such as the one shown in Pl. VII., where the sterno-chondro-humeral slip (tensor semivaginæ) occurs in combination with the M. sterno-chondro-coracoideus, associated with pronounced deficiency in the plane of the pectoralis major.

Subject number 133, 1898 (Pl. VII.), female, Ireland, æt. 42.

Left side.—Pectoralis major poorly developed, with deficiency of medial segment of clavicular portion, producing a wide clavi-manubrial interval. This space is occupied by a fusiform muscle, arising from the ventral extremity of the first rib and cartilage. Proceeding laterad the muscle divides into two fasciculi, of which one, overlying the normal subclavius, is inserted into the tip and adjacent portion of the medial margin of the coracoid process, close to the insertion of the pectoralis minor, while the other expands into a broad tendinous lamina which joins the subdeltoid aponeurosis.

Innervation.—A branch from the external thoracic nerve, passing mesad along the cephalic margin of the pectoralis minor, gives a filament to the lower muscle and continues on the deep surface of the sterno-chondro-coracoideus, penetrating the same a short distance from the origin.

This case evidently presents a combination of the tensor semivaginæ with the supernumerary pectoral muscle variously described as *pectoralis minimus, præ-clavicularis medialis, s. sterno-clavicularis anticus,*[1] *s. sterno-chondro-coracoideus ventralis.*

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[1] W. Gruber, *Reichert's Archiv*, 1865, p. 714.

ANALYSIS OF THE FIVE CASES OF THE M. TENSOR SEMI-VAGINÆ HERE RECORDED.

A comparison of the observations comprised in the above series leads to the following conclusions regarding the derivation and significance of the aberrant muscle and its relations to cognate variations of the pectoral region :—

1. The supernumerary intermediate muscle is clearly a displaced segment of the normal pectoralis major, as determined

(*a*) By the innervation, which in all five of the cases was furnished either through independent filaments from the external anterior thoracic nerve, or by twigs entering the substance of the variant muscles from branches supplying the normal pectoralis major.

(*b*) By the coexisting deficiencies in the muscular sheet of the pectoralis major, the gap being evidently produced by diversion of some of the fibres normally entering into the composition of the muscle to form the variant structure. This character is uniformly present in all of the above-described instances, although not equally pronounced in all.

In general it will be noted that the abnormal deviation of part of the pectoralis major to form the aberrant muscle usually involves the cephalic (manubrial) segment of the sterno-costal division, the origin of the variant centering at the second chondro-sternal junction and extending thence, in varying degrees in the different examples, cephalad toward the first cartilage, caudad toward the third, and mesad to corresponding points along the lateral sternal border (Cases 1, 3 and 4).

More rarely the central portion of the sterno-costal division of the pectoralis major furnishes the aberrant muscle, as in the second case above described, where the pectoralis is deficient over part of the second and third spaces and the intermediate muscle arises lower than in the other instances, viz., from the third and fourth cartilages. In this case the relation of the variant to the parent layer of the pectoralis major and its congruence with the deficiency in the same is especially clear and evident. With the more commonly observed higher origin of the intermediate muscle, as in Cases 1 and 4 of above series, the deficiency of the pectoralis sheet may appear as an increased development of the normal cleft between the clavicular and sterno-costal divisions of the muscle. The third instance above described is especially instructive in this respect. Here, with bilateral development of the abnormal muscle and high origin of the same, the deficiency in the pectoralis major appears on the right side as an enormously enlarged claviculo-sterno-costal interval, while on the left side an additional cleft in the sterno-costal division clearly betrays the source of the fibres diverted from their usual course to form the variant intermediate muscle.

2. In considering the etiology of the variation, the following conclusions appear justified:—

(*a*) It is apparent that the abnormal muscle develops in consequence of faulty processes in the normal cleavage of the common pro-pectoral mass into a superficial or ecto-pectoral, and a deeper or ento-pectoral plane.

Both ontogenetically, as shown by Lewis,[1] and phylogenetically, as presented in a former communication [2] to this Association by myself, the primate pectoral musculature appears first as a uniform mass, yielding by subsequent cleavage the ecto- and ento-pectoral layers. The former is in general confined in origin to the sternal region, and apparently favoured in its differentiation and subsequent development by the mechanical advantages derived from the firm connection with this fixed skeletal portion of the ventral thoracic wall. The latter furnishes, by further segmentation, in its own plane, a smaller cephalic element, the subclavius, or its more generalized representative, the sterno-chondro-scapularis, and a larger caudal muscle, the pectoralis minor and abdominalis. In this primitive disposition the abdominal portion of the pectoralis at first appears as a caudal prolongation of the deeper ento-pectoral layer, coming into view beyond the caudal margin of the ecto-pectoralis, or pectoralis major *sensu stricto*, but associated with the pectoralis minor at the insertion.

Subsequently the abdominal pectoral differentiates from the

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[1] *Loc. cit.*

[2] G. S. Huntington, "Present Problems of Myological Research, and the Significance and Classification of Muscular Variations," *Amer. Journal of Anatomy*, vol. xi., No. 2, pp. 157–175; 1903.

latter muscle, and this separation is further accentuated in man and the anthropoid apes by migration of the deep pectoralis minor insertion from the humerus cephalad to the coracoid process.

(*b*) In most of the lower primates the pectoralis minor retains the primitive humeral insertion in common with the pectoralis abdominalis and the axillary arch, when the latter structure is present, as a more or less distinctly specialized derivative from the thoraco-humeral panniculus, as is the case in the vast majority of the species composing the order below the group of the anthropoidea. It is only when these latter forms are reached that we begin to encounter typically the divorce of the two pectoral layers at the insertion, and the migration cephalad of the pectoralis minor from humerus to shoulder girdle, while the abdominal pectoralis remains secondarily connected with the pectoralis major, as a constituent of the dorsal plane of the tendon of insertion. Even among the anthropoid apes this secondary position of the pectoralis minor has not reached the uniformity and stability which characterizes it in the human species, where the occasionally-observed partial or complete prolongation of the minor tendon beyond the coracoid constitutes one of the more exceptional reversional variations of this region. Thus, while the coracoid insertion of the pectoralis minor obtains very generally, with minor specific differences, in the three remaining species of the great anthropoid apes, the arrangement of the muscle is subject to considerable variation in the chimpanzee. In the specimens examined by Broca and Humphry, and in two examples of my own series, the pectoralis minor was inserted altogether into the lateral tuberosity of the humerus. Hepburn and Champneys describe the muscle as passing over the superior surface of the coracoid to the capsule of the shoulder joint, and in one example dissected by myself this condition was approached, the pectoralis minor being only in small part attached to the coracoid, the remainder, separated from the cephalic surface of the process by a bursa, continuing into the shoulder capsule, closely associated with the supra-spinatus tendon. Alix and Gratiolet have previously described this divided insertion into capsule and coracoid in the chimpanzee. Finally Wilder reports a very significant example of this animal, in which the pectoralis minor insertion was humeral on the right, but into the coracoid process on the left side.

(*c*) It is reasonable to assume that the production of the variant muscle here considered depends upon the individual development of a fault in the cleavage of the common pectoral mass, by reason of which a portion of the primitive common muscle, normally destined for the pectoralis major, and more or less coincident with the same along the line of origin, becomes diverted from this original purpose and follows the lead of the pectoralis minor in shifting the insertion from the humerus toward the shoulder girdle. In the majority of the cases the displaced segment of the pectoralis major does not reach the coracoid process, but results in the production of a slip intermediate in position and insertion between the typical major and minor, viz. the *tensor semi-vaginæ* of Gruber and of the series here described, with indirect humeral attachment by expansion into subdeltoid aponeurosis (Cases 1, 2 and 3 of above series). In the fourth case above reported a striking example is offered of a well-developed intermediate muscle still incompletely differentiated at the insertion from the remainder of the pectoralis major, but tending in its cephalic portion to assume the independent fascial insertion characteristic of the typical tensor semivaginæ. This case, therefore, represents an early and still incomplete stage in the differentiation of the variant from the parent layer of the pectoralis major. On the other hand, in the instance above described, in which the tensor occurs in combination with the chondro-coracoideus-ventralis (Pl. VII.), the aberrant muscle is seen in its most advanced stage, the association with the insertion of the ento-pectoral plane being sufficiently close to lead to the production of a twin muscle, one segment representing the typical tensor semivaginæ, with subdeltoid fascial insertion and indirect humeral attachment, while the other, in direct combination with the normal pectoralis minor, reaches the coracoid process as M. chondro-coracoideus ventralis.

SUMMARY OF CONCLUSIONS BASED ON THE RECORDED OBSERVATIONS OF THE TENSOR SEMI-VAGINÆ.

I. DERIVATION.

Sheet of pectoralis major, as evidenced by

(*a*) The innervation (anterior thoracic nerves).

(*b*) The coexisting and corresponding deficiency in the plane of the pectoralis major.

II. ETIOLOGY.

Atypical cleavage of primitive pectoral muscular mass, a portion normally belonging to the system of the pectoralis major being partly diverted to the deeper ento-pectoral plane and following the lead of the latter in shifting the insertion cephalad toward the shoulder girdle.

A. Incomplete Type (Pl. IV.).

Insertion still largely associated with that of the normal pectoralis major, but partly continued into the subdeltoid aponeurosis.

B. Complete Type (Pls. I., II. and III.).

Insertion entirely into the subdeltoid fascia, intermediate between the attachments of the normal pectoralis major and minor.

C. Advanced Type (Pl. VII.).

Insertion partly extended to the coracoid process, resulting in the formation of a composite variant, the typical tensor semi-vaginæ appearing in combination with the M. chondro-coracoideus ventralis.

III. SIGNIFICANCE.

It is, of course, not advisable to reason concerning the morphological and physiological significance of these variations from the comparatively limited number of observations except along the most generalized lines. The following conclusions may, however, be fairly drawn:—

(*a*) The remarkably constant and uniform structural character of the recorded cases, both as regards the variant muscle itself and the innervation on the one hand, and the relation to adjacent muscular planes on the other, entitle it to recognition as an independent and well-established variation.

(*b*) This morphological value is further supported by the phylogenetic representatives of the human variant encountered as normal constituents of the pectoral complex in certain of the lower mammalia.

(*c*) We may define such variations as "reversional," or, as Eisler[1] proposes in the case of the sternalis, seek to justify their occurrence by saying that they "have become independent." After all, however, such statements convey little meaning as to the real purpose and significance of the aberrant structure. In the case of the muscle here under consideration we may, at least tentatively, advance a step further and dwell on the significance imparted to the structure by the evident analogy between the causes responsible for its production and the phylogenetic processes which have led, in primates, to the present morphological status of the elements composing the normal pectoral musculature. As above stated, both the differentiation of the individual segments and the migration of the pectoralis minor from humerus to shoulder girdle can be clearly followed in the primate series, man and the anthropoid apes being generally sharply differentiated by the coracoid attachment of the pectoralis minor from the remaining genera of the order, in which the muscle largely retains the primitive humeral insertion. It is possible that in case of the variant muscle here considered we are dealing with the individual expression of evolutionary processes at present operative in the ecto-pectoral plane, and strictly analogous to those which, during the phylogenetic development of the present normal anthropoid type, have led in the deeper ento-pectoral plane to the diversion of part of its component fibres, as pectoralis minor, from humerus to shoulder girdle. In this sense the occurrence of the tensor semivaginæ would be interpreted as a "progressive variation," constituting a myological condition at present attained by a very small number of individuals, but possibly destined to become more constant in future evolutionary periods, and ultimately to appear as a normal component of the primate pectoral group.

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[1] P. Eisler, "Der Musculus Sternalis, seine Ursache, und Entstehung, nebst Bemerkungen ueber die Beziehungen zwischen Nerv und Muskel," *Zeitschrift für Morphologie und Anthropologie*, Bd. III., Heft 1, 1901.

Again, in view of the transitional stage between the typical tensor semi-vaginæ and the præ-clavicular group of muscular variants, as illustrated in Pl. VII., it is possible to regard the former muscle as expressing one of the phylogenetic steps which have led to the establishment of the latter, *i.e.* to consider the tensor, so to speak, as representing arrest of development, or an intermediate stage, in the production of the præ-clavicular type of supernumerary pectoral muscle, especially of the sub-varieties of the ventral sterno-chondro-coracoid or sterno-clavicular forms. It is proper to recall in this connection that the various types composing the præ-clavicular group of variants are incomparably more frequent in occurrence than the tensor semivaginæ, and that the isolated instance of the latter muscle's occurrence in the anthropoid apes was recorded by Macalister in the chimpanzee, a form which, as above stated, has not yet attained a stable equilibrium in the coracoid attachment of the pectoralis minor, and hence may be assumed to offer a greater tendency to the production of atypical muscular elements associated etiologically with this process of migration.

These facts would speak, as far as they go, for the opposite interpretation of the muscle's significance, and would place the same in the category of "reversional variations" in the broader sense. This view, to which, considering all the available data, my own judgment inclines, would not regard the human tensor in any sense as representing a former component of the primitive primate pectoral musculature, and perpetuated as a normal element in some of the lower mammalia, as in the forms above described. The phylogenetic history of the primate pectoral mass is capable of complete and clear reconstruction, as previously shown,[1] and entirely contra-indicates such an assumption. The occurrence of a homologue in lower mammalia, morphologically equivalent to the human tensor, represents a specialization of the pectoral musculature in these forms and a wide departure from the primitive simple conditions which we may assume characterized the common primate type. Possibly, as above defined, such specialization indicates lines of election or of least resistance in the development of complicated components from a generalized mammalian pectoral type, and in that broad

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[1] Huntington, *loc. cit.*

sense brings the normal carnivore or artiodactyle sterno-humeralis into relation with the variant primate tensor. A closer phylogenetic connection between the two is, I think, excluded by the recorded facts. On the other hand, the aberrant human muscle possesses a broad reversional significance if we regard it, not as repeating an extinct component of the primate pectoral adaptation, but as representing results of faulty or exaggerated processes which in their normal scope have led, during the phylogenetic evolution of the present primate type, to the establishment of the regular component elements.

The fact that the subclavius is undoubtedly a product of further segmentation in the deeper or ento-pectoral plane is responsible for a large number and variety of aberrant muscular slips in the præ-clavicular region, and more extensive irregularities in the normal processes of cleavage and segmentation may very fairly be regarded as capable of producing disturbances in the adjacent ecto-pectoral plane of the pectoralis major, thus bringing the tensor into indirect genetic relation with the præ-clavicular group, to be presently considered in this connection. The muscle, therefore, represents an atypical deviation of part of the pectoralis major, possibly as the direct result of faulty cleavage in the separation of the deeper ento-pectoral plane from the superficial layer, such atypically displaced fibres of the pectoralis major tending in their insertion toward the type presented by the pectoralis minor, and sharing to a certain extent in the migration of the latter toward or to the pectoral girdle.

This interpretation appears to me sustained by a comprehensive valuation of all the known facts. The limited number of actual observations, and the purely speculative character of our assumptions regarding the physiological and morphological factors charged with the production of what we have tentatively come to define as "progressive" variations, contra-indicate the inclusion, even provisionally, of the tensor in this doubtful class.

3. *M. sterno-clavicularis* (*Præ-clavicularis medialis*) (Pl. VIII. figs. 1 and 2).

Certain of the variant præ-clavicular supernumerary muscles evidently belong to the morphological group here considered.

In the instance shown in Pl. VIII. figs. 1 and 2 the following conditions were noted :—

DESCRIPTION OF CASE :—

Fœtus near term, male, presenting numerous congenital malformations—viz., exstrophy of the bladder, malformation of the external genitals, imperforate urethra, spina bifida, club feet and hands.

Pectoral regions.—The manubrial portions of the pectorales majores are confluent by a broad tendinous band across the ventral midline, without attachment to the underlying sternum. The clavicular portions of both muscles are divided into a broader lateral part, closely applied to the ventral border of the deltoid, and a narrower medial slip, arising from the sternal end of the clavicle and the sterno-clavicular articulation, laterad of the sternal attachment of the sterno-cleido-mastoid. These divisions of the clavicular head of the pectoralis major are separated by a broad triangular interval in which portions of two præ-clavicular supernumerary muscles appear, arranged nearly symmetrically on both sides (Pl. VIII. fig. 1). The narrow medial clavicular slip is separated from the confluent manubrial portions of the sterno-costal head on each side by a distinct cleft. On the right side the cephalic fibres of the manubrial portion of the pectoralis major pass directly beneath the narrow medial clavicular slip, diverging at an acute angle from the rest of the muscle, and form the caudal one of the two variant præ-clavicular muscles (sterno-scapularis) seen in Pl. VIII. fig. 1, partially exposed by the deficiency in the clavicular portion of the pectoralis major. On the left side the same two præ-clavicular muscles are present, but there is no direct continuity with the manubrial fibres of the pectoralis major, which pass directly into the main mass of the muscle toward the humeral insertion. On reflecting the pectoralis major and clavicular deltoid on the right side, and after division and upward displacement of the clavicle near the acromial extremity (Pl. VIII. fig. 2), the præ-clavicular muscles show the following arrangement :—

1. *M. sterno-clavicularis anticus.*

A bundle of well-developed muscular fibres arises from the manubrium, close to the clavicular notch, and extends parallel with the clavicle laterad to its insertion into the ventral surface of the bone a little beyond the middle.

2. *M. sterno-scapularis* (var. *sterno-acromialis*).

Caudad of the preceding muscle, and entirely distinct from it, the cephalic fibres of the confluent manubrial segment of the pectoralis major turn cephalo-laterad beneath the narrow medial clavicular slip and continue as a fusiform muscle, caudad and under cover of the clavicle, beyond the insertion of the sterno-clavicularis, and across the cephalic surface of the coracoid, terminating in a slender tendon which is inserted with slight expansion into the medial border of the acromion, dorsad of the acromio-clavicular facet.

On the left side the same arrangement obtains, except that the sterno-scapularis arises directly from the sternum and is not continuous with the confluent manubrial portions of the greater pectoral muscles. Both muscles are apparently innervated by a common branch, which passes around the caudal margin of the sterno-scapularis to their deep surface. This nerve can be traced back to one of the anterior thoracic branches entering the deep surface of the pectoralis major above the cephalic border of the pectoralis minor. The normal subclavius muscle is absent on both sides. The variation just described suggests the following considerations:—

1. As in case of the two preceding variant muscles, viz., the *tensor semi-vaginæ* and *chondro-coracoideus ventralis*, the abnormal conditions are associated with faulty development of the pectoralis major and deficiency in its muscular plane, involving, however, in this instance the clavicular and manubrial heads of the muscle, whereas in the aberrant types previously considered the sterno-costal portion was atypically constructed and responsible for the production of the variation.

2. The two distinct abnormal muscles present in this case may be regarded as bearing the following relation to the pectoralis plane:—

(*a*) The sterno-clavicularis represents atypically displaced fibres of the deficient central portion of the clavicular head.

(*b*) The confluent manubrial portions of the two pectorales yield, on the right side directly, the second variant præ-clavicular muscle, which, as M. sterno-scapularis, replaces the absent subclavius, and represents the generalized mammalian type of this muscle (M. sterno-chondro-scapularis). Normally the primate subclavius, as previously shown,[1] appears as a segmentation derivative of the deep or ento-pectoral plane. The direct connection of its representative in this instance as sterno-scapularis with the superficial or ecto-pectoral plane of the pectoralis major suggests atypical development of the latter as the etiological factor responsible for the abnormal condition. The normal cleavage of the cephalic portion of the common pectoral mass into a deep stratum, yielding, by segmentation from the adjacent element of the pectoralis minor, the subclavian or sterno-scapular segment, and the superficial layer of the clavicular and manubrial pectoralis major has not occurred, possibly in consequence of the failure of the manubrial segment to gain the normal firm connection with the sternum. The resulting disarrangement of the pectoralis major in this region is manifested by the deficiency of the clavicular portion and by the deviation of part of the fibres normally composing the same to form the aberrant sterno-clavicularis, while the deeper layer, which should supply the typical primate subclavius, reverts in an incompletely segmented form, on the right side still directly continuous with the pectoralis major, to the generalized mammalian type of the subclavius, viz., the sterno-(chondro)-scapularis. In other words we are dealing here with another manifestation of the results produced by disturbances in the normal processes of cleavage in the pro-pectoral mass. In the case of the *Tensor semi-vaginæ* and the *sterno-chondro-coracoideus* previously considered, these disturbances involved the central (sterno-costal) division of the pectoralis major, and the muscular elements subtracted from the same formed the variant intermediate slips. These two muscles hence represent in a broad sense aberrations of development in the area of cleavage leading

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[1] Huntington, *loc. cit.*, p. 70.

normally to the complete and typical separation of the sterno-costal division of the pectoralis major from the pectoralis minor. The two aberrant præ-clavicular muscles, on the other hand, appear as the results of the same general atypical processes transferred to the region of normal differentiation of the superficial clavicular and manubrial portions of the pectoralis major from the deeper segment destined to form the sterno-chondro-scapularis, or its reduced representative in primates, the subclavius.

A very interesting example of similar conditions in the pectoral region was reported in 1899 by Dr Thos. H. Bryce,[1] in which in a female subject, æt. 62, with normal pectoral muscles on the left side, the manubrial portion of the pectoralis major defaulted in large part on the right side, and there were present three variant pectoral muscles—viz., sternalis, sterno-clavicularis, and chondro-epitrochlearis. The sterno-clavicularis, supplied on its deep surface by a branch from the external anterior thoracic nerve, arose from the side of the manubrium and by tendinous fibres from the second costal cartilage, the outer part of the tendinous origin being directly continuous with the upper tendon of the sternalis.

Comparison of the figure and description given by Dr Bryce with the instance here reported reveals a remarkable congruence in the disposition of the pectoralis and of the præ-clavicular aberrant muscles in both cases. There can be no question as to the complete correspondence between the single large sterno-clavicularis of Dr Bryce's observation and the double variation of the present case, divided into sterno-clavicularis and sterno-scapularis. The same manubrial slip crossing the præ-clavicular muscle to join the main sterno-costal division of the pectoralis major is present in both, as is also the wide interspace between this manubrial slip and the clavicular head, and while in Dr Bryce's case the sterno-clavicularis becomes in part continuous with the sternalis, the second aberrant muscle of our example—the sterno-scapularis—joins on the right side directly the confluent manubrial portion of the pectoralis major, a fact of much meaning in reference to the pectoral character of the sternalis (vide *infra*).

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[1] *Journ. Anat. and Phys.*, vol. xxxiv., pt. i., pp. 74–78.

Dr Bryce concludes in respect to the sterno-clavicularis of his case that "it evidently represents a portion of the deep lamella of the pectoral sheet arising from the manubrium, and it is significant that when present, either in its single or double form (inter-clavicularis anticus digastricus), there is frequently a defect in the pectoralis major."

He also quotes a similar instance reported by Dr Dwight.[1]

Further, in a case reported by Dr Stoker and quoted by Macalister,[2] the pectoralis major was absent. Two similar instances are described by Gruber,[3] in which the clavicular portion of the pectoralis major was deficient on the side presenting the præ-clavicularis medialis. I am in entire accord with Dr Bryce when he sums up his view concerning the sterno-clavicularis by saying that "it is therefore, in virtue of its position, a 'deep manubrial slip,' and, in virtue of its innervation, belongs to the same category as the pectoralis minimus and other slips derived from the same point. They may all be regarded as different forms of the part of the deep lamella of the pectoral sheet, usually suppressed in man, arising from the manubrium and supplied by the external anterior thoracic nerve."

I would amplify this excellent *résumé* of the morphological position of the sterno-clavicularis and pectoralis minimus by including in the same group the sterno-costal variants, tensor semi-vaginæ and transitional forms between it and the sterno-coracoideus, as well as the group of aberrant types involving, as various forms of the sterno-chondro-scapularis, the region of the normal subclavius.

As regards the etiological factors responsible for the production of the variations, I have above expressed the view that we are not dealing here with reversional structures in the strict sense, "usually suppressed in man," but with the results of very definite and limited developmental and phylogenetic influences peculiar to the pectoral region.

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[1] *Journ. Anat. and Phys.*, vol. xxii., 1888, p. 98.

[2] *Loc. cit.*, p. 50.

[3] *Reichert's Archiv*, 1865, p. 708.

SUMMARY OF CONCLUSIONS REGARDING THE THREE TYPES OF SUPERNUMERARY MUSCLES FORMING THE DEEP GROUP.

It is not difficult to correlate the morphological conditions offered by the three supernumerary muscles here considered and to recognize them as members of a continuous series whose individual position and relation to the entire pectoral complex may be schematically represented in Pl. IX.

The following conclusions regarding the group as a whole appear justified :—

1. The individual muscles share a common derivation from the pectoralis plane. This is established both by the constant innervation by the anterior thoracic nerves and by the nearly uniform coexistence of distinct deficiencies in the plane of the pectoralis major.

2. The etiology of the variants depends upon abnormal processes in the cleavage of the pectoral mass, disturbing the normal differentiation of the same into pectoralis major, pectoralis minor, and subclavius, and leading to the production of supernumerary accessory slips of greater or lesser extent.

3. The process of cleavage in these cases, while atypical for the primate disposition of the pectoral complex, may follow lines which are normal in the differentiation of the pectoral components in other mammalian orders. Hence some of the aberrant human muscles are morphologically homologous with intermediate pectoral elements normally found in some of the lower mammalia.

4. It is fair to assume that departures from the normal type of cleavage are favoured

(*a*) By the tendency to reversion, to a greater or less degree, to the primitive undifferentiated and unsegmented pectoral mass which, both phylogenetically in the primate order, and ontogenetically in the human embryo, forms the starting-point for the subsequent differentiation into the typical components.

(*b*) By the embryonic migration of the pro-pectoral mass from the cervical to the sterno-costal region, which affords opportunities for faulty completion of the secondary attachment to the ventral thoracic wall and shoulder girdle, and may thus give rise to the development of atypical muscles (vide *infra*, *Sternalis*).

5. These factors, operating over localized areas of the pectoral mass, produce the following individual aberrant forms, according to the position of the part of the pectoralis sheet involved (Pl. IX.):—

A. Central sterno-costal segment of pectoralis.

1. Tensor semi-vaginæ or sterno-humeralis, still associated with pectoralis major at insertion (Pl. IV. and Pl. IX. 5).
2. Typical tensor semi-vaginæ or sterno-humeralis inserted into subdeltoid aponeurosis, and thus obtaining an indirect humeral attachment (Pls. I., II. and III.; Pl. IX. 5).

B. Segment involved in the normal cleavage of pectoralis major and minor.

1. Typical sterno-chondro-coracoideus ventralis, S. pectoralis minimus (Pl. IX. 3).
2 Sterno-scapularis (Pl. VIII. fig. 2; Pl. IX. 2).

(A large number of recorded observations of so-called "reduplications" of the subclavius belong to this group.)

C. Intermediate pectoral segment between A and B.

Combination forms of sterno-humeralis or tensor and sterno-chondro-coracoideus ventralis (Pl. VII. and Pl. IX. 4).

D. Manubrial and clavicular segment.

By reduction and further migration of insertion to clavicle is obtained the sterno- or sterno-chondro-clavicularis ventralis in its various sub-types (Pl. VIII. figs. 1 and 2; Pl. IX. 1).

B. SUPERNUMERARY MUSCLES SUPERFICIAL TO THE PLANE OF THE PECTORALIS MAJOR.

This group includes in or near the ventral midline of the thorax the well-known sternalis, and further laterad in the delto-pectoral space the occasional infra-clavicularis. A careful consideration of these pectoral variants warrants their union, as regards derivation and significance, with the deeper intermediate supernumerary muscles just discussed into a common morphological group. The superficial supernumerary muscles, while differing from the deeper variants in their relation to the parent layer of the ecto-pectoralis, share with the latter the common derivation from this layer, and owe their production in part to the same etiological factors responsible for the development of the deeper muscles, in part to special conditions favouring atypical development on the superficial aspect of the pectoralis sheet.

I. STERNALIS.

So much has been written concerning the structure, innervation and probable morphological significance of the sternalis, that further contributions to the literature of the muscle seem superfluous unless thereby some additional light can be thrown on the still problematical character of this frequent variation. This is especially the case since the publication of the very able and comprehensive paper on the muscle by P. Eisler[1] in 1901, in which the author deals fully and completely with the neurological problems involved and advances a novel view regarding the factors responsible for the production of the variation.

An attempt to define the morphological position of the sternalis will be facilitated by the preliminary consideration of the present status of our knowledge concerning the innervation of the muscle, and by a brief review of the more important theories which have been advanced in explanation of the derivation and significance of the variant.

1. INNERVATION OF THE STERNALIS.

We owe our first definite knowledge concerning the nerve supply of the sternalis to the careful researches of Prof. Cunningham, who first laid stress on the importance of this criterion in the determination of muscular homologies, and to Prof. Shepherd, who has recorded the nerve supply in an interesting series of cases occurring chiefly in ancephalous monsters. Prof. Bardeleben of Jena has likewise contributed neurological data, and more recently Dr Christian,[2] in recording the nerve supply in two cases of sternalis observed by him,

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[1] *Loc. cit.*

[2] *Bulletin of the Johns Hopkins Hospital*, vol. ix., Nos. 90–91, p. 235, Sept.–Oct. 1898.

tabulates a series of 27 muscles with determined innervation, showing the following results :—

	No. of Sternales.	
Ventral branches of II.–IV. intercostal nerves alone,	14	muscles.
Ventral thoracic nerves alone, . . .	10	,,
Ventral thoracic and intercostal nerves combined, .	3	,,
Total, .	27	,,

Since the publication of these earlier records the number of careful observations on the nerve-supply of the sternalis has greatly increased, and of late years the conviction has steadily gained ground that the sternalis is always innervated by the anterior thoracic nerves, and not by the intercostals, the reported instances to the contrary notwithstanding. While frequently *perforated* by ventral cutaneous intercostal branches, the motor-supply is to be traced to the anterior thoracic complex. Hence neurologically the sternalis belongs to the domain of the pectoralis.

Eisler, in the paper quoted, joins the constantly-growing number of morphologists who have, with the multiplication of neurological determinations after improved methods, experienced more and more doubt as to the validity of the recorded cases of sternales with intercostal innervation, either alone o in combination with a supply from the anterior thoracic nerves and who have arrived at the conclusion that the muscle i uniformly supplied by the anterior thoracic nerves alone, and hence directly associated with the pectoralis musculature.

2. HYPOTHESES CONCERNING THE DERIVATION AND SIGNIFICANCE OF THE STERNALIS.

The main views heretofore advanced regarding the morphological position of the muscle may, for discussion and comparison be briefly enunciated as follows :—

A. Pannicular derivation of the sternalis.

This view, first presented by Turner[1] and adopted b a number of subsequent observers, regards the sternalis a

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[1] *Journ. Anat. and Phys.*, vol. i., p. 247.

a reversional persistent remnant of the thoracic cuticular muscle.

B. Ecto-pectoral derivation of the sternalis in the stricter sense.

Cunningham[1] clearly defined the relation of the sternalis to the muscular sheet of the pectoralis major, and held the variant to be a displaced and rotated segment of the latter.

C. Eisler's hypothesis.

Eisler,[2] in echoing Cunningham's view as to the direct derivation of the sternalis from the pectoralis major, assumes a definite mechanical cause for the abnormal development of the pectoral sheet leading to the production of the variation, believing the same to be due to an atypical widening of the ventral portions of one or more intercostal spaces, such widening being possibly caused by hyperplasia of the thymus and by the large size of the heart. The frequency of the sternalis in ancephalic monsters (twelve times greater than in "normal" individuals) is, according to Eisler, primarily produced by the factors indicated, and further favoured in these cases by the constant and marked lordosis of the cranial segment of the vertebral column. Eisler purposes, in fact, to place the sternalis in a separate group of muscular variations composed of atypical myological structures which have "become independent." The examination of a sufficiently extensive series of the variation, in the light of the three hypotheses above outlined, will convince the observer that a certain proportion of the individual cases are structurally in accordance with one or the other of the two main views which have been expressed in regard to the derivation and significance of the muscle, *i.e.* they appear either to fulfil the conditions demanded by what we can term briefly Turner's pannicular hypothesis, or they correspond, as clearly displaced segments of the pectoralis major sheet, to the mechanical theory of the Cunningham-Eisler conception. Furthermore, a certain number of individual instances will occupy a position intermediate between these two groups, the variant partaking of the structural character of both, although usually inclining

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[1] *Journ. Anat. and Phys.*, vol. xxii., p. 392.

[2] *Loc. cit.*

more to the one or the other. In other words a sufficiently comprehensive series of the variation will reveal the existence of the following types, which the muscle may assume in individual cases:—

A. Sternales, occurring usually as well-developed muscular bands, associated with disturbances in the typical development of the pectoralis major, and usually accompanied by more or less pronounced deficiency in the corresponding segment of the sterno-costal division of the muscle (Pl. X.).

B. Sternales characterized by the slender and delicate form of the aberrant muscle, varying in extent from a few scattered muscular fibres to a thin ribbon of pale muscular tissue overlying the pectoralis major, which appears fully developed and to all appearances normal in every respect. The terminal connections of the muscle in these cases are frequently fascial or aponeurotic, caudad the abdominal fascia or sheath of the rectus, cephalad the deep pectoral fascia, periosteum of the sternal midline, or sternal tendon of the sterno-cleido-mastoid.

As recently shown by Anthony,[1] it is possible to regard certain pre-pectoral fascial and fibrous bands as the metamorphosed and rudimentary representatives of the muscular sternales belonging to this group.

C. Sternales which in general partake of the structure of the second group, but which present a more direct connection with the pectoralis major. This is usually indicated, not by a corresponding deficiency in the pectoralis sheet, as in Group A, but by the continuation of some of the sternalis fibres into the pectoralis, or by the origin of part of the superficial layer of the latter muscle from the cephalic tendinous prolongation of the sternalis. At times the element appears as a superficial lamina of the pectoralis, continued separate from the main muscle well toward the insertion, as in the ancephalic specimen shown in Pl. XI. fig 1.

No observer, in critically examining a series of this kind, will for a moment doubt the general congruence of the different examples and the morphological entity of the variant as a distinct anatomical structure, possessing a common fundamental

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[1] M. R. Anthony, "Le muscle présternal ; ses formes fibreuses rudimentaires, leur fréquence chez l'homme et leur présence chez certain animaux," 11 fig., *Bull. de la Soc. d'Anthropol. de Paris*, 5 Livre, 1, 1900, pp. 486–509.

character, no matter what special features may induce the assignment of any individual case to one or the other of the general groups above defined. In other words, it would be impossible to hold that the different characters possessed by a selected series of individual instances of the muscle implied in any sense a fundamental difference in the derivation and significance. We are not dealing here with a number of structures morphologically differentiated by their origin and possessing merely a superficial resemblance to each other, but with a series of uniform derivation and significance, the individual members of which may, to a greater or less degree, present secondary differential characters. The sternalis is a muscular integer, and I am convinced that we can harmonize the apparently divergent phylogenetic and etiological views expressed concerning the history of the muscle by establishing a broader morphological basis for its derivation, which, according to the preponderance of secondary influences, may lead its development into one of several specific directions, resulting in the establishment of certain distinctive characters for the subdivisions of the muscle above enumerated. The fundamental basis for the morphological union of all the specific types assumed by the sternalis in individual cases must be sought in the ultimate derivation of the myological elements composing the variant from the pectoralis sheet. This final reference to the origin, clearly sustained by the innervation, is made the direct basis of the hypothesis advocated by Cunningham and Eisler. Furthermore, it is in entire accord with the pannicular theory of Turner, when the innervation of the thoraco-humeral skin-muscle and its relation to the superficial pectoral muscular sheet is correctly appreciated. With the acceptance of the general derivation of the sternalis from elements of the pectoral musculature, there remain the following points for consideration:—

1. The general etiological factors which lead to the remarkably constant percentage occurrence of the variation.
2. The striking numerical preponderance of the sternalis in the ancephalic fœtus.
3. The causes which determine the secondary group-characters of the muscle.
4. The relation of the sternalis to cognate variations of the

pectoral region, and especially the determination of the significance of instances in which the sternalis appears in conjunction with other pectoral variants.

I believe we can best arrive at a solution of these questions by provisionally retaining the classification of the types presented by the sternalis as above given, and by examining the individual groups seriatim.

Group A.—Well-developed sternales, with coexisting deficiency in the plane of the pectoralis major.

These cases furnish an advantageous starting-point for the general consideration of the muscle, since they offer very evident conditions, which pave the way for the subsequent study of the more obscure instances included in Groups B and C.

In examples of this type, as shown in Pl. X., the abnormal muscle appears clearly in Cunningham's and Eisler's sense as an atypically developed and displaced segment of the sterno-costal pectoralis major, whose connections with adjacent structures, as the frequent union with the sternal head of the sterno-cleido-mastoid or the aponeurosis of the external oblique, are secondarily acquired and morphologically unimportant characters. As previously seen, similar displacements of pectoralis elements, involving portions of the deeper plane of the muscle, lead to the production of the supernumerary intermediate pectoral muscles considered in the first part of this communication. In these instances the derivation and significance of the aberrant sternalis are perfectly clear and evident, and it only remains to gain what light we can on the question of the causes responsible for the atypical pectoral development. There is much in Eisler's conception of the sternalis which, if borne out by further and more extensive observations, would fill important gaps, heretofore left vacant, in our knowledge of these causes.

His mechanical theory of the production of the variation offers a plausible explanation of the cases of sternalis with exceptional defect in the sheet of the pectoralis major, either in the ancephalic fœtus or in adult subjects. Such cases do indeed correspond to the conception of an atypical development of the pectoralis with rotation or displacement of the muscle fibres involved in the disturbed area. I confess, however, that the atypical structure of the thoracic wall, and especially the abnormal widening of certain interchondral spaces, upon which Eisler lays stress as etiological factors of the first importance in the production of the variation, do not, as far as my present observations go, obtain, at least by no means uniformly. I have recently examined carefully the skeletal structures of the ventral thoracic wall in five instances of the sternalis occurring in adult subjects. Among these were two in which the muscle assumed the delicate ribbon form of Group B, and the example with extensive deficiency of the pectoralis major and strong muscular sternalis shown in Pl. X. In only one of the five instances—a case of superficial and slender sternalis—was a slight degree of asymmetry noticed. In the other four the thorax appeared perfectly normal, and the sternum and interchondral spaces of the subject shown in Pl. X. were remarkably regular and well formed (Pls. XII. and XIII.). In view of the frequency of asymmetrical development of sternum and costal cartilages in individuals who do not present any abnormality of the pectoral musculature, I am inclined to question the direct relation between thoracic asymmetry and the development of the sternalis. It is possible that we are dealing here rather with a coincidence than with an etiological element of moment. I am somewhat confirmed in this impression by the results of an examination of the ventral chest wall in eight ancephalic fœtus which presented no trace of the sternalis. In three of these marked atypical structure of the costal cartilages and irregular formation of the interchondral spaces were found. In one of these the fourth left rib presented the bifid termination occasionally seen. I should judge that ancephaly is apparently a favouring factor in the development *both* of the sternalis and of irregular formation of the interchondral spaces, but that the muscle does not depend directly for its production upon the latter condition. They may both appear in the same individual, or the malformation of the thorax may occur without the development of the sternalis, or the muscle may be found overlying a thorax normal in configuration. This question, however, will require definite determination on the basis of a very much larger series of observations than are at my disposal at present. On the other hand, these instances of sternalis with well-marked deficiency in the pectoralis major present features which clearly bring them into line with the muscular variants previously considered occupying the deeper layers of the pectoral complex. A comparison, for example, of the pectoral system of the two individuals shown in Pls. III. and X. will at once suggest the propriety of uniting them into a general group characterized by the correspondence of the abnormal development in the area of the pectoralis major, which has in the one case led to the production of the deep tensor semi-vaginæ, while in the other it has resulted in the appearance of the superficial sternalis. In both instances the derivation of the atypical segment is clearly indicated by the coexisting deficiency in the ecto-pectoral sheet.

We have previously characterized the deep supernumerary muscles of this region as products of atypical cleavage in the deeper strata of the pectoralis mass, resulting in departures from the normal type of myological evolution which in the human subject leads to the differentiation of the pectoralis major from the deeper layer composed cephalo-caudad of subclavius, pectoralis minor and pectoralis abdominalis.

In comparing the two examples referred to, the suggestion lies at hand that identical etiological forces have determined the disturbances of normal development, which in its final result furnishes us with two apparently entirely distinct muscular structures. In the one case these disturbing forces, operating in the deeper plane of the pectoralis mass, produce the tensor semi-vaginæ, or one of the group of allied intermediate muscles above considered. In the other the same forces, directed and perhaps specially modified by secondary etiological factors involving the superficial stratum of the pectoralis major, lead to the development of the sternalis as it appears in the group now under discussion.

If, therefore, based on the innervation and the coexisting deficiency of the pectoralis major sheet, we accept the common derivation of both the deep and superficial group of supernumerary pectoral muscles, we must seek further for the deciding causes producing this atypical development, and, moreover, consider what additional elements lead, on the one hand to the development of the atypical deep or intermediate series already discussed, and, on the other, to that of the superficial sternalis.

I have already expressed my belief that the deep group can be genetically considered as derived from the deeper lamina of the ecto-pectoral layer in consequence of faulty and incomplete cleavage in that portion of the embryonic pro-pectoral mass which is the site of the normal differentiation into the superficial element of the pectoralis major and the deeper layer comprising pectoralis abdominals, pectoralis minor and subclavius.

In the genesis of this group disturbances in and deviations from the normal embryonal process of *cleavage* or *differentiation* are primarily responsible for the development of the variant. I believe that we can ascribe the production of the sternalis to analogous disturbances in another part of the normal ontogenetic cycle which leads, when typically carried through, to the establishment of the pectoral relations as usually encountered, but which, by reason of the complex factors entering into the process, is prone to disturbances involving the superficial plane of the pectoralis and resulting in the development of the sternalis, as a part of the pectoral sheet deviated and rotated in Cunningham's sense to a position ventrad of the parent layer.

The three elements concerned in the ontogenetic history of the pectoral musculature, which must be considered together in their mutual relations in attempting to determine the etiology of aberrant pectoral muscles, are—

1. The cleavage of the entire mass into the superficial (ecto-pectoral, P. major) and the deep layer (ento-pectoral, including P. abdominalis, P. minor and subclavius).
2. The peculiar type of development of the pectoral muscles.
3. Certain stages in the development of the ventral thoracic wall.

As above stated, I am inclined to ascribe the deep or intermediate group of pectoral variants to disturbances in the first of the above embryonic elements, viz., the *cleavage* of the entire mass.

For the production of the sternalis I believe that we will have to reckon with the other two ontogenetic factors concerned:

1. *Development of the pectoral musculature.*—The researches

of Mall[1] and Lewis[2] have greatly augmented our knowledge of the embryonic details in the development of the trunk musculature. Lewis finds that the pectoralis major arises in common with the minor from a pre-muscle tissue located for the most part above the first rib. He examined by reconstruction and dissection embryos from 9–40 mm. The pro-pectoral mass is located chiefly in the neck, and lies at first in the region of its nerve-supply, receiving branches from the sixth, seventh and eighth cervical and first thoracic nerves, which proceed almost directly laterad with scarcely any caudal inclination. This mass gradually shifts caudad to the costal region, splitting into bundles during the process of migration. The clavicular portion is the first to segment from the common mass. Later the sterno-costal portion differentiates into the P. major and minor. During the migration the sterno-costal bundles overlap, so that the superficial fibres of each bundle descend farther than the deeper ones, possibly by reason of the latter acquiring an earlier attachment to skeletal points.

This ontogenetic migration of the pectoral muscle mass strongly suggests the possibility of finding in disturbances of the normal process the cause of the development of the superficial aberrant pectoral muscles, chiefly represented by the sternalis. Lewis, at the close of his very able paper, points out the etiological significance of his observations in reference to supernumerary pectoral muscles, and his suggestion appeals to me as the most satisfactory explanation of the conditions which *a priori* favour atypical muscular development in this region. If we seek for further contributory causes, it is proper to bear in mind the following facts:—

Lewis' observations have determined that in the pectoral migration the deeper planes are arrested earlier, while the superficial fibres continue to descend and thus come to overlap the deeper strata. The superficial portion of the pectoralis major is, therefore, longer in a condition of comparative independence of the skeletal points to which, in the normal progress

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[1] F. J. Mall, "The Development of the Ventral Abdominal Walls in Man," *Jour. of Morphology*, vol. xiv., No. 2, 1898.

[2] W. H. Lewis, "Observations on the Pectoralis major Muscle in Man," *Johns Hopkins Hosp. Bull.*, vol. xii., Nos. 121, 122, 123, April, May, June 1901.

of development, it becomes attached, and more subject to the influence of abnormal connections, established with adjacent structures, perhaps prior to or during the earlier stages of migration. The frequent cephalic fusion of the sternalis with the sternal tendon of the sterno-cleido-mastoid is perhaps to be interpreted in this sense. In case of an abnormal connection of that kind in the earlier developmental stages, we are, I believe, confronted by one of the causes which will lead to rotation of part of the pectoral plane from the typical position assumed in normal development, and which will carry the affected segment, during the continued migratory descent of the main mass, into the atypical vertical position characteristic of the sternalis, preserving, at the same time, in many cases the evident abnormal connection, as with the sterno-cleido-mastoid, which, by establishing a fixed point of early attachment for portion of the muscle, primarily led to its deviation from the normal direction assumed by the remainder. The fact that the *superficial* portion of the pectoralis is embryologically the last part to become definitely fixed in the usual sterno-costal attachment offers a ready explanation of the pre-pectoral position of the sternalis.

2. In studying in detail an extensive series of sternales, a surprisingly large number of muscles present a peculiar and definite relation to the mid-sternal line. The muscular fibres in these cases are directed cephalo-mesad from the caudal origin and appear in well-marked instances inserted entirely along the vertical mid-sternal line, while in other cases a partial or complete sterno-mastoid connection also exists. These conditions are, for example, well seen in the two individuals shown in Pl. X. and Pl. XI. fig. 2, and, while by no means of uniform occurrence, they are found in a sufficiently large percentage of cases in such a definite and characteristic form as to warrant their consideration in estimating the secondary causes which we may reasonably hold responsible for disturbances in the normal ontogenetic process of pectoral descent, and the consequent production of variant muscles representing portions of the pectoralis atypically displaced during migration. In this sense the cephalic attachment of the sternalis to the mid-sternal line suggests the possibility that in shifting from the

primary cervical to the subsequent sterno-costal position, portions of the pectoralis sheet may become included in the closure of the sternal bars in the ventral midline, and thus obtain a cephalic fixed point, which, in the continued descent of the superficial portions to overlap the deeper bundles—as it normally occurs—causes a larger or smaller segment of the superficial pectoral plane to deviate into the vertical position, and yield in course of complete development the sternalis of the type under consideration. In some instances, as in the example shown in Pl. XI. fig. 2, the oblique parallelogram described by the muscle is very striking, with the fibres ascending obliquely cephalo-mesad and terminating along the sharply-defined vertical insertion into the mid-sternal line. The facts just considered seem to afford a reasonable explanation not only of the principal and secondary causes leading to the atypical development of part of the pectoralis major as the sternalis, but also to account for the variability in size, attachments, relation to the parent layer and coexisting deficiencies of the latter, as represented by the various individual types of the variant muscle. In other words the sternalis appears as the product of several developmental factors, diverted from their normal course and acting in conjunction—viz., primarily, the ontogenetic migration of the propectoral mass and the later fixation of the superficial fibres, as compared with the earlier attachment of the deeper plane; secondarily, the possibility of atypical connections established prior to or during the early stages of this migration with adjacent structures, as the sterno-mastoid; lastly, the possible inclusion of part of the pectoralis major in the closure of the mid-sternal cleft. The various specific characters exhibited by individual instances of the muscle will be determined by the amount of pectoral tissue involved and by the preponderance of one or the other of the secondary causes.

Group B.—Sternales appearing as delicate scattered fibres or thin muscular bundles, overlying a normal pectoralis major, without evident deficiency in the substance of the latter.

From the statements just made concerning the first group, it is quite evident that the muscles classified under this second head may fairly be interpreted, in reference to derivation, as segments of the pectoralis sheet in cases in which the rotated and atypical displaced portion forms so small a part of the embryonic pectoral mass that its loss and diversion leaves no appreciable deficiency and produces no disturbance in the typical development of the main muscle. This is the most reasonable and evident interpretation of the special group of the variant here considered. Since this type of the sternalis has, however, furnished the basis of the "pannicular theory" of its derivation, it is well to consider the facts bearing on this interpretation in connection with the general discussion of this particular group.

It must be admitted that the structure of a certain number of sternales, belonging morphologically to this group, suggests at first sight that they represent abnormally persistent portions of the thoracic panniculus. Furthermore, the sternalis has been observed in conjunction and partial continuity with other aberrant pectoral slips of undoubted pannicular origin. These cases deserve special consideration. A marked example is shown in Pl. XI. fig. 2, presenting the following features:—

Female subject, æt. 43, Ireland.

1. Sternalis, confined to the right side, arises by a broad sheet of convergent aponeurotic fibres, continuous caudad with the aponeurosis of the external oblique over the rectus abdominis, corresponding to the level of the fifth costal cartilage. Mesally the fibres of origin continue with a curved course over the cephalic portion of the rectus to the xiphi-sternal junction, while the lateral border of the aponeurotic lamella continues directly into the origin of the second variant muscle, a well-marked pectoralis quartus. The sternalis measures 11·5 cm. in length and averages 2·75 cm. in width. It is inserted by short tendinous fibres into the ventral surface of the sternum opposite the second chondro-sternal junction. The cephalic fibres continue as a slender tendon—2 cm. in length—firmly attached in the mid-sternal line to the periosteum of the pre-sternum as far as the jugular notch, fusing with the mesal fibres of the sternal attachments of the two sterno-cleido-mastoid muscles, which meet in the middle line.

2. *Pectoralis quartus*, unilateral, confined to the right side, arises over the fifth right costo-chondral junction, the mesal fibres being directly continuous, as already stated, with the lateral margin of the origin of the sternalis, and not attached to the deeper parts, while the remainder of the muscle arises by short tendinous fibres from the fifth costal cartilage near its junction with the rib. The quartus, forming a flat band 18·5 cm. long, with an average width of 1 cm., continues laterad along the border of the pectoralis major, but entirely distinct from the same, across the axilla, to be inserted, together with the axillary arch, on the deep surface of the pectoralis major tendon.

3. *Axillary arch.*—Present on both sides.

On the right side it forms a muscular band, 5 cm. long and 0·75 cm. wide, which arises by a distinct tendinous intersection from the ventral surface of the latissimus dorsi, crosses the large vessels and nerves, and, joining the pectoralis quartus, is inserted with this muscle on the deep surface of the pectoralis major tendon.

On the left side the axillary arch, 7 cm. long, has a similar origin, and likewise fuses at the insertion with the deep surface of the pectoralis major tendon.

This case is of peculiar interest, since it shows the sternalis in combination with frequently-encountered supernumerary pectoral muscles of undoubtedly pannicular origin, and thus suggests the reference of the sternalis itself to the cuticular sheet. The theory of the pannicular derivation of the muscle was first advanced by Prof. Turner, and has found many supporters. The case just described gives the impression that all three of the variants encountered in this subject have a common origin and are to be interpreted as variant derivatives from the pectoral group in the larger sense, *i.e.* that they are to be regarded primarily as persistent portions of the ventro-lateral thoraco-humeral panniculus, and that they appear in turn more or less intimately associated with the subjacent layer of the pectoralis and latissimus by reason of the derivation of the thoracic and axillary cutaneous muscle from the ventro-appendicular system. It is quite evident that all three of the aberrant muscles belong to the same myological plane and are closely associated with each other. In fact, the sternalis and pectoralis quartus are in part directly continuous with each other. Certain general questions raised by this interpretation of the significance of these muscles may be considered under the following heads:—

1. Phylogeny of the panniculus, and its relation to pectoralis and latissimus, in reference to the pannicular derivation of the human variant muscles.
2. Innervation of the mammalian panniculus.
3. Innervation of the three variant human muscles here considered.

1. *Phylogeny of the panniculus, and its relation to pectoralis major and latissimus dorsi, in reference to the pannicular derivation of the human variant muscles.*

Comparative myology teaches us that the possession of a more or less extensive and differentiated skin-muscle is a very widely distributed mammalian character. In the monotremata the ventral portion forms an extensive sheet enveloping the ventral surface of the neck and trunk, and exhibiting connections with the deeper muscles of the anterior limb which will presently deserve our consideration. In other mammalian orders and suborders the muscle appears developed in varying degrees, presenting evidences of extensive reduction in the primates, and especially in man.

A very general disposition of the panniculus in the pectoral and axillary region is well described by Prof. Ambrose Birmingham in his able paper, "On the Homology and Innervation of the Achselbogen and Pectoralis quartus, and the nature of the Lateral Cutaneous Nerve of the Thorax" (*Journ. Anat. and Phys.*, vol. xxiii., p. 214). He says: "In animals we generally find the humeral panniculus as a thin sheet converging from the lateral region of the trunk towards the axilla, where it is inserted in connection with the pectoralis major on its deep surface as a rule; its ventral fibres overlie the great pectoral, the dorsal fibres cover the latissimus, and the intermediate fibres lie against the lateral thoracic wall." This excellent description pictures the panniculus as it is found in a large number of mammalia. In some forms the skin-muscle appears modified and specialized in accordance with special functional requirements, as in certain Rodents (Porcupine) and in *Erinaceus* among the Insectivora, forms in which the development of the protective spines calls a special modification of the cuticular muscle into existence. Mr Parsons, in his valuable contributions to the Myology of the Rodents, has shown that the members of this order offer many instances of a highly-developed and complex cutaneous muscle. In certain forms (Agouti and others) two layers of the panniculus are encountered in the thoracic and humeral region—one superficial to the pectoralis, while the other is placed upon a deeper level and closely associated with the pectoral muscles themselves. The same author[1] in another paper, in fact, suggests that the pectoralis group is derived from the panniculus, and that in reference to the sternalis it is immaterial whether we regard the muscle as part of the panniculus or as part of the pectoralis major. This

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[1] *Journ. Anat. and Phys.*, vol. vii., N.S., p. 505, "On the Morphology of the Sternalis Muscle."

intimate association of the panniculus with the pectoral muscular group is very important, and deserves careful consideration in determining the origin of the thoraco-humeral panniculus, and consequently the ultimate source of the human variant muscles which may be regarded as persistent portions of the cuticular muscular sheet. Phylogeny shows us that with the development of the shoulder girdle and anterior limb the primarily metameric disposition of the muscular system follows the lead of the skeletal apparatus and undergoes extensive and far-reaching modifications. Combination of a number of myomeres and the resultant production of individual muscles and muscle-groups, with the concomitant cleavage into layers and the alteration in the direction of the muscular fibres, change the primary simple conditions almost beyond recognition.

The ventro-appendicular muscles, pectoralis and latissimus, gain a relatively enormous surface development and are brought into contact with the integument over a largely-extended area. The development of a pannicular layer from the system of the latissimus and pectoralis is a result of this altered surface relation. I believe that we are justified in regarding the thoraco-humeral panniculus as a derivative from the ventro-appendicular muscular sheet, rather than considering with Mr Parsons[1] the pectoralis as a product of the panniculus.

The connection between pectoralis and panniculus is still to be traced in the monotremata, in which forms a considerable segment of the anterior ventral panniculus is derived from the humeral insertion of the pectoralis. The massive cuticular muscle of the American Manatee enters into extensive combination with the pectoralis and latissimus and with the musculature of the paddle. In birds a number of the deeper muscles—(Trapezius, Deltoid, Pectoralis, Serratus, Latissimus, etc.)—furnish muscular bundles which find their insertions in the patagium as tensors of this membrane. In mammalia in general the direct derivation of the ventral thoracic panniculus from the subjacent ventro-appendicular muscles is not so evident in all instances; and yet in many forms—as in the rodents examined by Mr. Parsons—the connection between

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[1] *Loc. cit.*, p. 507.

the two is well exemplified. As a matter of fact, it is not difficult within a comparatively limited number of types to illustrate a series of successive stages between the imperfectly segmented panniculus—still extensively united with the pectoralis—and the entirely free cuticular muscle. I believe that we are justified in regarding the panniculus and pectoralis as phylogenetically very closely connected structures; and in considering the former as a differentiated product of the superficial ventro-appendicular muscular group, which becomes variously modified—specially developed in some forms—while in others it appears greatly reduced—according to the demands of functional requirements in different animals. It is rational to regard the modifications of the muscular system resulting from the development of the pectoral girdle and anterior extremity as primary alterations of the metameric muscular type, and to consider the cuticular muscle as a further and secondary derivative of the appendicular muscular group, rather than to accept the panniculus as the primary structure from which the appendicular muscles are to be derived. This view of the mutual relationship of the muscular layers in question greatly simplifies the problems of innervation which are encountered.

The derivation of the variant human muscles forming the subject of this communication from the panniculus has been advocated by a number of authors. Sir William Turner [1] considered the sternalis as a remnant of the cuticular muscle, and his view has found many able supporters. Prof. Birmingham, in the paper quoted, proves conclusively that the axillary arch is a pannicular derivative. As regards the pectoralis quartus, he considers the muscle "a segmented portion of the great pectoral" (*loc. cit.*, p. 223), and denies its possible connection with the panniculus on the ground of *position*, basing his belief (1) on the conditions encountered in the kangaroo and wallaby, where the "pectoralis quartus is very large, its ventral fibres blend with the pectoralis major, and its dorsal fibres with the latissimus dorsi, while it is covered superficially by the panniculus"; (2) on two cases of Dr Brooks' in which the axillary arch was attached to the pectoralis quartus instead of

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[1] *Journ. Anat. and Phys.*, vol. i., p. 246.

to the lower border of the great pectoral—"here the quartus evidently took the place of part of the major"; (3) on the condition found in the cat, in which animal Prof. Birmingham finds the panniculus closely connected to the axillary borders of the pectoralis and latissimus. With care, however, it is possible to separate the panniculus from the underlying muscles, when the interval is seen to be very narrow, pectoralis and latissimus actually touching in one place. "In this narrow interval, and under cover of the adjacent part of the pectoralis major to a considerable extent, we find the pectoralis quartus, while the panniculus covers the interval and its contained muscle completely."

All these conditions appear to me capable of reconciliation with the derivation of the quartus from the panniculus if we keep in mind the *origin* of the cuticular muscle. The instances cited by Prof. Birmingham illustrate the same facts which the panniculus of the rodents demonstrates, namely that the panniculus is frequently encountered in two layers—a superficial portion corresponding in position to the human platysma, and a deeper stratum more intimately connected with the pectoralis. Regarding the entire skin muscle as a derivative from the ventro-appendicular sheet, it is not surprising to find examples in which the segmentation is, so to speak, incomplete, and in which, beneath a superficial free cuticular muscle, a portion of the same system, in process of separation from the parent ventro-appendicular layer, is encountered. In fact the pectoralis quartus, of the three variant human muscles here considered, is the one most prone to bear the evidences of its derivation from the pectoral division of the limb muscles. Again, the connection of the axillary arch with the latissimus can probably be regarded as representing the opposite condition, viz., a secondary fusion or reunion of a portion of the formerly free panniculus with the layer from which it was originally derived. Instead of considering panniculus and pectoralis as morphologically distinct units, a correct estimation of their relationship will reconcile the view which regards the pectoralis quartus as "a segmented portion of the great pectoral" with that which holds the muscle to be a deeper part of the panniculus, in the majority of instances *not yet* completely differentiated from the pectoralis major. That the axillary arch, which Prof. Birmingham and others have conclusively shown to be derived from the panniculus and the pectoralis quartus, are parts of the same system is suggested by the very cases of Dr Brooks' above quoted, and by the specimen here under consideration. I have likewise records of seven additional instances in which the axillary arch and pectoralis quartus united in the axilla, and similar conditions have been recorded by Prof. Humphry and others.

We may sum up the facts concerning the pectoralis quartus by saying that it appears as a derivative of the panniculus; that its lateral termination is more prone to exhibit complete pannicular character, as evidenced by its frequent union with the arch, an unquestioned cuticular derivative; that its mesal attachment preserves in many instances the connection with the pectoralis major more or less completely; that, in other words, the muscle is apt to represent an incomplete stage of that differentiation from the ventro-appendicular muscle which we must regard as the final step in the production of the general panniculus.

2. *Innervation of the panniculus.*

Mr Parsons finds that the ventral panniculus in Dasyprocta and other rodents examined by him is supplied by a large nerve, which also innervates the pectoralis, and which he identifies with the human internal anterior thoracic nerve.

Prof. Wilson[1] has shown that the panniculus generally receives its supply from "the lateral cutaneous nerve of the thorax," and Prof. Birmingham (*loc. cit.*) proves that this nerve is the homologue of the human lesser internal cutaneous, associated with another element representing a portion of the internal anterior thoracic nerve, which is usually absent in man, but appears as the nerve of the axillary arch when that muscle develops.

The nerve supply, therefore, confirms the derivation of the

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[1] J. T. Wilson, "The Innervation of Axillary Muscular Arches in Man, with remarks on their Homology," *Journ. Anat. and Phys.*, N.S. vol. ii., p. 294; "Further Observations on the Innervation of Axillary Muscles in Man," *Journ. Anat. and Phys.*, N.S. vol. iv., p. 52.

panniculus from the pectoral group, and affords conclusive evidence of the close morphological relationship between the two.

3. *Innervation of the three human variant muscles here considered.*

(*a*) *Pectoralis quartus.*—Both Prof. Birmingham and Prof. Wilson find the nerve of this muscle derived from the internal anterior thoracic nerve.

(*b*) *Axillary arch.*—The same observers have determined that the nerve supply of the axillary arch is also derived from the anterior thoracic trunks.

(*c*) *Sternalis.*—As above stated, modern investigations practically prove the anterior thoracic nerve supply of this muscle.

Conclusions regarding the possible interpretation of the sternalis as a reversional pannicular muscle.

1. The innervation of the sternalis demonstrates the variant to be either

(*a*) a portion of the pectoral mass in the narrow meaning, *i.e.* a displaced and a typical segment of the pectoralis major in Cunningham's and Eisler's sense; or

(*b*) a persistent reversional remnant of a portion of the superficial thoracic pannicular sheet, originally derived from the pectoralis, but normally not developed in man.

2. The innervation, therefore, not only indicates the close association of the sternalis with the pectoral muscle in the broadest meaning of the term, but it also correlates the same with the other superficial variant muscles of pectoral derivation and assembles them into a group, united both by the mutual relations of the individual components and by the common origin from the parent layer of the pectoralis.

3. Reference of the sternalis directly to the pannicular muscle is therefore not incompatible with either the innervation or the phylogenetic history of the cuticular layer, and, provisionally at least, this possible character of the variant should be considered in drawing general conclusions regarding the derivation and significance of the sternalis.

4. In estimating, however, the value of the etiological factors concerned in its production, it is evident that many cases of the muscle are to be referred directly to the pectoralis major, without pannicular intervention, as atypically displaced portions of this muscle in correspondence with the ontogenetic causes above defined.

5. The inference lies at hand that the types of the muscle belonging to Group B, and suggesting, either in their structure or in their association with other coexisting pectoral variants, pannicular derivation, are more properly to be regarded as less pronounced instances of the same displacement, involving merely such limited portions of the parent muscle that the gross conformation of the same does not suffer from this abstraction of a small segment, and that hence it presents a normal appearance.

6. It is, of course, conceivable that the general etiological factors previously considered should in individual cases become operative in conjunction with partial reversional appearance of a pannicular remnant. This interpretation might be assigned to instances in which the sternalis appears in combination with evidently pannicular supernumerary muscles, as in the above-described case of a sternalis in conjunction with the axillary arch and the pectoralis quartus.

7. On the other hand, these conditions may be regarded as examples of what we may, for want of a better term, call the "Variation diathesis," a strong tendency toward atypical or reversional formation affecting the entire muscular system in certain individuals, and producing multiple aberrant and supernumerary muscles in a single subject.

This view is sustained by the occasional observation of cases in which the sternalis occurs in combination with muscular variants of the thoracic region entirely outside of the pectoral sphere. Thus Prof. Ferris, of New Haven, recently communicated to me the records of an observation in which, with a well-developed bilateral sternalis, a typical supra-costalis was found on the left side. In this instance we are dealing with two muscular variations of the same topographical region in the same subject, one derived from the system of the pectoralis, the other associated with the sheet of the scalenus and external oblique. They are hence entirely independent of each other, and their simultaneous appearance in the same individual must be regarded as a coincidence, warranting perhaps the somewhat vague assumption that in cases of this kind a general, possibly hereditary, tendency to atypical development of the muscular system exists.

8. Again, the instances of sternalis occurring in combination with other variant muscles of direct pectoral origin deserve especial consideration in this connection. The most available instance of this is the case reported by Dr Bryce,[1] and already discussed in relation to the deep or intermediate group of pectoral variants. In this case the reverse of the conditions seen in Pl. XI. fig. 2 were found, namely, the direct continuity of the sternalis with the sterno-clavicularis, a variant derived, as above suggested, by atypical development directly from the plane of the pectoralis major, and not of pannicular character. Here we find direct union of a distinct pectoral element with the sternalis, and in this sense the case corresponds to the more frequently observed continuation of portion of a sternalis into the superficial layer of an otherwise normal pectoralis major. Its importance for our present inquiry lies, however, in the fact that it bridges the interval between the sternalis conjoined with additional variant muscles of *pannicular* origin, as seen in Pl. XI. fig. 2, and the occurrence of the sternalis as a solitary variant with or without defect in the sheet of the pectoralis major. In other words, the sternalis can appear either alone, or in combination with superficial aberrant muscles, or with deeper variants. In Dr Bryce's case the muscle is conjoined with the sterno-clavicularis, and there is coexisting atypical development and partial deficiency of the pectoralis major. The inference lies at hand to associate the abnormal form of the pectoralis not only with the sterno-clavicularis, but also with the sternalis, and thus to lead directly to the correlated group of isolated sternales, with derangement of the pectoral musculature, but without additional supernumerary muscles. In the same sense the case recorded and figured here (Pl. XI. fig. 2) may be taken as an example of those conditions in which, without gross disarrangement of the pectoral muscula-

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[1] *Loc. cit.*

ture, supernumerary elements appear as the result of slighter disturbances in the normal processes of pectoral development. These processes usually lead to the production of the solitary sternalis with underlying normal pectoralis, but in this instance, either by themselves or in association with the reversional appearance of pannicular rudiments, have led to the combination of muscular elements above noted.

9. It may therefore be concluded that the weight of evidence is *against* the assumption of a direct pannicular origin of the sternalis. No matter how varied the form, volume, attachments, relations, etc., of the muscle may be, all types of the structure can be satisfactorily united on the basis of direct derivation from the pectoralis sheet *sensu stricto.*

Group C.—The third group of sternales, in which the direct or indirect connection with the pectoralis major forms the distinctive morphological character, is, of course, readily coordinated with the preceding subdivisions, as examples of the variant in which, under the influence of identical etiological factors, the separation from the parent layer of the pectoralis major has not attained the complete degree characterizing the other types. Naturally a wide range of minor individual variation is here offered, and the development of the muscle may be to a marked degree irregular.

General conclusions regarding the derivation, morphological significance, and etiology of the sternalis.

1. Basing our conclusions on the facts of structure and innervation above outlined, we are justified in accepting the sternalis in its extensive range of individual and specialized forms as a product of atypical development of the pectoral mass in the wider sense.

2. Two general and fairly well-defined groups can be distinguished to which individual instances of the muscle can be more or less definitely assigned:

A. Sternales, occurring usually as well-developed muscular bands, associated with marked disturbances in the typical development of the pectoralis major, and accompanied by more or less actual deficiency in the corresponding segment of the sterno-costal division of the muscle. In these instances the abnormal muscle is clearly an atypical and displaced segment of the pectoralis major, whose connections with adjacent structures, as the frequent union with the sternal head of the sterno-cleido-mastoid, are secondarily acquired and morphologically unimportant characters.

B. A second general group of sternales is characterized by the slender and delicate form of the aberrant muscle, while the underlying pectoralis major appears in every respect normal.

Two possibilities suggest themselves in considering the derivation of this type:

A. Regarding the sternalis still as a displaced portion of the pectoralis major, it can be assumed that the rotated and atypical segment forms so slight a part of the entire pectoral mass that its loss and diversion from the same leaves no visible deficiency, and produces no disturbances in the typical development of the main muscles. This view is quite compatible with the known facts in the development of the pectoralis, which may be held responsible for the production of atypical derivatives.

B. A certain number of sternales suggest a derivation directly from abnormal persistent portions of a thoracic panniculus. The latter being in turn originally derived from the pectoral mass, the origin of the variant muscle is therefore again the pectoralis, although the derivation is less direct than in first group of displaced and rotated pectoral segments, occurring through the intervention of a pannicular antecedent.

This view is supported by the occasionally-observed instances of a sternalis occurring in direct continuity with other abnormal pectoral muscles which are both phylogenetically and by their innervation characterized as direct derivatives from the panniculus. In these cases the sternalis may possibly represent a reversion of part of the cuticular muscle. More probably, however, they are to be interpreted as examples of *coincidence* of several etiological factors simultaneously operative in the same individual, and leading to the production of several co-existing variants, of which the sternalis is to be regarded as produced by the same forces responsible for the development of the muscle in uncomplicated cases, while the others, such as the axillary arch and pectoralis quartus in the instance above described, represent pannicular reversions.

3. *Relation between the sternalis and the deep supernumerary pectoral muscles.*—We have, as previously seen in other portions of the pectoralis major, departures from the normal type of development leading to the production of deeper supernumerary muscles which represent clearly atypical and displaced pectoral segments, as the tensor semivaginæ, M. chondro-coracoideus ventralis, M. præ-clavicularis. This congruence of structural character in relation to the pectoralis plane strongly suggests the propriety of uniting the superficial and intermediate pectoral variants morphologically and genetically into a common general group, and this view is borne out by the cases, such as the one recorded by Dr Bryce, in which representatives of both the superficial and deeper division of muscular variants occur in the same individual, apparently in response to identical general causes leading to disturbances in the normal development of the pectoral musculature. In the usual cases, however, we find, contrasted with the deep position of the intermediate muscles, and requiring explanation based on the agency of secondary determining causes, the fact of the uniformly superficial ventral position of the sternalis, and of the graded series of stages by which the muscle in different individual instances passes from the massive muscular band with correspondingly deep deficiency of the pectoralis to the thin superficial ribbon with extensive fascial connections which leaves the underlying main muscle to all appearances normal and undisturbed.

4. *Etiology of the sternalis.*—The various questions raised by these considerations of the sternalis regarding the influences leading to the production of the variation as an atypical segment of the pectoralis major, and the modifying secondary conditions responsible for the appearance of the various types assumed by the muscle, find their explanation in the developmental history of both the pectoral musculature, and probably the ventral thoracic wall.

5. The preponderance of the sternalis in ancephaly is apparently due to mechanical conditions favouring disturbances in the normal migration of the embryonic pro-pectoral mass, and coincidently leading to atypical structure of the interchondral spaces. At the present writing the evidence seems to point to ancephaly as being responsible for *both* atypical muscular

development leading to the production of the sternalis and to asymmetry in the structure of the ventral thoracic walls.

The direct dependence of the muscular variation upon the latter condition, in Eisler's sense, is not apparent from the material so far available, and the observations at hand suggest that both anomalous conditions may, provisionally at least, be referred to the same etiological factors. They therefore appear frequently *coincident* with each other in the same individual, or may develop independently of each other.

6. The skeletal, fascial and muscular connections of the sternalis are, in the majority of cases, *secondary* acquisitions, such as the commonly-encountered junction of the cephalic extremity with the sternal tendon of the sterno-cleido-mastoid, and distally the connection with the aponeurosis of the external oblique, or the lower true ribs and cartilages. These connections are of little or no value in determining the significance of the variant or the muscular group to which it should be assigned. On the other hand, their early acquisition, preceding or during the embryonic migration of the pro-pectoral muscular mass, may very well be considered as one of the secondary factors determining the extent and character of atypical pectoral development leading to the various forms assumed by the sternalis.

7. Occurrence of the sternalis in combination or even direct continuity with certain other abnormal or supernumerary muscles of the pectoral region.

Three conditions are to be distinguished here:

(*a*) Sternalis, combined with deficiency of the pectoralis major, and with one or more of the deep group of supernumerary muscles above considered, as in the case reported by Dr Bryce.

These instances are to be interpreted in the same sense as the uncomplicated cases of sternalis described above under Group A. The disturbance of the normal type of development of the pectoral musculature is here more extensive and far-reaching in its results, leading to the production of both the superficial variant (sternalis) and one or more of the deeper intermediate group.

(*b*) Sternalis, combined with one or more superficial supernumerary muscles of pannicular origin, as the pectoralis quartus and axillary arch in the case above reported.

The evident pannicular derivation of the other aberrant muscles might suggest the possibility of a similar origin for the sternalis, the muscle then representing an *indirect* derivative from the pectoralis sheet, instead of—as in the first case—a *directly* displaced segment of the normal pectoralis major. More probably, however, these instances are to be interpreted as examples of coincidence in the same individual of atypical muscular structures, derived from the same morphological plane, but due immediately to a combination of etiological factors simultaneously operative.

(*c*) This is certainly the explanation of the third group, in which the sternalis occurs in combination with other aberrant thoracic muscles, not connected with the pectoralis. Thus in Dr Ferris' instance, where a double sternalis occurred in combination with a typical supra-costalis. Here a pectoral variant is associated with one belonging to the system of the scalenus and external oblique, and the case may be regarded as an example of what we may term a "Variation-diathesis," as so frequently observed in individuals with multiple muscular anomalies. These conclusions may be summed up in tabulated form as follows:—

SUMMARY.

I. DERIVATION AND SIGNIFICANCE.—Plane of pectoralis major, as shown

A. By the innervation through branches of the anterior thoracic nerves.

B. By the relations of the sternalis to its myological and skeletal environment.

Derivation from superficial pectoral layer in the majority of cases *direct*. A few instances of combination of sternalis with other supernumerary muscles of pannicular origin suggest possible phylogenetic *indirect* derivation of sternalis from pectoral mass, as reversional remnants of thoraco-humeral cutaneous muscle. More probably these cases represent *coincidence* of occurrence of multiple variations from several sources, the sternalis still *directly* pectoral in derivation, the associated variants *indirectly* derived from the same system through the panniculus.

II. Morphology.—Three general groups:

1. Sternalis with underlying normal pectoralis major.

2. Sternalis with coexisting deficiency and abnormal construction of pectoralis sheet.

3. Sternalis, combined with, or in direct continuity with, other muscular variants of the pectoral region, with or without coincident atypical development of pectoralis major.

A. With variants representing clearly misplaced portions of pectoralis major—Bryce's case. (Identical etiological factors affecting large area of pectoralis produce not only sternalis but additional variants of identical derivation.)

B. With superficial supernumerary pectoral muscles of unquestionably pannicular origin—Huntington's case. (Combination of various etiological factors of the same myological district leads to simultaneous development of sternalis from pectoral sheet, and other variants from remnants of the panniculus.)

C. With muscular variations of the thoracic region other than those derived from the pectoralis system—Ferris' case. (Atypical muscular diathesis leading to occurrence of multiple non-related myological variants.)

III. Etiology.

1. Ontogenetic pectoral migration.

2. Preceding or coincident atypical secondary muscular or skeletal connections leading to diversion of part of superficial pectoral layer to form the sternalis, and responsible for the minor variations presented by the muscle.

3. Closure of midsternal fissure as influencing atypical disposition of superficial pectoral elements during ontogenetic descent.

II. M. INFRA-CLAVICULARIS.

Supernumerary pectoral muscles, other than the sternalis, ventrad of the pectoralis major, are of comparatively rare occurrence. They belong to the same general morphological group as the variants previously discussed, and represent atypically diverted portions of the superficial pectoral lamina, usually derived from the clavicular head, and hence extending from the clavicle in varying degrees caudo-laterad over the subjacent pectoralis and deltoid. In their complete development they appear as the *M. infra-clavicularis*, a well-marked example of which is shown in Pl. XIV. A strong flattened muscular belly, arising from the mesal third of the ventral surface of the clavicle, extends laterad to terminate in a broad and firm fascial expansion covering the superficial aspect of the deltoid. There is no deficiency of the pectoralis major, but the delto-pectoral cleft, bridged by the aberrant muscle, is very distinct.

Innervation.—A branch of the external anterior thoracic nerve passing around the cephalic border of the pectoralis major enters the muscle on its deep surface near the middle.

EXPLANATION OF PLATES.

Pl. I. Columbia University Museum, No. 2533. Adult human subject. Left pectoral region with *tensor semi-vaginæ.*

Pl. II. From a fresh dissection. Adult human subject. Right pectoral region with *tensor semi-vaginæ* (intermediate ento-pectoral slip).

Pl. III. Columbia University, Study Collection. Adult human subject. Dissection of pectoral region, with bilateral *tensor semi-vaginæ* and extensive deficiency of pectoralis major.

Pl. IV. Columbia University Museum, No. 2334. Adult human subject. Right pectoral region with *tensor semi-vaginæ.*

Pl. V. Columbia University, Study Collection. *Putorius vison*, Mink. Dissection of pectoral region.

Pl. VI. Columbia University, Study Collection. *Cercoleptes caudivolvulus*, Kinkajou. Dissection of pectoral region.

Pl. VII. Columbia University Museum, No 2389. Adult human subject. Left pectoral region with *tensor semi-vaginæ* and *sterno-chondro-coracoideus ventralis.*

Pl. VIII. fig 1. Columbia University, Study Collection. Human fœtus near term. Pectoral region with *sterno-clavicularis* and *sterno-scapularis.*

Pl. VIII. fig. 2. Same specimen, with pectoralis major reflected on right side.

Pl. IX. Schematic representation of mutual relation existing between the members of the deep group of supernumerary pectoral muscles.

Pl. X. From a fresh dissection. Adult human subject. Right pectoral region, with *sternalis* and extensive deficiency of pectoralis major.

Pl. XI. fig. 1. Columbia University Museum, No. 935. Ancephalic fœtus. Pectoral region with bilateral *sternalis* and right superficial lamina of pectoralis major.

Pl. XI. fig. 2. Columbia University, Study Collection. Adult human subject. Pectoral region with *sternalis*, *pectoralis quartus* and *axillary arch.*

Pl. XII. From a fresh dissection. Ventral thoracic wall of subject shown in Pl. X. denuded of the pectoral musculature to exhibit sternum and formation of interchondral spaces.

Pl XIII. Columbia University Museum, No. 2218. Sternum and costal cartilages of same subject, macerated.

Pl. XIV. Columbia University Museum, No 2514. Adult human subject. Left pectoral region with *infra-clavicularis.*

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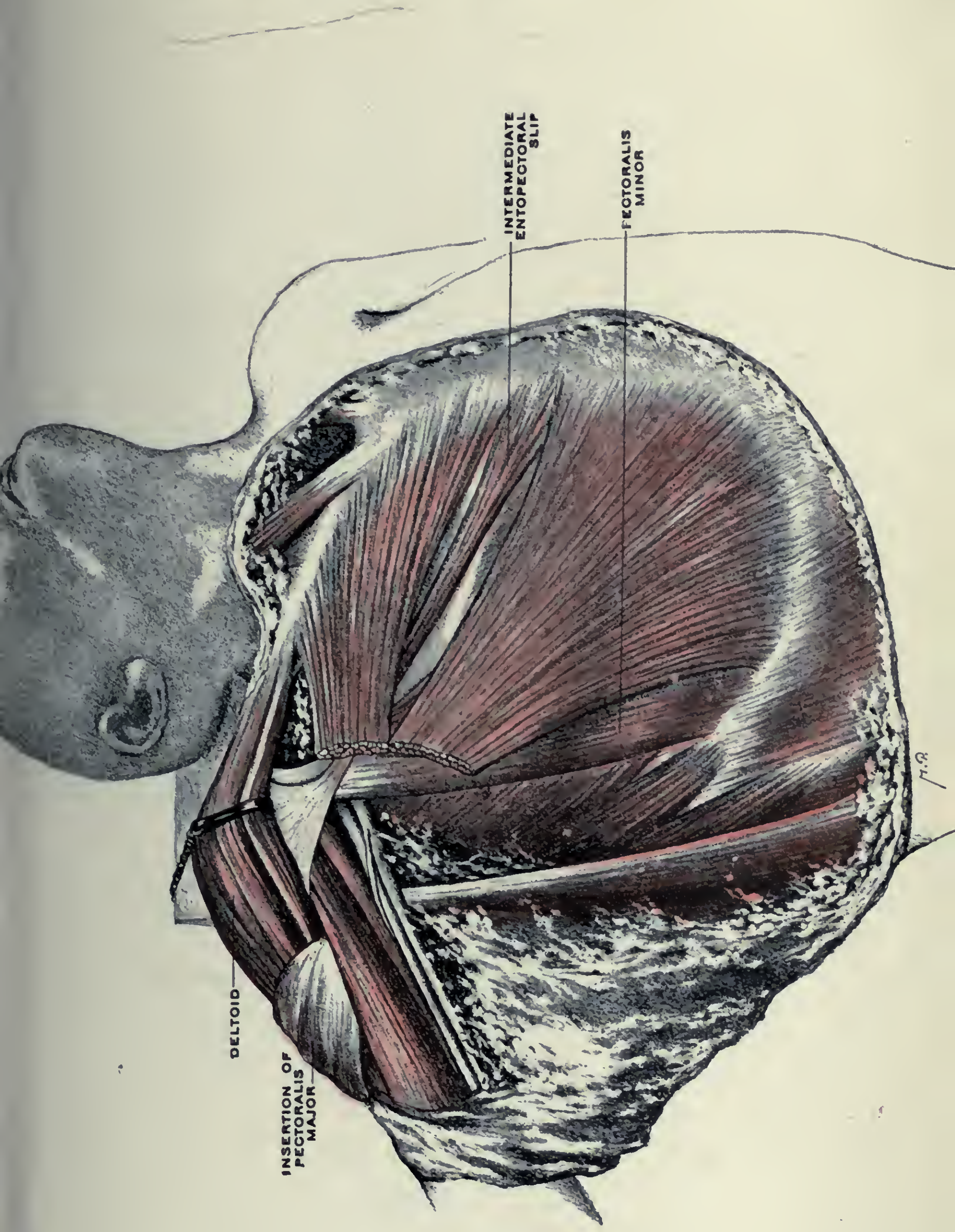
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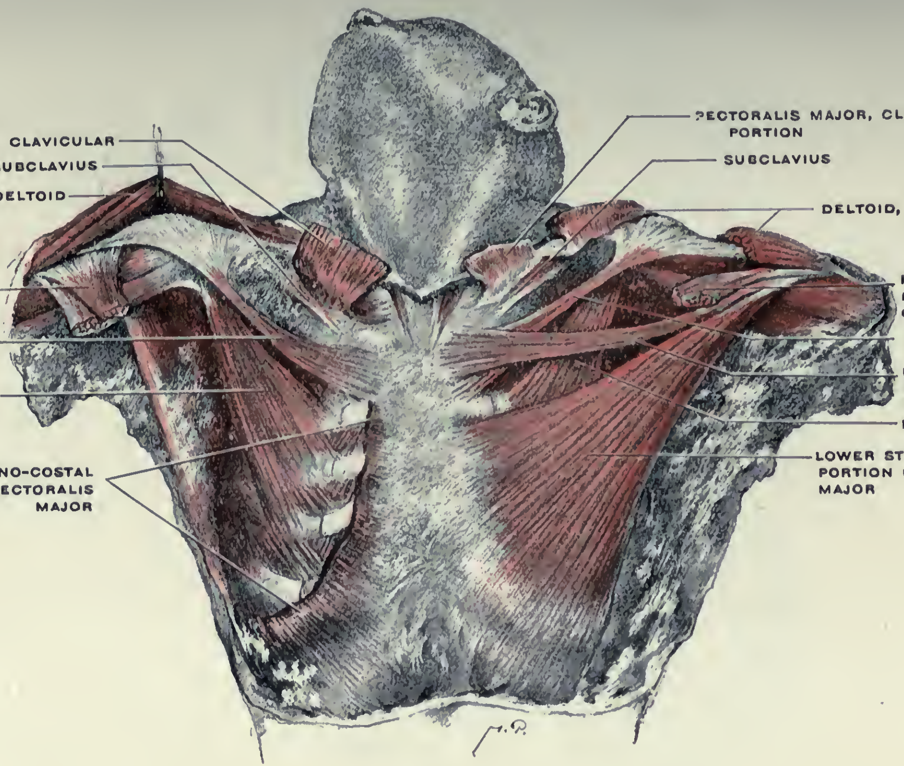

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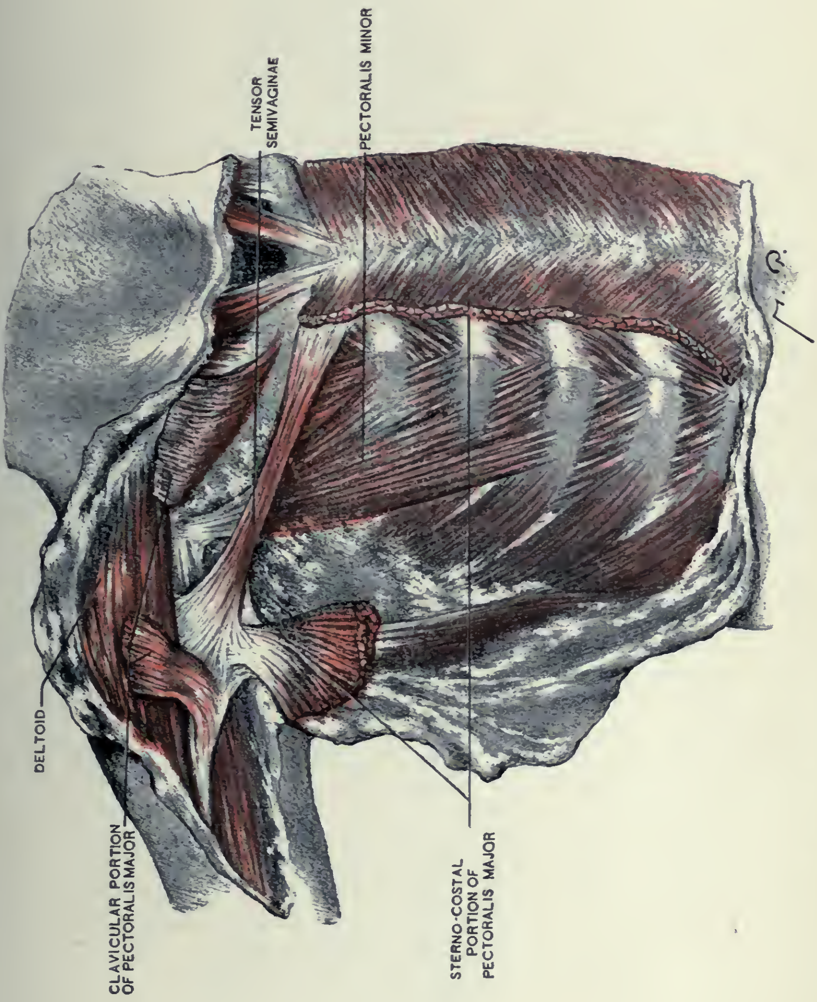

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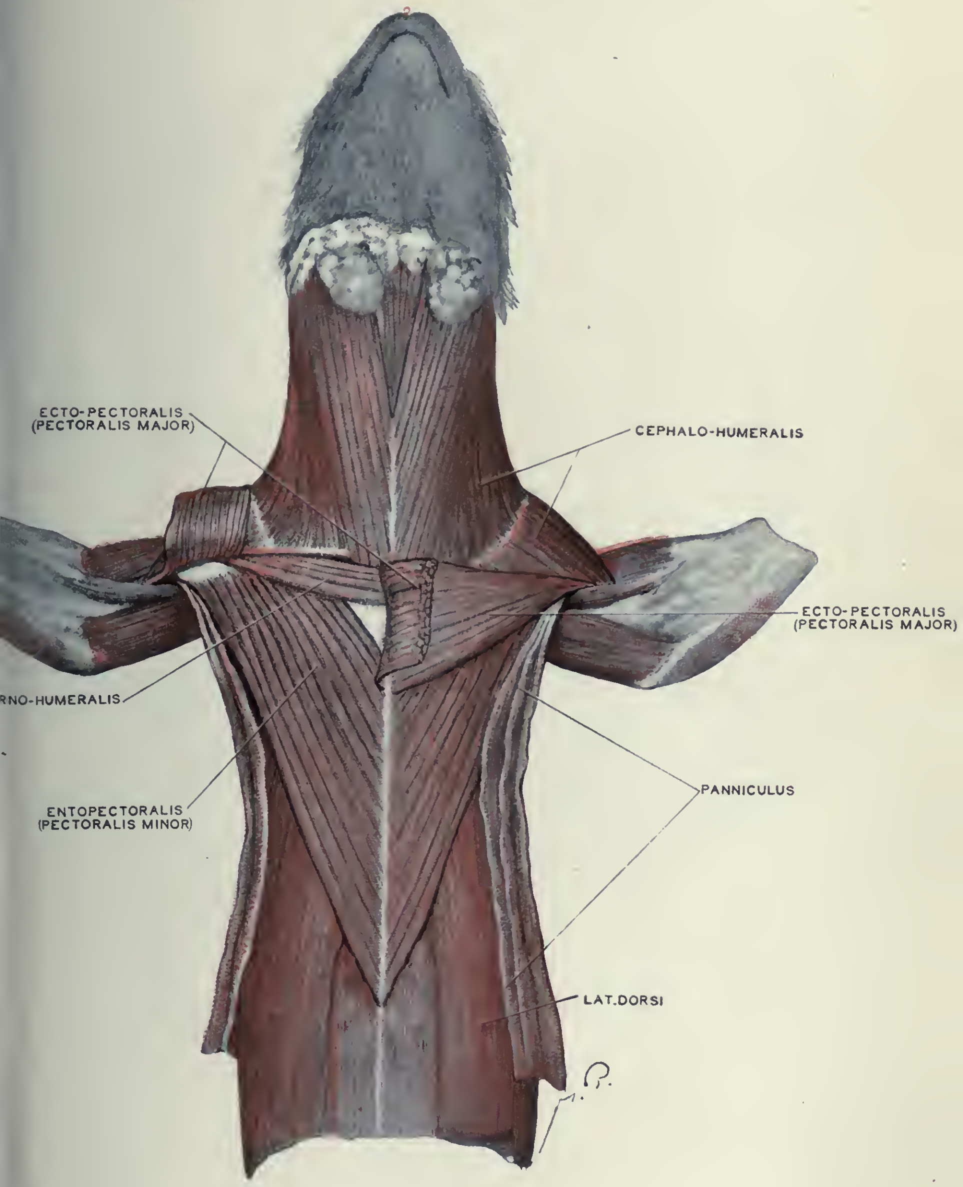

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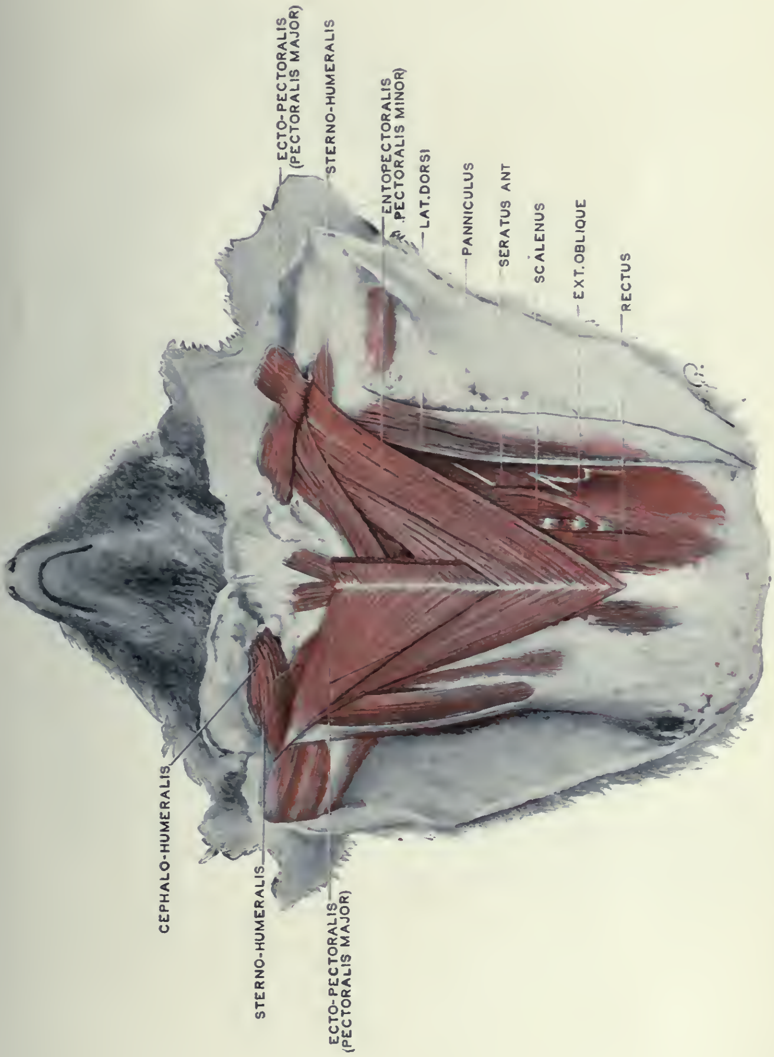

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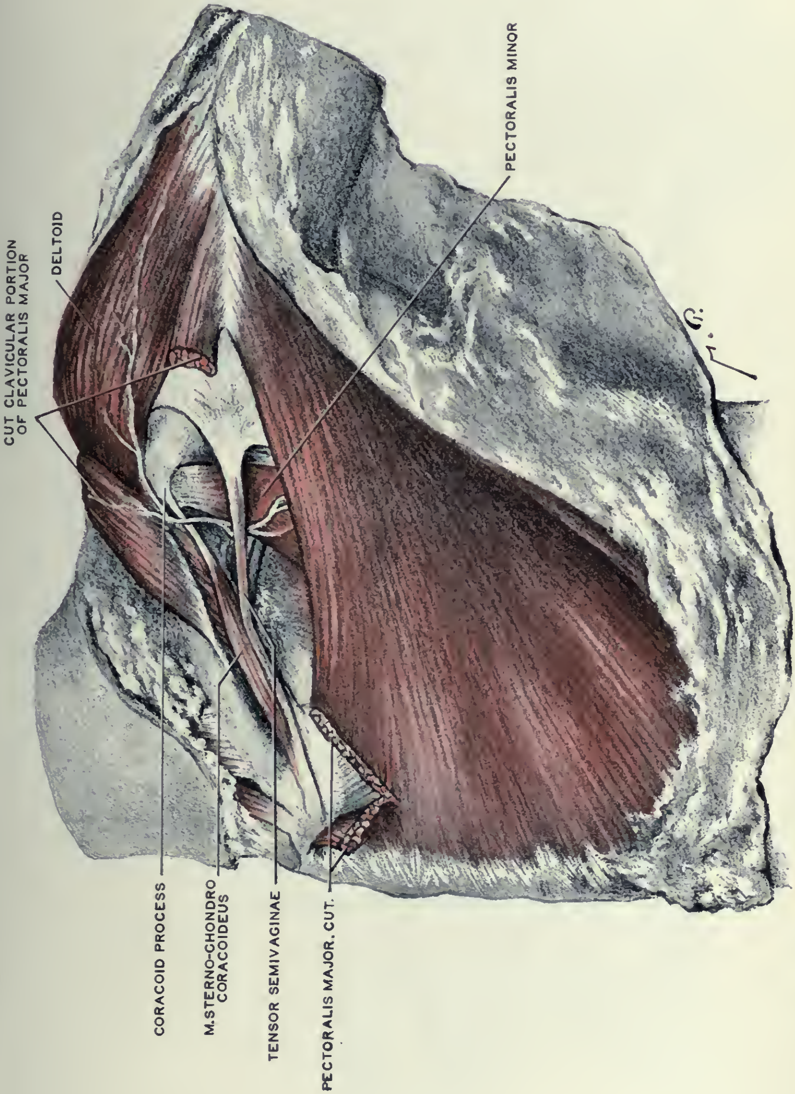

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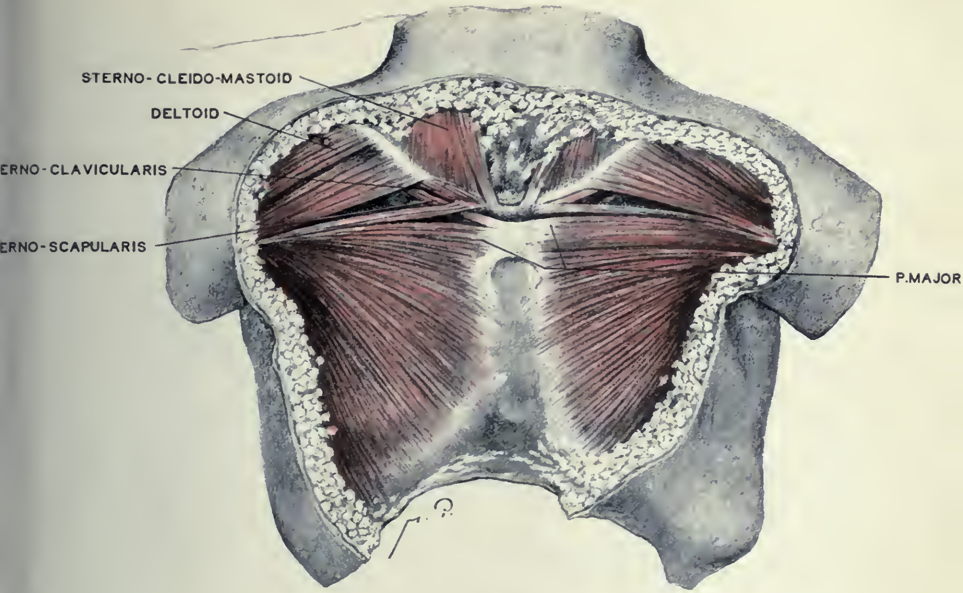

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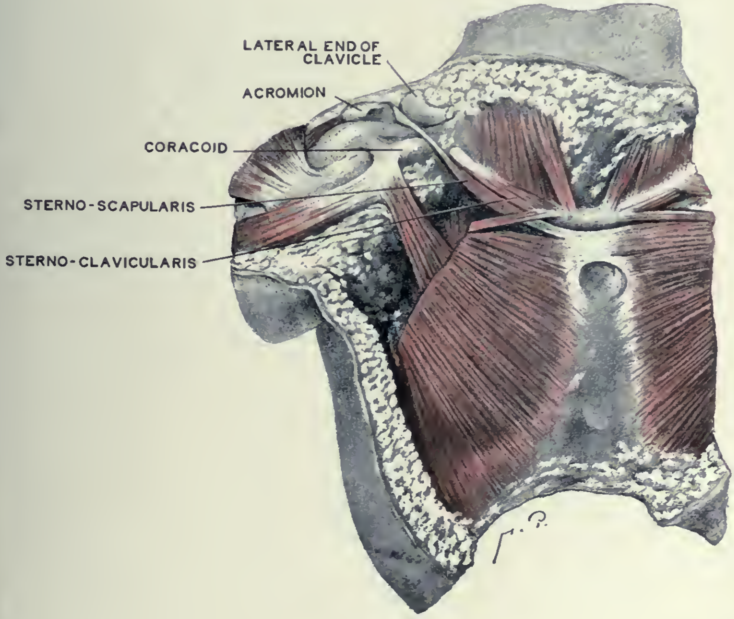

Fig. 2.

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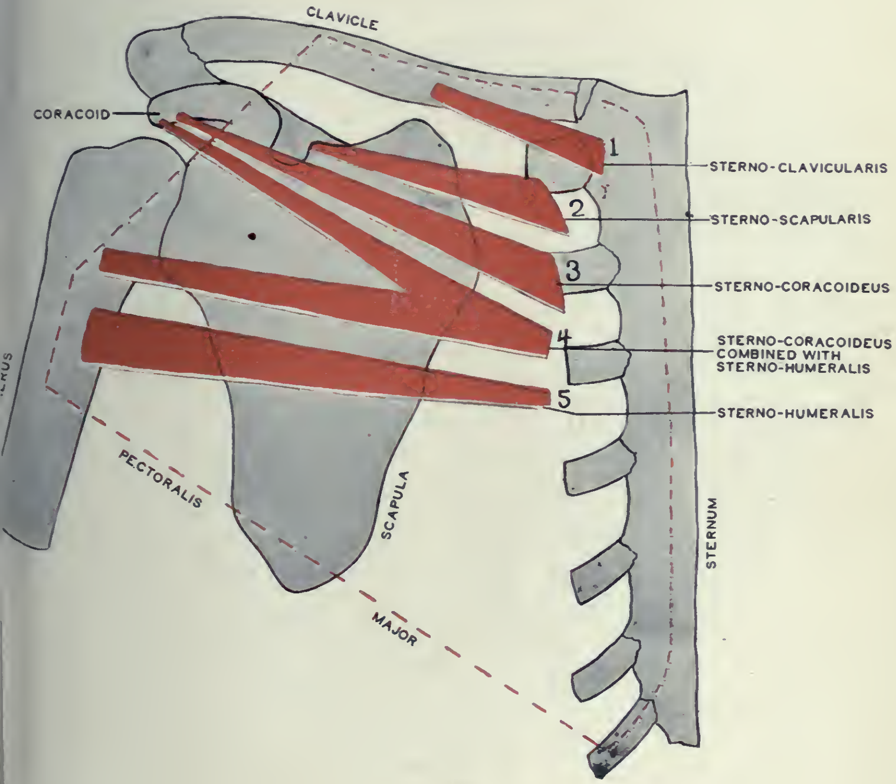

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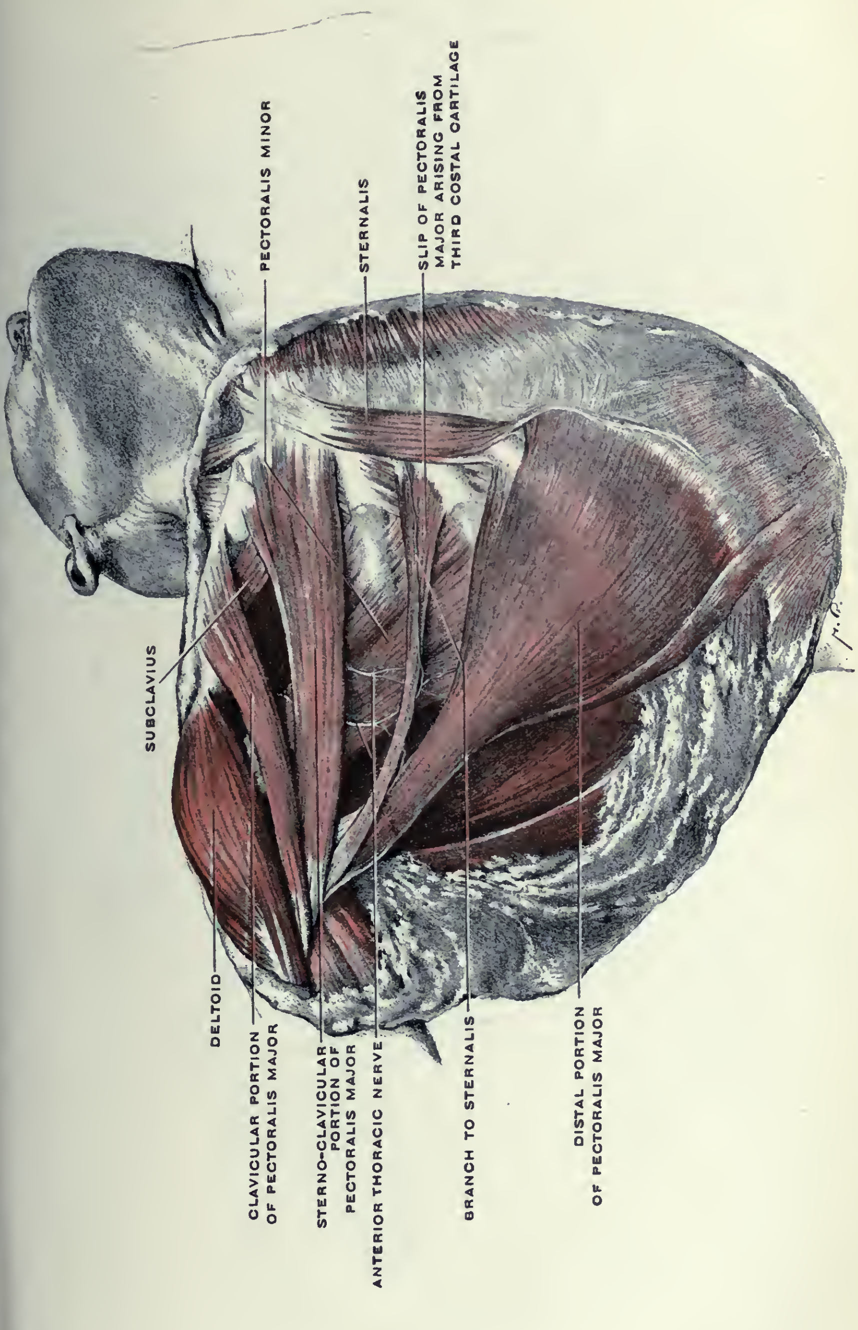

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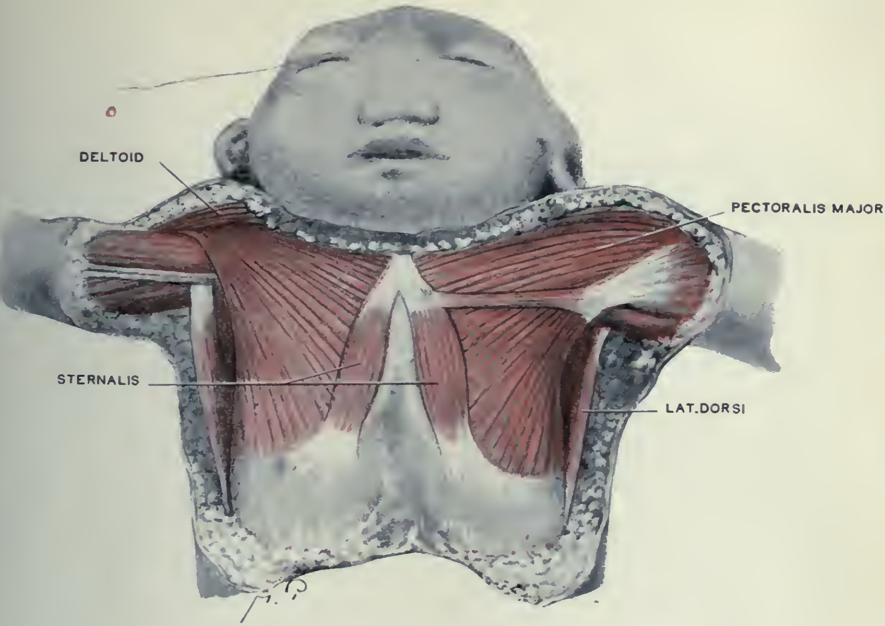

FIG. 1.

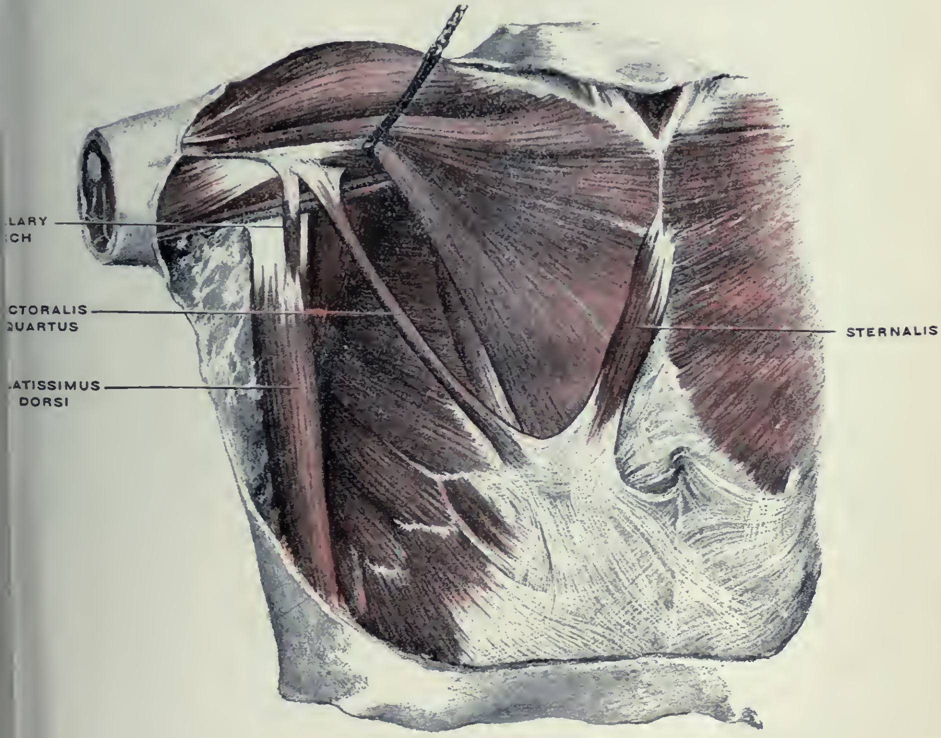

FIG. 2.

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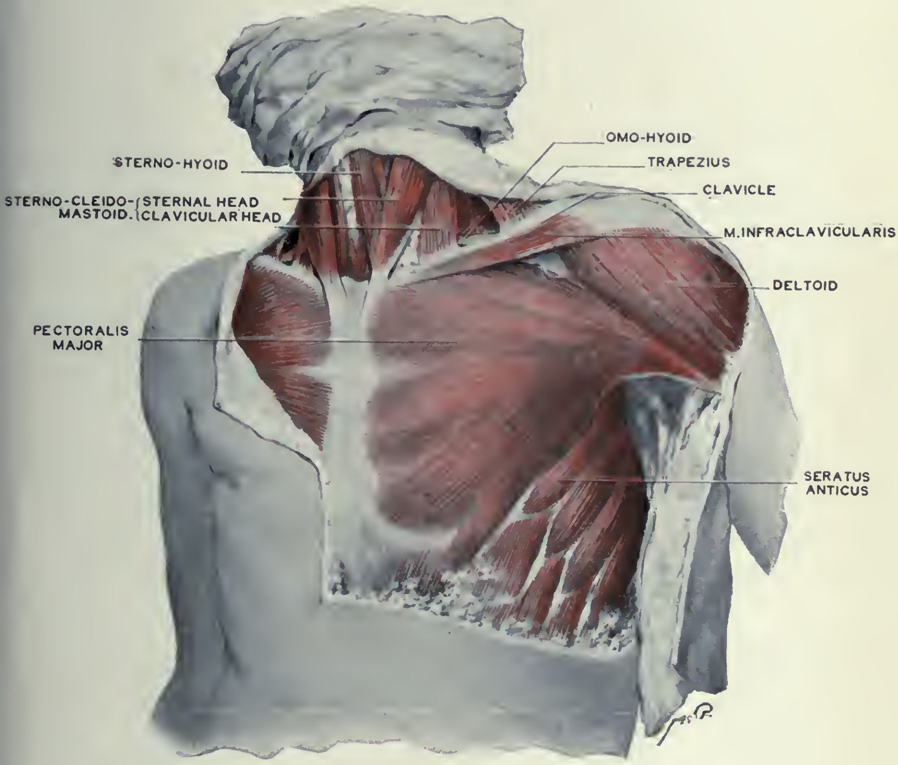
Journ. of Anat. and Physiology, October 1904.]

[Plate XIII.

Dr Geo. S. Huntington.

Journ. of Anat. and Physiology, October 1904.] [PLATE XIV.



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THE HISTOLOGY OF LYMPHATIC GLANDS: THE GENERAL STRUCTURE, THE RETICULUM, AND THE GERM CENTRES. By T. L. Bunting, M.D. (Plates XV.–XIX.)

Part I.

Under the name lymphatic glands I include only those lymphoid structures which have a separate existence, not being included within any other organ, and which have both afferent and efferent lymphatics. This excludes all peripheral lymph nodules, tonsils, etc., and also the so-called hæmolymph glands (38). Lymphatic glands are further separated from other lymphoid structures by the fact that all the cells formed in them go indirectly or directly into the blood.

I have examined numerous lymphatic glands from several of each of the following animals:—Ox, sheep, pig, rabbit, guinea-pig, cat, dog, badger, and man; also two glands from one civet-cat, two from an American opossum, one from an Australian opossum, and one from a jackal.

I worked chiefly with fine paraffin sections. For these the glands were fixed, about half of them in Flemming's weak solution, the remainder in Zenker's solution. The glands from the badgers, man, civet-cat, opossum and jackal were from subjects which had died from unknown causes, and they could not be fixed immediately after death. The others were from animals which had been killed either by the butcher, or by chloroform or carbon-dioxide poisoning, and these glands were in all cases placed in the fixative within a few minutes of death. I also used washed sections. These were some of them cut fresh, by freezing; the remainder were fixed as above and cut in paraffin. To wash the sections they were placed in a long test-tube about half full of water, and shaken for about fifteen minutes. Some sections were removed in the course of this time, and so showed the washing in progress. I fully agree with Thomé (36), and Sisto and Morandi (32), as to washing, pencilling, and digesting being too severe processes to give accurate results with so delicate a structure as lymph gland reticulum. But when controlled by a study of undisturbed sections, washing gives very valuable results, especially when the progress of the washing is watched.

My sections were stained on the slides by carmalum, alone, or followed by picric acid, safranin, safranin and kernschwarz, hæmatoxylin with and without eosin, thionin, Hansen's picrofuchsin, the Mallory-Stohr stain, the Israël-Pappenheim stain followed by hæmatoxylin, or Weigert's resorcin-fuchsin. The last four were used according to the directions of Thomé (36) and Retterer (27). Thirty glands were impregnated with silver-nitrate solution. Some of these were sectioned fresh, others were fixed as above and cut in paraffin. I also carried out certain manipulations which will be described later.

For finding glands too small to be readily discovered I found Retterer's method very useful. He takes a piece of tissue in which the glands lie, fixes it, passes it through alcohols, and clears it. The whole tissue is then transparent, except certain small nodules. These are the lymphatic glands; they are now easily seen and removed.

General Structure.

The classical schema of His is found only in the glands of cattle, as von Recklinghausen pointed out (26). Even in them it is not constant. I find that in the ox some glands have sinuses devoid of trabeculæ; while in the mesenteric glands of oxen it is usual for the cortical tissue to occupy one side of the organ and the medullary tissue to occupy the other, instead of the medullary being surrounded by the cortical. In other animals divergence from the classical arrangement is the rule. The relation of cortical and medullary tissue is found in every possible variety. In some glands even—for example, in the mesenteric glands of pigs—it is difficult to say whether tissue is medullary or cortical in nature. This is because the parenchyma is divided up very irregularly, by branching trabeculæ, into masses which might equally be regarded as very thick medullary cords, or as so-called cortical nodules. In consequence of these irregularities of distribution it is necessary to dissociate the terms medullary and cortical from their primary meanings, and to use "medullary tissue" as signifying parenchyma which is split up into moderately narrow bands called medullary cords, by intervening lymph channels; and "cortical tissue," parenchyma which is not so split up. There are equally great variations in the relations of trabeculæ to parenchyma. Some glands have no trabeculæ (most guinea-pig glands); in others the trabecular tissue is in excess of the lymphoid (chiefly in aged glands). These variations in the general structure of the glands are seen, as von Recklinghausen said, not merely in different animals but in the same individual; and I would add that some are seen even within one gland. For example, in rabbit glands the medullary sinuses at one end of the gland may contain numerous reticulum beams, while no beams whatever are present in the sinuses at the other end, which thus resemble those of birds. Great variations are also found in the glands of the same animal at different ages, as I shall show later.

Trabeculæ, when present, may occur as two separate systems. The cortical system really consists of processes running inwards from the capsule, which is frequently thicker at their points of origin. The medullary system consists of processes from the hilum, which run inwards through the medullary sinuses. Either of these systems may be present alone, or both may occur in one gland, leaving an intervening portion of gland free from trabeculæ. The latter is perhaps the commonest of all forms. In all these cases the free ends of the trabeculæ break up into a sort of brush, as Thomé (36) described, the strands of which become continuous with the beams of the reticulum. In some glands each system of trabeculæ is extended till it meets, and blends with, the other. This forms what we may call a complete trabecular system. When a complete system has trabeculæ so numerous that they occupy every sinus, as is usually the case in oxen, we have the classical schema of His. In cattle the cortical trabeculæ occur at approximately regular intervals. In most other animals their distribution is usually very irregular. Two may lie quite close together, and no others be found in the section.

The cortical trabeculæ are usually described, incorrectly, as septa or partitions forming loculi and dividing the cortical parenchyma into nodules (3, 19, 31). In single sections they have that appearance, but following through a series we find that each trabecula quickly disappears, and fresh ones appear in other positions. By cutting sections through the cortex, parallel to the capsule, it is seen that the cortical trabeculæ are really flattened bands of no great width, which lie scattered in a mass of continuous parenchyma, from which they are separated by an encircling sinus (Pl. XV. fig. 1). The trabeculæ can be dissected out from the cortex by needles, when their true shape as irregular bands is well seen (Pl. XV. fig. 2). In most animals in which they are found they run a fairly straight course, and do not communicate with each other until they reach the medulla. Sometimes they do branch, and the branches may anastomose in the cortex. This is notably the case in the Australian opossum. In this animal thick trabeculæ, with frequent branching, cause a closer resemblance to the traditional arrangement than I have seen elsewhere. But even here they do not enclose loculi; they only make, by their ramifications, a very irregular space, which is occupied by a continuous parenchyma.

It follows from this distribution of the trabeculæ that the cortical parenchyma is not divided into nodules or follicles, as is commonly described. It forms one continuous mass, pierced, but not interrupted, by the sinuses and trabeculæ, as shown in fig. 1. The term nodule is also sometimes applied to the germ centres. It is thus ambiguous, and is better avoided.

Germ centres are rare or absent in the newborn, as Gulland pointed out (12), and sometimes they are absent in adult glands. To distinguish them from the very different tissue which forms the remainder of the parenchyma, I call the latter the ordinary parenchyma. Though always most numerous at the periphery of the cortical tissue, they are usually scattered throughout the cortex with great irregularity, and a few are found in the medullary cords in some glands (*e.g.* in the rabbit). Even at the periphery there are often considerable areas of ordinary parenchyma between the germ centres. The germ centres at the extreme periphery often bulge outwards, causing little bosses on the exterior of the parenchyma, and thus giving it its nodular appearance.

Of sinuses the cortical one is sometimes the only one present. It may be interrupted in places by the parenchyma and the capsule coming into direct continuity. The medullary sinuses are the spaces between the medullary cords; though often quite narrow, they are sometimes, as in many rabbit glands, cavernous spaces occupying a large portion of the gland. Usually there are other sinuses, the intermediate sinuses, which connect the cortical sinus with those of the medulla. Medullary trabeculæ, when present, lie in the centres of medullary sinuses; they do not form their boundaries. Cortical trabeculæ, after crossing the cortical sinus, lie in the centres of the intermediate sinuses.

The Reticulum.

The nature of the reticulum is still an open question, and to previous divergent views is now added Retterer's opinion that no separate reticulum exists (27). Before discussing the various views upon the reticulum I shall describe my own observations upon it. In doing so I shall speak of its units as "beams," in order to avoid the use of question-begging terms.

The reticulum is continuous throughout the gland. The continuity can be distinctly traced between beams in the germ centres and those in the ordinary parenchyma, and between the latter and the sinus beams. The sinus beams at their peripheral extremities can frequently be seen to be continuous with fibres of capsule and trabeculæ, and many trabeculæ break up, as already described, into a brush of which the strands are continuous with beams of the ordinary parenchyma.

In the sinuses most beams have a general direction transverse to that of the sinus, crossing it straightly or obliquely. They branch comparatively little, and most branches run towards the parenchymal margin, so that more beams are inserted into it than take origin from the capsule and trabeculæ. In those medullary sinuses which have no trabeculæ the reticulum is more irregularly arranged, resembling in this respect that of the ordinary parenchyma, except that the mesh is larger. In some of these sinuses there is a special arrangement of beams, to be described later. Some sinuses may be devoid of reticulum in glands from cats and rabbits, as all sinuses are in birds (8). At their parenchymal extremities the sinus beams usually branch, and these branches unite with similar ones from the parenchyma to form the extremely close network which marks the boundary between sinus and parenchyma. Some of the sinus beams, however, run straight through this network without branching, and anastomose with beams in the interior of the parenchyma. In the ordinary parenchyma the reticulum is absolutely irregular; it forms a network of smaller mesh than that in the sinuses, though larger than that which lies at the periphery of the parenchyma. Round the outer part of nearly every germ centre the reticulum beams take a circular arrangement, forming a close network of elongated narrow meshes. This entirely surrounds these germ centres, except those which abut upon sinuses, when the side adjoining the sinus is free. Though this arrangement has somewhat the appearance of a capsule, as Gulland says (11), it is clearly a network with open meshes.

The beams are of very various diameters. The same beam may be narrow at one extremity and wide at the other. In the sinuses they tend to be narrow and long, though irregular. In the ordinary parenchyma they are more variable. Most are fine, as usually described, but amongst these a few coarse ones are usually found, and in places one finds patches of reticulum made up entirely of thick beams. In such patches the beams may be wider than the meshes, and the appearance of sections is rather that of a perforated plate than of a network. The contrast is exceptionally well seen in figs. 3 and 4 (Pl. XVI.), which show, under the same magnification, adjoining fields from the same section. Towards the lower left hand corner of fig. 4, and still more just beyond it in the section, the perforated plate-like appearance is seen. On beams in all situations we find plate-like expansions at the nodal points or in their course. In the sinuses these are usually small and rare, and a majority of them are at the parenchymal ends of the beams. In the parenchyma these enlargements are larger and more frequent. In parts it can be seen, on studying thick sections, that the apparently narrow beams are really profiles of membranes.

In other places we find the reticulum almost entirely made up of plate-like expansions (Pl. XVII.). These are the membranes seen on the surface instead of in profile. They are irregular plates, of varying and often of considerable size; they are inclined to each other at all angles, and are joined together sometimes directly, sometimes by the intervention of short thinner pieces. Thus they form a tissue the structure of which closely resembles that of a sponge, rather than a net. These expansions are no doubt identical with the expanded trabeculæ of Henle (13), and Vernon (37), and the membranes of Gulland (12). Most of the ordinary parenchyma is made up of the more or less cylindrical beams, with expansions scattered on them, but in the germ centres the thin beams are rarer, and the reticulum is largely a sponge-like tissue as just described. This can be seen in most undisturbed thin sections, though there the nuclei partly cover the plates, but it is more obvious in some which have been washed. The circularly-disposed beams around the germ centres are usually thick. A similar arrangement is sometimes found around the periphery of the ordinary parenchyma. I have seen a layer of three parallel beams thus running round part of the parenchyma of a dog's gland.

The nuclei of the reticulum are of varying appearances (Pl. XVIII.). Many are the round, or slightly oval, large, clear nuclei usually described. They are poor in chromatin; in each are several small chromatic spots. Gulland says that only one such spot is found in each (9). I find both their size and number variable. Occasionally only one is present; oftener there are several, in nuclei which undoubtedly belong to the reticulum. Other reticulum nuclei are narrow, but as long as or longer than the foregoing. These are occupied, largely or wholly, by structureless masses of chromatin. They show as spindles of deep colour upon the beams. These two classes of nuclei probably correspond to those described by Ribbert (29), who thought that the elongated ones belonged to the reticulum proper, and the round ones to cells which covered the reticulum. But between these two forms I find every possible variety. They may be a decided oval, narrower than the first described, angular, or crescentic. The chromatin in these forms varies between that in the other two in its arrangement. Some of it is often huddled together in one part of the nucleus, while other parts may still be clear. All the forms are found in every part of the gland, but the large clear ones are commonest in the germ centres, next in the ordinary parenchyma, and least frequent, though usually still plentiful, in the sinuses. The spindle-shaped nuclei are only rarely found inside the germ centres, many of which contain none of them. When found there they are usually towards the periphery. They are most frequent in the sinuses and on the circular beams around the germ centres, and next in the ordinary parenchyma, particularly at the border between it and the sinus. The intermediate forms are common in the sinuses and in the ordinary parenchyma, and are not infrequent, though much rarer than the large oval and round ones, in the germ centres. These proportions are sometimes reversed as between sinus and ordinary parenchyma, but they are constant as regards active germ centres. As these various forms of nuclei make a complete series, I regard them as variations of one form; and looking to their relative distribution they are probably variations due to age. The nuclei lie on or in the beams. When the beam is very narrow the nucleus forms a protuberance to one side, surrounded by a faint line of beam tissue. They are perhaps commonest on the plates or enlargements of the beams, but are often found also in the course of a beam, where there is no branching nor enlargement, except that immediately around the nucleus. The dark, spindle-shaped nuclei often cause no perceptible enlargement, even on narrow beams.

With ordinary stains no markings are shown which indicate cell margins, nor any distinction between the cell protoplasm and any other possible constituent of the beams. A few rare beams show signs of fibrillation. They stain very readily with eosin, which shows them to be granular. With hæmatoxylin and other basic stains they can be stained, though not so quickly. They then appear homogeneous, or patchy. Some beams always colour more deeply than others with these stains, but never so deeply as chromatin. Recently Thomé (36) has drawn attention to two stains which do differentiate the tissue of the beams, distinguishing between fibres and protoplasm. These are the Mallory-Stohr phospho-molybdic-acid-hæmatoxylin, which colours fibres dark blue and protoplasm light blue, and Hansen's picro-fuchsin, which colours fibres red and protoplasm yellow. I find that a similar differentiation is produced, though less satisfactorily, by staining for half an hour in Meyer's carmalum and then in an alcoholic solution of picric acid. The results by all these methods corroborate each other. The Hansen stain appears to me to be the most satisfactory of them. In addition to the fibres, the nuclear membrane and a few spots within the nucleus often take the red stain.

These stains show the beams to be composed in varying proportions of fibres and protoplasm (see Pl. XIX.).

In the sinuses a large but varying number are red, without a trace of yellow, with the Hansen stain. Usually the majority consist of red fibres, with some yellow about them. Many of these show as a red core with yellow borders. Often, however, the yellow is very irregular: it may be contained in the fork between two red fibres; it may extend for only part of the length of the fibre; it may be on only one side of it; and it may be either a very narrow yellow border or a wide and irregular cell body. In all the above there is a complete and continuous red fibre which takes the general direction of the beam without any undulations. In one or two preparations the fibres were all wavy. In addition to these beams with complete fibres there are some which show a fibre for only part of their length, and others which, instead of a fibre, show a number of indefinite dots and dashes of red. A few beams show two fibres side by side. There are also in the sinuses a few rare beams which are completely yellow, or protoplasmic. The nuclei lie in the protoplasm, and show no direct connection with the fibres.

In the germ centres fibres may be absent, and the whole reticulum be protoplasmic. As a rule a few fibres are present, thinner than those of the sinuses, and also many of the indefinite dots and dashes of red. These sometimes form a sort of feltwork in the plate-like beams. The circularly-disposed beams around the germ centres colour a decided red, with a small amount of yellow in parts.

In the ordinary parenchyma the condition is intermediate between that of the sinuses and the germ centres. Many beams are completely yellow, rare ones are entirely red. The majority show a red core with yellow margins, which are usually larger in proportion than the margins in the sinus beams. The plate-like beams frequently have fibres at their margins along one or more, or even all, of their sides; so that here we have plates of protoplasm supported by marginal fibres. The interior of these plates very frequently has no more than a few very indefinite slight dashes of red, and sometimes no red at all, but a few of them stain red throughout.

A further constituent of many reticulum beams is elastic tissue. This was pointed out by Henle (13), and Höhl (15). Retterer (27), Thomé (36), and Sisto and Morandi (32) have recently recalled attention to it. It is well shown by Weigert's resorcin-fuchsin method. It is seen on most cortical sinus beams as one fibre, or sometimes as two which branch and anastomose on the beam. In the parenchyma, and in many medullary sinuses, it is present in much smaller proportion, and may be entirely absent over considerable areas. It is commonest near the trabeculæ. The germ centres frequently show none, and at most only a few thin fibres. The circular beams around the germ centres often show them very markedly. Sometimes one, and more rarely two or three fibres together, pass through the cortical sinus, and run radially inwards through the cortical parenchyma, always upon beams. I have never seen groups of these radial fibres taking the place of trabeculæ, as Retterer described in the guinea-pig (27), except where the beams themselves have a trabecula-like arrangement, as I shall describe later. I have seen a few elastic fibres which cross the cortical sinus by themselves, without being united to any other beam tissue.

Variations in the reticulum at different ages have been described by Kölliker (20), His (14), Chievitz (4), Thomé (36), and Sisto and Morandi (32). I have studied this matter chiefly in the glands of cats. In the newborn the average width of the beams is greater than in the adult, and the reticulum nuclei are all either round or oval. In a cat about a quarter grown a few elongated nuclei are present. In the adult, though there are many thick beams and plates, there are more thin beams, and a still larger proportion of dark, elongated nuclei. With the Hansen stain the newborn cat shows a small proportion of fine red fibres which are found only in beams in the sinuses and ordinary parenchyma. The quarter-grown cat has already a few beams which consist entirely of fibres, and the germ centres have some slight red markings. At this age most of the plates stain yellow, with red fibres crossing them, or in their margins. The general distribution of fibres in the adult has already been described. Some of the plates, at this age, stain red throughout, though usually not so deeply as the fibres. Elastic tissue is rare in the reticulum of the newborn cat, but is certainly not absent, as Sisto and Morandi say it is, in that of the newborn infant. It occurs as thin fibres in a few of the peripheral sinus beams. Some of these fibres penetrate some distance into the cortical parenchyma. It increases in amount with age, and it spreads to the middle of the glands, appearing last in the germ centres. In the aged it is extremely plentiful throughout.

The foregoing description is given from the study of both undisturbed and washed sections. The latter gives, as I have said, valuable results when the progress of the washing is watched, and the observations are controlled by comparison with undisturbed sections. With washing, some of the purely protoplasmic beams are destroyed, most of the germ centres drop out bodily—no doubt owing to the poorness of their beams in fibres—the free cells of the parenchyma are removed very quickly, those in the narrow meshwork bordering on the sinuses being the last to go, and the nuclei of the reticulum are eventually removed, the large oval and round ones most readily.

I have described the sponge-like tissue chiefly from its appearance in washed sections. In undisturbed sections it is too closely connected with the free cells for any clear idea to be formed of it as a whole, especially as it must be studied in somewhat thick sections, because in thin ones most of the plates are cut down so as to look like cylindrical beams. But I have studied a sufficient number of these plates in undisturbed sections to be sure that my description applies to them also.

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DESCRIPTION OF FIGURES.

Pl. XV. fig. 1. Section, parallel to capsule, from gland of ox, showing the shape and distribution of the cortical trabeculæ, and the irregular distribution of the germ centres. The lymph spaces surrounding the latter are seen.

Objective 1″, Swift. Eyepiece A. A. Swift.

Pl. XV. fig. 2. Cortical trabecula, and parts of others, dissected from mesenteric gland of ox.

Objective 2″, Swift. Eyepiece A. Swift.

Pl. XVI. fig. 3. Washed section from gland of dog, showing ordinary fine reticulum. For comparison with figs. 4 and 5.

Objective $\frac{1}{5}$″, eyepiece C; both Swifts.

Pl. XVI. fig. 4. Washed section from gland of dog, taken from a neighbouring field of the same section as fig. 3, and with the same magnification. Shows the very thick beams, and in the lower left-hand corner an appearance as of perforated plate.

Objective $\frac{1}{5}$″, Swift. Eyepiece C. Swift.

Pl. XVII. Washed section from the gland of guinea-pig. Shows large plate-like beams forming a spongy tissue, and lower down the transition of this into fine reticulum. The magnification is lower than that of the two previous figures.

Objective $\frac{1}{5}$″, Swift. Eyepiece A. Swift.

Pl. XVIII. Reticulum nuclei, showing the various forms. A, from pig; B, from kitten; C, from badger. See note.

Objective $\frac{1}{12}$″, oil, Leitz. Eyepiece No. 4 Zeiss.

Pl. XIX. Beams with fibres and protoplasm, showing the various arrangements. A, from adult cat; B, from guinea-pig; C, from ox; D, from cat nearly adult. See note.

Objective D, Zeiss. Eyepiece 4 Zeiss.

N.B.—Plates XVIII. and XIX. were outlined with the aid of Zeiss' drawing camera. The outlines and proportions are therefore accurate; the details are approximations only.

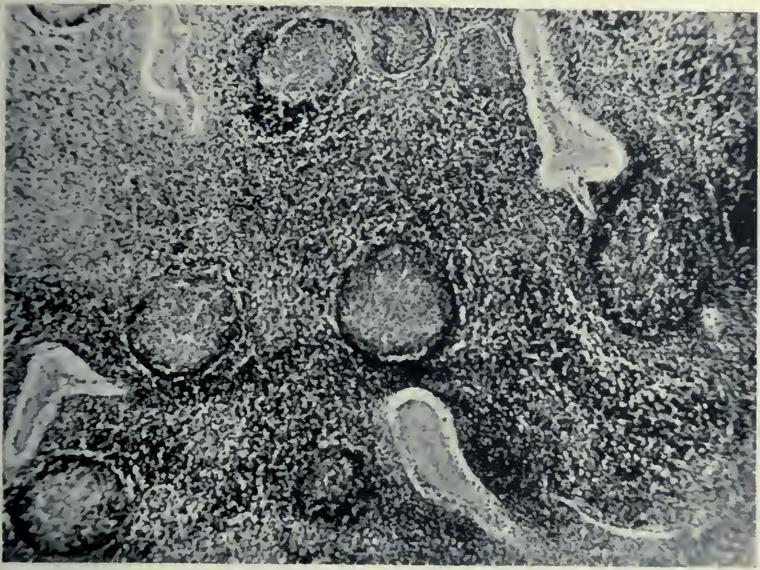

FIG. 1.

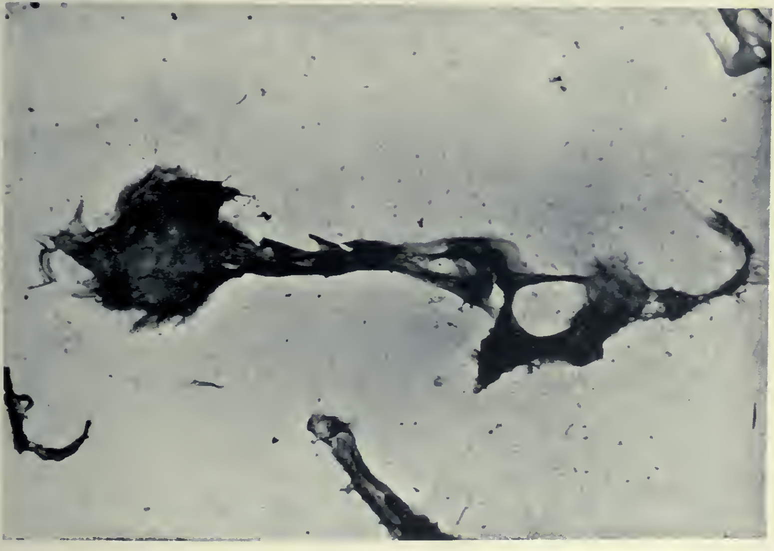

FIG. 2.

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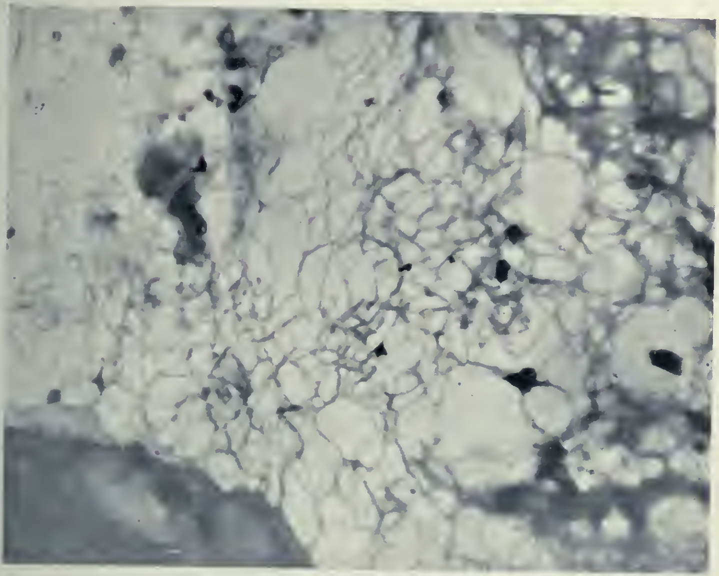

FIG. 3.

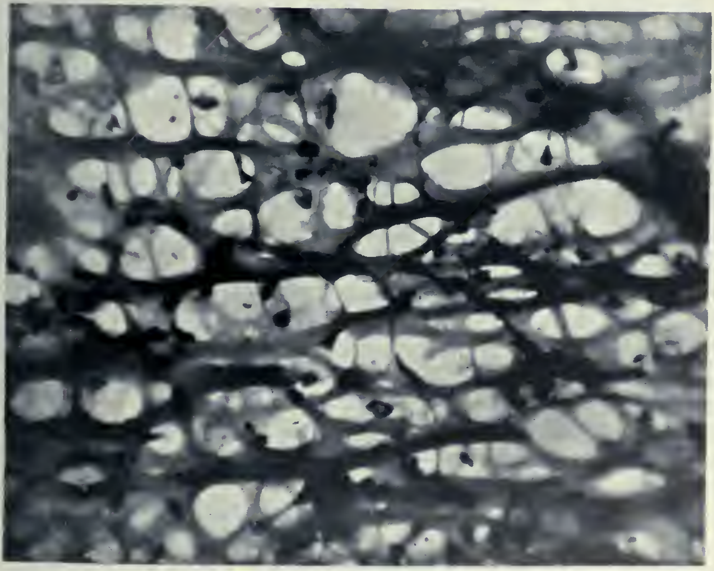

FIG. 4.

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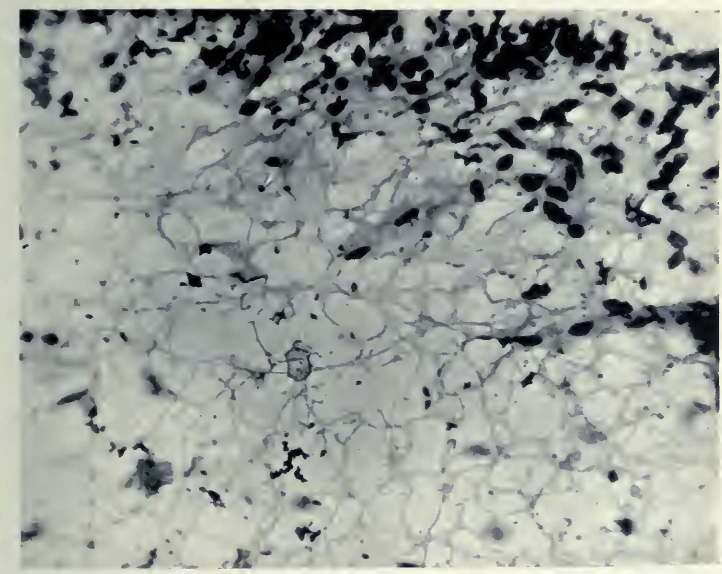

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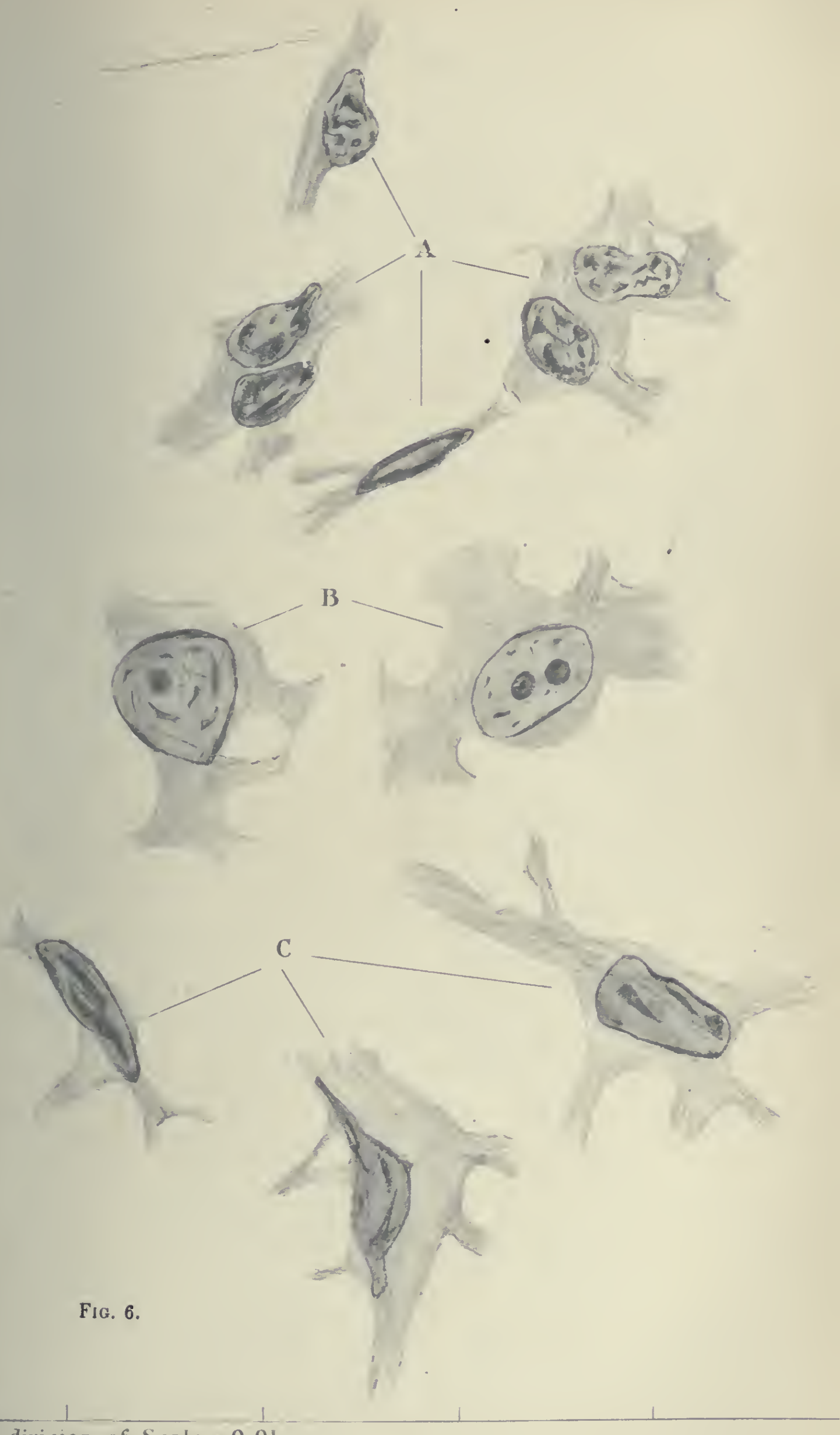

FIG. 6.

Each division of Scale = 0·01 mm.

FIG. 7.

ch division = 0·01 mm.

A HEART PRESENTING A SEPTUM ACROSS THE LEFT AURICLE.

By PETER POTTER, A.M., M.D., and S. WALTER RANSON, S.M. (*From the Anatomical Laboratory of the St. Louis University.*)

THE anomaly which we are about to describe occurred in the body of a healthy male negro, who died from asphyxia. The body is well formed and to all appearances normal. The heart shows no degenerative changes, and is normal in every way except for the presence of a septum across the left auricle. This septum divides the auricle into a right postero-superior chamber, receiving the five pulmonary veins, and a left antero-inferior chamber connecting with the auricular appendage and the left ventricle. Fig. 1 is taken from the upper surface of a horizontal section of the thorax through the articulation of the third costal cartilage with the sternum in front and the

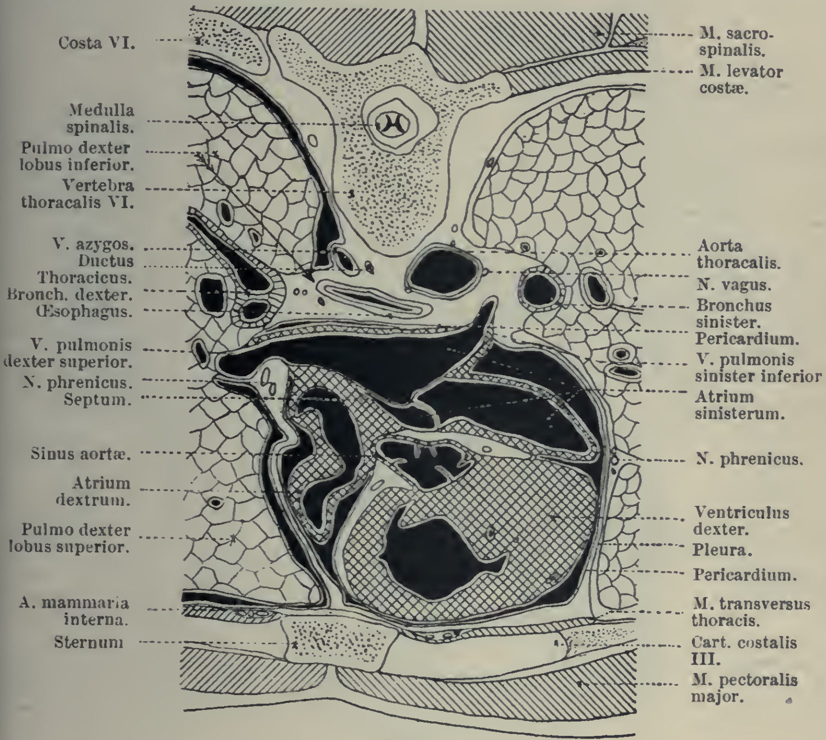

FIG. 1.

body of the sixth thoracic vertebra behind. The plane of the section is through the conus arteriosus of the right ventricle, the semilunar valves of the aorta, and the upper part of the auricles about 1 cm. below the opening of the superior vena cava. The left auricle forms the entire posterior portion of the heart. The right chamber of this auricle receives the left inferior pulmonary vein at its left end, and the right middle pulmonary vein at its right end. The septum is seen extending across the auricle from the interauricular septum anteriorly to the anterior margin of the left pulmonary vein posteriorly. The dotted line represents a branch of the septum, attached a little below the plane of this section to the anterior wall of the left chamber near its inner end, cutting off a small triangular space from the remainder of this cavity. Fig. 2 is taken

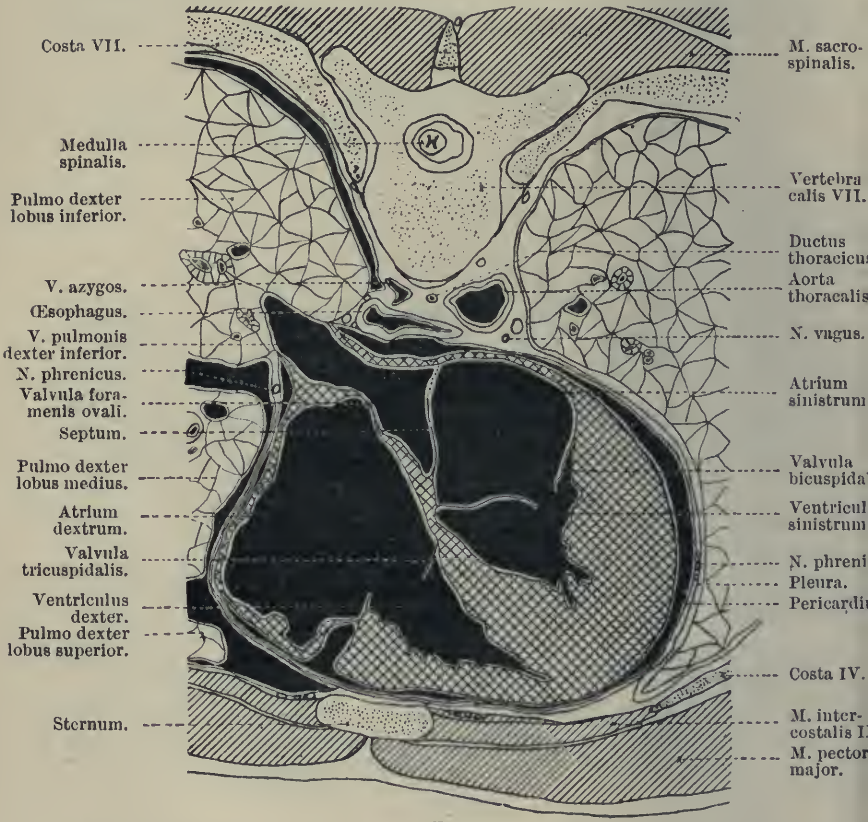

FIG. 2.

from the upper surface of a section through the third intercostal space in front and the body of the seventh thoracic vertebra behind. The plane of the section is through both auriculo-ventricular openings and the opening of the inferior right pulmonary vein, but below the left pulmonary veins. The septum extends backward from the anterior wall and ends in a free margin, which curves downward to become attached to the posterior wall 2 mm. below the plane of this section. The valve of the foramen ovale forms the middle third of the wall separating the right auricle from the right chamber of the left auricle. The muscular posterior wall of the right chamber is directly continuous with the musculature of the remainder of the auricle,

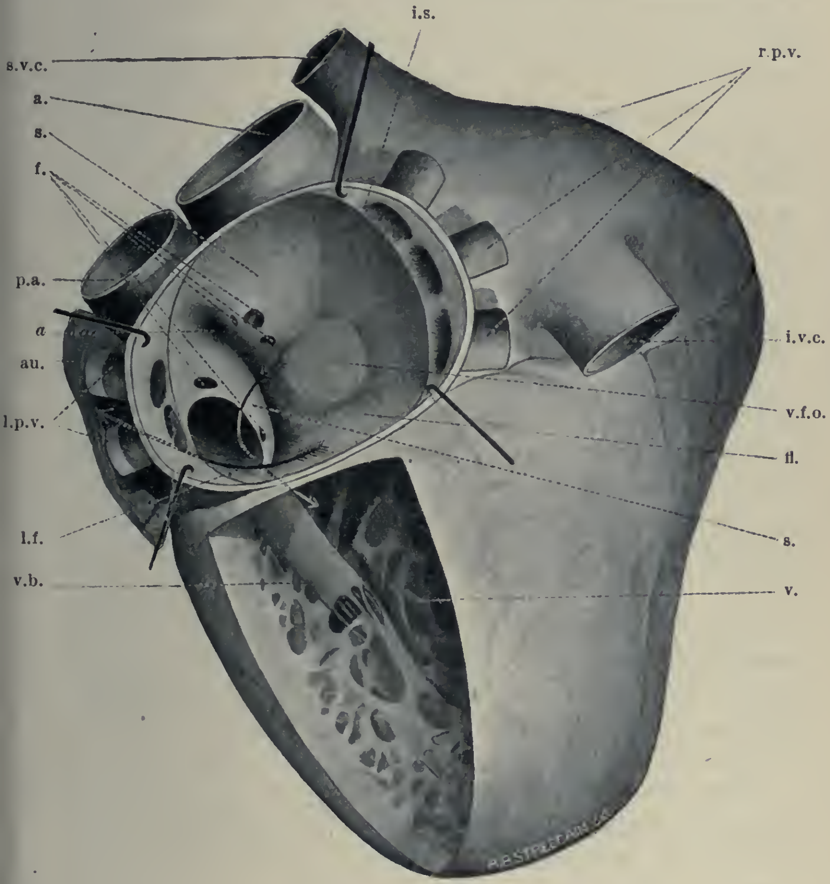

FIG. 3.

and is covered with pericardium. This same condition of the posterior wall is to be seen in fig. 1.

In order to give more clearly the position and shape of the septum, a reconstruction of the heart is shown in fig. 3. A portion of the posterior wall of the left heart is removed, and the interior of the right chamber of the left auricle is represented as viewed along the line of the arrow in fig. 1. The openings of the five pulmonary veins are seen on the reflected lateral walls. The right part of the farther wall is formed by the interauricular septum (*i. s.*), showing the membrane which completely closes the foramen ovale (*v. f. o.*). The remainder of the farther wall is formed by the septum (*s.*). The left chamber of the auricle lies beyond the septum, and communicates with the right chamber through six foramina in the septum (*f.* and *l. f.*). Of the two arrows which pass through the large foramen (*l. f.*) one follows the course of the blood downward through the auriculo-ventricular opening into the cavity of the left ventricle (*v.*), the other passes upward and to the left into the cavity of the auricular appendage (*au.*)

The septum is attached to the floor (*fl.*) of the auricle along the right posterior margin of the auriculo-ventricular opening. It passes directly up the anterior wall for about 2 cm., and bifurcates. The left limb continues vertically upward for nearly 1 cm., where it ends in the free margin shown in fig. 1 as a dotted line. The right limb, which forms the superior part of the septum, passes from the point of the bifurcation (*a*) downward and to the right as far as the left superior margin of the valve of the foramen ovale (*v. f. o.*), with which it is continuous.

From the foramen ovale it passes directly upward on the interauricular septum to the roof of the auricle, along which it is directed backward and to the left. It passes down the posterior wall along the anterior margin of the left pulmonary veins. From the lower margin of the inferior left pulmonary vein to within 5 mm. of the floor of the auricle the septum is deficient. This deficiency is due to the presence of the large foramen (*l. f.*) connecting the two chambers.

Of the six foramina which pierce the septum three are about 2 mm. in diameter, two others are about 6 mm. in diameter, the largest is about 20 mm. in the vertical and about 14 mm. in the horizontal diameter.

Henle[1] describes a small tubercle bearing an occasional semilunar valve-like process 6 mm. in breadth separating the openings of the pulmonary veins from the opening into the auricular appendage. From fig. 1 it will be seen that the septum is attached to the apex of this tubercle. That this septum is an overgrowth of the process he describes is very questionable.

Griffith[2] records a somewhat similar case, and refers briefly to four other cases which had come under his notice.

Two theories have been advanced to account for these cases. Martin[2] believes that his specimen is to be explained by the incomplete disappearance of the wall between the common sinus of the pulmonary veins and the left auricular cavity of the embryonic heart. In such a case one cavity must have been derived entirely from the common pulmonary sinus and the other entirely from the primitive auricle. This explanation fails entirely in the case under consideration, because the pulmonary veins open into a chamber, a part of the anterior wall of which is formed by the valve of the foramen ovale (fig. 2). This chamber must have been derived in part from the original auricle, since the foramen ovale develops within the primary interauricular septum.

Fowler[2] has offered the most plausible explanation of the condition. He believes it to be an overgrowth of the valve of the foramen ovale which is carried by the blood stream towards the auriculo-ventricular opening and becomes adherent to the walls by secondary attachments.

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[1] Henle, *Anatomy*, vol. iii., pl. 1, p. 42.

[2] *Journal of Anatomy and Physiology*, April 1903.

A STUDY OF THE ASTRAGALUS. By R. B. Seymour Sewell, B.A., *Christ's College, Cambridge, Fellow of the Anthropological Institute.* (Plates XX.–XXIII.)

Part III.

The Collum Tali.

Under this name, as we have seen in the first part of this paper, is included the more or less roughened region of bone lying between the corpus posteriorly and the smooth, rounded, articular surface of the caput anteriorly. In section, this portion of bone is more or less rhomboidal in shape, and we can distinguish four surfaces—viz., a superior, a lateral or external, an inferior, and an internal or medial.

Length.—As a measurement of the length of the collum tali, I have taken the distance between the middle point of the anterior border of the trochlear surface behind and the facies articularis navicularis in front, measured in a direction parallel with the outer border of the neck. This measurement I have found to vary very considerably in different bones. The average length of the neck was 15 mm., but in certain specimens it differed from this to a very considerable extent; in No. 741 it was as great as 24 mm., while in several other cases it only measured 11 mm.

As an index of the length of the collum, I have taken $\frac{\text{length of neck} \times 100.}{\text{length of bone}}$ (The total length of bone being taken as the distance between the floor of the sulcus musculi flexoris hallucis longi and the foremost point of the articular surface of the caput.) This, on the average, is found to be = 30, but the variations in the length of the neck, in specimens which possess the same maximum length measurement, give rise to very large differences in the values of this length-index, as will readily be seen from the following table:—

TABLE I.—*Showing Variations in the Length-Index of the Collum.*

No. of Bone.	Max Length of Bone.	Length of Neck.	Index.
514	45 mm.	11 mm.	24
431	45 ,,	16 ,,	36
446	50 mm.	11 mm.	22
327	50 ,,	.18 ,,	36
741	53 mm.	11 mm.	21
139	53 ,,	24 ,,	45

The length of the collum, in proportion to the maximum length of the bone, may differ in different races. Professor Havelock Charles notes that in the Punjabi the neck is much shortened in comparison with European bones (2). He does not, however, give any measurements, and I am inclined to think that this appearance is due mainly to the forward prolongation of the articular surfaces of the corpus.

The Superior Surface.—This surface is usually more or less rough. Both anteriorly and posteriorly it is sharply marked off by smooth articular surfaces, that in front being for the articulation of the scaphoid or navicular bone—the facies articularis navicularis—and that behind being the trochlear surface for the tibia. Externally the surface is marked off by a tubercular ridge from the lateral aspect, while internally it passes into the medial surface; occasionally all distinction into superior and medial regions is lost, and we get a continuous supero-internal surface, which is separated off from the external surface by the above-mentioned tubercular ridge, while inferiorly it ends abruptly at the border of the facies articularis calcanea media. This condition, however, seems to be of rare occurrence, and I have only found it in one specimen, No. 529.

Running parallel to the anterior border across the surface is a more or less well-marked ridge, which is continued internally on to the medial surface and may become continuous with the ridge which runs forwards on the internal aspect of the corpus from the anterior margin of the tuberculum mediale (9). In such cases we get a continuous ridge extending across the medial and superior aspects of the bone; such a condition, however, occurs in only 3 per cent. of the bones (Nos. 41, 65, 71, 82, 154, 160, 189, 193, 247, 257, 307, 319, 424, 349, 418, 419, 447, 452, 529, 569, 607, 733, 801, 913, 964, 971, 972).

This ridge has been noted by Professor A. Thomson in the astragali of the Australian and the Andamanese, and in these races he finds that its upper surface is "usually smooth and fits into a hollow on the inferior margin of the tibia" (10).

In the fresh state, the ridge serves as an attachment for the ligamenta talo-navicularia superficiale et profundum. As Barclay-Smith has pointed out (1), the superficial ligament arises from the outer and upper aspect of the neck, while the deep runs from the upper and inner aspect, the two sets of fibres crossing one another.

The vestigial ligamentum talo-metatarsale also gains an attachment to this ridge; as Keith has shown (6), this fibrous band, which runs from the astragalus to metatarsal 3, and also to some extent to 2 and 4, is well marked in the anthropoid apes, and can also be seen in the human fœtus, but becomes lost in adult life, owing to fusions taking place with other ligamentous bands.

The region of the neck lying in front of this ridge is usually smooth, so as to allow of free movement of the ligament, and is perforated by numerous small vascular foramina.

Externally, the ridge ends at the outer border of the neck, and occasionally its termination is marked by a rounded tubercle, situated somewhat towards the anterior end of the external border. Occasionally we come across a specimen in which the outer portion of the superior surface is produced upwards into a well-marked crest.

This condition was first described by Hyrtl (5), who gave to it the name of the *processus trochlearis* (fig. 21). It is situated at the point where the upper surface of the neck passes into the external surface, just posterior to the articular surface of the caput. In shape it is an oblong low protuberance, in which we can distinguish an anterior and a posterior surface.

The posterior surface, in the specimen which Hyrtl described, was saddle-shaped and covered with cartilage, and served as a groove in which the middle thick portion of the ligamentum talo-naviculare rested. In the specimens which I have examined, however, it was slightly convex in shape, and was more or less rough in character.

The anterior aspect is smooth and is slightly concave both from above downwards and from side to side; below, and to the inner side, this surface, in the great majority of cases, becomes continuous with the facies articularis navicularis.

The process is of infrequent occurrence: Hyrtl only obtained a single specimen. I have, however, found the condition occurring in 9 cases (Nos. 90, 185, 359, 529, 559, 585, 737, 774, 979).

I am inclined to regard this process as merely an abnormal development of the external portion of the ridge, which, as we have seen, runs across the upper aspect of the neck.

In a series of bones one can trace the gradual development of the small tubercle on the external border of the neck into, first, a low crest occupying the outer half of the superior surface, and continuous with the ridge internally, being separated from the articular surface of the caput by a smooth interval, and finally into a well-marked crest which completely obliterates the region of the neck in front of it.

The rest of the superior surface, that is, the part lying posterior to the ridge, between it and the facies articularis superior, is very vascular, and there are usually several large foramina situated along the anterior border of the articular surface.

Occasionally one comes across a specimen in which there is present a single very large vascular foramen, situated in the middle of the neck, which leads downwards into the substance of the bone; this condition seems to be of comparatively rare occurrence, and I have only found it in 13 specimens, which thus give us a percentage of 1·3. (The numbers of the specimens were as follows: 17, 29, 42, 50, 303, 353, 470, 583, 664, 709, 770, 869, 893.)

Facets on the Superior Surface.—As I have already pointed out (9), two articular surfaces are occasionally to be found on the upper surface of the collum tali, an internal and an external; when present, they articulate with corresponding facets on the anterior border of the distal extremity of the tibia during extreme dorsi-flexion of the ankle-joint.

Facies articularis interna colli tali.—This facet was first mentioned by Parker and Shattock (7), who found it present in a case of talipes equinus; but it was not until some years later that a careful account was given by Professor Havelock Charles of the occurrence of the facet in the Punjabi astragalus (2). The articular surface is usually of a quadrilateral shape, and is produced by a forward prolongation of the facies articularis superior corporis tali along the inner margin of the neck (Pl. XX. fig. 22).

It is convex from side to side, and slightly concave antero-posteriorly. Internally it becomes continuous with the forward prolongation of the facies malleolaris medialis. In no case have I found this facet to be present unaccompanied by such a forward prolongation.

With regard to the frequency of occurrence of this articular surface, this varies very considerably in different races.

In the Egyptians I have found it to be present in 189 specimens, or a percentage of 19 per cent., whereas in the Punjabi, out of 53 cases, Professor Havelock Charles found 25 examples of the facet, thus giving a percentage of 47·2 (2).

TABLE II.—*Giving Frequency of Occurrence of Internal Facet on Collum Tali in two of the Human Races and in the Anthropoid Apes.*

	No. of Bones examined.	Facet present.	Percentage.
Egyptian . . .	1006	189	19%
Punjabi . . . (Prof. Havelock Charles.)	53	25	47·2%
Gorilla	6	1	16·5%
Chimpanzee . . .	6	4	66·5%
Orang	15	13	86·5%

Professor A. Thomson also states that in the anthropoid apes, in some cases he found an extension forwards of the trochlear facet along the inner side of the neck, but in no instance did this articulate with a facet on the anterior margin of the inferior surface of the tibia (11).

I have also found this facet in the astragali of the anthropoid apes. It occurred most frequently in the orang.

Facies articularis externa colli tali.—On the external portion of the neck there is usually present a smooth tubercular ridge, which, in the position of extreme dorsi-flexion of the foot, fits into a hollow in the anterior margin of the distal or lower extremity of the tibia.

We may, however, find that its place is occupied by a definite articular surface, a corresponding facet being developed on the tibia, and between these two extremes we have all degrees of transition.

Professor Thomson, who was the first to describe this facet, distinguishes the following different conditions (10):—

1. Smoothing of the bone along the outer half of the upper margin of the neck.
2. The trochlear articular surface becomes insensibly blended with this smooth area.
3. The articular surface is well marked off: the facets may, however, differ in individual bones both in size and form.

In a well-developed specimen the articular surface presents a well-marked rounded anterior border, which separates it from the remaining non-articular portion of the neck; posteriorly we can recognise two conditions—in some cases the facet is separated off from the facies articularis superior corporis tali by a groove which runs horizontally across the articular surface (Pl. XXI. fig. 23), whereas in others there is no distinction between the two facets, the trochlear surface being continued forwards on to the neck.

The frequency of occurrence of this facet is found to vary very considerably in different races. In the Egyptian peoples I have found it to be present in 8·6 per cent. of the bones which I have examined—86 specimens in all. In the Punjabi, however, Professor Havelock Charles found it to be present in 34 cases out of 53, thus giving for this race a percentage of 64.

The facet occurs in the European race in very rare instances only; Professor Pfitzner only found a single specimen during the careful examination of 840 bones (8).

TABLE III.—*Giving the Frequency of Occurrence of the External Facet in some of the Human Races.*

	No. of Bones examined.	Facet present.	Percentage.
European . . (Pfitzner.)	840	1	...
Egyptian . .	1006	86	8·6%
Andaman . . (Thomson.)	29	16	55%
Punjabi . . (Havelock Charles.)	53	34	64%
Australian . . (Thomson.)	18	14	78%

(For particulars with regard to the occurrence of the facet in other races, I must refer the reader to Professor Thomson's papers in the *Journal of Anat. and Phys.*, vols. xxiii. and xxiv.)

Professor Thomson also states that he has found this facet to be present in the astragali of the anthropoid apes (10).

In one specimen, No. 751, the trochlear facet was prolonged forwards on to the neck not as two separate facets, but as one single large facet situated approximately in the middle line.

With regard to the frequency of occurrence of these facets and the factors concerned in their production, there can be no doubt that they occur much more frequently in those races which 'squat' on the ground, and are absent or occur only very rarely in races that do not possess this habit, as in the European races of the present day.

As Professor Havelock Charles points out, prehistoric man (Neolithic and Cave-dwellers) probably squatted on the ground, and hence seems to possess these facets (3).

In the case of the anthropoid apes, we have seen that the internal facet is present to a varying degree in the astragali of the different species. We must look for some reason, other than the above, to account for its presence in these animals.

According to Professor A. Thomson (10), it is probably due to the extreme dorsi-flexion of the ankle-joint during climbing, and hence is best developed in the Orang, which is acknowledged to be the most expert climber of all the anthropoids.

Another factor which we must consider is the size of the angle which the neck of the astragalus makes with the corpus in the vertical plane.

In the first part of this paper (9) we saw that in the European this angle possessed a much larger value than it did in the Egyptian. It is obvious that this must have a considerable importance, when we come to the question of the formation of facets on the neck of the astragalus; for there can be no doubt that facets would be much more likely to be formed in those bones which possessed a low value for this angle. That this is indeed the case is shown by a consideration of those bones which possess these facets: we have already seen that the average value for the angle between the collum and corpus, in the vertical plane, measures in the Egyptian astragalus 112°.

I have also measured this angle in those bones which have these facets, and I have found that in these cases the angle averages a value of only 110°.

This difference is certainly only slight, but the evidence becomes somewhat stronger when we come to consider the actual measurements. Thus, out of 72 bones examined, the angle was found to be less than 110° in 37 cases, thus:—

Value of Angle.	No. of Cases.
110°	2
109°	4
108°	5
107°	2
106°	7
105°	3
104°	5
103°	4
102°	...
101°	1
100°	2
98°	1
94°	1

Professor Havelock Charles points out that these facets are found in the Punjabi fœtus and infant, and he claims that we have here an example of the transmission of an acquired character. To quote his own words: "The facets are seen on the bones of the Punjabi infant or fœtus, and have been transmitted by the accumulation of peculiarities gained by habit in the evolution of its racial type, in which an acquisition having become a permanent possession, profitable to the individual under its conditions of life, is transmitted as a useful inheritance" (3).

Unfortunately for this view, however, it has been shown that these facets occur in the fœtus of the European, and probably in all other races, whether the facets are found to be present in the adult or not; and this is after all what one would expect to be the case, when one considers that during intra-uterine life the lower extremities of the fœtus are in the position most favourable for the formation of such articular surfaces, viz., one of extreme dorsi-flexion and inversion.

The External Surface.—This surface of the collum tali is the large, usually more or less quadrilateral area of bone which forms, in the natural condition of parts, the roof of the sinus tarsi.

It is markedly concave, and faces downwards, outwards, and slightly forwards.

Posteriorly, it is continuous with the narrow area of rough bone situated on the lateral surface of the corpus in front of the facies malleolaris externa.

Anteriorly, it is sharply defined by the smooth articular surface of the caput, while below and to the inner side this area of bone narrows somewhat abruptly, and becomes continuous with the roughened area of bone on the inferior aspect of the collum, which forms the roof of the sulcus interarticularis.

In a well-developed specimen, this surface of the bone presents somewhat anteriorly a roughened area, which is usually of a circular or oval shape.

This area, in the fresh condition, gives attachment to the ligamentum talo-calcaneum laterale. As we have already noted, we occasionally get a tubercle present on the external border of the neck, and when this is present it probably serves as an extra attachment for this ligament, for in almost all bones in which it occurs the area for the attachment of the ligament is continued on to the under surface of the tubercle.

In the fresh state the sinus tarsi is to a large extent occupied by the internal limb of the ligamentum fundeiforme: this band, as Barclay-Smith has shown (1), passes into the sinus behind the ligamentum talo-calcaneum laterale, and divides into an inner and an outer portion, the fibres of which spread out in a fan-like arrangement. The outer head passes downwards to be inserted into the os calcis, while the inner passes into the sulcus tarsi to gain an attachment to both bones.

The outer surface of the collum is usually rather vascular; several large foramina are frequently to be found in the groove between the rough area for the lig. talo-calcaneum laterale and the articular surface of the caput; several other large foramina are generally situated close to the point where the sinus tarsi runs into the interarticular sulcus.

In connection with this surface, a small ossicle is occasionally found.

Ossiculum in sinu tarsi.—This little ossicle was first described by Gruber (4). In the case which he records, the ossicle was situated in the sinus tarsi between the ligamentum talo-calcaneum and the ligamentum fundeiforme, but united with the periosteum of the collum tali by a short fibrous band. The ossicle was shaped like a somewhat compressed pyramid.

In size it measured 1·3 cm. in height, 1·4 cm. in the transverse direction at the base, and 1 cm. thick. Pfitzner (8) regards it as either a pseudo-sesamoid or a calcareous concretion.

In one specimen which I have examined, No. 351, there is present on the posterior wall of the sinus tarsi a small bony excrescence, which measured 1·5 cm. in length and ·7 cm. in breadth, the long axis being situated transversely.

I am inclined to regard this as an example of the ossiculum in sinu tarsi, which has become fused on to the posterior wall.

The Inferior Surface.—This aspect of the neck is subdivided into anterior articular and posterior non-articular portions.

The posterior part is occupied by a deep groove, the sulcus interarticularis, which in the natural position of parts forms the upper segment of the canalis tarsi. The sulcus varies very considerably in breadth in different specimens, and as we saw when we studied the corpus (9), it may be almost completely obliterated by the fusion of the facies articulares calcaneæ media et posterior.

Internally, the sulcus is shut off by the tubercular ridge which runs forwards from the anterior part of the tuberculum mediale to the facies articularis calcanea media, and serves as the dividing line between the inferior and mesial aspects of the neck (Pl. XXII. fig. 25).

In a well-developed bone, running forwards and outwards from this ridge, is another smaller ridge of bone, which divides the inner end of the sulcus interarticularis into two arms, an anterior and a posterior: this varies to a very great extent in its degree of development; in a large number of cases it is entirely absent, while in a few specimens (5 per cent.) it is, as we have already noted, largely developed, and bears a special facet for the calcaneum, the facies articularis accessoria inferior (9).

In the fresh state the sulcus is occupied almost entirely by ligaments: of these, two—the ligamentum interosseum and the ligamentum fundeiforme—are attached to this ridge; the latter ligament is, however, chiefly inserted into the os calcis.

Situated near the junction of the sinus tarsi and the sulcus interarticularis, and somewhat posteriorly, an elongated roughened area is usually to be recognised. This serves as an attachment for the ligamentum talo-calcaneum anterius, which is merely a thickened part of the capsule of the articulatio talo-calcanea posterior.

The roof of the sulcus tarsi is perforated by a number of vascular holes, which are usually arranged in two sets—an anterior, lying along the posterior border of the facies articularis calcanea media, and a posterior, along the anterior border of the facies articularis calcanea posterior.

The *anterior* part of the inferior surface of the collum is, as we have already mentioned, articular in nature, and is completely occupied by the facies articularis calcanea media.

Facies articularis calcanea media.—This facet is usually of an elliptical or rounded shape, being slightly concave in curvature antero-posteriorly, and flat or very slightly convex from side to side.

Posteriorly, it is usually marked off from the forward prolongation of the tuberculum mediale by a shallow groove, which externally becomes continuous with the sulcus interarticularis: in front, the articular surface passes continuously into the surface of the caput. The facet, however, is marked off from the facies articularis calcanea anterior and the articulation for the ligamentum calcaneo-navicularis by a low and usually not very distinct ridge; occasionally, however, this is of considerable prominence, the two articulatory surfaces on either side meeting at a considerable angle.

In several specimens the facet is separated from the articular surface of the caput by a notch which may be continuous with either the internal or external surface of the collum, and in a few cases there was a continuous groove bounding the facet in front and connecting the two lateral surfaces.

The facet presents numerous variations, which we may class as follows:—

1. Variations in size and shape.
2. Fusion with neighbouring facets.
3. Subdivision into two facets.

Variations in Size and Shape.—As we have already mentioned, the facet is usually of an elliptical shape, but it may occasionally be circular or even pyriform in outline, while in size it varies very considerably in different bones.

No. of Bone.	Total Length.	Greatest Length of Facet.	Greatest Breadth of Facet.
259	5·5	22 mm.	20 mm.
877	5·5	13 mm.	11 mm

Fusion with Neighbouring Facets.—The most common form of fusion is with the facies articularis calcanea anterior. This condition is found to occur in about 9 per cent. of the bones, and when present it gives rise to a single long facet, which reaches from the caput to the sulcus interarticularis. We also frequently find that the facet is prolonged backwards along the ridge towards the tuberculum mediale (Pl. XXII. fig. 26); as we have already noted, when this ridge is well developed we may get a special facet formed on it, the facies articularis calcanea accessoria. We must therefore regard this posterior prolongation of the facies articularis calcanea media as being produced by the fusion of these two facets; hence in such a condition we must recognise a pars propria in front and a pars accessoria behind. A similar condition is also found in the case of the facies articularis calcanea posterior, and in extreme cases we get a single long articular surface extending from the caput to the inferior aspect of the corpus tali.

We have also already pointed out that the facies articulares calcaneæ media et posterior may fuse directly and obliterate the sulcus interarticularis.

Subdivision in Two Facets.—This condition seems to be of rare occurrence, and I have only found it existing in a single specimen, No. 359.

In this bone the facet was replaced by two articular surfaces, separated from each other by a distinct ridge (Pl. XXIII. fig. 27). At first sight one is apt to mistake the most posterior of these facets for a facies articularis accessoria inferior, but on a careful examination the facet is seen to lie entirely in front of the anterior arm of the sulcus interarticularis, and one must therefore regard it as part of the facies articularis calcanea media which has become subdivided.

The Internal Surface.—This aspect of the neck comprises the rough non-articular area on the medial surface of the astragalus which is bounded anteriorly by the smooth articular surface of the caput and posteriorly by the facies malleolaris medialis; below this it becomes continuous with the non-articular portion of the internal aspect of the corpus. In the natural position of the bone the surface looks not only medialwards, but also to a slight extent upwards and backwards.

The breadth of this area is found to vary very considerably in different specimens; this is due chiefly to the variable length which the neck possesses, and to the variations in the extent to which the facies malleolaris medialis is prolonged forwards.

The articular surface of the caput is also in some specimens prolonged posteriorly, thus still further reducing the breadth, and in one case, No. 767, these two facets met, thus mainly obliterating the internal surface.

Inferiorly, the surface ends abruptly at the border of the facies articularis calcanea media; superiorly, however, it passes almost indefinably into the superior surface of the collum, and in rare cases, as we have already seen, all distinction into superior and medial surfaces is lost, and we get a continuous supero-internal surface.

In well-developed bones, we find that the ridge on the superior surface, which gives attachment to the ligamenta talo-navicularia, is continued on to the medial aspect for a variable distance: in the majority of cases it runs downwards and backwards to the border of the facies malleolaris, where it is lost, but in a few cases it becomes continuous with the ridge which runs forwards from the tuberculum mediale on the medial aspect of the corpus.

One occasionally finds that on this aspect of the neck there is developed a special facet: when present, it is caused by the articulation with the astragalus of a small ossicle, the *tibiale externum.*

The facet varies very considerably; it is usually situated near the lower border of the surface, and according to Pfitzner (8) is generally completely separate. In the specimens which I have examined, however, the articular surface was continuous with the smooth caput, being merely marked off from the articular surface for the tendon of the tibialis posticus muscle by a low ridge (Pl. XXIII. fig. 28).

It is of infrequent occurrence, and I have only succeeded in finding it in two specimens, Nos. 20 and 264.

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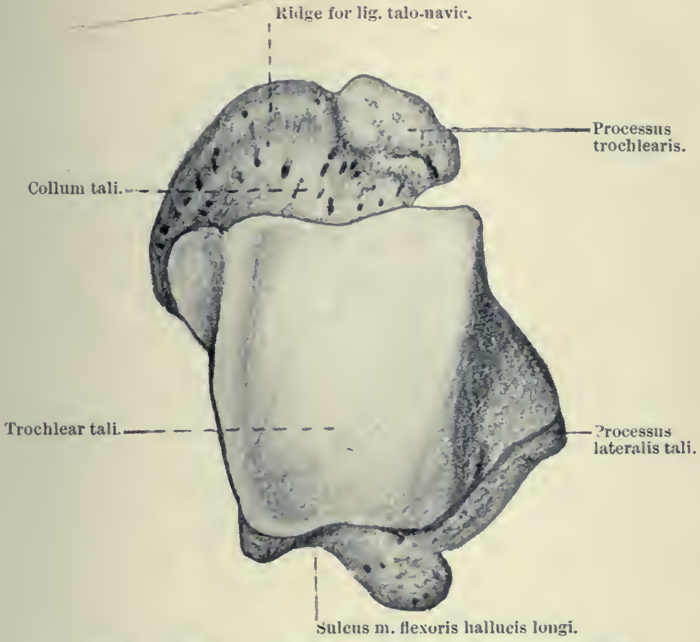

FIG. 21.—Norma verticalis—showing a processus trochlearis on the collum. No. 979.

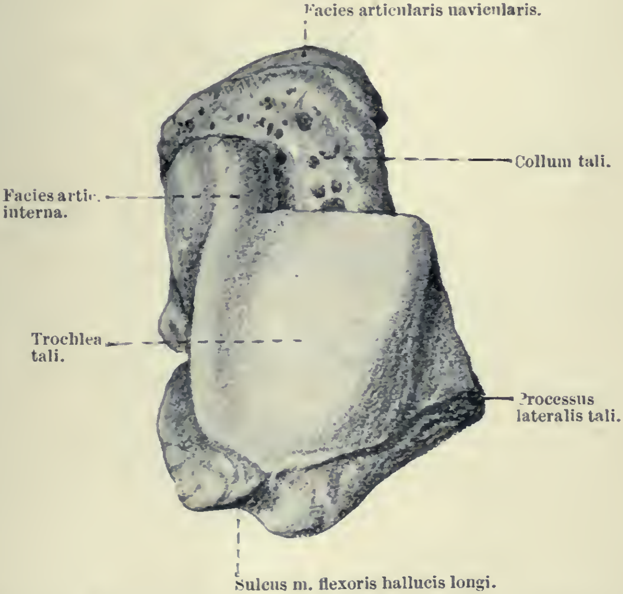

FIG. 22.—Norma verticalis—showing facies articularis interna on the superior surface of the collum. No. 619.

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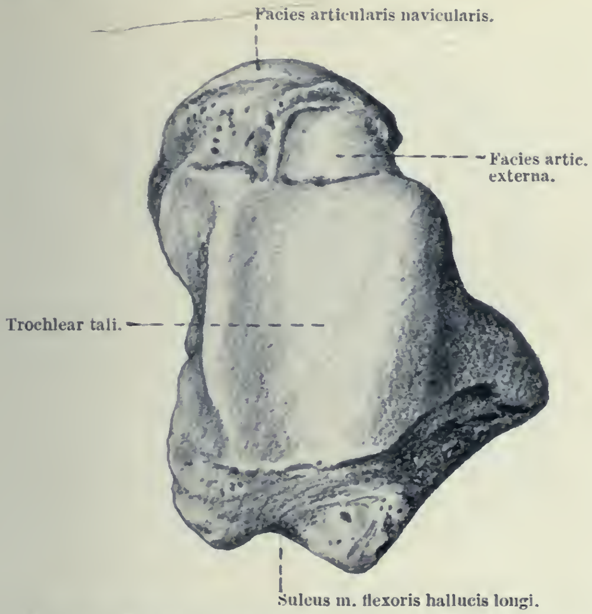

FIG. 23.—Norma verticalis—showing facies articularis externa on the superior surface of the collum. No. 362.

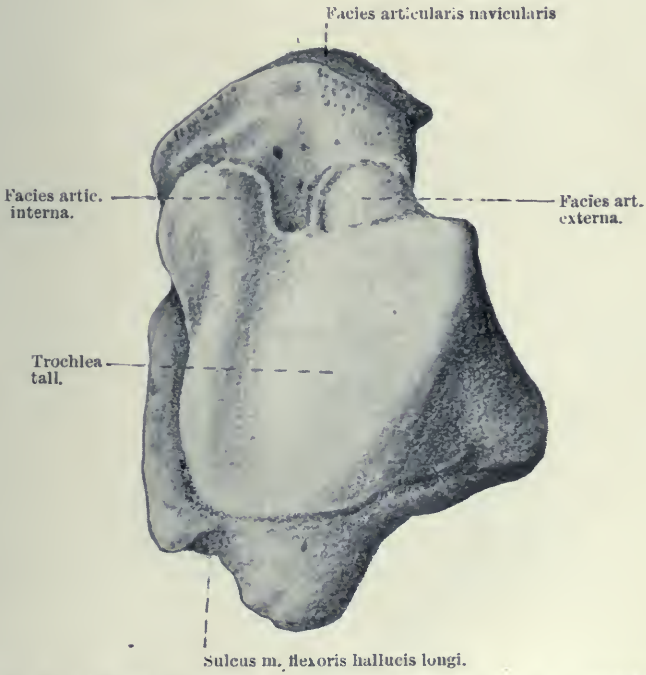

FIG. 24.—Norma verticalis—showing both facies articularis, interna and externa, on the superior surface of the collum. No. 732.

MR R. B. SEYMOUR SEWELL.

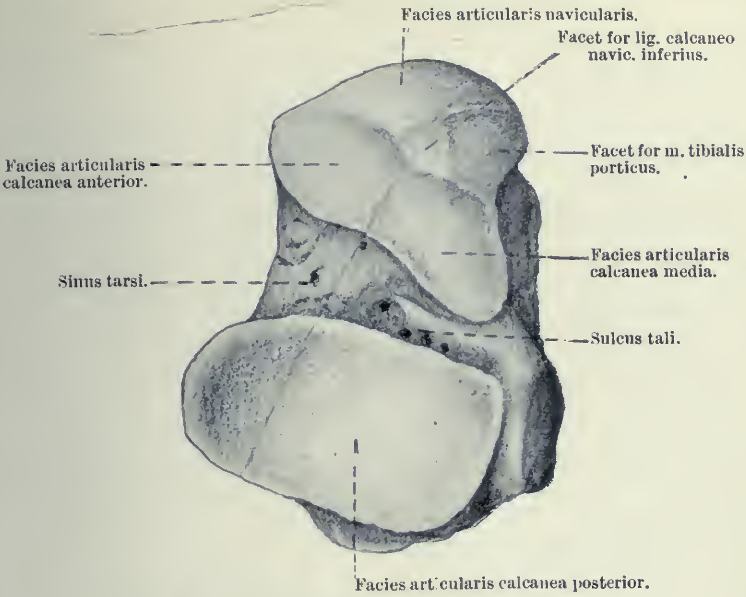

FIG. 25.—Norma basilaris—normal bone. No. 751.

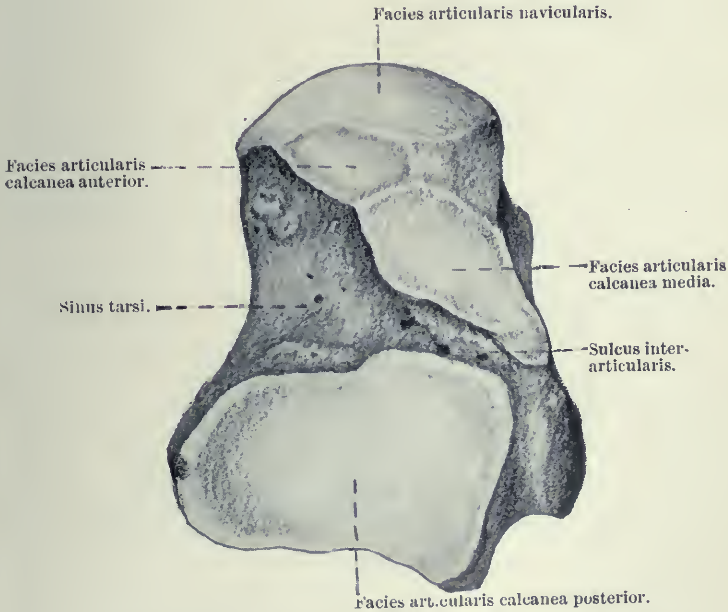

FIG. 26.—Norma basilaris—showing backward prolongation of facies articularis calcanea media. No. 794.

MR R. B. SEYMOUR SEWELL.

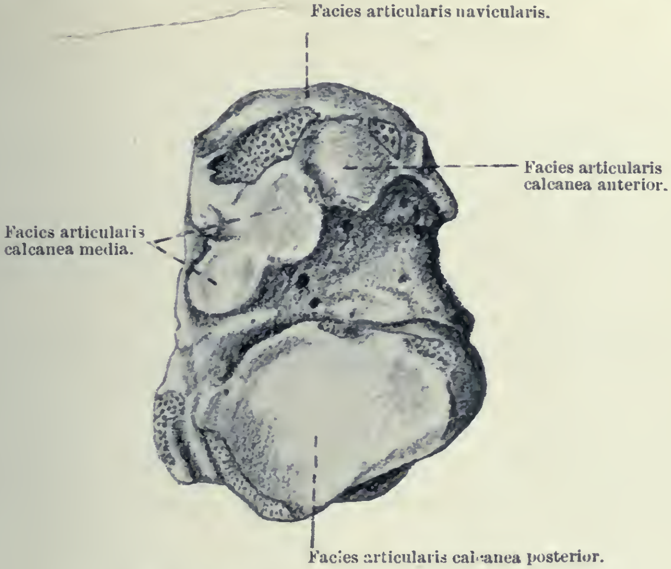

FIG. 27.—Norma basilaris—showing subdivision of the facies articularis calcanea media. No. 359.

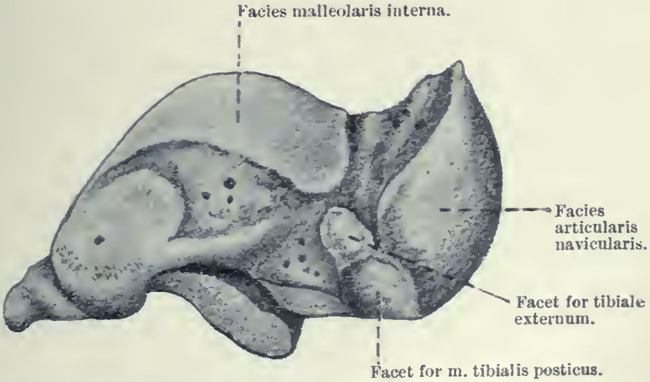

FIG. 28.—Norma medialis—showing facet for the ossicle, tibiale externum. No. 264.

MR R. B. SEYMOUR SEWELL.

AN ŒSOPHAGEAL POUCH WITH ABSENCE OF SIGNS OF ANY PATHOLOGICAL CAUSE.

By S. E. DENYER, C.M.G., M.D. (Cantab.), *Demonstrator of Anatomy, Cambridge University Medical School.*

THIS was observed in a male subject, of age unknown, but probably over 60 years, in the dissecting-room at Cambridge University.

The pouch is situated in the antero-lateral wall of the œsophagus on the left side, the upper end of the pouch being placed 47 mm. below the lower border of the posterior surface of the cricoid cartilage.

Measurements of the pouch.

Longitudinal vertical measurement	17 mm.
Transverse measurement	3·5 mm.
Depth of pouch	5 mm.

Relations of the pouch.

The pouch, the opening of which is sharply defined, lies entirely on the left side of the trachea. The posterior ends of the 6th, 7th, and 8th cartilaginous rings of the trachea form the edge of its inner boundary. Small diverticula run off from both upper and lower extremities of the pouch, so that it might be described as anvil-shaped.

It is situated at the convexity of the first curve the œsophagus makes to the left. It involves all the coats. A well-defined ridge in the interior of the œsophagus marks its lower boundary, the lower diverticulum of the pouch being prolonged 5 mm. below this.

The left recurrent laryngeal nerve runs between the anterior edge of the pouch and the trachea, while anteriorly and rather to its inner side lies the left subclavian artery, the lower part of which is in close relation to the pouch.

There are no adhesions, nor are there any signs of inflammation present in the neighbourhood of the pouch.

ON THE MORPHOLOGY OF THE HUMAN INTERTRANSVERSE MUSCLES.

By J. Dunlop Lickley, M.B., Ch.B., *Senior Demonstrator of Anatomy, Victoria University, Manchester.*

In the vertebrate series, from Amphibia upwards, small bands—generally muscular but sometimes fibrous—extend between the transverse processes of adjacent vertebræ. These bands vary in their arrangements and relationships not only in the different classes, but often in the separate regions of any individual form; yet they are generally described, from their position, as intertransverse muscles—a term which is therefore purely of descriptive importance, and has no morphological value.

In the following paper an attempt is made to indicate the homologies which exist between these muscles, with special reference to their arrangement in the human subject.

Dissections of the muscles and their relations to the spinal nerves have been made in members of the following groups:—

1. Amphibia—Anura.
2. Reptilia—Crocodilia.
3. Mammalia—Marsupialia, rodentia, insectivora, carnivora, cheiroptera, primates, and man.

Part I.—Descriptive.

I. In the frog the intertransversales are small, single, muscular bands extending between every two adjacent transverse processes. In each segment, the spinal nerve, after its exit from the intervertebral foramen, splits on the mesial border of the intertransverse muscle. The anterior primary division passes outwards along the ventral aspect of the muscle, while the posterior primary division passes directly backwards to the dorsal region. Under the extensor dorsi communis this posterior division divides into its internal and external branches.

The intertransverse muscles are supplied by the anterior primary divisions of the spinal nerves.

II. In the crocodile the muscles differ somewhat in the three regions. In the cervical region the muscles in each intertransverse space are paired. A ventral muscle has its attachments to the adjacent ventral roots—a dorsal, to the adjacent dorsal roots of the transverse processes.

In the dorsal region, throughout its whole extent, a set of distinct muscular bands is present—a single muscle being attached to the postaxial border of the transverse process of one vertebra, and to the preaxial border of the transverse process of the succeeding vertebra. In the lumbar region this arrangement is continued, a single muscle occupying each intertransverse space.

In the crocodile a considerable differentiation has taken place in the deep muscles of the back. A set of small muscular slips, readily defined in each region, is found extending between the articular processes. These slips, which may be called the interarticulares, are attached in front to the inferior articular processes of one vertebra, and behind to the superior articular processes of the postaxial vertebra.

In the cervical region, the spinal nerve divides at the mesial margin of the dorsal intertransverse muscle—its posterior primary division passing dorsalwards, its anterior running outwards between the two intertransversales. In the dorsal and lumbar regions, the nerve splits on the mesial border of the single intertransverse muscle—its posterior primary division again passing dorsalwards, while its anterior division courses outwards on the ventral aspect of the muscle. In all three regions the posterior primary division divides into its internal and external branches on the interarticular muscle.

The intertransversales are supplied by the anterior primary divisions—the interarticulares by the posterior primary divisions of the spinal nerves.

III. In mammals the arrangement of the intertransverse muscles is very similar in the various groups. In all mammals, the intertransverse muscles of the dorsal region—except in the case of the last one or two intertransverse spaces—are replaced by bands of fibrous tissue, more or less defined. The presence of muscular tissue in the last spaces seems to be related to the type of vertebra present. From a consideration of the articular processes in the vertebrata it is evident that, in mammals, the primitive form is most closely adhered to in the lumbar region (1). In man, the change from the lumbar to the dorsal type occurs between the last two dorsal segments, the 12th dorsal vertebra being the last to retain the lumbar type. In some of the lower mammals the change is a more gradual one, involving the last two or three dorsal vertebræ; and in these cases, muscles occupy the last intertransverse spaces.

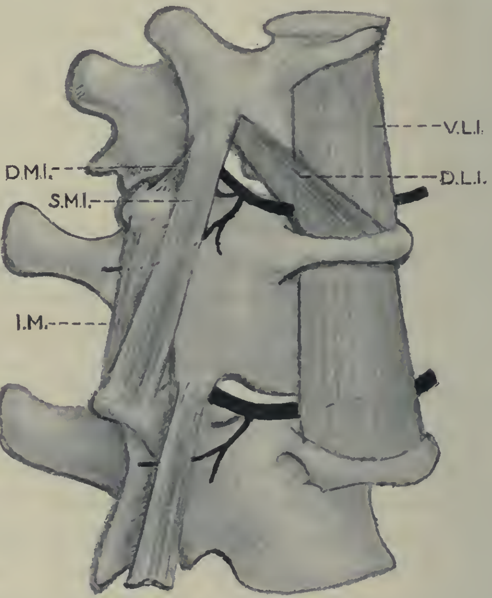

Diagram showing the relations of the spinal nerves to the inter-transverse muscles in the lumbar region of the kangaroo. In the lower space the dorsal slip of the lateral inter-transverse muscle has been removed. The processes have been separated a little beyond normal in order to show more clearly the individual muscular slips.

V.L.I. = ventral band of lat. inter-trans.
D.L.I. = dorsal band of lat. inter-trans.
D.M.I. = deep portion of mesial inter-trans.
S.M.I. = superficial portion of mesial inter-trans.
I.M. = inter-mammillary.

In forms such as the kangaroo, the arrangement of the muscles can be very clearly demonstrated on account of the prominence of the mammillary and accessory processes in the lower dorsal and lumbar regions.

As the muscles do not, however, differ essentially from those of man, it will be better for the purposes of this paper to note briefly their chief characteristics in the human subject.

Cervical region. — In each segment two intertransverse muscles are present on each side—one anterior, the other posterior, attached respectively to the anterior and posterior tubercles of the transverse processes.

Dorsal region.—Intertransverse muscles are in this region replaced by single feebly marked fibrous bands, although in the lowest spaces on each side small muscular slips may be present.

Lumbar region.—As in the cervical region, two muscles are present in each intertransverse space, but their relationship is different. A lateral muscle extends from the inferior border of the transverse process of one vertebra to the superior border of the transverse process below, while a mesial muscle runs from the accessory process of one vertebra to the mammillary process of the vertebra below.

The lateral intertransverse muscle may be further split up into two portions: (1) a ventral portion attached to the adjacent borders of the transverse processes, and (2) a dorsal portion which extends from the accessory process of one vertebra to the upper border of the transverse process of the vertebra below. In the kangaroo, where the muscles are well developed, the mesial intertransverse muscle may be differentiated into three bands: (1) a small slip extending across between the accessory process of one vertebra and the mammillary process of the succeeding vertebra; (2) a larger portion lying superficial to this slip rising from the accessory process of one vertebra, passing across the succeeding vertebra, and gaining an attachment to the mammillary process of the next vertebra; (3) a muscular band extending between the mammillary processes of adjacent vertebræ. The accessory processes are joined to one another by fibrous bands.

In the cervical region the spinal nerve divides on the mesial border of the posterior intertransverse muscle. Its anterior division passes outwards between the two intertransversales. Its posterior division passes backwards and divides under the deep muscles of the neck into internal and external branches.

It may be noticed that, in the case of the rectus capitis lateralis, the anterior primary division of the first spinal nerve passes through the bundles of the muscle.

In the dorsal region, the spinal nerve undergoes division close to the posterior border of the external intercostal muscle—its anterior primary division passing outwards along the ventral aspect of that muscle. The posterior primary division splits on the intertransverse band into internal and external branches.

In the lumbar region, the spinal nerve divides into its anterior and posterior primary divisions on the mesial border of the lateral intertransverse muscle. The posterior primary division divides into its internal and external branches, and of these a branch from the internal pierces or passes round the deep surface of the mesial intertransverse muscle.

The chief differences observed in the mammals dissected were related to this splitting of the posterior primary division. With the modifications of the dorsal muscles, the branches of supply have in some cases become enlarged, and the regular arrangement is not preserved in the lumbar region. Large muscular branches are given off from the internal division before it passes round the deep aspect of the mesial intertransverse muscle. One branch, however, is constantly found in this typical position.

The two intertransverse muscles in the cervical region and the lateral intertransverse in the lumbar region are supplied by the anterior primary divisions – the lumbar mesial intertransverse muscles by the posterior primary divisions of the spinal nerves.

PART II.—MORPHOLOGICAL.

In dealing with the morphology of the intertransverse muscles it is necessary, in the first place, to consider the homologies of the points of attachment of the muscular slips. It has been pointed out by Cleland (2) that the transverse processes and rib arches are continuous parts of a primary costal circle.

Albrecht (3) distinguishes between the two portions—the transverse processes lying between the protovertebræ, the ribs between the myocommata; but he acknowledges their intimate relationship under the term "homotropie." This differentiation is a superficial one of considerable descriptive value, but the important fact to recognise is, that the transverse processes and ribs are morphologically continuous structures, forming with the vertebræ in typical segments complete arches. The adjacent borders of successive arches are joined by muscular bands, which belong to the ventrolateral group of muscles, and receive their nerve supply from the anterior primary divisions of the spinal nerves.

In the lowest forms, the transverse processes are simple, and are described as purely "costal" processes. In the higher forms, special small tubercles are developed on the transverse processes, in relation with the differentiation of the dorsal musculature. These are described as "muscle" processes to distinguish them from the "costal" processes, and they are associated with the axial group of muscles which receive their nerve supply from the posterior primary divisions of the spinal nerves.

The articular processes bear a varying relationship to the transverse processes, with which, however, they are always intimately associated. In some cases the articular pillar is a compound of the articular processes and part of the costal process, so that the muscle processes may be found in connection with either the apparent transverse or apparent articular processes. This close relationship of the articular costal and muscle processes has an important bearing on the relations of the muscles associated with them.

In the complete arch of the thoracic region of the crocodile, the simplest arrangement of the intertransverse muscles is present. The ventrolateral musculature is represented by—

(1) The external intercostals, continued dorsalwards into the intertransverse muscles — merely a thin fibrous band between the tips of the transverse processes marking the separation.

(2) The internal intercostals and their continuation dorsalwards into a fibrous membrane.

(3) The group of extracostal muscles—lev. costarum, subcost., etc.

The axial group of muscles is represented in the interarticulares.

In the lumbar region, the transverse processes contain both the costal process proper and part of the rib arch. Only the single external intercostal sheet of muscle is here retained, forming a single intertransverse muscle which is homologous with the fused intertransverse and external intercostal muscles of the dorsal region.

In the cervical region, the transverse process is again composite. Its ventral root is part of the rib arch, while the dorsal root is made up partly of the costal process and partly of the rib arch. The dorsally placed intertransverse muscle is therefore similar to the intertransverse muscle in the lumbar region, while the ventral represents the internal intercostal muscle.

In the case of the frog, each transverse process consists partly of costal process and partly of rib arch. The single muscular slip present in each intertransverse space is, from its relations to the spinal nerve, representative of the outer layer of the ventrolateral musculature, *i.e.*, it consists of inseparable intertransverse and external intercostal muscles. In the frog the axial musculature is very simple, and there are no defined interarticular muscles present.

In man, as in most mammals, the arrangement of the intertransverse muscles is rendered somewhat complex by the modifications in the position of the muscle processes.

In the lumbar region, the muscle processes are distinct as: (1) the mammillary process connected with the superior articular process, and (2) the accessory process at the root of the transverse process. The muscles extending between these—mesial intertransversales—belong to the axial musculature, and, from their relations to the posterior primary divisions of the spinal nerves, are comparable with the interarticulares of the crocodile. The lateral intertransversales of this region are again formed of the continuous intertransverse and external intercostal muscles.

In the dorsal region—as Bruce Young (4) and others (5) have shown—it may be deduced from other muscular attachments that the accessory processes are carried out towards the tips of the costal processes, while the mammillary processes remain at their roots. With this translation of the processes a corresponding translation of the associated muscles has taken place. The change has been accompanied by a degenerative one in the muscle fibres, so that the original interarticular muscles are replaced by bands of fibrous tissue, which, however, retain their relationship with the posterior primary divisions of the spinal nerves. Intertransverse muscles as distinct structures are absent.

In the cervical region, both muscle processes have been transferred to the articular pillars, but I have been unable to define any muscular tissue related to them in this region. The transverse processes have similar homologies to those in the crocodile, and the intertransverse muscles—anterior and posterior—are therefore homologous respectively with the internal and external intercostal muscles of the dorsal region.

The homologies of the muscles in man may be thus summarised :—

Cervical region :—
Anterior intertransversales = internal intercostals.
Posterior do. = external do.
Dorsal region :—
Intertransverse bands = interarticulares.
Lumbar region :—
Mesial intertransversales = interarticulares.
Lateral do. = external intercostals.

Muller (5) suggested that the posterior intertransverse muscles were similar to the mesial intertransverse muscles of the lumbar region and to the dorsal intertransverse muscles. Bruce Young, in criticising this statement, gives the following as the arrangement of the muscles :—

Cervical region :—
Anterior intertransversales = internal intercostals.
Posterior do. = levatores costarum.
Lumbar region :—
Mesial intertransversales = thoracic intertransversales.
Lateral do. = levatores costarum.

Sutton holds the view that the levatores costarum of the lumbar region are represented by a set of radiating fibrous bands passing out from the tips of the transverse processes into the middle lamella of the lumbar aponeuroses. It seems possible that the levatores costarum may be included in the posterior intertransverse muscles of the cervical region, although they cannot be separated. In the lumbar region, however, they must be referred to the dorsal slips of the lateral intertransverse muscles previously noted. Both Müller and Young are agreed as to the homologies of the dorsal intertransverse bands and the mesial lumbar intertransverse muscles, although they have not traced their origin from an original interarticular muscle.

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(2) Cleland, *Nat. Hist. Review*, 1863.

(3) Albrecht, *Sur les copulæ intercostoidales et les hémisternoides du sacrum des mammifères*, Bruxelles, 1883.

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(6) Sutton, *Ligaments, their Nature and Morphology*, 1902.

THE MAMMALIAN CEREBELLUM: ITS LOBES AND FISSURES.

By O. CHARNOCK BRADLEY, M.B., F.R.S.E., *Royal Veterinary College, Edinburgh; Goodsir Fellow, University of Edinburgh.* (PLATES XXIV.–XXVIII.)

PART II.

The Cerebellum in Primates.

THE brains of *Hapale jacchus*, *Nyctipithecus trivirgatus*, *Cebus capucinus*, *Lagothrix humboldti*, *Ateles ater*, *Macacus rhesus* (two specimens), *Cynopithecus niger*, and *Cercocebus fuliginosus* have been examined. The description of the cerebella of the first two had better be given separately, as they differ in many respects from those of the remaining monkeys. The other specimens will be described together, since they do not differ sufficiently widely to justify individual consideration.

Hapale jacchus (Pl. XXIV. figs. 48, 49, 50 and 51).—At the very first glance, one is struck with the remarkable simplicity of this cerebellum. It is certainly not a simplicity of so severe a type as that met with in some other small mammals, but it is sufficiently pronounced to call for remark. Paramedian sulci are exceedingly faint in lobes A, B and C. In the remaining lobes they are easily recognisable, but not deep. The number of folia in the vermis is small enough to allow one to speak of the different lobes as being composed of a certain number.

Fissure I. is very easily recognised in mesial sections. Its depth is about as great as that of any other fissure with the exception of II. Lobe A consists of five folia, three of which go to lobule A_1, the remaining two to A_2. Fissure *c* is undoubted. It is difficult to say if lobe A assists in the formation of the hemisphere, owing to the doubtful character of the paramedian sulcus at this point.

Fissure II. is placed farther back than one would expect, in view of the comparative simplicity of the cerebellum as a whole. Consequently, lobe B is relatively large in the vermis, but becomes more restricted in the hemisphere, owing to the course of fissure II. in a downward and forward direction. Only one, or possibly two, of the intralobular fissures is what Bolk would describe as 'complete,' *i.e.* runs completely across the cerebellum.

Lobe C calls for a detailed description. It consists of four folia in the vermis, but in the hemisphere—following the customary behaviour of this lobe—its folia are more numerous. Three of the folia pass outwards and forwards to the border of the cerebellum without undergoing much alteration. The fourth folium is connected with several short folia, which are arranged in a radiating manner, their centre of radiation being towards the middle line. This increase in the number of the folia, with a corresponding increase in the size of lobe C, is what we have been led to expect; but the point to which attention is asked is the comparative simplicity of their arrangement in a cerebellum in which, as will be shown immediately, certain parts are much better developed than is customary in a cerebellum with a simple lobe C. Neither fissure a nor b can be determined, though serial sections through the half of the cerebellum have been made and examined microscopically, in order to settle this and some other particulars to be presently detailed.

Lobe D is divided into two lobules by a very distinct fissure d. Lobule D_1 consists of two folia in both vermis and hemisphere, there being no difficulty in determining the connection of the two districts, owing to the shallowness of the paramedian sulcus. Lobule D_2 also carries two folia, but does not reach the hemisphere.

Lobe E is likewise composed of two folia, or one compound folium, and microscopic sections show that it entirely disappears at the limits of the vermis, and that a white area takes its place. Considerable difficulty has been experienced in arriving at any conclusion as to the line of separation of flocculus and paraflocculus. There is a well-developed and clearly-defined lobulus petrosus which, attached to the rest of the cerebellum by a narrow neck, is closely surrounded by a capsule of bone. In addition, there are five folia lying anterior to the point of attachment of the lobulus petrosus; and it becomes a question as to how many—if any—of these belong to the paraflocculus. Unfortunately Bolk (13) affords no assistance in the reading of the riddle, since he does not mention these folia in the text of his paper, nor do they appear in his text figures. In fig. 2, taf. ii., he apparently shows two of them. But here they are simply labelled "*Form. verm.*" (formatio vermicularis). An examination of serial microscopic sections leads one to conclude that, as in the rabbit, these folia anterior to the lobulus petrosus all belong to the flocculus. In looking over sections beginning in the middle line, it is first noticed that a trace of grey matter appears in the small area of white matter which has been left on the disappearance of lobule D_2 and lobe E. This gradually increases in amount until a veritable folium is formed, which is ultimately divided into two, an upper and a lower, to the former of which the lobulus petrosus is attached. There can be little doubt that this is the paraflocculus; and, incidentally, it may be remarked that its mesial commencement lies far under lobule D_1, *i.e.* it commences within measurable distance of the vermis. No microscopic connection can be traced between the paraflocculus as just described and the five folia in the anterior part of the cerebellum; they are therefore held to constitute the flocculus, which, as in the rabbit, is far removed from the vermis.

Nyctipithecus trivirgatus (Pl. XXIV. figs. 52, 53 and 54).—The cerebellum of this Douroucouli is not unlike that of Hapale, except that it is a little more complex. In this specimen, as in the preceding, microscopic sagittal sections have been made of one-half of the organ. Instead of giving a detailed description, it will suffice to compare the cerebellum of Nyctipithecus with that of Hapale.

The differences in the anterior region are too slight to require mention, and lobe C need not be dilated upon. It is with lobes D and E that it was found especial attention was necessary. In this part of the cerebellum paramedian sulci are very pronounced, and their presence removes the obvious connection of the parts of lobule D_1 which is so clear in Hapale. When a series of sections are examined, it is found that lobule D_2 (which is larger than in Hapale) ends somewhat abruptly about the paramedian sulcus. At the same time lobule D_1 adds to the number of its folia, so that there are three of these visible in the hemisphere when the intact cerebellum is examined. Sections show a very definite continuity of them with the paraflocculus, which, though not very large, is of good size, and carries a bulky lobulus petrosus.

The mesial part of lobe E retains its grey matter slightly more laterally than lobule D_2 extends. Then all that remains is the edge of the medullary velum, above which lies fissure IV., which can be followed without difficulty until it separates the paraflocculus and flocculus.

Cebus, *Lagothrix*, *Ateles*, *Macacus*, *Cynopithecus*, and *Cercocebus* (Pl. XXV. figs. 55 to 62; Pl. XXVI. figs. 63 and 64).—These cerebella will be described together, as their resemblance is very great. In the anterior part of the organ there is little to note. Until lobe C is reached, the lobes, lobules and fissures are not unlike those met with in animals with a cerebellum of about the same degree of complexity. And it may be further stated that in all six monkeys the corresponding parts are of about the same relative size and disposition. It is in the district which lies behind fissure II. that the main features of interest are encountered.

Lobe C is marked by a pronounçed antero-posterior increase in the hemisphere. With the exception of Cebus, there is little difficulty experienced in finding fissure *b*, which cuts the vermis fairly deeply, and curves downwards and forwards to the margin of the hemisphere. Lobule C_1, thus bounded posteriorly, is of about equal antero-posterior diameter throughout, and its intralobular fissures run approximately parallel. It is a perfectly good exhibition of Bolk's *lobulus simplex*. In Cebus, however, it is difficult to decide upon a *sulcus posterior* such as is figured and described by Bolk (13), fig. 13. In the other monkeys the deepest fissure in the vermis in lobe C can be traced as a continuous and deep sulcus to the margin of the hemisphere. But in the specimen of Cebus, examined for the purpose of this paper, the deepest fissure in the vermis is neither deep nor continuous in the hemisphere. Judging from the condition as described by Bolk, I can only conclude that my specimen was one illustrating the subsidiary morphological position of the fissure.

Lobule C_2 is not quite the same in all the specimens. In Cebus, as noted above, fissure *b* cannot be determined; therefore the exact limits of lobule C_2 cannot be defined. In Macacus, C_2 has *apparently* no existence in the vermis, because fissure *a* runs into fissure *b* in the paramedian sulcus. That part of it which does exist, however, has the same form as the hemisphere portion of the lobule in the other monkeys, *i.e.* it consists of a number of folia arranged in the form of a half-opened fan, the handle of which is directed towards the vermis. The fissures between the folia all disappear before reaching either fissure *a* or fissure *b*, with the exception of one which arrives at the apex of the triangle, and therefore opens into the conjoint fissure $a+b$ (Pl. XXV. fig. 61). In Cercocebus and Cynopithecus fissure *a* is deep in the hemisphere, but in the vermis is traceable into a shallow interfoliar cleft in the depths of fissure III. Lobule C_2 is therefore present and of some size in the vermis. In the hemisphere it need only be noted that it is relatively larger than in Macacus. It has the same radial arrangement as in the latter animal, and there is the same fissure running inwards towards the point of convergence of fissures *a* and *b*. It should be noted that there is a very narrow link connecting the three parts of lobule C_2 on each side, this being invisible on the surface. In Lagothrix and Ateles fissure *a* cannot be followed into the vermis, therefore the limit between lobules C_2 and C_3 is problematic.

Lobule C_3 in Cebus and Macacus consists of a narrow part in the vermis, continued into a much larger portion in each hemisphere, there being a slight stricture in the paramedian sulcus. In Cercocebus and Cynopithecus, owing to the peculiarity of fissure *a*, lobule C_3 can hardly be said to have any existence in the vermis. The most that can be said of it is that it is represented by three or four folia on the anterior wall of fissure III. In the hemisphere, however, it is large, and resembles the homologous part in the other cerebella.

Lobules D_1 and D_2 are very similar in all the specimens. D_1 is largely developed in the hemisphere, and there is little difficulty in finding its connections with the vermis. This is very easily done in Cebus, owing to the comparative lack of depth of the paramedian sulci (Pl. XXV. fig. 57). Lobule D_2 belongs entirely to the vermis. In order to ascertain if there was any continuation whatever beyond the vermis, microscopic sections of this region were made in Cercocebus. It was found that lobule D_2 ends somewhat abruptly, and gives place to a considerable stretch of white matter which underlies lobule D_1 in the mesial part of the hemisphere.

In all but Cebus, lobe E also ends at the level of the paramedian sulcus. In Cebus, however, the lowest folium is continued outwards, undiminished in size, underneath lobule D_1 (Pl. XXV. fig. 58). It proceeds laterally for some distance and then fades away, giving place, as it appears, to the posterior medullary velum to which it has been previously adherent.

The same general arrangement of the flocculus and paraflocculus obtains in all the monkeys examined. The paraflocculus consists of a single row of transverse folia, which turns downwards a little in front and *appears* to be continuous with the flocculus (Pl. XXV. figs. 55 and 60). This appearance would lead to the description of the paraflocculus as composed of dorsal and ventral parts, and to the statement that the flocculus is wanting, were it not for two circumstances which cannot be put on one side unconsidered. The one is that there is a deep sulcus separating the anterior end of the flocculus from the paraflocculus. Again, the flocculus is closely related to, and partly adherent to, the lateral prolongation of the posterior medullary velum. This is best seen in Cebus, where, owing to the lateral extension of lobe E (as described above), there is very little interval between flocculus and lobe E (Pl. XXV. fig. 58).

The paraflocculus carries a lobulus petrosus, springing from its lateral face close to the anterior end. The extent to which the paraflocculus proceeds backwards and inwards varies in some degree.

In Cebus, lobule D_1 passes on to the inferior surface of the hemisphere, and consequently sets a limit to the paraflocculus. In the other monkeys, however, the paraflocculus is continued unarrested in a mesial direction until it almost reaches the vermis. But it is not fused with any part of the vermis, as microscopic sections show; and for this reason the term paraflocculus is applied to the whole of it, however nearly it may approach the middle line.

In no specimen could one feel convinced that there was a dorsal and a ventral limb to the paraflocculus, such as Elliot Smith indicates (10). I am inclined to think that the paraflocculus of the monkey corresponds to the ventral limb of that structure in the majority of mammals, and that the dorsal paraflocculus has been replaced, so to speak, by the enlarged hemisphere segment of lobule D_1.

The Human Cerebellum.

Thanks to the kindness of Professor D. J. Cunningham, I have been enabled to examine a number of human fœtal cerebella. Although several of them are of approximately the same age, and none is illustrative of the earlier stages of development of the fissures and lobes, there are at least four of them which throw light upon some of the problems of the growth of the fissures in man. The remainder have been of the greatest use in enabling me to check my results, and in showing in what manner some of the fissures are liable to variation. Seeing that the several cerebella had been separated (along with the pons and medulla) from the rest of the brain, no definite idea could be formed as to the age of the embryos from which any one had been taken. This is perhaps not of the greatest importance, since the literature contains figures illustrating several different stages in the growth of the human cerebellum, with the age or size of the embryo appended. Anyone who is curious on the matter may compare the figures given herewith with those of previous writers (Stroud, Kuithan, Elliot Smith). The cerebella mentioned here will be known by numbers.

In *Cerebellum No. I.* (Pl. XXVI. figs. 65, 66, 67, 68 and 69), the anterior part of the organ is already provided with a fairly numerous set of folia. In the posterior part the fissures are less numerous, and it is on this district that especial attention will be bestowed, for the reason that here are located the lobes and lobules concerning which there is most difficulty in arriving at conclusions regarding homologies. In all parts of the organ a distinction can readily be made into a vermis and two hemispheres, this being the more easily done in the posterior district. When the cerebellum is viewed from the front (fig. 65), fissures *c*, I., II. and *b* can be at once recognised, their disposition being very similar to that in the adult brain. Special attention is asked to the appearance presented by a mesial sagittal section (fig. 69). A noteworthy feature here is the large size of what is no doubt to become the 'lingula.' Further, the depth of fissure I. is to be noticed, since this, as previously tentatively stated, is not recognised by the human anatomist as a fissure of any importance in the division of the vermis into its several lobes. Between fissures *c* and I. there is only one folium visible when the surface is examined, this folium being even narrower in the hemisphere than in the vermis. That part of the organ which lies posterior to fissure II. is of great interest, chiefly because, as already said, its development is not so far advanced. Appearances seem to point to the development of fissure *b* as having been from two lateral halves, which have gradually grown towards the middle line. These two halves, in this particular specimen, seem to have missed arriving at exactly the same point in the middle line, with the result that they overlap to some extent (fig. 66). In a mesial section the fissure is double, appearing as two shallow depressions (fig. 69). Fissure *a* is still in the form of two halves, which are approaching each other in the vermis. It will be observed that fissures *a* and *b* develop in man in the same manner as has been found in the pig, rabbit and sheep. Fissure III. has obviously commenced its development in the middle line (*cf.* Kuithan). It is deep in the vermis, but gradually becomes shallower as it curves outwards and downwards into the hemisphere, to disappear finally before reaching the margin of the cerebellum (fig. 67). Fissure *d* is as deep as III. in the vermis, and in each hemisphere is continuous with a curved groove which reaches the border of the organ. It is well to remark that *d* is very shallow in the paramedian sulcus.

Lobe E is small, and confined to the vermis. A simple unfoliated flocculus is visible when the cerebellum is looked at from behind or from the side (figs. 67 and 68). There are no paraflocculi in this specimen.

A few intralobular fissures have appeared in the vermis in lobules D_1 and D_2; and that part of the hemisphere which lies between fissures *a* and *d* is marked by a groove, which begins at the border of the cerebellum and, passing for some distance towards the middle line, becomes gradually less deep, until it finally ends before reaching the vermis (fig. 67). There seems little reason to doubt that this groove ultimately becomes continuous with III., and so separates lobe C from lobe D (*cf.* Stroud's figure 62 (1), and Elliot Smith's emendation of it in his figure 9 (12)). If this supposition is correct—and there seems little reason to question it—then the similarity of development of fissure III. in its entirety in man, and in the rabbit, pig, sheep and calf, is very striking.

Cerebellum No. II. (Pl. XXVI. fig. 70), in addition to showing further growth of the fissures and lobes, is interesting, since it illustrates an asymmetry in lobe C. It will be observed that fissure *b* of the left side is continuous with fissure *a* of the right; and *a* of the left and *b* of the right half of the cerebellum cross the middle line to terminate in the opposite hemisphere. If any instance were needed in the support of the contention that these fissures are of secondary importance merely, their tendency to irregularity of disposition might be cited. In this cerebellum the posterior portion has developed very considerably as compared with the same region in No I. Fissure III. is now complete, forming a series of graceful curves, of which that in the vermis is the most acute, and has its convexity looking upwards. Fissure *d* and lobule D_2 have not altered materially from the condition in the preceding specimen. The vermis portion of lobule D_2 has become foliated, but the hemisphere segments remain smooth. The flocculus is now foliated. There is a paraflocculus on one side only, and it is much smaller than the flocculus. Its connections cannot be followed with any degree of satisfaction, it being quite clear that only in much younger material can the origin of the paraflocculus and flocculus be determined beyond question.

Looking at this cerebellum as a whole, it is observed that there has been a more pronounced growth in the hemispheres than in the vermis. This growth has taken place more particularly in lobules C_3 and D_1, lobule D_2, as previously stated, being still unfoliated in the hemisphere. As a consequence of this marked local development, the hemispheres project farther posteriorly than the vermis, and overhang the medulla to a greater degree than they did in cerebellum No. I. The paramedian sulcus is deepest and best marked in lobule D_2, and it will be noticed that the connection between the three parts of lobule D_1 has become very narrow.

In *Cerebellum No. III.* (Pl. XXVII. figs. 71, 72 and 73), there is a marked resemblance to the adult organ. There is now a fairly pronounced vertical flattening. On inspecting the cerebellum from above, fissures I., II. and *b* are seen to run uninterruptedly across the surface, and lobes A and B and lobule C_1 now carry folia. Fissure *a* is still in the form of two lateral halves which approach each other, *i.e.* the vermis, but have not yet fused (figs. 71 and 72). Because of this lack of continuity there is still a portion of the vermis common to lobules C_2 and C_3. This common connection is of only small antero-posterior diameter, as indeed was the case in the younger specimens. Lobule C_2 is relatively small, and its intralobular fissures are few. Lobule C_3 in the hemisphere has again grown at a rapid rate as compared with the surrounding lobules. There is little to remark in fissures III. and *d*. They present much the same features as have been mentioned in connection with Cerebellum No. II., their depth of course being greater. Lobule D_1 has not grown as rapidly as appeared to have been the case in the interval between No. I. and No. II. The connecting link between that part of it which lies in the vermis and its more lateral segments is narrow (as in No. II.) and consists of a single folium. Lobule D_2 has not grown in a manner which calls for remark, and those portions of it which are placed lateral to the paramedian sulci are still smooth. A small and simple paraflocculus is present on both sides (fig. 73). The flocculus does not appear to have made any noteworthy progress.

The external features of *Cerebellum No. IV.* (Pl. XXVII. fig. 74) are very similar to those of No. III. There are rather more intralobular fissures, but the lobes, in the main, present no additional points of interest. It should be noticed that the two halves of fissure *a* have at length joined in the middle line. This is obvious in a mesial section (fig. 74). Attention is again directed to fissure I. as seen in section. Its depth in the middle line is great, being not much less than that of *c*. The importance of this fissure is once again insisted upon.

The only other fœtal cerebellum (*No. V.*) to which any reference is necessary is useful as affording evidence of the parts of the adult organ formed from the various lobes of the younger specimens. This cerebellum has arrived at such a stage that it, at one and the same time, resembles No. IV. and also the fully-developed structure. Its approaching identity with the adult organ removes any necessity for a detailed description. It will suffice to indicate what changes occur in the transition from the fœtal to the adult condition. It may be said, in general terms, that the most striking alteration in the form of the whole organ is produced by a growth in the hemispheres out of proportion to that of the vermis. This we have seen to begin in the comparatively early stages illustrated by the material the description of which is given above; it becomes still more evident in the later stages. As a consequence of this disproportionate growth, the vermis becomes a comparatively insignificant part of the human cerebellum, and the mesial connections of the corresponding parts in the two hemispheres is relatively reduced in a sagittal direction. This feature of development is not equally marked in all regions. In lobes A and B it is very trifling. In lobe C it is decidedly obvious, and particularly so in lobule C_3.

The growth of the hemispheres within this lobule is so great, and the fissures which cut its surface are so deep, that human anatomists have found it expedient to divide it into three parts. This enormous growth of lobe C is very characteristic of the human brain. Indeed, Bolk has said (14) that "the distinguishing feature of the human cerebellum depends upon what may almost be called the monstrous development of the *crus primum* of the *lobulus ansiformis*" (*i.e.* lobuli semilunares superior and inferior and gracilis), with the corresponding reduction of other parts to which attention will be directed later. The lateral portions of lobule D_1 also share in this developmental activity, but to a smaller extent. Lobule D_2 does not become nearly so conspicuous a focus of growth. Because of the backward projection of the hemispheres in the region of lobe C, the vermis appears to sink into the depths of a narrow valley, bounded by the steep heights of the hemispheres. For the same reason, the lateral portions of lobe D are constrained to form part of the sides of the valley. That part of lobule D_2 which contributes to the formation of the hemisphere is, indeed, so confined by the masses lying lateral to it that its growth has to take place in a sagittal direction. In the adult brain it is found to consist of two rows of folia—or rather one row doubled upon itself—radiating out from what Ziehen (15) describes as the *fossa axialis.*

Throughout the present paper, and also in the one which has preceded it, the various lobes and fissures have been known by means of letters and numbers. This plan has been followed with the intention of avoiding the use of terms—such as those employed in Human Anatomy, for instance—which would in any degree hamper us in our endeavour to approach the subject without preconceived ideas of any kind. It need hardly be said that these letters and numbers here employed are merely a temporary convenience, but I do not propose to substitute any other form of nomenclature for them in this communication except in the case of the human brain, and in this case merely in order that the conclusions as stated in the preceding paragraphs may be the more readily appreciated by the human anatomist.

Fissure *c*, then, is the *sulcus postcentralis* of man, and therefore forms the posterior (upper) limit of the *lobus centralis* (lobule A_1). Fissure I. is not recognised as being of any great importance, and is therefore unnamed in books on Human Anatomy. That it should not be relegated to a subordinate place has, it is hoped, been made clear by embryological evidence, and also by the testimony of comparative anatomy. Lobule A_2 is considered in the text-books as a part of the *lobus culminis*, though there are not lacking those who consider this lobe to be composed of two parts. Lobe B constitutes the upper part of the lobus culminis. There seems to be want of agreement between Professor Elliot Smith and the present writer in connection with the subdivision of this part of the cerebellum. What has been referred to as fissure *c* in the foregoing descriptions is evidently equivalent to the *fissura præculminata* of Elliot Smith, who, nevertheless, states that the 'culmen' of the human brain is divided into two lobules by a fissure (*a* in his figures) which may be as deep as, or even deeper than, the *fissura præculminata* (11).

Fissure II. is the *sulcus preclivalis*, fissure *b* is the *sulcus postclivalis*, fissure *a* the *sulcus horizontalis magnus*, and fissure III. the *sulcus postpyramidalis.* Lobe C therefore comprises a very large proportion of the human cerebellum. Its lobule C_1 is the *lobus clivi*, consisting of a *clivus monticuli* and its *lobi lunati posteriores.*

Lobule C_2 is the *lobus cacuminis*, with its diminutive *folium cacuminis* in the vermis, and its much expanded *lobus postero-superior* in the hemisphere. To this, and to lobule C_3, as has been said, the human cerebellum owes not a little of its distinguishing characteristics. Lobule C_3 is the *lobus tuberis* with a vermis segment, the *tuber valvulæ*, and the enormously developed appendages in the hemisphere which anatomists have found necessary to subdivide into *lobus semilunaris inferior*, *lobulus gracilis anterior*, and *lobulus gracilis posterior.* The *sulci postgracilis* and *intragracilis*, being confined to man and the anthropoid apes, have found no place in the foregoing descriptions. They are of no interest as forming primary subdivisions of the cerebellum; for, not only are they limited to one zoologic locality, so to speak, but in those animals in which they do occur, they are tardy in their appearance in the embryo.

It is scarcely necessary to apologise for the somewhat cavalier treatment of the sulcus horizontalis magnus, as various writers, during the past eight years, have borne witness to its utterly subsidiary position among the cerebellar fissures.

In lobe D of the human cerebellum are found points of primary importance to the morphologist. Lobe D_1 consists of the *pyramis* and its *lobi biventralis*, constituting the *lobus pyramidis.* Lobule D_2 is the *lobus uvulæ*, with its *uvula* in the vermis and the *tonsils* in the hemisphere. That part of lobe D which is so well developed in the majority of mammals, and which has come to be known as the paraflocculus, is either unrepresented in man, or, when present, is of small size. But, on the other hand, that connection between the paraflocculus and lobule D_1 in the vermis (pyramis), which is always comparatively small and often apparently absent in the lower mammals, is largely developed in man, forming that very considerable lobule, the *lobulus biventer.* And, again, that continuation of lobule D_2 into the paraflocculus, which apparently has only an existence in the embryo in the lower mammals, is persistent as the *tonsil* in man. Lobe E is the *lobus noduli* (nodulus and flocculus), which, though subject to some variation in size in different animals, does not show such extreme degrees of fluctuation as are found in many of the other lobes.

No mention has been made of the *lingula* of the human cerebellum, and this because it is not considered to be a separate and distinct lobe of the cerebellum. It must be admitted that a very prevalent idea, as expressed in many text-books on Human Anatomy, is that the 'lingula' stands on the same level of importance as the 'nodulus,' and that these two structures should be further held of equal status, since they are similarly related to the anterior and posterior medullary vela respectively. But such assertions are not supported by comparative anatomy. The 'nodulus' is always present in mammals (Meta- and Eu-therian, at any rate), but the 'lingula' is not so constant. In the smaller mammals with a simple cerebellum, there is no trace of grey matter on the dorsal surface of the anterior medullary velum. In the larger mammals this absence also mainly obtains; and even when there is an invasion of the velum by grey matter, it is usually very small in amount. For example, in the monkeys examined, with the exception of Hapale, the velum appeared to spring from the edge of a folium of the cerebellum, instead of from the central mass of white matter as is most frequently found to be its mode of attachment. Certainly 'lingulæ' do occur of a moderate size in animals other than man but such instances are not numerous. A 'lingula' may be found in one specimen and not in another of the same species of animal. And even where a 'lingula' is accepted as being always present, as in man, for example, it is liable to great variation in size. There is certainly a degree of variability in size of the 'nodule,' but this is not nearly so marked as it is in connection with the 'lingula.' Further, the development of the anterior and posterior vela and their adjacent parts is not quite the same. The anterior velum is produced by the upward and forward growth of the cerebellar lamina, which causes a thinning, so to speak, of the roof of the neural tube. The posterior velum is originally a thin non-nervous membrane, attached to the sharp margin of the cerebellar lamina. It is readily conceivable that in the development of the anterior velum there may be an overflow into it from the cerebellar lamina of some of those cells which go to produce the grey cortex of the fully developed cerebellum. If this view be correct, then one may look upon a 'lingula' as an accidental circumstance. The 'nodule,' on the other hand, grows directly from the posterior edge of the cerebellar lamina, and makes its appearance at a very early date. Elliot Smith apparently holds a different opinion as regards the morphologic status of the 'lingula,' for he not only considers it in his paper on the human cerebellum, but also includes it in his latest diagram "representing the fundamental and more constant secondary fissures of the mammalian cerebellum" (11).

Having now signified my conception of the homologies of the human lobes and fissures in terms of the human atatomist, I shall again revert to the provisional use of numbers and letters.

THE CEREBELLUM OF PRIMATES IN GENERAL.

Whatever opinion one may hold regarding the inclusion or exclusion of the Lemuroidea in or from the order of Primates, there can be no doubt that, so far as the cerebellum is concerned, the lemurs do not range alongside the Anthropoidea. Elliot Smith has shown that among the lemurs many types of cerebellum are to be found (12). In many respects the cerebellum of the Anthropidea stands apart from the rest of the Mammalia; and, from the Hapalidæ upwards, forms a graded series of forms, culminating in man. It may be permitted to summarise some of these gradations.

In the Hapalidæ the lobes are simple and of few folia; and the general direction of the fissures is transverse, *i.e.* there is none of that marked local obliquity so commonly met with in most cerebella. Lobe C can hardly be said to be subdivided at all. This circumstance, were it not relieved by an attempt at the obliquity just mentioned, would bring the lobe down to the level of the corresponding part in the rodents, insectivores, etc. Another feature of note is the small size of the paraflocculus (that is, if the statements set forth upon this point in a previous part of this paper are substantiated by further research).

In all the monkeys examined, as well as in those described by Bolk (13), there is no possibility of overlooking fissure I. In most monkeys lobule A_2 is, relatively speaking, small, whereas lobe B is well developed. In lobe C we find a gradual increase in size as we ascend from the Hapalidæ, this increase being mainly, but not entirely, in a sagittal direction. Associated with this expansion in the hemisphere is a relative reduction of the vermis posterior to fissure *b*, and an arrangement in the hemisphere of the folia belonging to lobules C_2 and C_3 in a radiating manner.

The characteristic feature of lobule D_1 is the constancy and size of those parts of it which belong to the hemispheres. So far as the marmosets and monkeys are concerned, there is nothing very striking in the form, size and disposition of lobule D_2. In all of them of which we have any account this lobule is similar to that of mammals belonging to other orders. There is therefore a remarkable difference between this lobule in the monkeys and the apes. From Stroud's observations on the Ape Cerebellum (16), it appears that in the chimpanzee, orang and gorilla, at any rate, there is a lateral continuation of lobule D_2 as in man, but in these animals it "is a relatively small tetragonal mass." It would be very interesting to find some monkey in which this condition, but on a smaller scale, is present, for then the gradations up to man would be complete in this region of the cerebellum.

The fairly uniform size of the flocculus and lobe E in general in different monkeys is noteworthy. In no order of Mammalia is there any very great variation in the dimensions of these parts; but in monkeys and apes (Stroud) the variation is even less than might reasonably be expected in a group of animals differing widely in other particulars. In monkeys, too, the paraflocculus is fairly uniform, and is peculiar in all of them in consisting of only one well-developed row of folia. In a previous paragraph it has been stated that there seems reason to suppose that this single limb corresponds to the ventral paraflocculus of other mammals, the dorsal limb being probably taken up in the development of the large part of lobule D_1 which lies within the hemisphere. It would be interesting to see what embryology has to say on this point.

In the apes, Stroud found that the paraflocculus was variable. In a gorilla he describes it as "very large and almost entirely exposed." In two orangs "it is small and concealed on the left side, only the tip showing on the right side." And in a chimpanzee it "is small and concealed on the left side; the tip is visible on the right side." The paraflocculus of the apes therefore forms a link between the well-developed lobule of the monkeys and the small, insignificant and inconstant structure in man, which is generally referred to as the "accessory flocculus."

ARBOR VITÆ CEREBELLI.

It has become a practice—not invariable, but certainly common—for those who write on the cerebellum to devote some attention to the figure presented when sagittal sections (particularly in the middle line of the vermis) are made. It is obvious that the form assumed by the white matter will vary greatly, depending upon the depth of the primary fissures, and the number, depth and disposition of the subsidiary fissures. For this reason the appearance of the arbor vitæ cerebelli differs in different animals, presenting the least intricacy in those brains in which the cerebellar fissures are few and the lobes and lobules are simple. For example, in the smaller bats the rays proceeding from the central mass of white substance are only five in number, and each ray is undivided. In the larger cerebella the rays are much more numerous and sometimes very copiously branched. Moreover, not only does the form of the arbor vitæ differ in different species of animal, but there is also variation to be noticed in different animals of the same species.

For these reasons it is difficult to arrive at any precise conclusion as to the absolutely typical form of arbor for any one class, or even species of animal, unless one is fortunate enough to be able to examine numerous specimens of that order or species. Bearing this in mind, it is with a certain amount of reserve that one speaks of the form and definite arrangement of the branches of the arbor vitæ cerebelli in any given animal. At the same time general statements may be made as to their disposition in the average mammalian cerebellum.

In all cerebella the central white mass is divided more or less into two parts by the fastigium cutting into it from below and fissure II. indenting it from above (Pl. XXVIII. fig. 76). The degree of division is far from being constant, nor is the result of the division always the same. In probably the majority of mammals the anterior area of white matter is the larger and more compact. The posterior area has a greater tendency to be drawn out in an antero-posterior direction. Springing from the anterior and posterior portions of the white mass are two strong main branches, which pass upwards into lobes B and C respectively. To these two branches Ziehen (15) has applied the names of *truncus verticalis* (to the anterior) and *truncus horizontalis* (to the posterior). It is unfortunate that these names do not indicate the direction of the branches in all, or even in most, mammals. Most frequently they are both more or less vertical.

In all but the simplest forms there are five prominent branches in addition to the two just mentioned, so that the average mammalian cerebellum has seven rays of white matter spreading out from the central mass. These seven rays pass into the following lobes and lobules. The lowest of the anterior branches passes into lobule A_1, and is very frequently not a single ray, but rather two or three. The next ray passes into lobule A_2, and arises either from the central mass directly or from the third branch. Not infrequently it is difficult to decide if these two branches come from a common point, or if the third branch gives origin to the second. The third branch, which is one of the two main and constant rays, is always thick; it forms the core of lobe B, and very frequently divides into two (sometimes more) parts. The fourth branch is usually the strongest of the seven. It curves upwards into lobe C, and in all cases, except where this lobe is incompletely or not at all divided, splits into three sub-rays—one for each lobule. The fifth branch arises in one of four ways. It may leave the central mass independently; it may arise in common with the fourth branch; it may spring from this branch; or it may have a common origin with the sixth branch. Whatever its mode of origin, its destination is lobule D_1. The sixth branch mostly arises separately and independently; but, as just said, it may share a common origin with the fifth. It runs into lobule D_2. The last branch is always the smallest; indeed in the simplest forms it is not more than a small projection from the white centre. It forms the axis of lobe E.

Seeing that there is so much diversity of form of the hemispheres in different animals, it would be exceedingly difficult to make any serviceable general remarks upon the arrangement of the white matter in these parts of the cerebellum.

General Summary.

It may be well to briefly summarise the result set forth in this paper and in the one which has preceded it, and to state the conclusions at which one has arrived. The writer is fully alive to the possibility that these conclusions may require modification in the light of further research. But at the same time they are such as have emerged from a conscientious attempt to add facts as well as theories to the literature of that part of the brain concerning which, even at the present time, opinions are far from uniform.

From the examination of embryological as well as adult material, it is again made clear—if this were in any way necessary after the work done by Stroud, Kuithan, Elliot Smith, Flatau and Jacobsohn, and Ziehen—that in all mammalian cerebella, from the simplest upwards, there is one transverse fissure of pre-eminent importance. Its future status is foreshadowed at an early period of development, and is attained to and maintained in all adult forms. Were it not that it is to a degree inconvenient to do so, the cerebellum might be described as consisting of two lobes, separated by this fissure. Largely for the sake of convenience, but also and mainly from the consideration of the comparative anatomy of the mammalian cerebellum, it is better to recognise five lobes. Each of these has its own characteristics, and, in a series of cerebella, is found to undergo modifications along certain lines. The lobe in which variation is least marked is the most posterior, or E. The greatest amount of diversity of form occurs in lobes C and D. Lobes A and B change somewhat, but to a less extent. Lobe A, in all but the simplest cerebella, is divided into two parts by a transverse interlobular fissure. Lobule A_1, the lower of the two, may remain simple, or, in the higher forms, be in its turn composed of more or less independent parts—generally two or three in number. Lobule A_2, the upper part of lobe A, is generally the smaller, and frequently remains unsegmented. The deep fissure in lobe A has been known as *c* throughout these communications; its importance has been recognised for long by human anatomists. Fissure I., which separates lobes A and B, has not been accorded that attention to which, it appears to me, it is entitled. Lobe B varies in different animals within certain limits, but these limits are fairly well defined. In all the small bats, for example, it is a single, undivided folium. It increases in size *pari passu* with the increase in size of the other lobes, until it is found to be subdivided by deep sulci. Examples of the commencing division of this lobe are supplied by the squirrel and opossum. In these animals, not to multiply examples, the lobe is found to be crossed transversely by a fissure which divides it into two practically equal portions. When there is dissimilarity of size the advantage nearly always rests with the more posterior division. In Phoca the division is very clear. In forms more complex than the opossum and squirrel the two portions of lobe B are themselves subdivided. This is also well exemplified in Phoca. Lobes A and B differ from the remaining lobes in the shallowness of their paramedian sulci, and in their small transverse expansion. These points have been emphasised by Bolk (14), and are excellently demonstrated in some of the Ungulates (Bos, for example). The embryology of lobes A and B is also different from that of C, D and E. In the earlier stages they lag behind in development; then comes a period of activity, in which they outdistance the posterior lobes, and so come to resemble the adult lobes while C, D and E are still comparatively rudimentary.

Lobe C occupies a developmental and anatomical position peculiarly its own. Even in the simpler forms its surpassing importance is obvious, for even here its great antero-posterior diameter in the hemispheres attracts attention. In higher forms it is clearly divided into three lobules by two fissures—*a* and *b*. These two fissures are not of equal consequence. From what has been seen in the embryos examined, *a* probably always (horse excepted?) begins its existence in the hemisphere and grows into the vermis. Fissure *b* seems to begin either in the hemisphere (rabbit and pig) or in the vermis (sheep), and nearly always becomes complete, *i.e.* grows across the whole cerebellum. It is highly probable that fissure *a* frequently remains as two lateral segments which do not join in the vermis, or if they do, their union is apparently later than the conjunction of the two parts of *b*. Even when fissure *a* is complete, it may not cut the vermis very deeply. These variations, and the potentiality for irregularity, demonstrate the secondary importance of fissures *a* and *b*.

Lobule C_1 apparently corresponds to Bolk's *lobulus simplex*, and does all that Bolk claims for it. It is unmistakably of a like constitution with lobes A and B, but it differs from them in its greater lateral extent. Lobules C_2 and C_3 are peculiar in possessing a power of growing in a sagittal direction, especially in the hemispheres. Upon this peculiarity depends the most striking differences in a series of mammalian cerebella. For this reason Elliot Smith gave the name of *area crescens* to the lateral part of what he then called the *lobus centralis* (now named by him *lobus medius*). Sagittal expansion is also possible in the vermis, but it is generally smaller in amount here than in the hemisphere. Phoca may be used as an example of the possible exuberant expansion of the hemisphere, and Bos as an instance of a similar growth, but to a less extent, in the vermis.

The two lobules which compose lobe D have different characters. Lobule D_2 is much the simpler. It is usually limited to the vermis except in the highest forms (apes and man), and does not show any sagittal expansion such as will produce distortion of the vermis. Lobule D_1 may be confined to the vermis, but is frequently continued into the hemisphere (as shown in man, apes and monkeys in the greatest degree). When lobule D_1 has a segment in the hemisphere, this is generally connected with the dorsal paraflocculus. This connection is clearly indicated in the ungulates. In monkeys it seems within the bounds of possibility that the dorsal paraflocculus is replaced by the large portion of lobule D_1 which lies in the hemisphere.

Lobe E is subject to some modifications in size, but the variation is not notably great. Its continuation into the hemisphere is not of common occurrence, but in Cebus and *Viverra civetta* it was found to be so continued; and in Didelphis and Herpestes the continuation of its grey cortex reaches as far out as the flocculus. Like the mesial part of lobe E, the flocculus does not vary to any great extent. It appears to reach its lowest point in some of the carnivora.

The difference in the size of the paraflocculus in different mammals is very striking. In its most highly developed condition it is composed of two rows of folia, to which may, or may not, be added a lobulus petrosus. This lobulus, when present, is generally attached to the posterior end of the ventral paraflocculus, but there are exceptions to this rule. The peculiarity of the paraflocculus in the monkeys has received some detailed attention. In the apes it shows various stages of diminution, and in man it has entirely disappeared in many, if not in most cases.

Although throughout these papers the paraflocculus and flocculus have been described by themselves in the accounts of the various cerebella, this has been done merely for the sake of convenience. It is perhaps well to repeat the assertion that the paraflocculus is an outlying part of lobe D, and the flocculus bears the same relation to lobe E (fig. 75). Both embryology and comparative anatomy demonstrate this. The separation of the paraflocculus and the flocculus, either in part or entirely, from the more mesial portions of the lobes of which they are parts, depends solely on secondary development. They are apparently crowded to one side, and their connections with the vermis weakened or broken down by the growth of the superposed parts of the hemisphere.

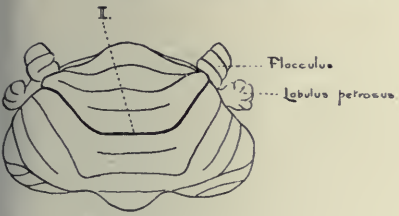

FIG. 48.

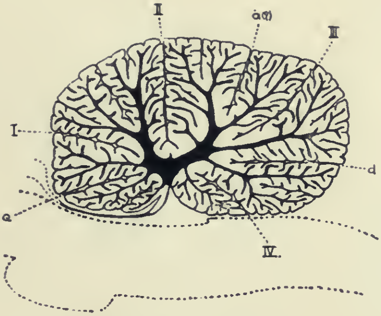

FIG. 47.

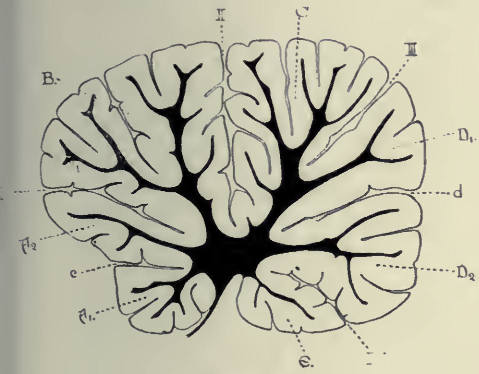

FIG. 54.

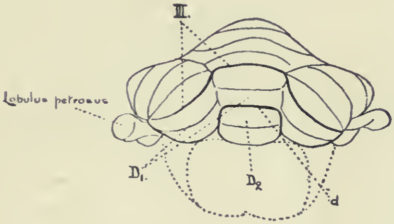

FIG. 49.

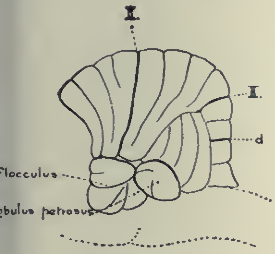

FIG. 50.

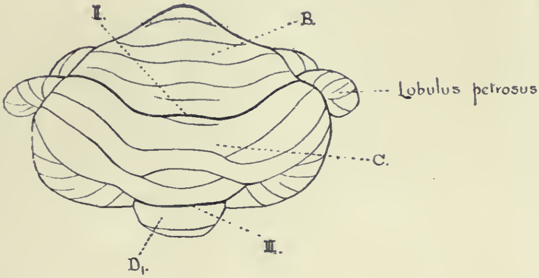

FIG. 52.

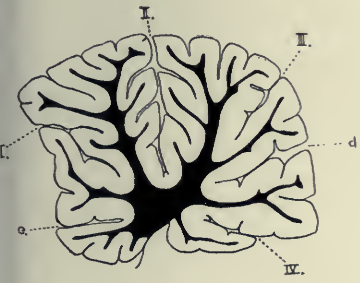

FIG. 51.

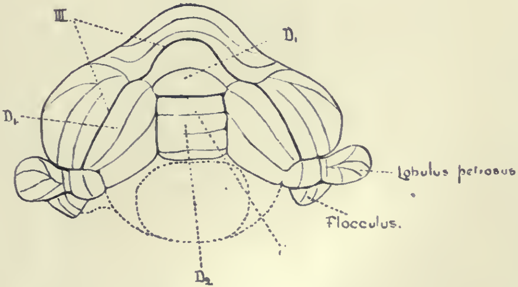

FIG. 53.

Professor O. CHARNOCK BRADLEY on the Mammalian Cerebellum: its Lobes and Fissures.

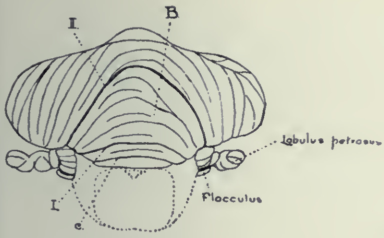

FIG. 55.

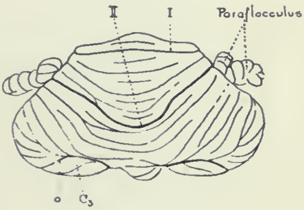

FIG. 56.

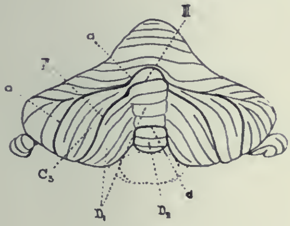

FIG. 57.

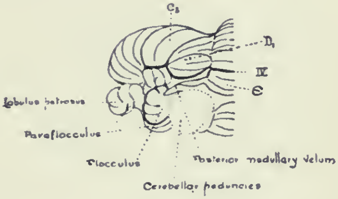

FIG. 58.

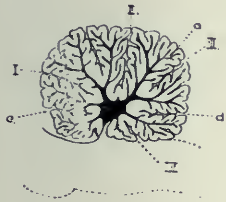

FIG. 59.

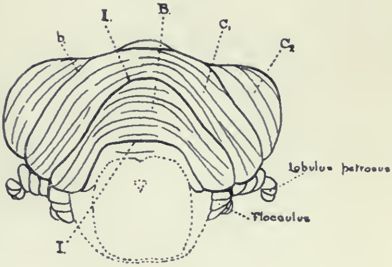

FIG. 60.

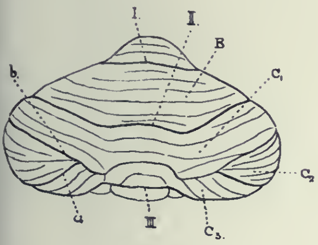

FIG. 61.

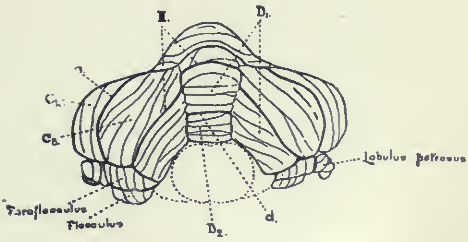

FIG. 62.

Professor O. CHARNOCK BRADLEY on the Mammalian Cerebellum:
its Lobes and Fissures.

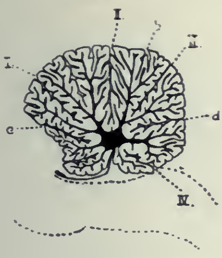

FIG. 63.

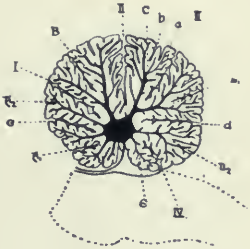

FIG. 64.

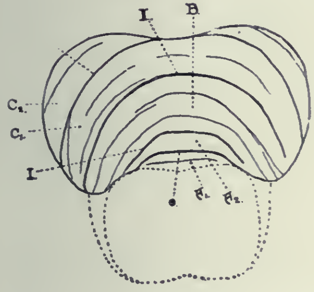

FIG. 65.

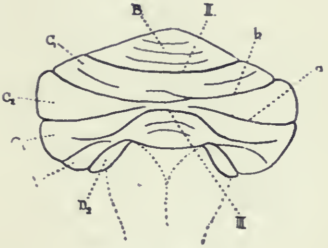

FIG. 66.

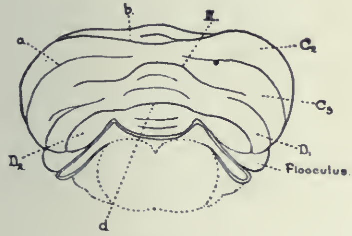

FIG. 67.

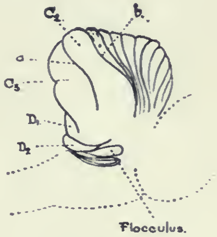

FIG. 68.

FIG. 69.

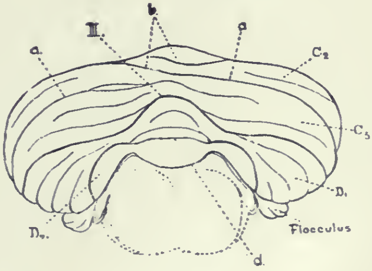

FIG. 70.

Professor O. CHARNOCK BRADLEY on the Mammalian Cerebellum:
its Lobes and Fissures.

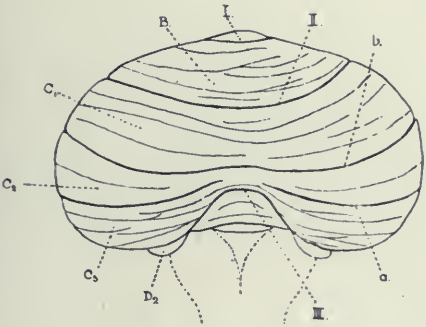

FIG. 71.

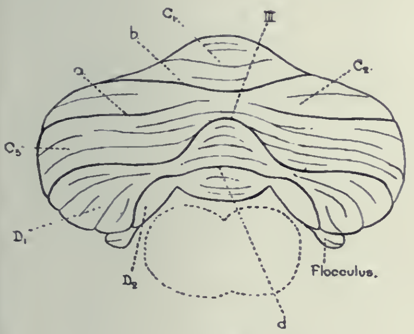

FIG. 72.

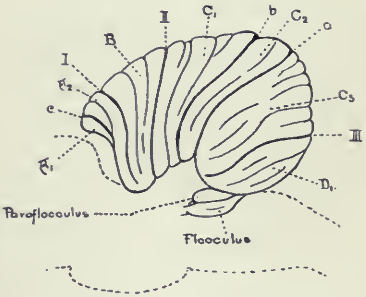

FIG. 73.

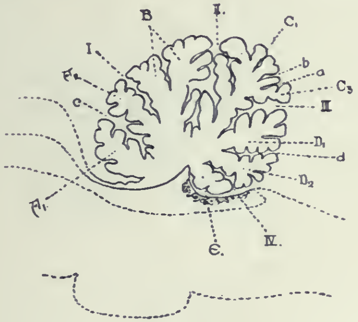

FIG. 74.

Professor O. CHARNOCK BRADLEY on the Mammalian Cerebellum: its Lobes and Fissures.

Journ. of Anat. and Physiology, October 1904.] [PLATE XXVIII.

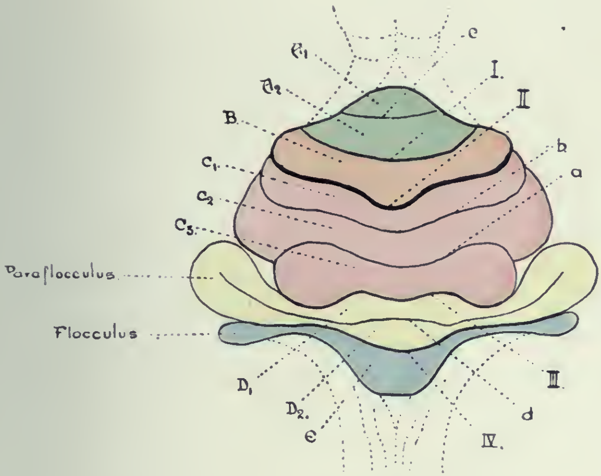

FIG. 75.

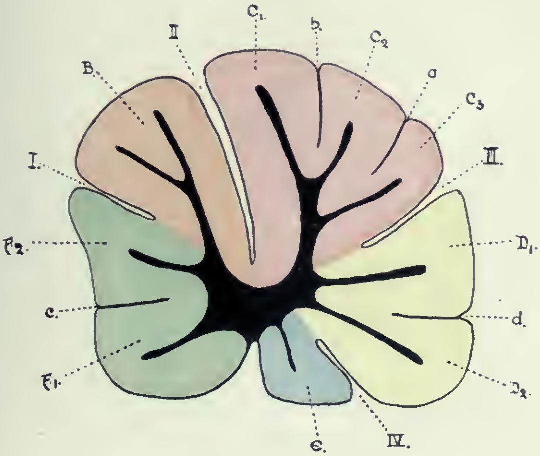

FIG. 76.

Professor O. CHARNOCK BRADLEY on the Mammalian Cerebellum: its Lobes and Fissures.

EXPLANATION OF THE FIGURES.

Fig. 47. Phoca vitulina. Mesial sagittal section. × 1.
Fig. 48. Hapale jacchus. Superior view. × 2.
Fig. 49. ,, Posterior view. × 2.
Fig. 50. ,, Left lateral view. × 2.
Fig. 51. ,, Mesial sagittal section. × 3½.
Fig. 52. Nyctipithecus trivirgatus. Superior view. × 2.
Fig. 53. ,, ,, Posterior view. × 2.
Fig. 54. ,, ,, Mesial sagittal section.
Fig. 55. Cebus capucinus. Anterior view. × 1.
Fig. 56. ,, Superior view. × 1.
Fig. 57. ,, Posterior view. × 1.
Fig. 58. ,, Inferior view. Left half. × 1.
Fig. 59. ,, Mesial sagittal section.
Fig. 60. Macacus rhesus. Anterior view. × 1.
Fig. 61. ,, Superior view. × 1.
Fig. 62. ,, Posterior view. × 1.
Fig. 63. ,, Mesial sagittal section.
Fig. 64. Cercocebus fuliginosus. Mesial sagittal section.
Fig. 65. Human embryo. No. I. Anterior view. × 2.
Fig. 66. ,, No. I. Superior view. × 2.
Fig. 67. ,, No. I. Posterior view. × 2.
Fig. 68. ,, No. I. Right lateral view. × 2.
Fig. 69. ,, No. I. Mesial sagittal section.
Fig. 70. ,, No. II. Posterior view. × 2.
Fig. 71. ,, No. III. Superior view. × 2.
Fig. 72. ,, No. III. Posterior view. × 2.
Fig. 73. ,, No. III. Left lateral view. × 2.
Fig. 74. ,, No. IV. Mesial sagittal section. × 2.
Fig. 75. Schema of the lobes and lobules of the average mammalian cerebellum arranged in one plane.
Fig. 76. Schema of the mesial sagittal section of the average mammalian cerebellum.

Notice of Book.

A Treatise on Applied Anatomy. By Edward H. Taylor, M.D., University of Dublin. London: Charles Griffin & Co., Ltd., 1904.

This volume is one of the largest and fullest treatises on Applied Anatomy which has been issued in this country, and it is one which, from many standpoints, will attract attention. The object of the work is, in the words of the author, "to provide an account of the regional anatomy of the human body in its more important applications to Medicine and Surgery," and the author's qualifications to do this—since he is now a surgeon, and was formerly lecturer on Applied Anatomy in Trinity College, Dublin—have enabled him to produce a book which will appeal both to the Surgeon and to the Teacher of Anatomy. As is pointed out, many of the operations which it is now in the power of the surgeon to perform—thanks to anæsthetics and antiseptics—are of the nature of carefully planned and extensive dissections, so that a thorough knowledge of Anatomy is now, more than ever, an essential part of a surgical training. It might be further stated that recent advances in special departments of anatomical science, and especially in Embryology, are more and more being made use of both by the surgeon and the physician, and one is, therefore, glad to see the accounts of the development of different organs and regions which are introduced throughout the book.

The general arrangement of each section consists of, first, a careful description of the anatomy of the part, followed by a description of the commoner surgical affections met with in it, and an explanation of the manner in which the signs and symptoms of pathological changes are influenced by anatomical facts, as well as of how such facts determine or modify the proper treatment.

A special feature of the book is the numerous and beautiful illustrations, and in both the illustrations and descriptions the author has made use of the most recent advances in Anatomy. This is specially noticeable in the sections dealing with the Head, in which the X-rays have been used to elucidate the topographical anatomy of the Brain and Ear, and in those relating to the Thorax and Abdomen, which are illustrated and described from formalin specimens, with results which for beauty and accuracy are much in advance of anything of the kind.

The volume is dedicated to Professor D. J. Cunningham, and the Dublin School is to be congratulated on the production of a work which will be of great value to surgeons and physicians, as well as to teachers of anatomy.

It will also be of use to senior students; but, in spite of what the author seems to imply in his preface, we consider that it is of the greatest importance for the junior student to have a sound training in scientific anatomy. It is only at a later stage in his course that he is in a position to appreciate the practical bearing of anatomy on medicine and surgery.

David Waterston.

Journal of Anatomy and Physiology.

TWO CASES OF FOURTH MOLAR TEETH IN THE SKULLS OF AN AUSTRALIAN ABORIGINAL AND A NEW CALEDONIAN.

By J. T. Wilson, M.B., *Professor of Anatomy, University of Sydney, N.S.W.*

(Plates XXIX., XXX.)

Through the courtesy of my former pupil, Mr H. O. Lethbridge, I was enabled to obtain possession of an Australian male aboriginal skull from the Maranoa River district, Queensland, in which a fourth molar tooth had been developed on each side of the upper jaw. In the specimen the tooth is actually present only on the left side: on the right it has, unfortunately, been lost *post-mortem.* The existence of the well-formed alveolus upon the right side testifies to the presence during life of a tooth equal in development to the one actually present on the left side.

With the exception of the missing fourth molar, and of the right mesial incisor lost during life (probably through extraction in accordance with the common aboriginal custom), the teeth of the upper dentary arcade are complete (Pl. XXIX. fig. 1).

The degree of wear of the molar teeth answers to Broca's grade No. 2, except in the case of the third molars, in which the dentine has been exposed only at one small point of the right tooth. The fourth molar, not being opposed by a corresponding tooth in the mandible, is unworn, with the exception of a minute area of the enamel close to the anterior margin of the crown. Here it had experienced slight contact with the posterior edge of the crown of the third mandibular molar tooth.

The supernumerary tooth (fig. 1), though somewhat smaller than its companions in front of it, is a well-formed molar.

The occlusal surface of its crown shows a somewhat modified, but quite recognisable, H-shaped furrow. The four cusps of a typical upper molar are evident, but the ridge of enamel joining the mesio-lingual and distal-labial cusps is suppressed. A small fifth cusp is also present, intercalated between the two distal cusps, and the grooves marking out the intercalated cusp are continued downwards upon the distal aspect of the crown. Precisely similar cusps, proportionately larger though still small, are present on the third left, and on both second and third right molars. In addition, the third left molar has an accessory cusp projecting from the labial aspect of its crown, just above the mesio-labial cusp. The point of this accessory cusp does not, however, reach the level of the rest of the crown. The corresponding place on its fellow of the opposite side (third right molar) shows a less-developed form of the same accessory cusp, in the shape of a tolerably prominent tubercle.

In the mandible the molar series is represented only by the typical three molars on each side. These are on the whole slightly larger than the corresponding teeth in the upper jaw, especially mesio-distally. The series as a whole projects slightly both in front of, and behind, the upper molar series, exclusive of the fourth. The distal end of the lower wisdom tooth is placed pretty close up to the curve of the commencing ramus, leaving no room for a possible fourth lower molar of any moderate size. Nevertheless there is a small and rough triangular depression immediately distal to the wisdom tooth, best marked upon the right side, and here measuring 5 mm. from its base at the wisdom tooth to its apex directed towards the ramus (Pl. XXIX. fig. 2). This is doubtless one of those shallow fossæ (" Dellen ") which Zuckerkandl (1) has noted as occurring in this situation, and as representing, though not actually constituting, rudimentary alveoli. A very good example of such a " Delle " in the mandible of another aboriginal Australian is shown in Pl. XXX. fig 3.

The accompanying tables show the dimensions of the teeth of the molar series in the specimen under consideration :—

TABLE I.

Total Mesio-distal Length of 1st to 3rd Molars.	
Upper.	*Lower.*
Left, 31 mm.	Left, 34·5 mm.
Right, 31 ,,	Right, 33·5 ,,

TABLE II.

Mesio-distal Length of Individual Molars.	Labio-lingual width, Individual Molars.
Upper Left.	*Upper Left.*
1st = 10·5 mm.	1st = 11 mm.
2nd = 10·5 ,,	2nd = 12 ,,
3rd = 9·5 ,,	3rd = 11 ,, { exclusive of accessory cusp; with cusp, 13 mm.
4th = 8·0 ,,	4th = 8 ,,
Upper Right.	*Upper Right.*
1st = 10·5 mm.	1st = 11·5 mm
2nd = 10·5 ,,	2nd = 12·0 ,,
3rd = 9·5 ,,	3rd = 11·0 ,, { exclusive of accessory cusp; with cusp, 13 mm.
4th, missing	4th, missing
Lower Left.	*Lower Left.*
1st = 11·0 mm.	1st = 11·5 mm.
2nd = 11·5 ,,	2nd = 12·0 ,,
3rd = 11·5 ,,	3rd = 12·0 ,,
Lower Right.	*Lower Right.*
1st = 10·5 mm.	1st = 11·5 mm.
2nd = 11·5 ,,	2nd = 12·0 ,,
3rd = 11·5 ,,	3rd = 11·5 ,,

The second case is that of a very fine male cranium from L'Ile Noule, New Caledonia, recently added to the collection of the Australian Museum, Sydney. I am indebted to the Curator, Mr R. Etheridge, for bringing it under my notice.

Both of its dentary arcades are quite perfect and the teeth are very slightly worn, only the incisors and the upper canines showing the least trace of dentinal exposure (Pl. XXX. fig. 4).

On each side of the upper jaw, behind fairly large and well-formed third molars, a small supernumerary fourth molar is to be seen. On the left side it is bicuspidate, and its crown measures about 3 × 3·5 mm. in thickness. On the right the crown is tricuspidate, and its diameter is 4·5 mm. in either direction.

On neither side does the small tooth occupy the whole width of the much-thickened and tuberculated hinder end of the alveolar border of the maxilla. It is quite possible that, as in Turner's latest case (*v. infra*), further exploration of the swollen alveolus in the neighbourhood might reveal an additional tooth-rudiment. Even without opening up the alveolus it is evident that, distally to the alveolus of the small supernumerary molar, the posterior end of the alveolus is hollowed out in its interior.

The question of the occurrence of a fourth molar in man was treated of at some length by Zuckerkandl of Vienna in a paper published in 1891 (1). This paper contains a review of various cases of the occurrence of supernumerary molars recorded by previous observers. From this it appears that the existence of what may be called true fourth molars (*i.e.* in series with, and behind, the wisdom teeth) is far from common. The following summary of cases is mainly condensed from Zuckerkandl's analysis.

In the skull of a Kalmuck, Magitot found a fourth molar on both sides of the upper jaw; and again in a negro a similar condition was found, but on both sides of both jaws. In the latter case the supernumerary teeth were smaller than the other molars.

In an Irish skull Harrison found a right upper molar, full-sized and typical.

Amongst 268 African skulls, Mummery discovered fourth molars in six cases. In one case the supernumerary tooth was present on each side of the upper jaw, regularly arranged in the arcade, and well-developed. In another somewhat similar case the supernumerary tooth was inclined to the labial side of the molar series. A third case showed a well-formed fourth upper molar on the left side only, whilst in the three remaining instances the supernumerary teeth were more or less malformed.

Amongst ten cases of supernumerary molars described originally by Busch, that observer found none in which the superfluous teeth were well-formed or in series with the normal molars. Subsequently, however, Busch recorded three cases exhibiting these latter features.

Out of 148 anomalies of the teeth catalogued up to 1884 in the Catalogue of the Odontological Society of Great Britain, 17 were of the nature of supernumerary molars. Only 3 of these occurred in the lower jaw. In only a few cases of the 17 were the supernumerary molars in series with the normal molars behind the wisdom teeth.

Langer described an interesting case of a negro skull which possessed a fourth molar behind the wisdom tooth on each side both above and below, which was normally formed, though smaller than the other molars. There was also a supernumerary premolar.

Four cases of supernumerary molars are described by Zuckerkandl himself. Two of these showed fourth molars in series with, and behind, the third molars. In one of these, an Austrian skull, the fourth molar was present on both sides of the upper jaw; its crown was tuberculated and somewhat stunted. In the other case, that of an African negro skull, from an individual aged about nineteen, there was seen on each side of the lower jaw, distal to the wisdom tooth, a fourth molar, which had not yet attained its full growth. The crown showed six small unequally-sized cusps. On the left side of the upper jaw there was also a fourth molar of about equal size and similar in form to those in the lower jaw. These teeth are illustrated in figs. 27 and 28 of Taf. II. accompanying Zuckerkandl's paper.

In the same communication the author describes, as normally occurring, an epithelial process of the hinder end of the dental lamina, forming a backward prolongation of it beyond the developing wisdom tooth. This small epithelial mass is lodged either in an open groove, or in a funnel-shaped pit or niche with blind extremity, in communication with the alveolus of the wisdom tooth. Such a pit, or recess, or groove, is, according to the author, frequently found in the skulls of individuals from the period of from ten years of age up to adolescence. In the lower jaw the cavity is usually an actual pit or imperfect alveolus; in the upper jaw it is generally groove-like, though it may become a pit later on. In 43 skulls of individuals from fourteen to nineteen years of age such rudimentary alveoli were met with no less than 28 times, and the groove in the upper jaw 17 times, the two co-existing in 13 cases. In far the larger number of instances all trace of these rudimentary alveoli must disappear in the adult, for in 300 adult skulls there were only five cases of either pit or groove representing the actual rudimentary alveolus of a fourth molar. On the other hand, however, it would appear that, in a larger proportion of adult skulls, there persists in the lower jaw a shallow triangular depression (Delle), whose base is at the wisdom tooth and whose apex is directed to the ramus of the mandible. Zuckerkandl found this no less than 44 times in the 300 skulls examined. He regards it as evidence of the earlier existence of such a rudimentary alveolus as he found so commonly present in young skulls. Corresponding to this depression he found in the upper jaw, though less frequently, a shallow grooved depression between the wisdom teeth and the tuber maxillæ. It co-existed with the depression in the mandibular alveolus 25 times, and was present alone only twice, amongst the 300 skulls.

The same author has demonstrated that appearances like these, interpretated as indications of an effort after the production of a fourth molar, are closely similar to those which characterise the early stage of the development of the alveolus of the wisdom tooth. The latter appearances may be taken as the key to the former, and in their light it is clear that in a large number, perhaps in the majority of cases, there exists at one period of molar developmental activity a more or less rudimentary alveolar niche or recess, probably in every case lodging an epithelial back-growth of the dental lamina beyond the third molar germ, which must be taken as the rudiment of a possible fourth molar.

From the not too abundant statistical evidence it would appear that well-developed fourth molars are of more frequent occurrence amongst the African negro race than amongst Europeans.

Sir William Turner (2) has noted the presence, in the skull of an aboriginal Australian female, of a rudimentary bicuspidate tooth behind the last wisdom tooth in the upper dentary arcade.

More recently the same author (3) has recorded a case of an Australian aboriginal skull in which there was on the right side a shallow socket behind the right upper wisdom tooth, in which had been lodged a supernumerary molar. Behind the left upper wisdom were two sockets, in each of which a supernumerary molar was contained. The more anterior of these teeth had erupted and was partly destroyed by caries. Its crown measured 6 mm. in diameter. The additional supernumerary tooth behind this had not erupted. Its crown was 5 mm. in width and irregularly cuspidated.[1]

In his 'Challenger' report Turner (2) notes that in many of the Australian crania examined, "the maxillary tuberosity had grown into a roughened mass which prolonged the dentary arcade from 1 to 1·5 cm. behind the last molar tooth."

W. Krause also (4) found the average backward prolongation of the alveolar process of the maxilla behind the wisdom tooth in 109 Australian skulls to be 1 cm. He further states elsewhere (5) that he frequently discovered in this alveolar prolongation small smooth-walled cavities, either closed or open, of a few mm. in dimensions. Krause draws attention to the fact that whilst Zuckerkandl found rudimentary alveoli behind the wisdom teeth in only 5 cases among 300 adult skulls, he himself had found such cavities in no less than 9 per cent. of 188 Australian skulls. This interesting fact may be correlated with the frequent backward prolongation of the tuberosity of the maxilla above noted as of common occurrence in skulls of this race.

As regards the relative percentage, however, of rudimentary alveoli, it does not appear from Krause's paper that any account was taken of the distinction which was drawn by Zuckerkandl

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[1] He describes (3) in an African skull from the Gambia district an additional tooth on each side in the interval between the 1st and 2nd permanent molars.

between (*a*) the actual rudimentary alveolus ('Rinne' in the upper and 'Grübchen' in the lower jaw) occurring only rarely in fully adult skulls, and (*b*) the shallower and less sharply defined grooves or fossæ ('Dellen') found by Zuckerkandl in a much larger number of additional instances amongst the 300 adult skulls examined. Thus if we put aside the 5 cases of actual rudimentary alveolus, there yet remain 27 other cases amongst the 300 in which Zuckerkandl found a hollow of varying size behind the upper wisdom tooth, *i.e.* in 9 per cent. It is quite possible that Krause's phrase (5), "kleine, glattwandige, nach unten entweder geschlossene oder offene, nach oben sich in einen Knochenkanal fortsetzende Höhlen," may be taken to imply that he excluded all except the more definite rudimentary alveoli, presumably similar to those included in Zuckerkandl's five cases; but in a comparison of results this should be definitely ascertained.

In his reference to the occurrence of rudimentary fourth molars in the jaw of the Australian aboriginal, Professor Krause remarks that we must go down to the marsupials in order to find amongst living mammals an example of the normal possession of four molar teeth in the upper jaw.

As an occasional variation, however, fourth molars are found not only in the human species, but also in a not inconsiderable percentage of the skulls of the Primates, as well as in other mammals. Thus Bateson (6) records having examined 35 otherwise normal skulls of the chimpanzee and having found either fourth molars or their empty sockets in four cases. The common assumptions (*a*) that such variations find their inevitable explanation in inheritance from an ancestral stock which normally possessed the larger number of molars, and (*b*) that individual homologies are maintained amongst the various molars throughout the mammalian series, find in Bateson an energetic opponent. His extensive observations upon cases of variation in 'meristic series' have led him to maintain that "on the analogy of what may be seen in the case of Meristic Series having a wholly indefinite number of members, it is likely that the attempt thus to attribute individuality to members of series having normally a definite number of members should not be made." Thus in reference to a case in which four premolars were present instead of the normal three, and to which there was nothing to indicate that any one of them was supernumerary rather than the other, he submits "that the four premolars must be regarded as collectively equivalent to the three premolars of the normal. The epithelium which normally gives rise to three tooth-germs has here given rise to four," and he believes that "it is as impossible to analyse the four teeth and apportion them out among the three teeth as it would be to homologise the sides of an equilateral triangle with the sides of a square of the same peripheral measurement" (7, p. 114).

He would doubtless apply the same dictum to the occurrence of four molars in the Eutheria. He has, in fact, pointed out that in cases in which a fourth molar occurs as a variation, the third molar, in such case penultimate, tends to be larger and better developed than the corresponding, but ultimate, tooth of a same size. In these cases, he remarks, the new number of the normal animal of the series seems, as it were, to have been reckoned for in the original constitution of the series.

It will be difficult to eradicate from the biological mind the conviction that, amongst teeth as well as with other organs, a genuine return to more primitive conditions does actually take place in at least some instances of variation.

Bateson would appear definitely to reject the doctrine of tooth-homology which is implied in the assumption "that if we had before us the whole series of ancestors from which the form has sprung, we should then be able to see the history of each tooth distinctly and severally in the jaws of each of these progenitors." But is it not true, on almost any theory of variation open to the morphologist at the present time, that this is precisely what we *should* be able to see if we really "had before us the whole series of ancestors"? If the summons to the whole ancestral series to appear before us were obeyed, it is difficult to see, at least on any evolutionary hypothesis, how the "history of each tooth distinctly and severally" could possibly be concealed. It is indeed conceivable that that history might show that the now supposed homologous teeth of various modern mammalian forms are neither individually homologous in the sense of being definitely '*homogeneous*' in the phraseology of Lankester and Osborn (8), nor homologous in the '*homoplastic*' sense of these authors. But even should the survey of such a hypothetically complete series succeed in convincing us that variation has not exhibited any consistent method determined by pre-existing dentitional conditions, it would surely, nevertheless, be possible at least to frame an empirical history, by the ear-marking of every aberrant member of a tooth-series, and the following out both of every precedent condition and of every derivative and result of its occurrence, including its own more or less persistent recurrence.

But, again, is it not the case that, in the comparative and palæontological data bearing upon, *e.g.*, the evolution of the molar cusps in mammalia, we have a very tolerable approximation to a genuine ancestral history of the evolution of the molar form? Professor H. F. Osborn (8) has recently submitted arguments in further support of the view that a quite definite homology can be shown to subsist as regards the appearance in mammals of the various molar cusps. It is true that it is only with regard to the three most primitive cusps that he claims for that homology a strictly 'homogenetic' significance. But his conception of that more limited homology, to which he has applied Lankester's term 'homoplasy,' is rooted no less firmly in phylogenetic fact, although the actual determining causes of those variations which give rise to the evolution of homoplastic structures remain for him unsolved and obscure.

Bateson himself admits that "variation may sometimes respect the individual homologies." This would appear to amount to an admission of the occasional determination of variation by descent, and a recognition of actual homogenetic relationship. Even if the homology admitted be interpreted in the homoplastic sense, there is yet an implied reference to a phylogenetic standard.

No one would maintain that all variations possess an equal and similar morphological value. It is beyond question that numerous instances of variation are of purely 'teratological' significance, not only ontogenetic, but also in cases in which the phenomenon of hereditary recurrence shows an affection of the strip. The existence of these need not be allowed unduly to discount the value of others which are almost inevitably suggestive of reversion. Such a variation as hexadactyly may perhaps be merely teratological. Can we, on the other hand, refuse a phylogenetic explanation of the occurrence of, say, an os centrale in the human carpus? Notwithstanding his admissions, Bateson's argument, logically carried out, amounts to a destructive criticism of the doctrine of homology as grounded in descent. He admits that the statement that an organ of one form is homologous with the organ of another form implies that there is between the two some connection by descent, and it is in its application to series of multiple parts that he more especially questions the validity of the belief. But he has shown no ground in principle for the distinction thus set up, and it is difficult to discover a justification for a restriction of the scepticism thus introduced.

In support of the more special phase of his criticism (*i.e.* in the case of multiple or 'meristic' series), he points out that the body of the varying organism "has never *been* the body of its parent." But this only amounts to a denial of a material identity, which, of course, no one affirms. On the other hand it is certainly not an adequate conception to represent the regeneration of the form in the offspring from the parent form, under the simile of the re-creation of the form of a plastic model after the return of its constituent wax to the melting-pot, as Bateson graphically expresses it. It is obviously untrue to fact to suggest, by means of such a metaphor as that of the melted wax, that with each germinal generation there is a return to morphological indifference and homogeneity. Surely it may safely be conjectured that, whatever may be the nature of the normal form-determinants of the organism—be they material or dynamic—they are in some very real sense morphologically persistent in the germ. And I cannot see why these should be conceived as either wholly inoperative, or even habitually unreliable in operation, within series of multiple parts, even when it is admitted that many variations, there as elsewhere, are incomprehensible as mere phenomena of reversion. That there is good reason for regarding some variations as cases of true reversion pure and simple, is shown anew by Professor Charnock Bradley (9), who, after producing evidence to this effect in the case of the ruminant dentition, remarks that from the evidence "we may judge that there is at least an attempt at tooth formation in the canine and incisor region of the upper jaw of, at any rate, some ruminants. Both comparative anatomy and embryology point to the possibility of the reappearance of these lost teeth." Variation in this direction, he holds, "may reasonably be taken as an instance of reversion towards an ancestor provided with a fuller complement of teeth than is present in the modern Bovidæ."

Even if a faith in the phylogenetic significance of some numerical tooth-variations be retained, it may be that the occurrence of supernumerary fourth molars is not one of the cases in which a direct phylogenetic interpretation can quite readily be entertained. In dealing with some cases of the same variation in the dentition of the horse, Professor Charnock Bradley (9) adopts Mr Bateson's view that the appearance of a supernumerary fourth molar cannot well be explained by reference to ancestral conditions, since the four-molar type must be regarded as too remote. He regards it as the most feasible conclusion "that the supernumerary tooth is merely a variation resulting from a more than usually extensive backward prolongation of the dental lamina, and the formation from it of one dental germ in excess of the normal number." With this non-speculative conclusion I am strongly disposed to agree. I would point out, however, that it implies a somewhat different conception of the nature of a tooth-series than that apparently entertained by Bateson. The latter writer seems to conceive of a tooth-series as in its origin a totality or mass of germinal material, shareable amongst the various tooth-germs of the series. The precise causes which determine such a partition he leaves as a problem unsolved, though it is, as he says, "not a physical, but a physiological, process of division" which results in such a series of multiple parts. Bradley's suggestion involves no such idea of a totality of germinal material in the case of the molar series, and it would, I submit, be a mistake to represent that series as possessing any 'specific original constitution' at all, in Bateson's sense, apart from just that hereditary tendency to organise itself on lines phylogenetically determined, which it is the general tendency of Bateson's argument to minimise.

In support of Bradley's view I would point out that the development of the fourth molar rudiment in man, as investigated by Zuckerkandl, practically repeats in all essentials the previous process by which the molars in front of it were differentiated from the free-growing hinder end of the dental lamina. And, like these too, the fourth molar is in its development directly conditioned by the development of the alveolar process of the jaw.

Wherever a true 'fourth' molar appears in the human subject, the alveolus appears to be prolonged backwards. Either this alveolar prolongation condition determines the appearance of the fourth molar, or *vice versa.* But it is not the latter, as the centimetre-long average prolongation of the tuber maxillæ in aboriginal Australians, without fourth molars, bears witness; whilst at the same time there is a high probability that the true fourth molar appears more frequently in this race than, *e.g.*, in Europeans. This would seem to indicate that the occurrence of the fourth molar is largely conditioned by the exuberant alveolar growth.

The mode of origin of the third molar, its not infrequent existence as a non-erupted tooth, and its occasional suppression or obliteration, are paralleled exactly in the case of fourth molars, though of course with an enormously greater degree of rarity in the case of the latter. In other words the appearance of the fourth molar would appear to be governed by laws and conditions precisely similar to those which govern the appearance of the normal third molar. The question is merely one of relative frequency dependent upon favouring conditions.

It is true that we are quite in the dark at present with regard to the actual and efficient embryonal causes which determine the appearance of those enlargements of the primitively continuous dental lamina which constitute the first rudiments of the teeth. The subsequent cupping of the rudimentary enamel-organs is doubtless the result of functional interaction between the ectodermal dental lamina and the surrounding mesoderm; and so, in all probability, is the primary local thickening of the dental lamina itself. It is, however, easier to assume heterogeneity as manifested first in the mesoderm, rather than in the ectodermal lamina (*e.g.*

from vascular and other differentiation in the former), and it therefore seems not unreasonable to suppose that the unknown organ-forming stimuli in the case of the teeth may be primarily mesodermal, perhaps vascular, or at least vasoformative.

Given a continued proliferative activity of the free-growing posterior end of the dental lamina, co-operating with an alveolar-segmental repetition of vasoformative stimuli, and there might result a repeated differentiation of enamel-germs so long as the alveolar elongation afforded the space necessary for the addition of further members of the series. After this fashion we might account, amongst the Marsupialia, for such a numerical excess in the molar series as is exhibited in Myrmecobius. It is to be observed that such an inherent capacity for the production of new enamel-germs might still be regarded as dependent upon phylogenetic inheritance. It would become unnecessary to limit the inherited capacity to any definite number of teeth. A limit to the molar series would be placed partly by the limit of elongation of the alveolus, partly by the growth-capacity of the ectodermal lamina, whilst other causes of limitation and suppression are easily conceivable as operating in varying degrees in various mammalian forms.

It may be admitted that this mode of explanation of the occurrence of what has been referred to as a 'true' fourth molar is of itself insufficient to explain the phenomenon of a supernumerary premolar intercalated in the ordinary premolar series, as well as of those cases of aberrant supernumerary molars existing outside of the ordinary molar series. But even if for the time we put aside, with Bateson, all direct phylogenetic interpretations of numerical variation, yet if the above suggestions regarding the nature of the causes of tooth-differentiation in general be entertained, the underlying idea may without much difficulty be extended so as to yield something in the way of an explanation of other supernumerary teeth.

Thus it may be suggested that the form of the future tooth, including its serial character, may likewise be dependent upon the precise character or extent of the assumed extrinsic mesodermal organ-forming stimulus (or upon the interaction between this and the growth-activity of the ectodermal lamina) which accounts for the actual appearance of the tooth itself. Since all the teeth pass through the stage of simple cupped enamel-organs there is no necessity to assume that the ultimate multicuspidate character of, *e.g.*, a molar is the result wholly, or even predominantly, of an intrinsic tendency towards that form on the part of the ectodermal dental lamina alone. And if that be so, then the premolar or molar character of the tooth may be regarded as to a large extent an impressed character which may easily be conceived as capable of variation owing to variations in the surrounding vascular or vasoformative conditions. And aberrant vasoformative foci may well be regarded as in some cases determining the appearance of wholly superfluous and irregular tooth-germs, which may ultimately attain maturity.

Further, it must not be forgotten that vasoformative foci, wherever occurring in the body, are just as much subject to hereditary influences as anything else. The vascular system is conspicuously characterised by its variability. Yet very frequently are its variations interpretable only as due to the recurrence of ancestral conditions.

Is it not possible, then, that by some such circuitous course of reasoning we may do justice to the hereditary factors and the phylogenetic aspect of the phenomena of tooth-variation, whilst yet recognising the force of some of Bateson's objections against regarding tooth-series as fixed and definite entities, involving a rigid homology of the individual members of each in different animal groups?

DESCRIPTION OF PLATES.

Pl. XXIX. fig 1. Palate and upper dentary arcade of skull of Australian aboriginal from Maranoa River district, Queensland, with supernumerary fourth molar tooth *in situ* on left side, and empty socket for similar tooth on right side.

Pl. XXIX. fig. 2. Mandibular molars on right side in same skull, showing triangular fossa or 'Delle' distal to third molar.

Pl. XXX. fig. 3. Mandibular molars on left side of mandible of another Australian aboriginal skull, showing extremely well-marked example of a fossa or 'Delle' distal to third molar, which had probably lodged the swollen posterior end of the dental lamina.

Pl. XXX. fig. 4. Palate and upper dentary arcade of skull of native of New Caledonia (L'Ile Noule), showing small supernumerary fourth molar teeth *in situ* distal to the wisdom teeth.

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FIG. 2.

FIG. 1.

PROF. J. T. WILSON.

FIG. 4.

FIG. 3.

PROF. J. T. WILSON.

THE DEVELOPMENT OF THE RETINA IN AMPHIBIA: AN EMBRYOLOGICAL AND CYTOLOGICAL STUDY.

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(Plates XXXI. and XXXII.)

PART I.

CONTENTS.

1. LITERATURE.

THE Vertebrate retina has for many years provided histologists with a favourite field of research The beauty of its many-layered structure and the complicated arrangement of its constituent elements have for long commanded attention. The interpretation of many of the appearances presented by the retina still remains a matter of difficulty, however; and a great deal of research will be necessary before a true and correct understanding of its intricate structure is arrived at. The study of its development has also proved equally attractive, so that the literature relating to both the histology and embryology of the retina has now assumed vast proportions.

A large amount of research on this structure has been carried out by Kölliker (18 and 19), working chiefly with embryos of the rabbit and also with human embryos His main conclusions are, that the internal molecular and the ganglionic layers first appear, while the outer and inner nuclear layers are differentiated much later by the interposition of the external molecular layer. He and Babuchin (3) were the first to point out that the rods and cones develop as prolongations from the cells of the external nuclear layer—a better explanation of the origin of these structures than that adopted by Max Schultze (26) and W. Müller (24), who described them as cuticularisations of the same cells. His (14 and 15) also has made several important communications on the development of the retina in the human embryo; but his observations are chiefly confined to the mode of formation of the optic vesicle, optic cup, and choroidal fissure. He and Kölliker (18 and 19) were among the first to show that the optic nerve-fibres develop as axis-cylinder processes of the retinal ganglion-cells. This has now been accepted as their correct mode of origin, although for a long time it was disputed by many competent authorities, who still clung to the erroneous idea that they were developed from the cells of the optic stalk. Müller (24) has contributed to the literature of the subject an interesting account of the development of the retina in *Ammocœtes.* Researches on the rabbit embryo have been conducted by Löwe (22), but his conclusions differ in some degree from those of Kölliker (above). He describes three stages in the differentiation of the retinal layers, and considers the outer limbs of the rods and cones to be derived from metamorphosed cells. This, however, is now known to be a wrong interpretation of the origin of these structures. Regarding the development of the *membrana limitans interna* there was for some time much doubt. Arnold (1), Löwe (22), and Lieberkühn (20 and 21) considered it to be formed from the mesoblast, but Kölliker (18) eventually proved that it was developed from the optic cup. The pigment layer was found by Gunn (13), in the course of a research on the Teleostean retina, to develop from cells which grow in from the deep layer of the cuticular epiblast, and which are distinct from the cells of the optic cup. A general discussion on the development of the Vertebrate retina is given by Cajal (25) at the close of his researches on that structure in the adult, and he makes a number of references to the work of earlier observers (Kölliker, His, etc.). The mode of formation of the optic nerve-fibres and choroidal fissure in Amphibia was traced by Assheton (2), who showed that the former are developed as axis-cylinder processes from the retinal ganglion-cells.

An interesting paper has been recently published by Cirincione (11) dealing with the embryology of the retina in Reptilia, in which the author treats chiefly of the mode of development of the optic vesicle and cup in this class of Vertebrates. In 1900 Levi[1] published a paper on the development of the rods and cones in the Urodela; but, unfortunately, I have been unable to consult this memoir. Another recently published account of the embryology of the retina is one by Kerr (17), who furnishes an interesting description of the formation of the visual elements in *Lepidosiren paradoxa.*

Bernard has made an extensive series of communications on the retina, chiefly of Amphibians (both larval and adult forms), but

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[1] "Osservazioni sullo svillupo dei coni e bastoncini della retina degli Urodeli," *Lo Sperimentale,* 1900.

also of other Vertebrate types. These have all been published during the progress of this research, and some of them during my absence in Leipzig, so that I did not see these memoirs until some time after my return to this country. It is of interest to note at this point that many of my observations agree in the main with those of the above author, but in some other instances a somewhat different conclusion has been arrived at with regard to the interpretation of the various phenomena presented. The following are Bernard's chief results:—

(1) The retina consists of a syncytium or cytoplasmic reticulum in which nuclei are suspended. These nuclei are not stationary, but are capable of migrating outwards, ultimately to become rod-nuclei (4).

(2) The rods are prolongations of the cytoplasm of the retinal syncytium; but a great part, if not all, of the fluid, which is first protruded to form the rods, comes from the associated nuclei (5). He also shows that absorption of pigment by the rods occurs during the tadpole stage (6).

(3) The cones in Amphibia are the early stages in the formation of new rods (7).

(4) The fibres of Müller are streams of absorbed pigmentary matter finding its way through the retina (8). These appear only after the eye has begun to function; no such preformed structures exist.[1]

On looking through the literature of the subject, it is to be noticed that most of the descriptions deal chiefly with the mode of formation of the Vertebrate optic vesicle and cup, while the study of the development of the various retinal layers from its walls has received much less attention. The embryology of the optic, or (as I prefer to call it) the retinal cup, is thus well known, but the mode in which the layers of the retina are formed from its walls is less perfectly understood. This fact was admitted by the late Professor Milnes Marshall in his *Text-Book of Vertebrate Embryology* (p. 279). Professor Schäfer, in Quain's *Anatomy* (vol. i. pt. i. p. 86), also states that the development of the retina from the inner layer of the optic cup has not been fully worked out. An investigation into the subject therefore seemed desirable, and the description contained in this paper is the result of a research begun about four years ago. The work has been done partly in the Anatomy Department of the United College, St Andrews University, and partly in the Laboratory of the late Professor His at Leipzig. To Professor Musgrove I wish to express my best thanks for many kind facilities which have been granted to me during the progress of the work. I also desire to place on record my deep sense of gratitude to the late lamented Professor His for his kindness and courtesy in granting to me the

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[1] Bernard (9) has made a still more recent communication on retinal structure, in which he shows that the various layers are connected together by a system of fine fibres which pass directly between the nuclei. This memoir has been published since the present paper was submitted as a thesis to the University of Edinburgh.

honour and privilege of prosecuting research in his laboratory. The work was done as a Research Student, and later as a Research Fellow, of St Andrews University. It is necessary to mention that part of the expenses was paid by the Royal Society, through its Government Grant Committee, while the cost of the illustrations has been defrayed by a grant from the Executive Committee of the Carnegie Trust. I wish here to tender my best thanks for the pecuniary aid so generously furnished from these two sources towards covering the expenses of the research.

2. Special Methods of Preparation adopted.

(*a*) *Fixation.*—In conducting a research on the retina, the greatest difficulty that has to be encountered is the proper fixing of its elements, more especially the rods and cones. These latter structures are so delicate and fragile that subsequent manipulations easily injure or even completely destroy them if they are imperfectly fixed. After a trial of several agents, I eventually decided to employ the fixative known by the name of Bles' fluid. The formula I use is as follows—

70 per cent. alcohol, ...	90 parts.
Glacial acetic acid, ...	3 ,,
Formalin, ...	7 ,,

This has yielded in my hands perfectly satisfactory results. A week's immersion in this fluid was found sufficient to completely fix the tissues.

(*b*) *Dehydration.*—From this mixture the tissues were directly transferred to 90 per cent. alcohol for 24 hours. Subsequently, two baths of absolute alcohol (each of 24 hours' duration) sufficed to complete dehydration.

(*c*) *Clearing.*—The tissue was then placed in cedar-wood oil, which was kept heated to a temperature of 55° C. for 24 hours. In the case of very young embryos a shorter time was found sufficient (12 hours).

(*d*) *Embedding.*—From the cedar-wood oil the tissue was transferred to a first bath of melted paraffin, and after 1 hour to a second. It was found that the paraffin into which the tissue was placed directly from the cedar-wood oil was apt to 'crystallise' when poured into the mould. This was obviated by the second lot of paraffin, in which the tissue was kept for 6 hours, and afterwards used for pouring into the mould. Paraffin of a m.p. of 51° C. was employed, but in the height of summer at Leipzig a paraffin of 54° C. had to be resorted to.

(*e*) *Section cutting.*—The sections of the frog-tadpoles were cut with a Minot microtome, and those of the toad-tadpoles with a Cambridge rocking microtome, each section being of a thickness of 3·3 *micra.*

(*f*) *Section mounting.*—The sections were fixed on to the slide by a method for which I am indebted to Dr Fraser Harris. The 'ribbons,' cut into lengths of suitable size, were placed on the surface of warm water, of such a temperature that the paraffin flattened out perfectly, and were floated from this on to the slide. The slides were then placed edgewise in the paraffin stove (top shelf) for 12 hours. It was found quite unnecessary to previously albuminise the slides, for not one of the many thousand sections which I mounted in this way came off during the subsequent staining processes.

(*g*) *Staining.*—After experimenting with many staining agents, I found that the most satisfactory results were obtained with the iron-alum-hæmatoxylin stain (Heidenhain). By this the rods and cones are especially well stained throughout their whole extent, even to their tips; but it also brings out in a wonderful way the fibres of Müller and the molecular layers. In order that these favourable results might be obtained, it was found necessary to depart somewhat from the ordinary methods of using the stain.

The method which I employ is as follows:—The slides are first placed in the iron-alum solution for 10 minutes, rinsed in tap water, and then left in the hæmatoxylin solution until the sections show a bluish-black colour when held between the eye and the shade, such as is afforded by the upper margin of a window (if the slide be examined by direct daylight the sections appear black). This tint is usually produced in about 20 minutes in the case of sections which are 3·3 *micra* thick; but for sections 6·6 *micra* thick only 10 minutes are necessary. The slide is then rinsed in tap water, and again dipped into the iron-alum solution, when, almost immediately, the bluish black is brightened, so that the sections when held up to the window, as before, appear of an ultramarine-blue tint, the black element of the previously blue-black colour having disappeared. The slide is now placed in a fresh quantity of tap water for 15 minutes, when the colour will be found to have become even richer in hue. Overstaining in the hæmatoxylin prevents successful differentiation, while understaining leads to rapid bleaching in the iron-alum solution. In the latter case the slides should be rinsed once more in tap water and replaced in the hæmatoxylin. Old solutions of hæmatoxylin, even when frequently filtered, are apt to deposit small black specks on the sections. When this occurs the solution must be renewed. In the *Microtomist's Vade Mecum* it is recommended to dissolve five germs of hæmatoxylin crystals in 100 c.c. of distilled water. Only a small quantity of this, however, goes into solution, the rest becoming disintegrated to form the deposit mentioned above. Quite as good staining results are obtained when only a crystal or two are used, while the tendency to the formation of deposit is considerably lessened. The iron-alum solution is rather unstable, and must be renewed whenever it becomes turbid.

By the above method of staining the nuclei show a brilliant ultramarine blue colour, and under the high power the intranuclear structure is very well demonstrated.

The other stain employed was Mayer's hæm-alum, followed by eosine or by Mann's methyl-blue-eosine. With these the various retinal layers are well shown, but the rods and cones are only faintly stained. It may be observed that when Mann's solution is used, the eosine stains the outer segments while the methyl-blue stains the inner segments of the rods and cones. The staining effect on these structures is, however, very slight compared to that of the iron-alum-hæmatoxylin. The Golgi method was also experimented with, but in my hands yielded very unsatisfactory results in the embryonic retina.

(*h*) *Dehydration and clearing of sections.*—After two baths of 90 per cent. alcohol the sections were completely dehydrated by absolute alcohol, and cleared in exotic oil of lavender. This latter substance, while clearing the tissue perfectly, does not tend to cause shrinkage. The most convenient way to use it is to immerse the slide in the oil contained in a small glass trough, which can be rocked about in order to remove all traces of alcohol. It is advisable to leave the slide in the oil for about 5 minutes. After draining off the excess of oil, a small piece of dried filter-paper is laid over the sections, and the surface of this is gently stroked so as to remove the most of the oil. A drop of Canada balsam is then applied, followed by the cover-glass.

(*i*) *The procuring of the embryos.*—Two frogs which had already paired were placed in a large tank containing water plants, and after two days an abundant deposit of spawn was obtained. This was placed in a large dish with water plants and kept in the laboratory. Under these conditions the ova and resulting tadpoles developed very successfully. The toad spawn was found at the side of a pool in a disused quarry, and when found the ova had reached practically the same stage of development as the frog's ova when first discovered. The toad spawn was placed in another dish and allowed to develop under similar conditions. From these dishes embryos were removed every second day for the purpose of examination. The series of frog-embryos is fairly complete, leading to the end of the metamorphosis (94 days). Owing to occasional spells of hot weather in Leipzig the paraffin cut badly, and some specimens were consequently lost. The series of toad-embryos is less complete, the supply of tadpoles having become exhausted by the 76th day (the ages of the embryos are calculated from the date of impregnation of the ova). After the 25th day the tadpoles were kept in the dark for 3 hours before killing, so as to ensure full retraction of the pigment-cell processes, which were found to become active under the influence of light about that date.

3. EARLIER STAGES OF DEVELOPMENT OF THE RETINA.

As already stated, the mode of development of the optic vesicle and cup has been previously very fully described by numerous observers. This research, therefore, deals with the mode of origin of the various retinal layers from the walls of that cup. It is convenient to consider first the inner wall, and note its condition in the youngest embryo shown (Pl. XXXI. fig. 1). In this figure it is interesting to observe that the inner and thicker wall of the optic cup is continuous with the basal portion of the thalamencephalon. At the same time it may be noticed that the lens is developed from the deeper layer of the epiblast, and is at first solid, the cavity appearing somewhat later. The description which most observers furnish with regard to the structure of the inner retinal wall is, that it is quite uniform—that is to say, composed entirely of the same kind of cells. Thus it is stated in Quain's *Anatomy*,[1] with reference to this inner wall, that "in its earlier stages it closely resembles in structure the wall of the cerebral vesicles, consisting of elongated epithelium-like cells, apparently arranged in several interlocking layers." Somewhat similar statements are made in Balfour's *Comparative Embryology*, Foster and Balfour's *Embryology*, and Marshall's *Vertebrate Embryology*. If this wall be minutely examined, however, it will be found to contain all the structures which His (15) has described as being present in the spinal cord of the human embryo, and I propose that the corresponding structures in the retina receive names in accordance with this view. There are, firstly, cells (*spongioblasts*[2]) whose processes unite with those of neighbouring spongioblasts to form a network (*myelospongium*). The outer and inner extremities of this myelospongium network of the retina form the external and internal limiting membranes respectively. It may be noted, however, that the external limiting membrane of the retina is next to the original cavity of the optic vesicle, and thus corresponds to the internal limiting membrane of the embryonic spinal cord. In the meshwork of the myelospongium are found two kinds of cells—(1) *germinal cells*,[3] which are always situated immediately underneath the external limiting membrane, and (2) *neuroblasts*, which are formed by division of the germinal cells. The importance of recognising the presence of these four structures in the inner retinal wall can hardly be overestimated, since the subsequent processes of development of the various layers are much influenced by them; and undoubtedly a large amount of the difficulty in the interpretation of the mode of development

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[1] Vol. i. pt. i. p. 86.

[2] Certain cells in the inner nuclear layer of the adult retina have been wrongly termed spongioblasts, for they are derived from the neuroblasts of the embryonic retina.

[3] This term requires slight modification, as will be shown later.

of the retinal layers has been due to the fact that the presence of the above structures during the earlier stages has not been fully recognised.

The late Professor His kindly permitted me to examine some of his sections of the embryonic human retina, and in these, as well as in some of my own preparations (human), I have been able to demonstrate the presence of the same four structures. I have also studied the retinæ of fish-embryos and of the chick, with exactly similar results.

The layer of germinal cells is never a complete one, and indeed no karyokinetic figures may be seen in some of the sections. It is interesting to note that the plane of division of the germinal cells is always in one direction, namely, at right angles, or nearly so, to the external limiting membrane, so that the two daughter-cells lie at first side by side, and later one of them is moved towards the deeper layers of the retina (Pl. XXXI. fig. 3). The first formed neuroblasts are therefore to be found in the site of the future ganglionic layer, while those of a more recent generation are situated at varying distances from the external limiting membrane according to their age—the newly formed ones being, of course, placed nearest to the layer of germinal cells. It will be at once understood from this, that those neuroblasts which become the retinal ganglion-cells are the first to be formed by the division of the germinal cells, and they are, on the whole, rather larger than the younger neuroblasts. The germinal cells in the middle of the convexity of the retinal cup cease to divide at a very early stage of development, and become directly transformed into rod and cone cells, from which the rods and cones develop as processes. They constitute the youngest generation of retinal cells, and no karyokinetic division can be seen to occur in this region after the rods and cones begin to make their appearance. The germinal cells, however still persist under the external limiting membrane, nearer to the margin of the retinal cup, and by their division the growth of the retina results (see Pl. XXXII. fig. 10). The rods and cones thus appear first over the middle of the convexity of the cup, and from this point the development of these structures extends in all directions towards the cup-margin, and they gradually encroach upon the germinal cell-area as development proceeds. The writer has already observed this fact in the retina of Teleostean embryos and of the chick, while Bernard[1] refers to the same point in his paper.

A most striking characteristic which is displayed by the retinal neuroblasts is, that their nuclei all show a progressive diminution in size as development proceeds. This is well seen on comparing figs. 4, 5, and 6 (Pls. XXXI. and XXXII.), which represent nuclei of the ganglionic layer at the 19th, 35th, and 94th days respectively, drawn to exactly the same degree of magnification. Bernard[2] in his paper states that he has observed certain of the cone-nuclei in a collapsed condition, as if their contents had been forced into the basis of the cones, and I have certainly noticed this phenomenon; but apart from this there is a *progressive* diminution in the size of the nuclei of all the layers, which is so gradual as only to be noticed by comparing figures of early with those of late stages. In some cases the nuclei are reduced to less than one-fourth of the size which they possess in the early stages. This observation led me to make a closer examination of the neuroblasts in the Amphibian retina with the highest powers of the microscope, the result being that I have been unable to demonstrate the existence of protoplasm around the structures by the use of cytoplasmic stains. It is true that tissues fixed in Bles' fluid often do not stain with aniline cytoplasmic stains, such as eosine, so well as tissues which have been fixed in corrosive; but even after corrosive fixation, this protoplasmic investment cannot be demonstrated. Other observers state that protoplasm is present, but very scanty in amount, and what there is of it is prolonged into the processes of the neuroblast. After studying these neuroblasts carefully in the wall of the cerebral vesicles and spinal cord, as well as in the retina, I have come definitely to the conclusion that this protoplasmic investment is absent, and that these processes cannot therefore be derived from it, but in reality issue from the substance of the nuclei, and cause the gradual diminution in the size of the latter. His' drawings[3] of these neuroblasts also certainly suggest this conclusion. The processes of the retinal 'ganglion-cells' and of

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[1] *Quart. Jour. Micr. Sci.*, vol. xliii. p. 43.

[2] *Quart. Jour. Micr. Sci.*, vol. xliv. p. 453.

[3] Figured in Quain's *Anatomy*, vol. i. pt. i. p. 58.

the cells of the internal nuclear layer first show themselves as protrusions of the nuclear contents, while the rods and cones are at first also protrusions from the nuclei of the external nuclear layer. A clear unstained vesicle can often be seen at one pole of a nucleus of the retinal wall (two such nuclei are shown in Pl. XXXI. fig. 2), and appears to consist of the achromatic nuclear matrix which is about to be protruded. The nuclear wall may also frequently be observed to extend into the base of the process in the form of a pointed prolongation—an appearance which seems to suggest the withdrawal of some of the nuclear contents (examine three of the nuclei in Pl. XXXI. fig. 4). I find that this diminution in size of the nuclei is practically universal throughout all embryonic tissues, and is especially evident in striped muscle, where the nuclei in the earlier stages are of gigantic size, and, later, some of them give off their contents so suddenly that they appear quite collapsed. I refer to this fact very briefly here, because it is to form the subject of a future communication.

The above observations regarding the appearance and behaviour of these embryonic nuclei are further supported by an examination of the germinal cells. It is stated in text-books that the nuclei of these cells (in the embryonic spinal cord) are usually in one or other of the stages of karyokinesis, and are surrounded by a zone of 'clear protoplasm'—the term 'clear' being no doubt applied because this material stains only very faintly. After having tested the reaction of this substance to numerous cytoplasmic stains, I am convinced that this clear protoplasm (in the Amphibian retina at least) is simply the achromatic[1] nuclear matrix in which the chromatic karyokinetic figures are lying (Pl. XXXI. fig. 3). This achromatin has been set free by the disappearance of the nuclear membrane — a phenomenon which occurs during karyokinesis. It ought to be noted that the term 'achromatic' which is here employed is not an absolute one, for this nuclear substance does stain to a slight extent, which varies with the stage of karyokinesis.

These germinal cells, then, and the neuroblasts to which they give rise, are simply nuclei. Further, the progressive diminution

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[1] The nomenclature given in Quain's *Anatomy*, vol. i. pt. ii. p. 179, has been adopted.

in the size of the nuclei is due to the extrusion of this achromatic nuclear matrix in the form of processes. Hence the difficulty experienced by every observer in demonstrating these latter structures by means of staining agents. Moreover, the rod and cone elements, when they first appear, do so as perfectly clear spherical globules, consisting of nothing more than the nuclear achromatin. This fact will be much more fully alluded to when I come to consider the development of these elements. At this early stage of retinal development the only material present which can be at all considered as representing cytoplasm is the myelospongium network. The germinal nuclei by their division give origin to all the nuclei of the inner retinal wall, and what appears to happen is, that some of these nuclei become imbedded in the 'cytoplasm' to form spongioblasts, while others remain free in the meshwork of the cytoplasm as neuroblasts. This observation regarding the mode of development of these structures does not support the theory advocated by Gaskell (12), namely, that the inner wall of the Vertebrate retina is to be considered as consisting of two parts (Müllerian fibres and retinal ganglion), each with a distinct and separate origin.

The diminution in the size of the retinal nuclei is sufficient to account for the growth of all the processes of the nuclei in the internal nuclear layer, since these are very short; but, on the other hand, it is insufficient to account for all the contents of the rods and cones, as will be explained later when I come to describe the mode of origin of these structures.

The axis-cylinders of the optic nerve arise as processes of the nuclei in the ganglionic layer, and therefore the drain on these nuclei is greatest. This is well demonstrated by the fact that their relative rate of diminution is the most rapid; but, as already shown, they are the largest nuclei in the inner retinal wall, and their diminution in the early stages is due to the ingesting of food-material by them being insufficient to enable them to retain their previous size while their contents are being extruded in the form of processes. The great difficulty which is experienced in staining the individual fibres of the retinal nerve-fibre layer is due to the fact that they are composed of the achromatic nuclear substance from the ganglionic nuclei.

Miss Huie (16) has shown that in *Drosera* the cytoplasm of the gland-cells is produced by the cell-nucleus absorbing food-material, metabolising it, and then excreting it into the body of the cell. So also, in the case of these retinal ganglion-cells, there is ample proof that their protoplasm is excreted from their nuclei. The origin of the axis-cylinders from these nuclei before they show any trace of surrounding protoplasm supports the contention of those who insist on the fact that the axis-cylinder process of a nerve-cell can be traced right into the nucleus of that cell.[1] It is also of interest to note here Bernard's observations regarding the presence of fine fibrils which he has detected connecting together the retinal nuclei (9).

The newly-formed optic vesicle and also the walls of the cerebral vesicles are loaded with yolk-granules, but these disappear at an early stage (by the 20th day), and it is quite easy to demonstrate that they are ingested by the neuroblast nuclei as food-material; for the nuclei of the inner retinal wall at this period often show large irregular masses (which may be termed nucleoli) of deeply-staining material. These obscure the intranuclear network and give to the nuclei a very coarse structure, but this tends to disappear later, so that the network again becomes evident. Moreover, in the early stages (*e.g.* 12 days) yolk-granules may actually be seen in the substance of some of the nuclei—apparently undergoing the process of digestion. This action of these nuclei on the yolk-granules affords ample substantiation of Mann's view (23) that the nucleus has the power of absorbing and metabolising food—a theory which has been ably supported by Miss Huie's researches (16) on the gland-cells of *Drosera.*

4. FORMATION OF THE MOLECULAR LAYERS.

The myelospongium network plays a most important part in the formation of the molecular layers. Its presence can be recognised in the very earliest stages, and its general arrangement is as follows:—

(1) The outer ends of the fibres are attached by broad bases to the external limiting membrane, and between these the germinal nuclei are found lying (Pl. XXXII. fig. 7).

(2) Immediately internal to the layer of germinal nuclei each

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[1] See Quain's *Anatomy*, vol. i. pt. ii. p. 318.

basal portion, as a general rule, divides into two branches, which unite with their neighbours so as to form a sort of arcade, within the arches of which lie the germinal nuclei and, later, the nuclei of the rods and cones. The site of the future sense-epithelium layer is thus mapped off at a very early stage of development (Pl. XXXII. fig. 8).

(3) Between this arcade and the internal limiting membrane the myelospongium is arranged in the form of an irregular network, within the meshes of which lie the neuroblasts; and its inner extremities divide into two branches, which blend to form the internal limiting membrane.

When the internal and external molecular layers develop, then those myelospongium fibres which run in a radial direction become thicker, and therefore better marked, and give rise to the fibres of Müller, while the other portions of the network do not tend to become thickened, and now appear as lateral offshoots from the radially-directed fibres. These latter fibres may thus be termed the rudiments of the fibres of Müller. Bernard (8) considers that the fibres of Müller are entirely formed from streams of absorbed pigmentary matter finding their way through the inner retinal wall, and he further states that they appear only after the retina becomes functional, as no such preformed structures exist. I am certainly convinced that the thickening of the radially-directed myelospongium fibres is due to streams of altered pigment passing along them, and this is evident in the retinæ of adult frogs, for in these the fibres of Müller have usually a characteristic corkscrew-like course through the internal molecular layer, and this suggests the passage of the streams through that layer. I quite agree with Bernard's conclusion that such streams of absolved pigmentary matter pass through the retina, but I wish to point out that the rudiments of the fibres of Müller exist before these streams have made their appearance.

5. Formation of the Internal Molecular Layer.

When the internal molecular layer first makes its appearance it is seen to consist of a dense plexus of myelospongium, the meshes of which are so small that cells are unable to remain imbedded in it, and are thus pushed to either side. At this early stage the fine structure of the internal molecular layer can be observed to be directly continuous with the myelospongium fibres, especially in the toad, where these are of a coarser nature than in the case of the frog.

For an explanation of the mode of origin of the internal molecular layer it is necessary to study the wall of the cerebral vesicles (the fact that the retina is developed from the wall of the cerebral vesicles must never be lost sight of), where a somewhat analogous change occurs; for at a very early stage of development—before the appearance of the internal molecular layer of the retina—this becomes mapped off into an outer portion which is devoid of neuroblasts, and an inner portion which is crowded with neuroblasts. The outer portion is found to consist of a dense mass of myelospongium, and to have exactly the same appearance and staining reactions as the internal molecular layer. In the case of the retina, however, the formation of the internal molecular layer maps off a layer of nuclei—the ganglionic nuclei; but no such phenomenon occurs in the wall of the cerebral vesicle. This can probably be explained by the fact that these retinal ganglionic nuclei very early give off their axis-cylinders, which at once pass over the choroidal fissure, and thus serve to keep the ganglionic nuclei anchored close to the internal limiting membrane, and the dense plexus of myelospongium is on that account formed to their outer side.

The internal molecular layer always stains well from its very first appearance, and to exactly the same degree of tint as the myelospongium. This layer has always been understood to be composed for the most part of the arborising processes from the cells on either side of it; but, as already shown, these processes are for the most part achromatic in nature, and thus stain very feebly, and could not give the tint of colour which the internal molecular layer shows with staining agents *from the date of its very first appearance.*

These processes from the nuclei on either side soon begin to grow into this layer, and ramify within it, so that it may be compared to a sort of trellis-work on which the growing nuclear processes are trained after the fashion of the tendrils of a plant; and this would perhaps account for the extreme degree of arborisation which these processes show in the adult retina by means of the Golgi impregnation-method. In the case of the embryonic retina the chief indication of the giving off of these achromatic processes is the diminution in the size of the nuclei, for, as already stated, I obtained very unsatisfactory results with the Golgi method in the embryonic retina.

The internal molecular layer first makes its appearance at the centre of the retinal cup, corresponding to the point where the rods and cones first develop, and from here its growth extends in all directions towards the cup-margin. If the growing edge of this layer be examined, it is at once observed that it presents a bevelled surface towards the internal nuclear layer. Thus it is much thicker in the centre than at the growing margins, and therefore presents in sections the shape of a very thin crescent (Pl. XXXII. fig. 10). This characteristic shape suggests to one the idea that growth must occur on the convex surface of the crescent, and that very little growth occurs on the concave surface (next to the ganglionic layer). This is confirmed by carefully examining those nuclei of the internal nuclear layer which lie next to the internal molecular layer. Each lies in a sort of cup, as if the tissue of the internal molecular layer were attempting to surround it.

Another point to note about these innermost nuclei of the internal nuclear layer is, that they are the first in that layer to give off processes into the internal molecular layer. As the latter grows in thickness these nuclear processes become imbedded more and more deeply in it, but the processes themselves gradually elongate, and this prevents the nuclei from becoming enclosed in that layer.

The nuclei of the internal nuclear layer, which lie further out, give off their internal processes somewhat later, and these do not, therefore, become so deeply imbedded in the internal molecular layer. This may explain the appearance presented by the internal molecular layer in Golgi preparations of the adult retina, which show that the internal processes from the nuclei of the internal nuclear layer reach to varying depths in this layer.

6. FORMATION OF THE EXTERNAL MOLECULAR LAYER.

The site of the future external molecular layer is early denoted by the arcaded arrangement of the myelospongium-fibres towards their outer ends, which has been already referred to. In these early stages the centres of the arches are rather pointed, owing to the fact that these fibres join one another to form an acute angle (Pl. XXXII. fig. 7). Somewhat later in development the pointed character of the arch tends to disappear, and it becomes more and more flattened. The outline of the external molecular layer is therefore at first somewhat sinuous (fig. 8); and when the arch becomes quite flat, then the external molecular layer comes to possess a straighter outline (Pl. XXXII. fig. 9). This rearrangement causes the radial fibres of the myelospongium to have a slight lateral bend at the external molecular layer (well seen in fig. 9), so that at this stage they do not run an exactly straight course between the external and internal limiting membranes. Somewhat later, however, when the altered pigment already referred to begins to pass along these fibres, and thus thicken them, they possess a straighter course between the limiting membranes.

It will be understood from this description that the myelospongium forms the first groundwork of the external molecular layer, just as it forms that of the internal molecular layer. The rod and cone fibres and the external processes of the internal nuclear layer grow into and arborise within the external molecular layer.

This layer does not tend to increase very much in thickness as development advances, so that in the adult frog it still forms quite a thin stratum in the inner retinal wall. A slight degree of growth occurs in its outer surface in the form of small projections around the rod and cone nuclei, the result being that the latter structures rest in little cup-like depressions.

The free margin of the external molecular layer extends forwards into the undifferentiated region of the inner retinal wall, but it is a short distance behind the growing margin of the internal molecular layer (Pl. XXXII. fig. 10).

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EXPLANATION OF PLATES XXXI. AND XXXII.

List of Abbreviations.

cav. of optic vesicle.	cavity of optic vesicle.
cav. of thal.	cavity of thalamencephalon.
ex. ep.	external epiblast.
ex. l. m.	external limiting membrane.
ex. m. l.	external molecular layer.
ex. n. l.	external nuclear layer.
f. of m.	fibre of Müller.
floor of thal.	floor of thalamencephalon.
ga. l.	ganglionic layer.
ga. n.	ganglionic nucleus.
g. n.	germinal nucleus.
i. l. m.	internal limiting membrane.
i. m. l.	internal molecular layer.
i. n. l.	internal nuclear layer.
lat. wall of thal.	lateral wall of thalamencephalon.
lens.	crystalline lens.
myel.	myelospongium.
neur.	neuroblast.
neur. ep.	neural epiblast.
r. p. c.	retinal pigment cells.
sp.	spongioblast.

All the figures were drawn with the aid of the *camera lucida* apparatus of Zeiss. For figs. 1 and 10 Zeiss's A lens and ocular No. 3 were employed; for figs. 2, 7, 8, and 9, Zeiss's D lens; and for figs. 3, 4, 5, and 6, Leitz's $\frac{1}{12}$-inch oil immersion lens.

Fig. 1 is a vertical section of the optic cup of a 12th-day toad-tadpole. The relation of the outer and inner layers of the cup to

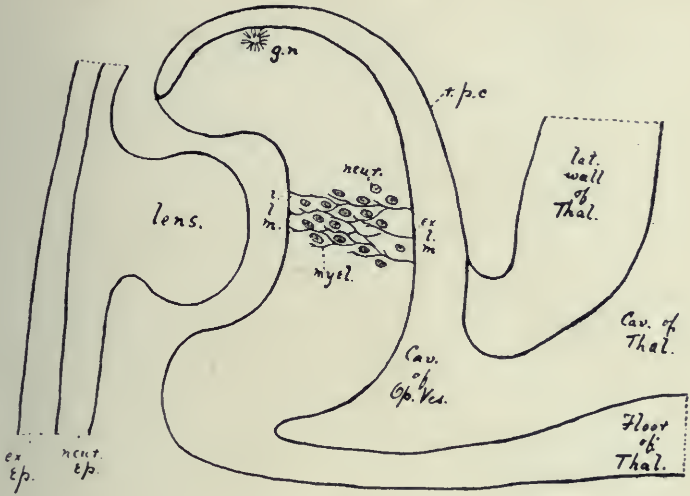

FIG. 1.

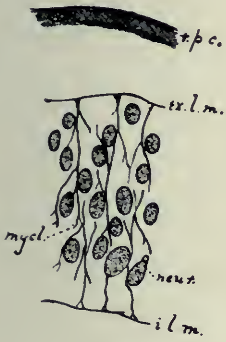

FIG. 2.

FIG. 3.

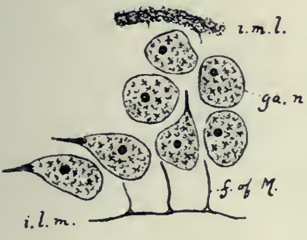

FIG. 4.

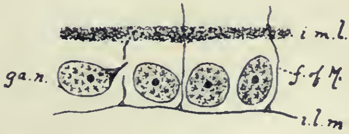

FIG. 5.

Dr John Cameron on the Development of the Retina in Amphibia.

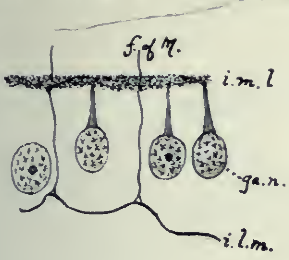

FIG. 6.

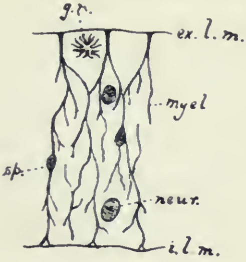

FIG. 7.

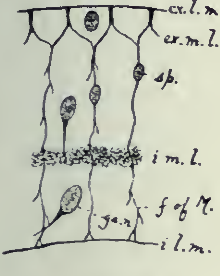

FIG. 8.

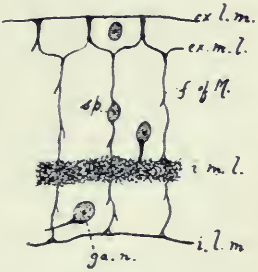

FIG. 9.

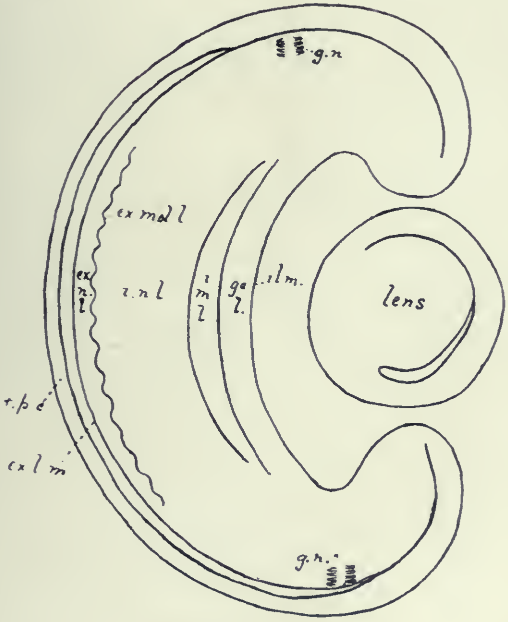

FIG. 10.

Dr JOHN CAMERON on the Development of the Retina in Amphibia.

the walls of the thalamencephalon are well shown. A portion of the inner retinal wall has been filled in to show its structure. The formation of the lens from the deeper or neural layer of the epiblast is also represented.

Fig. 2 shows the structure of the inner retinal wall in a 12th-day toad-tadpole. The limiting membranes, myelospongium network, and neuroblasts are all well marked at this stage. Two neuroblasts show globules of nuclear achromatin about to be protruded.

Fig. 3. The relation of the germinal nuclei to the external limiting membrane and to the neuroblasts is shown. The clear zone around the karyokinetic figures consists of nuclear achromatin. The dotted outline represents the nuclear-membrane (frog-tadpole at the 17th day).

Fig. 4. Several nuclei of the ganglionic layer of the retina of a 19th-day frog-tadpole are shown giving off their achromatic processes. Note the pointed prolongation of the nuclear wall in three cases.

Fig. 5 shows four nuclei of the ganglionic layer of the retina of a 35th-day frog-tadpole, which exhibit a marked diminution in size when compared with those of fig. 4.

Fig. 6 shows four nuclei of the ganglionic layer of a frog's retina at the end of the metamorphosis (94 days). Note their processes and their size when compared with fig. 4.

Fig. 7 is a representation of the myelospongium network of the retina of a 12th-day toad-tadpole. The arrangement of the outer and inner ends of the fibres is clearly shown, as also their relationship to the germinal nuclei and neuroblasts.

Fig. 8 is the myelospongium network in a 19th-day frog-tadpole. Note the appearance of the internal molecular layer and the flattening of the arches near the outer ends of the fibres to form the external molecular layer.

Fig. 9 shows a still further stage in the flattening of the arches, and the formation of the external and internal molecular layers. Frog-tadpole at the 25th day.

Fig. 10 is for the purpose of showing that the differentiation of the various retinal layers begins near the central point of the retinal cup and progresses in all directions towards the cup-rim, where the germinal nuclei still persist. Note the crescentic shape of the internal molecular layer and the sinuous outline of the external molecular layer. Frog-tadpole at the 21st day.

THE RELATIONS OF THE SUPERIOR OBLIQUE MUSCLE OF THE EYE IN THE MAMMALS. By

FRANK S. POOLE, B.A., *Sidney Sussex College, Cambridge.*

MORE attention has probably been paid by students of anatomy and physiology to the muscles of the eye than to any other group of muscles in the whole body; all are supposed to know their relations and actions. Yet when, a short time ago, I became interested in the superior oblique, both from the morphology and from the mechanical structure of that interesting muscle, I was surprised to find that the literature, both on the subject of its development and of its action, was strangely deficient.

With regard to its development, it is usually regarded as derived from the first head cavity, described by Balfour, along with four other of the orbital muscles. This has been worked out in the Elasmobranchs by Marshall (1), but he himself expresses uncertainty as to this origin for the superior oblique. The subject is one which certainly requires further investigation.

I do not propose, however, at present to deal with the development of this muscle, but rather with its structure and its relations with the orbital cavity. To this I was led originally by a paragraph in a paper by John Struthers (2), published in 1854, which I will quote in full:—

"Among mammals the direction of the (visual) axes varies considerably. When they look much forward—as, for instance, in the cat—the line of action of the oblique muscles is directed backwards, as in man. When the axes are turned quite outwards—as in the rabbit and the hare, in which the axes of both eyes cannot possibly be directed to the same object—the oblique muscles are then directed forwards to the axis, but in most quadrupeds—in which the eyes look forwards and outwards (so that, if both eyes are used on one object, the visual axis cannot correspond to the axis of the eye)—they may be said to meet the axis at a right angle as well as to embrace the middle of the eye."

The same author also discusses the action of this muscle, pointing out that there is considerable disagreement on the subject, and he comes to the conclusion that it is evidently intended for the purpose of producing a rotatory movement of the eye—an opinion, I believe, not generally held by physiologists at the present time.

The only other authority I have come across is the writer of a paper in the *Bibliographie Anatomique* (3), who states the same facts, and gives as a reason that in the higher mammals the trochlea is situated nearer to the orbital margin, and that this is correlated with the more and more marked convergence of the optical axes as we ascend the zoological scale.

I have also had recourse to a paper by L. Johnson (4), on the mammalian eye, which contains some interesting numerical data as to the divergence of the visual axes measured on living mammals. Finally I wish to convey my thanks to Dr Marett Tims for all the assistance he has given me, particularly in looking up references.

From hints afforded by these few papers on the subject, several interesting points presented themselves:—

1. That the development of the superior oblique and trochlea, though suggested, and evidently regarded as fact at present, is not decided and would well repay reinvestigation.

2. That two authorities agree in ascribing different relations to the superior oblique in different species of the mammalia, but neither of them attempts to give any numerical facts or states the extent of these differences.

3. That until more is known regarding the relations of the muscle, no definite statement can be made regarding its action—an essentially mechanical problem.

The second of these questions is the one to which I have paid more attention, as I think that the question of the action of the muscle cannot be solved until more is known of its attachments. For the purpose of testing the statements in these papers, and as a preliminary step towards obtaining some definite facts concerning the relations of this muscle, I have dissected a few of the commoner mammals; and it is the results gained by these dissections which I now wish to communicate, as the differences observed in the relations of this muscle in the different specimens have turned out even more remarkable than I had expected. In most of the dissections only sufficient fat and other tissue was removed to expose the parts required, as by this means the muscles were as little displaced as possible.

Three angles have been measured and tabulated. The first is the angle which the superior rectus muscle makes with the centre line of the head, and denotes as near as possible the angle of divergence of the orbital cavity. The second gives the angle of divergence of the superior oblique from the middle line, before traversing the trochlea, while the third angle measured is that between the two parts of the superior oblique before and after passing through the trochlea. These angles I have put in the form of a table in their order of magnitude, and I have also added the values given by Johnson (4) for the divergence of the visual axes in certain animals as nearly allied as possible; these last will be seen to agree very closely in order of magnitude with values found for the divergence of the orbital axes.

I. Divergence of orbital axes.		II. Divergence of superior oblique.		III. Angle between two parts of superior oblique.		IV. Divergence of visual axes (4).	
Rabbit,	66°	Bullock,	43°	Bullock,	100°	Hare,	85°
Bullock,	63	Pig,	35½	Sheep,	99½	Ox,	52
Sheep,	59	Sheep,	28½	Pig,	91	Wild Sheep,	50
Pig,	53½	Rabbit,	25	Cat,	79	Pig,	33
Monkey,	28	Cat,	8	Rabbit,	54	Cat,	7–9
Cat,	25	Monkey,	0	Monkey,	36	Monkey,	0

These results will, I think, perfectly satisfy anyone that there is a considerable difference in the disposition of the superior oblique with regard to the eye in the mammals. What is perhaps most surprising is the enormous range (64°) through which the trochlear angle (*i.e.* that between the two parts of the superior oblique) varies, a range considerably greater than in the case of either of the first two angles measured (41° and 43° respectively). Further, in Struthers' paper (2) it is suggested that the trochlear angle is greater with increased divergence of the eye, while in higher types, when vision is more nearly parallel, the angle becomes smaller. This is evident from these measurements, but is particularly well shown in the case of the three Ungulates.

In these the only discrepancy which occurs is in the angle of divergence of the superior oblique of the pig and the sheep, but I think that this is largely due to the relatively large size of the eyeball in the sheep as compared to that in the pig, the muscle being pushed further towards the centre line.

A very strange discrepancy also occurs in the trochlear angle

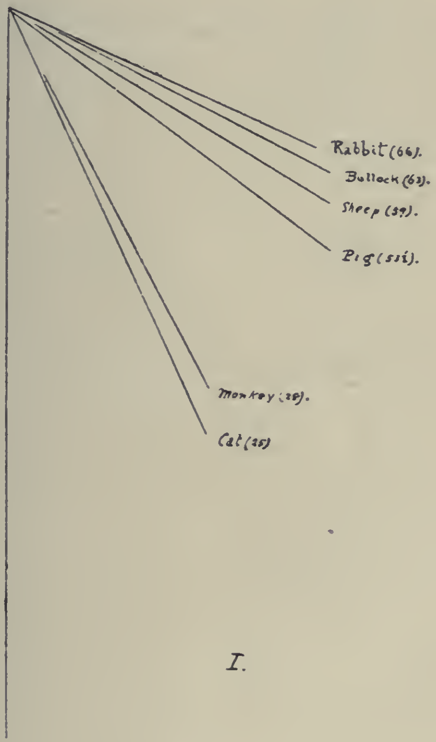

FIG. 1.

of the rabbit. Here, with a large orbital divergence, we should expect to find a large trochlear angle, but instead we find an angle considerably less than a right angle. This I am unable to explain, but I think it may possibly be due to some variation in the individual selected, of which I shall have to speak later. Among the other species which have been dissected no such regularity, as shown in the Ungulates, occurs, and I think this shows that such regularity will be found only to exist among species closely allied, as perhaps we should expect.

Apart from the mere question of the disposition of the superior oblique, several remarkable facts were noticed in the trochlea itself and its attachments to the orbital wall. Various forms of trochlea occur, with and without cartilage, and attached in a variety of ways. In some, again — *e.g.* in the cat and bullock —a fibrous or cartilaginous band passes from its inner (orbital) aspect superficial to the other ocular muscles to be inserted into the outer wall of the orbit in relation to the lacrymal gland. These arrangements I do not intend to describe in detail now, but hope to do so at a future date, when more specimens have been examined.

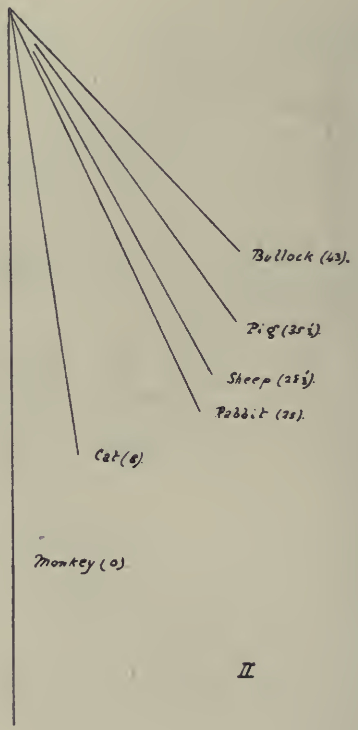

Fig. 2.

So far enough measurements have not been made for any conclusion to be drawn as to the cause or object of this alteration in disposition. It is clear that it must considerably influence the muscle's action, and that this is in some way connected with different degrees of divergence of vision, but in what way they are connected is a question which can only be answered when more facts are known, and when the regularity which is suggested by the Ungulates is shown to hold more extensively.

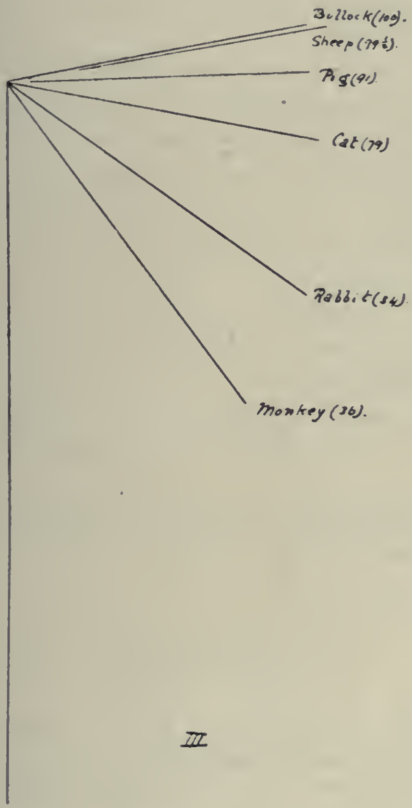

FIG. 3.

In the next place it is necessary to investigate the question as to how far the arrangement in an individual can be taken to represent that in the species. Considerable individual variations may exist and would have to be taken into account. I propose, therefore, as the next step in the investigation, to work upon a number of individuals of one or two common and easily attainable species, and if these show a tolerable uniformity and freedom from individual variation, I propose to continue the measurements on individuals of as many species as can be obtained and conveniently dissected. The results of this investigation, when tabulated, should give interesting results and if such is the case I shall communicate them in a further paper on the subject.

In order to render the angles, which I have already tabulated more evident, I have prepared three figures, showing them in their actual sizes. They are in each case measured from the vertical line, which in figs. 1 and 2 represents the median line of the head. The three figures correspond respectively to the three first columns of the table.

Fig. 1 gives the angles of divergence of the orbital axe measured along the superior rectus.

Fig. 2 gives the angles of divergence of the superior oblique from the middle line.

Fig. 3 gives the actual values of the angles which the two parts of the superior oblique make with one another at th trochlea.

In this graphical way a clearer notion may perhaps be obtained as to the extent of variation in these angles.

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THE OS CALCIS. PART II. By P. P. LAIDLAW, B.A., *Scholar of St John's College, Cambridge.* (PLATES XXXIII.–XXXVII.)

PART II.—THE PROCESSUS POSTERIOR.

THIS division of the bone includes all that portion posterior to the corpus. It presents five surfaces—internal, external, superior, inferior, and posterior; which, with the exception of the posterior and inferior, show very small variation in contour.

The posterior surface approximates to a triangle apex upwards, and includes that portion of the bone seen in norma dorsalis. It is markedly curved from above down, and slightly so from side to side. Its lateral margins are marked out by two rounded ridges, which meet superiorly in the apex of the triangle. In the greater number of cases the apex is slightly truncated, an acute angle being only found in 9 per cent. The lateral margins follow the line of junction of the epiphysis, and in all young bones this may be made out, and thus the posterior surface includes the greater part of the *one-time* epiphysis. The inferior boundary is not so well defined, a sudden increase in curvature from above downwards being all that delimits the plantar surface from the posterior.

This surface is subdivided into three areas:—

(i.) *The Trigonum Achilleum*, a triangular area at the top of the superior surface, which forms the apex of the triangle. It is invariably smooth, and presents the usual characteristics of a bursal surface. It is marked out inferiorly by a well-marked narrow groove from

(ii.) *The Tuberositas Achilleas*, a rough surface of polygonal outline which receives the insertion of the tendo Achillis. This is, in its turn, separated by a narrow ledge from the lowest area.

(iii.) *The Tuberositas Calcanei.*—This area varies in shape, according as the *processus lateralis tuberis calcanei* is or is not a portion of the plantar surface in the natural position of the bone.

In cases (84–5 per cent.) where the *processus lateralis tuberis calcanei* is in the same horizontal plane as the processus medialis, the inferior border of the posterior surface of the *processus posterior* is horizontal, and the tuber calcanei is consequently trapezoidal.

But in some 10 per cent. the *processus lateralis tuberis calcanei* is not a part of the plantar surface proper, and in these the area of the *tuber calcanei* seen from behind is diminished, and is then triangular in outline, apex downwards. This is brought about by the inferior surface of the *processus posterior* beginning at the lower outer angle of the tuberositas Achillea in these cases, and the angle delimiting the posterior and inferior surfaces occurring at a gradually lower point in the perpendicular plane, as one passes inwards towards the *processus medialis* (Pl. XXXIII. figs. 9 and 10).

Sheer.

Angulated.

Terraced.

This area is rough and ridged where the dense connective tissue of the heel obtains firm attachment.

The profile view of this region is variable, and between two extremes all intermediate conditions are found.

The first extreme is a *sheer* drop vertically downwards from the apex of the *trigonum Achilleum* to the plantar surface. In this form the groove and ridge separating *trigonum* and *tuberositas* from *tuberositas* and *tuber* respectively are poorly developed.

According as these grooves and ridges become more and more marked we obtain a series of *angulated* forms, culminating in a form which descends in steps which may be termed the *terraced* type.

Variations other than those already mentioned are pathological, the most common being an over-extension of ossification into the *tendo Achillis*, which may reach a very considerable height. In one case this extended as a shelf-like projection beyond the apex of the *trigonum Achilleum.*

The inferior surface consists of two rounded tubercles, connected by a narrow isthmus. These are respectively *processus lateralis tuberis calcanei* and *processus medialis tuberis calcanei.*

Anteriorly and laterally the margins of the two tubercles form the boundaries, and posteriorly this surface is confluent with the posterior surface.

The *processus medialis* is considerably larger than the *processus lateralis*, and transmits nearly all the body pressure to the ground. In 10 per cent. it transmits the whole, as in these cases the lateral tubercle is displaced upwards, and consequently is not a part of the true plantar surface. In these also the inferior surface is of greater extent, the lateral angle being bevelled off towards the *processus lateralis tuberis calcanei* in the manner mentioned previously.

The *processus lateralis* is a variable structure and is almost peculiar to man, the anthropoids I have been able to examine showing only a trace of it.

Its variations fall into three main groups:—

(i.) Separation from the *processus medialis* by a deep groove just at the point where the isthmus usually connects the two. This occurs in rather more than 2 per cent. of cases.

(ii.) Separation from the *processus medialis* by a similar groove associated with displacement forwards.

In these cases the tubercle seems to be a slightly differentiated part of the retrotrochlear eminence. This occurs in rather less than 2 per cent.

(iii.) Displacement upwards, the tubercle not taking part in the plantar surface proper.

(iv.) This variety is much more common, and occurs in 10 per cent. It is not always present, being absent in about 1 per cent., and in these there is, of course, no true trigonum plantare, a rounded ridge, becoming broader behind, taking its place.

The inconstancy of this element I believe to be due to its recent acquisition, and its most developed form is the most common, viz., a well-developed tubercle in the same plane as the processus medialis, and connected to it by an isthmus.

This conformation gives a broader and more secure basis for the heel, a point of no small importance in the erect position, and more particularly in walking.

From a survey of the specimens at my disposal, I find that this element is composed of two parts—(1) a projection from the bone itself, (2) an epiphysis (see Pl. XXXVI. fig. 15).

A series of bones may be readily traced (among the variations just mentioned) in which the posterior end of the retrotrochlear eminence becomes enlarged, and is gradually displaced downwards and backwards until it reaches the point just external to the *processus medialis.* This forms the basis of the tubercle, but when the point is reached an epiphysis develops, either from the single epiphysis at the posterior end of the bone, or, as I consider more probable, a secondary epiphysis of its own, which becomes incorporated with the first at an early date.

I take this view as very young bones show a sound epiphysial surface isolated from the primary by smooth surface bone. It is a point, however, difficult to decide.

The anthropoid bones which I have been able to examine show the most primitive human type, viz., a small tubercle at the hindmost part of the retrotrochlear eminence, and never any more than this. I have not examined a large number, but those at my disposal included 6 gorilla, 6 chimpanzee, 11 orang bones.

In two chimpanzee feet which I dissected this theory of the formation of this tubercle received additional support from the arrangement of the soft parts.

The outer head of the accessorius arose from a tubercle on the hinder part of the retrotrochlear eminence, and the musculus abductor metatarsi quinti digiti and ligament arose from the same point. This condition was symmetrical, and it will be remembered that these in man arise from the processus lateralis.

We have, then, strong evidence in favour of the view put forward, and I am convinced further investigation will only confirm the same.

The degree of downward projection of these tubercles is very variable; and although I have attempted to correlate the amount of this with other measurements of the bone, I have been unable to find any regularity in the figures.

The surface is rough, for insertion of the plantar fascia and connective tissue of the heel. Pathological ossification may extend along the plantar fascia, giving a well-marked projecting ledge. In one case this projected as far as the cuboid tubercle anteriorly as a shelf-like projection.

The lateral external surface is concave from above downwards and before backwards. It is bounded by the curved ridge marking the line of epiphysial union posteriorly, and by the imaginary line dropped from the *facies articularis posterior* to the *processus lateralis tuberis calcanei* anteriorly. Superiorly a round smooth border separates it from the superior surface, and inferiorly the margin of the *processus lateralis tuberis calcanei* forms its boundary. It presents no features of interest, and varies merely in extent according as the external plantar tubercle is displaced upwards or forwards.

Vascular holes are an inconstant feature. The bone in this region is very delicate, and in a large number of the Egyptian specimens has been broken.

The mesial surface presents similar boundaries and similar contours.

The concavity from before backwards is more marked, and due to the greater size of the internal plantar tubercle. From above downwards a convexity is noticeable in all cases, particularly in the lower half of this surface, again due to the prominence of the *processus medialis tuberis calcanei.*

The musculus accessorius marks the bone in this region in 9 per cent., a curved line of roughness showing its origin, which runs a short distance away from, and parallel to, the line of epiphysial union.

The superior surface has for its boundaries the margin of the *facies articularis posterior* anteriorly, and the ridge forming the boundary of the *trigonum Achillcum* posteriorly. Latterly the margins are rounded of into the external and internal surfaces respectively, and a definite line of separation is impossible.

The whole is typically saddle-shaped. The curvature from before backwards varies with the degree of projection of the *facies articularis posterior* and the apex of the *trigonum Achilleum* posteriorly.

A small tubercle is met with in 7 per cent., just internal and anterior to the centre of the surface, for the *ligamentum talo-calcaneum posterior*.

I have noticed a small mesial pit just posterior to the *facies articularis posterior* in 2 per cent. Its meaning I have not been able to determine.

The length of the processus posterior in relation to the whole is variable, and an index of $\frac{\text{length} \times 100}{\text{greatest length of bone}}$ shows variation from 22–40, and this averages slightly more in Egyptian bones.

One hundred Egyptian bones had an average value for this index of 33·3, and have on the whole a fairly constant index, ranging between 30 and 36.

One hundred modern bones had an average value of 29·8, but showed a greater range of variation than the Egyptian, in 22 to 35 the deviation from the average being commonly great.

Topinard remarks on the greater prominence of the negro heel, but his generalisation is denied by the more recent American writers.

In measurements of this index an *os trigonum*, if present, is best excluded, as otherwise a specious value is obtained.

There is, as a rule, a higher index in laterally-compressed bones than in those compressed from before backwards.

PART III.—THE PROCESSUS ANTERIOR.

The *Processus Anterior* presents five surfaces also, of which four will be immediately considered, the mesial surface being more conveniently included along with the lateral process, which occupies the greater part of the surface.

The superior surface is limited posteriorly by the anterior margin of the *facies articularis posterior*. Anteriorly and externally the margins of the bone perceived in norma verticalis form its boundaries, and internally a line drawn from the anteromedial angle of the *facies articularis anterior* to the mesial edge of the *facies articularis posterior* serves as a line of demarcation from the processus lateralis. This line passes between the *facies articularis anterior* and *facies articularis media* when these two facets are markedly separate. In cases of fusion it serves as a line of division of the compound facet. The degrees of fusion and separation between these facets will be considered later.

The superior surface is very variable, but as a rule the following four features may be made out:—

(1) *Facies Articularis Anterior*.—A small oval facet situated at the extreme antero-internal angle of the surface. Its long axis is directed antero-posteriorly and slightly outwards. It is flat, with the anterior part raised, forming an inclined plane where the angle it makes with the horizontal one is very small.

The articular surface is continuous at the antero-mesial edge with that of the cuboid.

This facet is only present as a separate entity in 32 per cent. of cases. In 69 per cent. it is partially or completely confluent with the *facies articularis media* of the sustentacula. Out of 750 bones examined, it was completely absent in seven cases.

In three cases there is noticeable a fine line of incomplete ossification, partially separating this inner angle of this facet from the main mass of bone. Calcaneus secundarius of Gruber.

Calcaneus secundarius.—There are several examples of this on record, Stieda, Gruber, and Pfitzner having described instances.

Those of Professor Pfitzner occurred in 2 per cent. of the feet examined, but all except one were of small size, and in all but four cases were free, and not ankylosed with the os calcis. Pfitzner's largest example occurred, curiously enough, in an Egyptian mummy, and the best specimen under my observation is also an Egyptian bone, and both these are partially synostosed with the os calcis.

The very low percentage in the bones examined (3 in 750) is explicable by the fact that it is only in the fused cases that it will remain in the macerated specimen, and it is impossible to determine with certainty whether a facet in this position is for calcaneus secundarius or os navicularis. In five more cases, I believe, an ossicle was present in the region.

In bone 587 it measures 16·5 mm. in length by 6·5 mm. in breadth and 6 mm. thick. It is firmly attached to the os calcis at one point, viz., the superior external angle, and presents surfaces for articulation with the talus above and cuboid inferiorly and anteriorly. The navicular does not come into contact with this specimen, as is the case with Pfitzner's specimens (Pl. XXXIV. fig. 11).

Stieda's and Gruber's examples are very similar to Pfitzner's large example—15 mm. long by 8 broad and 5 thick. In Gruber's example a true articulation occurred between the ossicle and the calcaneum. In Stieda's cases synostosis had begun.

Stieda found it in three cases out of 120, Gruber one in 719. Professor Pfitzner regards this ossicle as a "true but rudimentary" tarsal element, which is gradually becoming absorbed into the calcis. He found it symmetrically disposed in five cases, in various degrees of fusion and separation, in 400 subjects. There does not seem to me to be much evidence in favour of this view, but it would be presumptuous to criticise from one dried specimen the result of careful examination in fresh specimens such as Professor Pfitzner's.

Gruber explains this ossicle as an epiphysis, which in a few cases fails to fuse, and in a few rare cases forms a joint with the main mass of the bone; while it usually occurs fused, and is that part of the bone articulating with the *caput tali*, and is termed by him *sustentaculum tali anterior*, and is, as a rule, not developed from a separate centre.

(2) *Crista lateralis.*—A rounded linear elevation running along the outer margin of the superior surface. It is narrow and prominent at the apex of the *facies articularis posterior*, where it arises, and spreading out as it passes forward, is lost on the anterior portion of the *processus anterior*.

Its prominence depends entirely on the depth of the next feature to be considered—the *fossi calcanei*. The bone here is very dense and hard, and it probably functions as a strenthening beam at what is the weak point of the whole bone.

(3) *Fossa calcanei* is a deep depression just in front of the *facies articularis posterior*. The general surface converges towards the lowest part of this depression, and there are usually at its lowest point one or more holes opening into the *antrum calcanei*, a space free from cancelli in the interior of the bone. Where there is one hole it is of large size and funnel-shaped.

(4) *Supracalcanean Tubercle.*—In the median line and a little in front of the centre of the superior surface this eminence is met with, from which the *ligamentum fundiforme* and a slip of the *musculus extensor brevis* arise.

This feature varies considerably, and the varieties fall into three types:—

(*α*) A uniform smooth eminence, without subdivision for the various structures arising from it.

(*β*) A flat eminence, slightly raised from surrounding parts, which may have secondary mammillary projections.

(*γ*) A series of three small tubercles for the points of origin of ligaments and muscle.

In one case (bone B92) an articular facet occurs here, which may, I think, be for *ossiculum in sinu tarsi* (Pl. XXXV. fig. 14).

Just anterior to the supracalcaneal tubercle at the anterior margin of the bone a slight ridge marks the origin of the *ligamentum calcaneo-cuboideum dorsale*.

At the outer edge of this ridge, in 6·7 per cent. of the bones examined, there occurs a more or less marked secondary projection of bone which overhangs the cuboid facet anteriorly, and is faceted for its reception. In one-half of these cases there is noticeable on the facet side a line of holes separating this added portion of the bone, and giving all the appearance of a fused ossicle.

This structure has been termed the *processus trochlearis calcanei anterior* by Hyrtl and Zuckerkandl (Pl. XXXIV. fig. 12).

Professor Pfitzner dismisses this projection, which appears so like an ossicle in some specimens, as a pathological development, not necessarily associated with flat-foot, and is in part brought about by the anterior border of the calcaneum overshooting the cuboid. His main argument for a pathological origin seems to be that this is found in bones which are otherwise well marked, and these bones are to him abnormal.

He states that he has repeatedly proved that bones with spicular projection are derived from physically imperfect individuals, and that the strongest physically and best developed muscularly are not marked by sharp crests or tubercles, but are smooth and round. He lays great emphasis on this point.

He hence adds the term *spurious* to the name of this structure.

From the number of specimens under my observation, a series may be traced from these which appear to be a spread of ossification into the *ligamentum calcaneo-cuboideum dorsale* to a large shelf-like projection 15 mm. wide, but it is difficult to understand how a pathological condition should occur in such a high percentage at this part of the bone. In favour of it, again, we have the fact that on the superior surface of the bone there is no line of ossific union (this only occurs on the anterior surface in the cases examined) such as would indicate separate ossicle, and I know no case in which a free ossicle has been found at this point. However, the condition of fusion of ossicles in which one margin becomes completely united while the other remains separate is often met with elsewhere.

Zuckerkandl regards it as simply an over-development of the anterior margin of the *supracalcanean tubercle*, where the *ligamentum calcaneo-cuboideum dorsale*, a slip of *musculus extensor brevis digitorum* and *ligamentum talo-calcaneum laterale* arise, and remarks that the feet which he examined (two cases) were otherwise perfectly normal.

I am, on the whole, inclined to agree with him, as—

(1) No separate ossicle has been described just at this point.

(2) Incomplete ossific union *only* occurs at the front.

(3) It is similar to other cases mentioned by various observers, where small doubt exists as to the probability that the appearance is merely higher development of a normally occurring tubercle (*e.g.* astragalus, the *processus trochlearis* of Hyrtl).

(4) One limb in a skeleton in the Cambridge museum shows the structure coexisting with a *processus trochlearis* on astragalus and tibia, all well developed.

The external surface is the pretrochlear portion of the bone viewed in *norma lateralis*, and its boundaries are the margins of the bone viewed from the same position, except the posterior, which has already been remarked on under the heading *corpus.*

This surface presents few features of interest which have not already been noticed in Part I.

Thus the trochlea and tendon grooves occupy its posterior half in those cases already noted.

The general contour shows a marked convexity from above downwards, and flatness from before backwards. At the middle point of the anterior margin of the surface a roughness is observable for the *ligamentum calcaneo-cuboideum laterale.*

The *sulcus musculus peroneus longus* is of exceptional depth in 5·6 per cent., and winds round to the inferior surface of the *processus anterior* as a well-marked groove. Just at the inferior anterior corner of this surface a second trochlea is developed in those cases—the inferior trochlea of Moresten.

In Pl. XXXV. fig. 13 a typical instance of this is given. It will be noticed that a deep groove just on the external lateral border of the cuboid tubercle marks the path of the tendon of *musculus peroneus longus*, and this is kept in position by (1) cuboid tubercle internally, (2) a secondary trochlear eminence and articulation.

This condition is usually associated with a well-marked processus trochlearis.

The plantar surface of the processus anterior is of small size, and consists of the cuboid tubercle and a small strip of bone between that and the cuboid facet.

The cuboid tubercle is a small square mass of dense bone, forming the apex of the trigonum plantare (Part I.). Its sides are about 1 cm. in length, and it is faintly convex in all directions. Its surface is smooth where that portion of the plantar ligaments arising from the trigonum plantare plays over it. Its anterior edge is, however, rough, for the reception of a deeper slip of the plantar ligaments.

The strip of bone just anterior to this is much weaker and is of small size, and presents no feature worthy of notice. In cases of increased size (anything above 4 mm.) the cuboid facet does not extend so low down as usual, and consequently leaves a large strip of greater width than usual between tubercle and facet.

The anterior surface of the processus anterior is coextensive with the *facies articularis cuboidea.*

This facet is of triangular outline, base horizontal and apex down. The angles are rounded off. The surface in 90 per cent. of cases is saddle-shaped, being convex from side to side, and markedly concave from above downwards.

The superior margin of this facet juts out as a shelf-like projection at the internal angle, and here overhangs a tongue-like extension of the cuboid facet on to the lateral aspect of the processus anterior, the *recessus cuboidalis.*

At the super-internal angle also the *facies articularis cuboidea* is continuous with the *facies articularis anterior.*

The internal margin is almost straight, and is only distorted when the recessus cuboidalis is over-developed. The boundary of the facet is in these cases ill-defined.

The external margin is always obvious, and is the most anterior part of the bone.

In three cases, the angles of the triangle projecting more than usual and the cuboid bay being absent, this facet was converted into a typically glenoid form.

In almost 9 per cent. flatness from side to side, and in the lower half from above down, destroyed the typical saddle-shape usually observed.

As has been already noticed, at each superior angle there may occur ossicles—the procalcaneum, calcaneum secundarius.

At the inferior angle I have not seen an instance of the apicularis which has been described. This is a secondary ossification in the plantar ligament, which may become fused with the apex of the facies articularis cuboidea.

PART IV.—SUSTENTACULUM TALI.

This is the smallest of the primary divisions of the bone, and varies very considerably in general character. It projects as a bracket-shaped process from the mesial superior border of the *corpus,* and extends forwards for a variable distance on to the *processus anterior.* The degrees of the extension forwards divide the bones into two great groups.

(1) Bones with short *sustentacula.*—Where the sustentaculum

ends suddenly at the middle point of the supero-mesial border of the processus anterior. This condition is always associated with the complete separation of *facies articularis anterior* and *facies articularis media*, a deep notch separating these two facets along the inner borders. This condition prevails in 32 per cent. of cases examined.

(2) Bones with long *sustentacula*.—Where there is no notch defining the anterior part of the *sustentaculum*, but its mesial border passes gradually on to the processus anterior at an acute angle. About 40 per cent. In these cases the *facies articularis media* and *anterior* are fused, and no line of separation is noticeable.

It will be seen that between these two types—(1) where there is a definite anterior border to the sustentaculum caused by the presustentacular notch, and (2) where there is no notch developed—intermediate forms are possible, depending on the degree of development of the indentation in question, and these are met with in all gradations. The appearances are intimately connected with the appearances in the facets, which may be classified as follows:—

(1) Small presustentacular notch, correlated with figure-of-eight conformation of the facets, where the constriction in the figure is slight.

(2) Half-formed notch, where the constriction in the figure-of-eight is great, a small isthmus merely connecting the two facets.

The sustentaculum thus has two surfaces, superior and inferior, and two or three borders, posterior and internal (and possibly anterior), and one margin, a hypothetical line separating it from *corpus* and *processus anterior*.

Viewed from above, the structure is of triangular shape, and from behind is bracket-like. The base of the triangle juts out from the bone directly at right angles, and the apex is directed forwards.

The posterior border is that small area of bone seen in norma dorsalis. It arises at the middle point of the supero-internal border of the corpus and runs out at right angles in most cases, though slight obliquity forwards is met with, and more rarely obliquity backwards. The surface is continuous at its origin with the *sulcus calcanei*, and inferiorly passes off on to the tendon groove for flexor longus hallucis. The border becomes thickened at its outer extremity, and presents a spicular projection upwards —the suprasustentacular spine.

The internal border is of triangular outline, apex forwards; its base is the suprasustentacular spine; from this to the apex a gradually decreasing thickness is noticeable to the point where the sustentaculum joins the processus anterior. The apex is truncated when presustentacular notch is present. There is noticeable (*a*) an infra-articular groove just at the upper margin of the border, which either (1) fades away anteriorly, (2) passes round at the presustentacular notch to the processus anterior; (*b*) a roughened area just below this for the *ligamentum deltoideum*, which is interrupted at its posterior lower third by (*c*) a glide facet for the tendon of *flexor longus digitorum.*

The anterior border is rough for ligamentous attachment when present, and is rounded off on to the processus anterior at its junction with the internal surface of the bone.

The superior surface is for the most part occupied by the *facies articularis media.*

This is an elongated oval facet, concave from before backwards, and flat from side to side. Its variation at its anterior extremity has already been remarked on, and needs no further comment.

The long axis of the facet is oblique, being directed forwards and outwards. The whole facet is raised slightly from the surrounding parts except at its posterior extremity where the suprasustentacular spine occurs.

Absence of the suprasustentacular spine is not frequent— 1·5 per cent.—a flat depressed articular area, passing across a ridge to the main facet, taking its place (Pl. XXXVII. fig. 18). This is either a facet for the *os sustentaculi proprium* or for an exceptional development in the astragalus.

The suprasustentacular spine may be a separate ossicle— *os sustentaculi proprium.*

The os sustentaculi proprium is a small pyramidal mass of bone situated at the inner and most posterior part of the sustentaculum; it, as a rule, does not form a true joint, but is partially fused with the upper surface of the sustentaculum.

Pfitzner found a frequency of about 1 per cent., and in the cases examined by him found it symmetrically disposed in two subjects. He regards it as a true skeletal structure, and believes it to be the point where ossification by over-extension brings about fusion between the *os calcis* and *talus.*

I have only found two well-marked cases of separate ossicles, though possibly another three cases are instances where it has been removed during maceration.

Professor Pfitzner's view of the individuality of this ossicle does not seem to me to have much to support it. As I have before mentioned, the separate epiphysial ossification centre has been shown not to have such definite and fixed value as was at one time supposed.

Division of the facet into two was observed in bone (Pl. XXXVI. fig. 16), the meaning of which I am at a loss to understand.

Fusion with *facies articularis posterior* has already been noticed (Part I.).

The remainder of the superior surface is occupied by the *sulcus calcanei*, a deep narrow groove separating *facies articularis media* from *facies articularis posterior.*

This groove is narrow posteriorly, and opens out anteriorly into the *fossa calcanei.* It is, in cases of short sustentaculum, joined near its termination by another groove, narrower and shallower, which lies between *facies articularis media* and *anterior.*

These and the fossa form the floor of the *canalis tarsi*, which is completed by the astragalus above.

Two planes of ligament arise from the sulcus, which are medial and lateral, for the *facies articularis media* and *facies articularis posterior* respectively. As Barclay-Smith has shown, these are not as strong as was supposed, and they rarely leave any impress on the bone. If they do mark the bone, the origin is marked by a faint longitudinal ridge, which becomes knobbed anteriorly.

Vascular holes are an inconstant feature.

The inferior surface of the sustentaculum is markedly curved from above downwards, and the bone in this region is dense and hard, supporting by its bracket-like formation the whole weight thrown on the sustentaculum. A line of separation between it and the mesial surface of the corpus is impossible, the one passing into the other imperceptibly.

It is bounded by the edge of the *facies cuboidea* anteriorly, superiorly by the rounded lateral border of the sustentaculum, inferiorly by the rounded edge of the trigonum plantare, and by an arbitrary line dropped vertically from the root of the process posteriorly.

It presents three features of constancy, but is otherwise uninteresting:—

(1) A sulcus for the *musculus flexor hallucis longus*, which begins at the posterior border at about its middle, and runs forwards and slightly downwards, to be lost just posterior to the extremity of the surface. This feature varies slightly in being occasionally displaced downwards.

(2) Two narrow ridges, well marked and rough, for the attachment of the tendon sheath.

(3) A vascular hole of large size, just below the posterior third of the lower of these two vesicular ridges. This is not always present.

(4) A roughness, just above the cuboid tubercle, for the *ligamentum calcaneo-cuboideum mediale.*

The Architecture of the Bone.—The cancelli are disposed very favourably to ensure the greatest strength in the bone.

The outer case is of exceptional thickness at the facets, the fossa calcanei and crista lateralis, the cuboid tubercle, the plantar tubercles, tuberositas Achillea, and the inferior surface of the sustentaculum. Elsewhere the case is thin, and easily broken by rough handling. From the *facies articularis posterior* a system of bony plates pass downwards and backwards to the processi plantares in gentle curves, taking a very large amount of the thrust in this region. These plates are on the outer margin turned obliquely outwards so well as that the outermost reach the external wall of the bone about its middle, and these are determining factors in the formation of the retrotrochlear eminence.

This system is connected by horizontal series sagittally and coronally, which add greatly to the strength.

A second series of trabeculæ run from the dense *tuberositas Achillea* in wide curves forwards and downwards to the cuboid tubercles, knitting the first together posteriorly, and converging in front to the cuboid tubercle.

FIG. 9.—Bone B 92—Posterior view. Typical position of the processus lateralis tuberis calcanei. (Most developed human form.)

FIG. 10.—Bone 494—Posterior view, showing processus lateralis not a part of the true plantar surface. (Approaching anthropoid form.)

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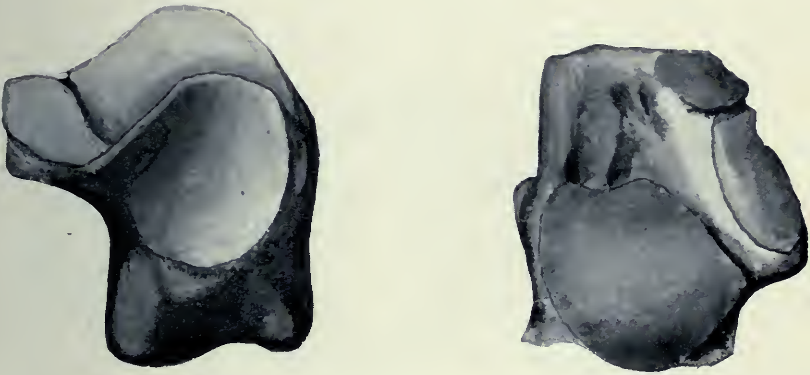

FIG. 11.—Bone 587—Calcaneus secundarius.

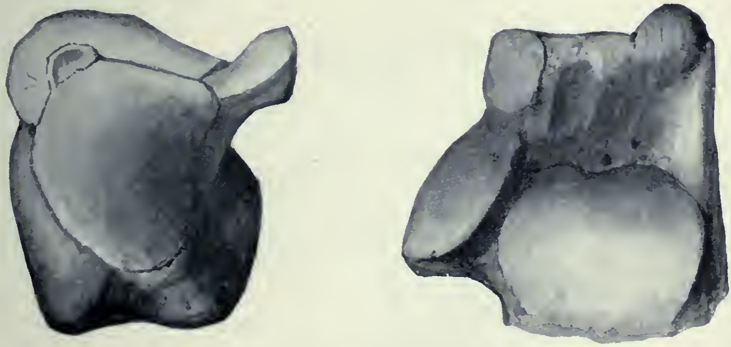

FIG. 12.—Bone 584—Processus trochlearis anterior calcanei (spurius) (procalcaneum).

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FIG. 13.—Bone 101—Inferior trochlea of Moreston.

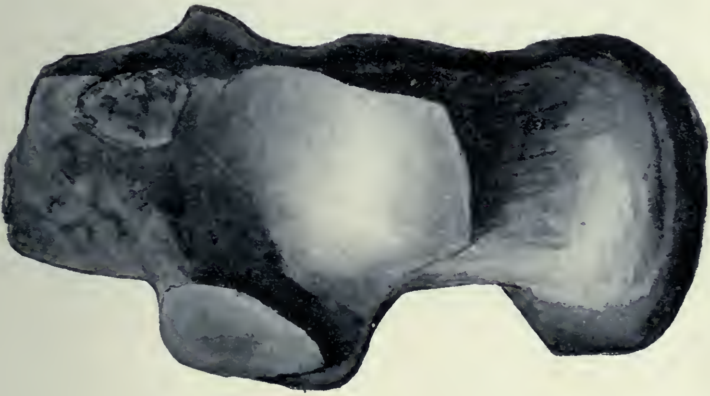

FIG. 14.—Bone B 92—Facet at point of supra-calcaneal tubercle. (Ossiculum in sinu tarci?)

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FIG. 15.—Young bone, showing the epiphysis on processus lateralis tuberis calcanei.

FIG. 16.—Facies articularis media, divided.

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[PLATE XXXVII.

FIG. 17.—Os sustentaculi proprium.

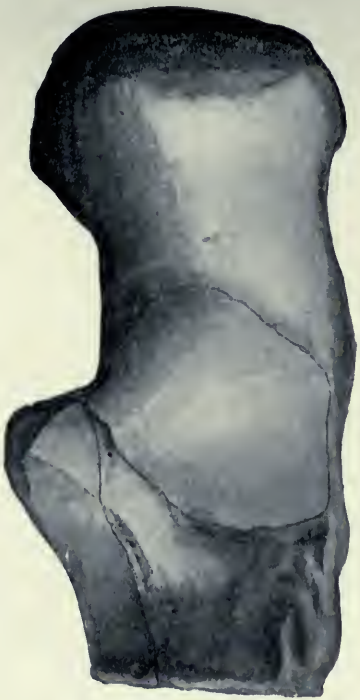

FIG. 18.—Facies articularis media, half divided.
(Os sustentaculi proprium ?)

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The strain of the *tendo Achillis* is thus distributed (1) through the first series of trabeculæ to the *facies articularis posterior*, and (2) to the dense bone of the cuboid tubercle, and so through the plantar ligaments to the rest of the tarsus.

A third series run in curves from the *facies cuboidea* backwards and upwards in curves to the *facies articularis anterior* and the dense bone of the superior surface of the *processus anterior*, the forward and downward thrust being thus distributed through the long arch of the foot.

Between series I. and III. there are no cancelli; a space exists in the *antrum calcanei.* The weak point of the system is the fossa calcanei, and it is here that the outer case is most dense and hard.

A fourth series runs from the middle astragalar facet downwards and inwards to the dense bone forming the inner wall of the case and the inferior surface of the sustentaculum; this is thick down to the cuboid tubercle, and weight from this region is thus thrust downwards and inwards on to the system of cancelli and ligaments, made up of long plantar ligaments, cuboid tubercle, and series II. of calcanean cancelli. This system is also knit together by cross trabeculæ, and gives appearance seen in figure in transverse section.

The whole is thus admirably adapted for the strains put upon it by the movements during life, and the needs of the organism in the erect position.

In conclusion, I wish to acknowledge the great help kindly given me by Professor Macalister, without whose aid this paper would never have been written.

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THE HISTOLOGY OF LYMPHATIC GLANDS: THE GENERAL STRUCTURE, THE RETICULUM, AND THE GERM-CENTRES.

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(*Continued from* page 68.)

Part II.

I leave my observations on three points—the relation to the reticulum of pigment-containing cells, of the trabeculæ and capsule, and of the endothelium—until after I have discussed the nature of the reticulum in the light of my own and previous observations.

In doing so it is necessary to first consider the views of Retterer, who, in a long series of articles (27, 28), denies the existence of any separate reticulum. He believes that the middle of each germ-centre consists of a "plein tissu," which is a collection of cells lying edge to edge without any gaps whatever between them. In these cells are a number of chromophil filaments, which are connected from cell to cell and form a network which lies in the other constituent of the cell protoplasm—a clear substance which he calls hyaloplasm. Further out some of the hyaloplasm has disintegrated, setting free, as leucocytes, the nuclei surrounded by most of the remaining hyaloplasm; while a little hyaloplasm also usually remains adherent to the chromophil filaments and with them does form a reticulum in this part of the gland. The chromophil filaments eventually become elastic fibres. In certain strands the hyaloplasm persists, and becomes converted into white fibrous tissue, thus forming the trabeculæ and capsule. As this is a theory touching the whole gland structure it cannot be fully considered until I discuss the germ-centres, but points especially touching the reticulum may be mentioned now. I cannot find a "tissu plein," and have no doubt as to the existence of irregular empty spaces, even in the middle of the germ-centres in undisturbed sections. They are clearly seen in thin sections, though they might be missed in thicker ones. These must indicate a reticulum of some kind. On Retterer's theory the chromophil reticulum in the "tissu plein" and the fibres in the sinus beams are of different nature from the fibres of the trabeculæ. But they all take the characteristic red colour with Hansen's stain. Also continuity can be distinctly traced from the beams in the germ-centres, through those of ordinary parenchyma and sinuses, to the fibres of the trabeculæ and capsule; while, according to Retterer's theory, the continuity should be between the trabecular fibres and the hyaloplasm. These considerations are all free from the fallacies due to washing, and to other conditions, which Retterer admits to produce a reticulum. To Retterer, however, belongs the credit of having first described the sinus beams as consisting of protoplasm with a fibre developed within it, though he mistook the nature of the fibre. He also was amongst the first to lay due stress on the elastic tissue in the reticulum.

It is unnecessary to follow in detail the literature of the discussion as to whether the reticulum consists of branching cells or of fibres. Hoyer's digestion experiments (16) proved the presence of fibres, but they did not disprove the presence of protoplasm as an integral part of the reticulum. They did, however, finally disprove His' idea (14) that the fibrous matter develops on the outside of the protoplasm.

Stöhr (33), Gulland (10), and others have described the development of reticular from ordinary connective tissue. Gulland describes the development in a long series of preparations. If his account be complete, it proves not only that the reticulum is fibrous from the first, but that its fibres are identical with ordinary white connective fibres. But there are indications in his account of changes which he failed to describe. He says that in the tissue which is developing into glands the reticulum gets finer, and at the same time the nuclei become larger and more numerous than in the connective tissue outside. These changes must mean an increase of the cellular element in the tissue, which may possibly be accompanied by an, unnoted, delay in the formation of fibres. Gulland describes the beams of the cortical sinus (except a few which originate in the septa between the lymphatics from which it is formed) as appearing only after the development of the gland is nearly complete. This cortical sinus, according to him, consists of closed lymphatic vessels lined by a continuous endothelium. It is difficult to see how beams inside these vessels, which contain no connective tissue, can be, or develop from, connective-tissue fibres. Yet these beams are admittedly similar to those in other parts of the gland.

Apart from the foregoing considerations, the belief that the reticulum is purely fibrous rests upon direct observation. Ranvier (25), Bizzozero (2), and others distinctly saw the beams as fibres composed of fibrils, and clothed by endothelium. I have quite failed to demonstrate any endothelial markings upon the beams, as I shall describe later, and Ranvier's own figure of them in the *Traité Technique* shows lines so broken and indefinite that they are quite inconclusive. The Hansen and Mallory-Stöhr stains show clearly that many beams are entirely protoplasmic. The other beams which show a fibre more or less surrounded by protoplasm might be held to consist of a fibre surrounded by endothelium or by clasping cells. But Thomé (36) describes and figures cross-sections with the fibre lying entirely within uninterrupted cell protoplasm, with no limiting membrane anywhere. So that the protoplasm all belongs to one cell, and is quite continuous around the fibre, if Thomé is correct. The gradual increase in the number and thickness of the fibres with age, and their frequent appearance as detached fragments within the beams, which I have pointed out, both argue strongly against the theory of fibres with clasping cells. Bizzozero said that some endothelial cells instead of clasping the fibres were framed by them. He had doubtless seen some of the plate-like beams, which I have described, with fibres in their margins.

The theory that the reticulum is purely cellular is disproved both by Hoyer's experiments and by the use of Hansen's stain. It need not be further discussed.

Possibly the supporters of these rival theories have been misled by studying the reticulum—the one in young, the other in old subjects. Kölliker (20), His (14), and Chievitz (4) noticed the changes with age, and described both anastomosing cells and fibres. Thomé (36) and Sisto and Morandi (32) have recently repeated these observations, and made them more exact. The reticulum certainly consists of both anastomosing cells and fibres, the former predominating in the newborn, the latter in the aged.

My observations of the reticulum in the main confirm those of Thomé. The chief difference is that he does not describe the plate-like beams which I find make a considerable part of the reticulum. Other points in which his description differs from mine are as follows: He describes most of the fibres as undulating. I find that they closely and directly follow the course of the beams. In one or two glands I found that most of them did undulate; but as this condition was exceptional, and yet common in those glands in which it occurred, I attributed it to faulty preparation. He says that the fibre is usually in the centre of the protoplasm. I find that it often lies toward one margin in the narrow beams, and that it usually does so in the plate-like beams. He describes the protoplasmic borders as always straight. I saw them sometimes irregular, clinging like torn drapery to one edge or other of the fibre. He says that no beams consist of fibres without protoplasm. I found many such beams. He considers the comparative scarcity of nuclei in the aged as being apparent only, and due to the nuclei being hidden by the growth of fibres. I believe the nuclei to be really fewer, as one would expect from the disappearance of protoplasm from some of the beams. He says that the circular arrangement of beams is continued only for two-thirds of the way round the germ-centres. I find that it goes all the way, except where interrupted by proximity to a sinus. Lastly, I have not definitely confirmed his statement that in beams cut across one can see the fibre situated in the midst of uninterrupted protoplasm. Many fibres, as I have described, do not stretch the whole length of the beam which contains them, and the ends lie loose in the beams. I find it difficult to distinguish with certainty between this appearance and that which Thomé describes and figures. Nevertheless, for the reasons already given, I agree with him that the fibres are so surrounded.

Sisto and Morandi describe two separate reticula. One is fibrous, the other consists of anastomosing cells. These are often in contact, the fibres supporting the cells; but the two networks are essentially separate structures, and are nowhere continuous with each other. Their reason for this statement is that cells and fibres lie in different optical planes from each other. I can find no evidence of this; but when protoplasm surrounds fibres, it, of course, comes into focus slightly earlier and might give rise to a false impression. They describe some fibres as being surrounded by cell processes: in this case, there can be no question of the protoplasm and fibres lying in different planes, and no mention is made of any visible separation between them, nor of anything to show that one is merely attached to the other. So that this description agrees exactly with that of Thomé of a fibre lying within protoplasm. They describe the changes with age very fully, and point out that in glands from old subjects the fibres have very greatly increased, while the cells have so shrunk as to no longer form a network, and to be merely attached to the fibres. This suggests that the cells have never been truly independent of the fibres; and as there is no inter-cellular matrix in the gland, in which fibres could be formed, one is at a loss to know how the progressive formation of fibres goes on if they and the cells are really independent of each other. The belief that they are not really independent is supported by the fact that I many times saw beams with fibres in them directly continuous with others without fibres; and I do not doubt that all the beams, both narrow and expanded, and those with fibres as well as those without, form one continuous whole, and not two separate networks.

In almost all other respects Sisto and Morandi's account agrees with my observations. They remark that in the very young considerable areas of gland may be free from fibrous reticulum; in other words, fibres have not yet developed in the beams. They describe swellings, which are themselves fibrous, upon the fibrous reticulum. In the cellular reticulum they describe large cells, which often have membranous expansions. Some of these cells are supported by fibres of the fibrous reticulum, which are in contact with the cells along one or more or even all of their edges. These evidently correspond to my plate-like beams. The large cells are the plate-like beams while purely protoplasmic, or with fibres developed in one or more of their margins. Sometimes, as Sisto and Morandi point out, two cells lie edge to edge to form one plate. The fibrous swellings are similar beams which have become fibrous throughout, and colour a diffuse red with Hansen's stain, as I have described. Their description of the elastic tissue, and its increase with age, agrees essentially with my observations. They agree with me, and therefore disagree with Gulland, in describing the nuclei of the reticulum cells as containing several obscure points—nucleoli or net-knots. They state that a considerable proportion of the fibres have longitudinal striation. While I found such striation occasionally, I should say that it occurs only in a small proportion of the fibres.

The relationship between the fibres of the reticulum and those of ordinary connective tissue is still undecided. Mall (21) and Orth (24) have established that there are some chemical differences, and Thomé (36) insists upon the fibrillar nature of the one and the non-fibrillar nature of the other. On the other hand, the optical continuity of fibres of the reticulum with those of the capsule, and of the latter with those of the surrounding connective tissue, is established by numerous observers, and I can confirm it. The nuclei of the two tissues either very closely resemble each other or they are identical. Thomé, admitting this, suggests that the same cells can at different times construct fibres of different nature (36). Gulland (10), in his observations on the development of reticular tissue, shows that it is developed in and probably from ordinary connective tissue. Delamere (6) points out that the fact of reticular tissue not producing gelatin on boiling constitutes a resemblance to embryonic connective tissue.

I can add to these considerations the fact that subcutaneous connective tissue from over the ulna of the newborn kitten contains a few fibres which gives the same result as narrow reticulum beams with Hansen's picro-fuchsin, one or both sides showing a distinct though thin yellow margin. Taking this, together with the foregoing points, it seems possible to consider the reticulum fibre to be a connective-tissue fibre so modified in its development that the protoplasm of its formative cell remains longer about it, and that it either is not fibrillar or does not show its fibrillar nature until an advanced age. In fact, that its development has been delayed. This would involve an acceptance of the view that connective-tissue fibres may, at all events sometimes, be developed within the cells, for in the glands there is no other matrix from which the new fibres, which certainly do develop, can be formed. Such a relationship as I suggest is not contradicted by the chemical differences demonstrated by Mall. They are differences of degree rather than of kind, depending chiefly upon the exact temperature, or the exact percentage strength of the reagent, and not showing any essential dissimilarity. This is shown by the fact that as regards the hydrochloric acid reaction, Mall admits that tendon from different parts even of the same animal varies in its reaction. While the differences on boiling seem actually confirmatory of my view, according to Delamere.

I may now summarise my views on the reticulum as follows: In the newborn animal it consists chiefly or entirely of branching cells, some of which already contain fibres or particles of a fibrous nature which increase and amalgamate to form fibres in course of time. Fibres develop eventually in all the cells, and the cell protoplasm shrinks so that some fibres are eventually left with no protoplasm at all. Many of the cells are widely expanded, with only short processes, so that a sponge-work is formed rather than a network. These are the yellow stained plates of my preparations. Some of these plates consist of two or more cells, with margins in apposition. In the plates the fibres develop either along the margins, or as a diffuse deposit of fibrous particles all over the cell. The former are the yellow plates with one or more red margins, the latter become the red plates which I have described in adult glands, and correspond to the fibrous expansions of Sisto and Morandi. The beams of the germ-centres either are younger than those of the sinuses and ordinary parenchyma, or else for some reason they resist the fibrous change longer. The nuclei of the reticulum are at first large, light, and round or oval. With age many, or all, of them lose their rounded shape, and become angular or spindle shaped. The chromatin at the same time increases, and runs together in shapeless masses. These degenerate nuclei are most frequently found upon the beams with much fibrous matter and little protoplasm. The fibres are related to ordinary connective-tissue fibres, of which they may be merely a developmental variation.

To complete the study of the reticulum it is necessary to examine its relations to pigment cells, endothelium, and trabeculæ.

Trabeculæ.—Many sinuses which have no true trabeculæ have in their centre, as von Recklinghausen (26) said, an unusual disposition of the reticulum beams. These take an almost longitudinal direction, and by crossing each other they form a plexus which looks like a very loose trabecula, while they retain their characters as independent beams. Thomé describes another arrangement (36), which I have seen in many animals. This is, that at the place where a cortical trabecula might be expected to exist, there is no true trabecula, but instead several separate thick reticulum beams come off from the capsule in a bunch, cross the cortical sinus, and run inwards, almost parallel, through the cortical parenchyma. They are so close that there is scarcely room for one layer of lymphocytes in between them. They run straight on for some distance, and eventually lose themselves by anastomosing with other beams. Where these bunches of beams spring from the capsule there is often a thickening of the capsule protruding into the gland, just as at the base of an ordinary trabecula. In other cases, true trabeculæ which do not reach right through the cortex break up into similar bundles of almost parallel beams. Even well-formed trabeculæ always contain some leucocytes, and often whole rows of them, while their tissue varies from very compact to a looseness which suggests reticular tissue. So there exists a complete series of forms, from that of the most irregular sinus reticulum up to that of definite compact trabeculæ. In many glands, notably in dogs, all these conditions can be noted in one section.

These facts, together with the optical continuity of their fibres, suggest a close relationship between the reticulum and the trabeculæ. Apart from the unstriped muscle in some, and the elastic tissue in all, the trabeculæ consist of a mass of fibres usually described as ordinary connective tissue. Mall, on chemical grounds, believes them to be really reticular tissue (21). Thomé says the same, because he can find no trace of fibrillation in them. He, however, could not prove their reticular nature by the Hansen or Mallory-Stöhr stains, because the fibres lay too close together for accurate observation. This difficulty is overcome by the loose nature of the trabeculæ in the badger, and the mesenteric glands of the pig. In both these animals I have been able, with Hansen's stain, to demonstrate in the trabeculæ red fibres with the characteristic yellow margins. Fibres so bordered are not numerous, but they are sufficient to establish the identity. The nuclei of this tissue bear out its reticular nature. They are like those of the reticulum, but there are fewer of the large round and oval, and more of the angular and elongated varieties. I may add that I have also demonstrated typical reticulum fibres in the loose textured capsules of glands from the civet-cat and jackal.

Thomé believes that the special arrangements of reticulum just described are trabeculæ in process of formation, and he builds his new schema for lymphatic glands upon this belief. It is supported both by the larger number of trabeculæ in adult than in younger glands, and by the fact that the state of the nuclei and the rarity of protoplasm on the trabecular fibres suggest that they are at a late stage of development. On the other hand, one sometimes sees very thick and well-formed trabeculæ in young glands.

The Endothelium.—There is great diversity of statement, even amongst recent authors, as to the presence and distribution of endothelium in lymphatic glands. I have investigated it by the injection of silver nitrate solutions of strengths varying from 1–100 to 1–500, and I also treated sections with the same solutions. I made most of the sections thick, and so ensured having in them many places in which I was looking at the undisturbed surfaces of trabeculæ and medullary cords, and not at sections of them. I found clear endothelial markings within blood-vessels, and therefore my methods were not at fault. I examined thirty glands from ox, sheep, pig, dog, and cat. In some sections I could find no endothelial markings except in blood-vessels. In the remainder there were patches upon one or more trabeculæ or within the capsule, but the great majority of the trabeculæ showed none, nor did the greater part of the capsule. I found markings on the surface of the parenchyma in only two cases, and in these they were very indefinite. I have also stripped pieces of capsule from the cortical side of three mesenteric glands of oxen, and, after freeing their internal surface as far as possible from adherent pieces of parenchyma, have treated them with silver nitrate solution. These preparations showed some patches of endothelium, but for the greater part they were free from it. It is, however, possible that in making these preparations I tore some endothelium from the capsule. I have never been able to demonstrate any endothelial markings on the reticulum beams. Von Recklinghausen had much the same experience, and doubted the existence of endothelium on the parenchyma; while he said that having seen it frequently on capsule and trabeculæ, he might "venture to say" that it is there throughout the gland (26). Other more recent writers speak very confidently of its presence even on the parenchyma (Stöhr (33), Clarkson (5), Fleury (8)). Delamere (6) says that on the parenchyma it is inconstant, except over the germ-centres. Other writers (Böhm and Davidoff (3), Schäfer (31)) do not describe it on the parenchyma at all. With Ranviers' opinion (25) that it clothes every reticulum beam I have dealt already. My own view is that even upon the trabeculæ and capsule it is not found sufficiently often to warrant the belief that it exists upon them throughout the gland. It was only in a decided minority of places where the surface of capsule and trabeculæ could be examined that I found endothelial markings. It is true that in many parts one finds the border between parenchyma and sinus composed of a definite line with enlargements, which looks like the section of an endothelial membrane and its nuclei. But usually such appearances are more definitely seen in thick than in thin sections. They can, therefore, equally well be explained as reticulum beams, with thin nuclei, running approximately parallel to the direction of section, and showing best in thick sections, because there they are not cut through as they would be in thinner ones. In any case, this appearance is seen only in parts, and usually only in the cortex. It is sometimes seen as two or even three parallel lines one within the other: in these cases it is still less likely to be endothelial. On the other hand, nearly all medullary cords, and much cortical parenchyma, show a quite irregular margin when cut across, and their border is marked only by the closer network and the presence of more free cells than are found in the sinuses. If the cortical sinus is developed from closed lymphatics, it must at one time have had a complete endothelial lining, but this may have partly disappeared. Von Recklinghausen's observation that injection, either artificially, or naturally by the chyle, forces particles through into the parenchyma, proves that the channels do not remain closed. On the capsular side of the cortical sinus of the badger I have observed that the loose spaces of the interior of the loosely built capsule open freely into the sinus without any intervening endothelium. In the ox I have cut through the capsule at an extremely acute angle, and find that its internal surface presents an absolutely ragged edge of loose fibres, instead of the somewhat regular surface which one should find in cutting an endothelium at whatever angle.

I therefore conclude that the sinus endothelium is found only in patches, which are frequent upon the capsule and trabeculæ, but rare upon the parenchyma. These I would compare to the patches of endothelium found in areolar tissue and within synovial membranes. Both have doubtless been formed in the same way. The cells and nuclei of these patches present no peculiarities distinguishing them from reticulum cells. Where reticulum beams lie close together, the cell margins must often touch each other, thus bridging the intervening space, and so producing all the appearances described. As these cells are mesoblastic in origin, they may, when so arranged, be rightly called endothelial, but I agree with Saxer (30) and Thomé (35 and 36) that they are really reticulum cells.

Pigment-containing Cells.—These are sometimes spoken of as being only in the sinuses. They are really found all over the glands, but in the parenchyma they are always most numerous at parts near to sinuses. They are often absent, and usually rare in germ-centres, yet I have counted as many as six in one section of a germ-centre from a civet-cat. They contain black or brown pigment in granules, and also leucocytes, red corpuscles, particles of hæmaglobic matter, and other objects. They are irregular in outline, branching, and, when numerous, anastomosing by their branches to form a network. They vary in size. They usually contain only one nucleus. When there are more than one, the remainder often, and perhaps always, belong to ingested cells. Their minute structure is obscured by the pigment and enclosures, and it is difficult to say how many types of pigment cells there may be. Thomé distinguishes two kinds (35): the first, found in the sinuses, branch, and have sparing chromatin. The others, found in the parenchyma, have no processes but more chromatin. The former are, he says, continuous with and descend from the smaller cells lining the sinuses, which he calls endothelial, though he considers them to be ordinary reticulum cells. The latter, he says, are free, and are really leucocytes. It is on all grounds probable that many of these pigment-bearing cells are really free leucocytes, but many even in the parenchyma are certainly identical with those in the sinuses, and are really reticulum cells. They branch—in the American opossum I have found them forming an anastomosing network in the parenchyma, and they were still present in a section which had been washed so that the free leucocytes had disappeared from it. Woodhead says that foreign particles in the glands are taken up sooner or later by the fixed cells of the gland (39), thus confirming my view that, at all events, many of these parenchymal pigment-bearing cells are really reticulum cells.

We must therefore add to the description of the reticulum—(1) that its elements form a great part, and often the whole, of the trabeculæ; (2) that its cells in places form patches of endothelium at the borders of the sinuses; (3) that its cells are often phagocytes.

The Germ-Centres.

Their distribution and their reticulum have already been described. Most of them present the typical appearance of a light middle surrounded by a dark ring, but some are dark throughout, and others have no dark ring. The middle portion of the typical germ-centres contains numerous nuclei of two distinct kinds. The first are large, round or oval, lightly stained, and contain one, or usually more, dark spots. Some of these are certainly reticulum nuclei. The second kind are small, dark, rounded nuclei. The two kinds are in about equal numbers, and are both evenly distributed amongst each other. There may also be one or two angular, or elongated, reticulum nuclei, and a few pigment-containing cells. Between these nuclei is a mass of protoplasm, in which no border line can be seen between the protoplasm of the reticulum and the cell bodies surrounding the nuclei. There are always irregular empty spaces in this protoplasm, the meshes not being completely filled. The protoplasm is less, and the spaces between it greater at the periphery than at the middle of this portion of the germ-centre. The light middle passes suddenly into the dark ring. This has the circularly arranged reticulum already described, and a plentiful supply of blood capillaries, also circular in arrangement. The meshes are filled by a multitude of small dark nuclei, like those just mentioned, each of them surrounded by a very small protoplasmic body. There are also reticulum nuclei, of which the angular and elongated usually predominate, though sometimes there are most of the oval and rounded ones. Immediately outside the dark ring, or between the circular fibres, or sometimes within the ring, there are a number of lymph lacunæ, or small sinuses. These are rarely absent; often they are so numerous that they enclose the germ-centre in a complete plexus of narrow sinuses. Sometimes they are large, and, on section, half of the germ-centre may appear to hang free in a lymph space.

In some germ-centres the large light nuclei are rare or absent, and the whole is filled with the small dark nuclei. Sometimes all the germ-centres in a gland are in this condition. These are the germ-centres which are dark throughout. A very similar appearance, which must not be confused with it, is obtained when a section passes through the periphery of a germ-centre cutting only the dark ring. This is readily detected by following through the series of sections. The circular beams around germ-centres may be few or many; sometimes they are absent altogether. In rarer cases both the circular beams and the dark nuclei of the periphery are absent, and their place is taken by ordinary reticulum with empty meshes. These are the germ-centres with no dark ring. Some of them also have no dark nuclei in the middle portion.

In washed sections the germ-centres usually disappear bodily, leaving circular gaps. The circular arrangement of beams, or a part of it, is often left, the reticulum having given way just within this, where the beams are weakest because they are thin without being fibrous.

It will be seen that the above description is incompatible with the existence of Retterer's "tissu plein." For I have no doubt of the real existence of irregular empty gaps even in the middle of the germ-centres; they are clearly seen in thin sections. Retterer admits that the classical appearance is really found, as a pathological or post-mortem change, in animals which have been starved or have died from disease, and in glands which have not been fixed for some time after death. But these conditions do not hold for the majority of glands I have examined, nor for those studied by other recent observers who also failed to find a "tissu plein." In addition to this point of direct observation, and to the considerations already described under the head reticulum, there are the following objections to Retterer's account: According to him, the cells in the middle are all young, and the age of the others varies as their distance from the middle. We should therefore expect the different kinds of cells to be arranged somewhat concentrically. In reality, we find the small dark nuclei evenly distributed amongst the large light ones in the middle. Further out we find a ring composed of dark ones, and still further out, in the ordinary parenchyma, is a loose arrangement, with both kinds present, though dark ones are in a majority. Retterer accounts for the dark ring by saying that toward the outside of the central part of the nodule the nuclei become chiefly chromatin, but on his theory I cannot understand the reappearance of light nuclei scattered amongst the others outside the dark ring. Retterer acknowledges the production of a reticulum by washing, but considers this to be due to a destructive process which has broken up the "tissu plein." It is doubtful if such an explanation could account for the extremely rapid disappearance of most of the free cells from the ordinary parenchyma in the early stage of washing, and it is significant that the last part of it to be freed from them is always the outside margin bordering on the sinuses; that is to say, the very part at which, according to Retterer, they are most free. Again, if the whole parenchyma be one tissue, thinning and weakening toward the outside, it is impossible to understand why nearly all the germ-centres are carried bodily away during washing, while the more peripheral and presumably more fragile ordinary parenchyma remains. In conclusion, Retterer's view of leucocytes as cell fragments, which move only in virtue of disintegrating processes, is quite at variance with the opinion of nearly all observers; for example, since Retterer published his articles, Jolly (17) has carefully described the movements of lymphocytes, while Maurel (22) has followed their life-history, and found them at first motionless and afterwards mobile. We may, therefore, put aside Retterer's "tissu plein," and regard the germ-centres as really having a reticulum.

The small cells with dark nuclei correspond in all respects with ordinary lymphocytes. There remain to discuss the cells which divide in the germ-centres. As mitoses are much more frequent amongst these than in any other part of the gland, it is certain that they are the mother-cells of most of the lymphocytes formed in it. Flemming pointed out (7) that they may be either fixed cells belonging to the reticulum or the capillaries, or they may be free cells derived from the blood. He left the point undecided, though he inclined strongly to the latter view. Stöhr has recently said much the same thing (34). Beard (1), from studies of the development of *Raja batis*, has proved that the thymus is the first source of leucocytes in the body, and he concludes that it is the parent source of all leucocytes, because any other source would be superfluous. If this conclusion could be substantiated, it would, of course, decide the source of the mother-cells in the germ-centres. But, however superfluous, other subsequent sources may exist. Beard brings forward no reasons to show them inherently improbable, and they can therefore be disproved only by a detailed exclusion of each one of the many possible sources. Beard accepted Stöhr's refutation of Retterer's epithelial theory—the other possible sources he left untouched. We cannot therefore exclude the fixed cell theory on general grounds.

On the other hand, the early presence all over the body of leucocytes, which are of thymus origin, makes it impossible to conclusively prove the existence of any other later source unless by direct observation of their development. Klein gave a very definite account of such a direct observation (18), the endothelium of a lymphatic proliferating, and the young cells breaking away to form lymph cells; but he was working with old methods, and it is impossible to be sure that what he saw were really leucocytes. In the absence of any more satisfactory direct observation, we have no proof of any source of leucocytes subsequent to the thymus.

Gulland believes, on other grounds, that the mother-cells come from the blood (9 and 10). He found that the first kind of leucocytes to appear in developing adenoid tissue were wandering cells with lobate nuclei, and these being adult forms must have come from outside, *i.e.*, from blood or lymph. Dividing leucocytes and daughter-cells were not found till later, and he considered that there was no other source for these but the leucocytes with lobate nuclei. But the presence of leucocytes, which we may admit to have been introduced from without, does not exclude the possibility of other leucocytes being formed from the fixed cells previously within the tissue. The time relation—daughter-cells appearing only after leucocytes with lobate nuclei had become plentiful—would be more significant, were it not for the equally significant fact, which Gulland records (10), that, shortly before the daughter-cells appear, the connective-tissue cells proliferate rapidly and their nuclei become larger. Gulland also remarks that it is very difficult to identify the dividing cells as leucocytes; they are certainly different from all known forms of leucocyte. Gulland describes their difference from the reticulum cells (9). This lies chiefly in the facts that reticulum nuclei have only one dark spot or nucleolus, and that they are smaller and more oval in shape than those of the mother-cells. On the first point I have already said that I disagree with him, as do Sisto and Morandi (32). As to the second, I find that the large light nuclei in the germ-centres present so many gradations of size and shape that it is impossible to draw a dividing line between them on these points, and some of these nuclei are undoubtedly reticulum nuclei. A further point against Gulland's theory is the fact that leucocytes with lobate nuclei are extremely rare, or even absent, in the germ-centres, as he himself has said (9), and the transformation of the incoming leucocytes into the very different mother-cells could scarcely be so sudden as to account for this extreme rarity.

There is still, therefore, no certainty as to the nature of these mother-cells. To further investigate it I have made the following manipulations: By pressing with a needle on the cover glass over a section many of the free cells can be made to move to and fro. Those of the ordinary parenchyma move most readily, and most of those in the germ-centres do not move at all. Germ-centres can be separated from sections under low magnifications by means of needles without much difficulty. Many small cells escape while this is being done. I cannot be sure whether these come from the germ-centre, the surrounding parenchyma, or both. When once the germ-centres are separated, I find great difficulty in disintegrating them further. I tore them to pieces by means of needles, using Zeiss' A objective and No. 2 eyepiece during the process. They separated readily into fragments, but the cells did not come away individually. Reticulum beams could be seen here and there projecting from the torn edges of the fragments, but only minute portions of them were thus laid bare. I also pencilled sections under the same magnification. Cells very readily escaped from the ordinary parenchyma, so that the reticulum was laid bare, but from the germ-centres only a few escaped, and when I attempted to carry the process further the germ-centres were destroyed.

These experiments show an unusual adherence of the mother-cells to the reticulum. This is not sufficiently explained by saying that their large size prevents them escaping from the meshes, for they did not escape even when the germ-centres were torn across, and the meshes broken. Though this adherence is far from being enough to establish a belief that the mother-cells are part of the reticulum, it does suggest further inquiry on that point. At present we must leave the problem where Flemming left it, except that we may regard rather more favourably the possibility that these mother-cells are really reticulum cells.

Flemming's objection to this, that the mother-cells are not branching as are reticulum cells, is uncertain, and, if correct, is really not important. They are equally different from leucocytes, and if derived from either must have undergone considerable transformation before dividing.

Whatever be the origin of the mother-cells there still remains the question of how and why germ-centres are formed. Mitosis occurs amongst the cells of the ordinary parenchyma without germ-centres resulting, and it is frequent in the glands of the fœtus and the newborn in which, as Gulland pointed out (12), germ-centres do not exist; so that mitosis is not a sufficient determining factor. Beard gives the simple explanation that some leucocytes do not wander, but remain and divide, forming little groups of two and four, and cell nests, which are the original germ-centres (1). But he does not tell us why they do not wander. Gulland attributes their formation to the richness and peculiar distribution of the blood-supply (12), which causes a profuse diapedesis at these spots; and then the leucocytes, being caught by the reticulum, remain and germinate. But he also describes the arrangement of capillaries as being preceded by an increased collection of leucocytes, so that he does not really differ from Beard. Neither of these theories takes into account the difference between the reticulum in the germ-centres and that in the ordinary parenchyma of an adult gland. This might possibly be due to a difference of blood-supply; it could scarcely be caused by an accumulation of leucocytes.

This difference really is that the reticulum in the germ-centres is always in the condition of young reticulum. It may be that it is really old reticulum which is kept permanently in this condition by a peculiar richness of blood-supply, or some other cause. Or it may be that it really consists of young, newly-formed beams. The latter alternative is most in accord with Flemming's belief that the germ-centres are transitory structures. This belief is confirmed by my observation of the two varieties of a-typical germ-centres. Those with all their nuclei of the small dark variety seem to me to be germ-centres which have recently lost their activity, while those which have a light middle but no dark ring of daughter-cells seem to be germ-centres just commencing activity. The occasional occurrence of these two varieties therefore, by confirming the transitory nature of germ-centres, supports the idea that the reticulum of germ-centres really consists of newly-formed beams. But if so, I have not been able to follow the process by which the germ-centres, with their surrounding circular beams, assume later the arrangement of ordinary parenchyma. In any case, the state of their reticulum must be taken into account in any satisfactory theory of the origin of germ-centres. The idea which seems to me most feasible, though it does not meet all difficulties, is that germ-centres are points at which not merely new leucocytes but new gland tissue is being formed.

The dark ring at the outside of the germ-centres is caused by a great accumulation of daughter-cells, which, being small, have probably been washed through the interstices in the germ-centre, as Gulland suggests. From the dark ring most of them probably pass into the lymph sinuses, which I have described in and about the dark ring, and thence proceed to the main sinuses of the gland. It is improbable that any large proportion of them passes directly into the surrounding parenchyma, or the change from the crowded state of the dark ring to the looser ordinary parenchyma would not be so sudden. But some daughter-cells doubtless miss the sinuses, and pass into the ordinary parenchyma.

[For the literature referred to in the text, see Part I. of this Paper — Vol. XXXIX., *Journal of Anatomy*, October No., 1904, p. 66.]

ON THE PRESENCE OF A SUPERNUMERARY MILK INCISOR IN THE HUMAN DENTITION. By CHARLES EARLE, B.Sc., *Mt. Vernon, New York, U.S.A.*

THE presence of supernumerary permanent teeth in the mammalia is of frequent occurrence. Bateson in his study of variation has recorded a great many cases of extra permanent teeth, but as far as I am aware there are few records referring to the addition of teeth to the deciduous dentition.

In the case of extra teeth in the mammalia, according to Bateson this phenomenon has occurred most frequently in the Anthropoidea among primates. On the theory of reversion we would not expect this to happen most often in the highest group of mammals, but among the lower and more primitive forms.

In the lower primates the addition of extra incisors to the deciduous series has been noticed by Filhol in the genus *Adapis*, an extinct generalised type from the Upper Eocene of Europe. In *Adapis* there are three incisors on each side in the milk series, in contrast to two of these teeth of the permanent set. This reversion in *Adapis* surely points to the fact that the primates have originated from a more primitive Eutherian, which had the typical number of teeth, viz.:—

I. 3/3. C. 1/1. Pm. 4/4. M. 3/3 = 44.

In *Hyopsodus* of the Middle Eocene of the United States we meet with a primate which has the full number of teeth, and the only one known in this respect. However, in this genus the true molar pattern is already quite specialised, and probably too much so to have led to higher and permanent results.

The object of this brief paper is to record the presence of an extra incisor in the upper milk dentition of a boy about five years of age. This tooth was the third to be erupted, and came in position between the left median and lateral incisor. It is slightly less in breadth than the superior median, and has the same proportions nearly as the lateral incisor. The milk dental formula in this case is:

$$\text{I. } \frac{2-3}{2-2} \quad \text{C. } \frac{1-1}{1-1} \quad \text{M. } \frac{2-2}{2-2} = 21.$$

In the case of the present subject the upper milk incisors do not seem to be especially crowded in the premaxillary bone, and the median teeth are symmetrically arranged in relation to the symphysis. I here remark that the single lateral incisor on the right side is much smaller than either the left lateral or the supernumerary incisor on that side.

In conclusion, it appears that the presence of this extra tooth is simply an anomalous case, and can be compared with that of extra digits. I believe it has no significance from an evolutionary standpoint, and cannot be considered as a case of reversion.

THE THEORY OF NERVE COMPONENTS, ESPECIALLY WITH REGARD TO ITS RELATION TO THE SEGMENTATION OF THE VERTEBRATE HEAD. By

Onèra A. Merritt, B.Sc. (Lond.), M.Sc. (Birm.).

The object of the following paper is to give an account of the Theory of Nerve Components, and some of its recent developments, which may prove of interest to those physiologists and morphologists who may not have time or opportunity for studying the extensive and rapidly increasing bibliography dealing with this aspect of comparative neurology.

CONTENTS.

INTRODUCTION.

In early anatomical works the nerves of the body were divided into two systems, the motor and the sensory, which were primarily defined by their physiological characters. This method was prevalent until 1886, when Gaskell (12) subdivided these two main systems according to the histological and physiological characters of the component fibres of the nerves.

Gaskell made two radical changes: he used the histological method to differentiate nerves, and substituted nerve fibres for nerves as morphological units. According to the modern nerve component theory, of which Gaskell may be regarded as the founder, the principal types of nerve fibres are classified into systems, each system being termed a 'component of the whole system.' A system may be defined, according to Herrick (13), "as the sum of all fibres in the body which possess certain physiological and morphological characters in common, so that they may react in a common mode, and each is defined by the terminal relations of its fibres, by the organs to which they are related peripherally, and by the centres in which the fibres arise or terminate. The fibres of a single system may appear in a large number of nerves, repeated more or less uniformly in a metameric way (*e.g* cutaneous for the spinal nerves), or they may be concentrated in a single nerve, as the optic." A knowledge of nerve components is essential to the understanding of the evolution of the nervous system, for "the arrangement of the components in its main outlines, including the terminal centres of the special sensory systems, is a palingenetic character of great permanence throughout the Vertebrata, which is not due to the direct influence of the present environment."

This modern conception has shown how comparative gross anatomy of the nervous system may lead to erroneous results, especially when attempts are made to homologise the condition in the lower Vertebrates with an apparently similar condition in the higher. For example, there are said to be ten pairs of true cranial nerves in Mammalia; hence, without regard to the conditions in Fishes, their nerves also were divided into ten pairs, and further the nerves of Mammals and Fishes were homologised with one another because they were both represented by the same numerals, and the functions of the nerves of Fishes were defined by the function of the so-called homologous nerves of the Mammalia. This, however, is no longer considered the right method of argument, the condition of the mammalian nerves not helping to explain the condition of the nerves of a Fish, for only by a thorough understanding of the nerves of the Fish can we comprehend the value of a single mammalian nerve.

To understand nerve fibres, it is necessary to study the distribution of nerves in both adult and embryo, as well as the histological and physiological characters of the component nerve fibres. Having defined the number and characters of the components of any species, certain interesting questions now arise. Which of these components are primitive and occurred in a typical primitive segmental nerve? Which nerves of the present form are most primitive? And lastly, can we determine the primitive number of segments in such a structure as the brain by the study of the nerves connected with it? Unfortunately, this last question has been discussed from two different points of view: that of the embryologists, who depend entirely upon neuromeres, out of which nerves of unknown components and destiny grow, and that of the ordinary neurologist, who argues from the condition of the nerve and its components in the adult, but disregards the history of the nerve in ontogeny and phylogeny. It is the work of the neurologists of the future to correlate these two points of view, and solve the question of the segmentation of the head. The theory of nerve components is now accepted in its main outlines by all zoologists as the most far-reaching and important morphological conception of the nervous system. Certain important but as yet doubtful details need further investigation, such as, for example, the analysis of the afferent splanchnic system and the relations of its parts to one another, and the determination of the nature of the components of the Optic and Olfactory nerves.

The Evolution of the Nerve Component Theory.

The first step towards an accurate knowledge of nerve components was made in 1810 by Bell (6), and subsequently by Magendie. According to their theory, each spinal nerve has two components, motor and sensory, the sensory elements coming from the dorsal root, which was ganglionated, and the motor from the ventral non-ganglionated root. The next important work was that of Gegenbaur, who in 1871 demonstrated the compound nature of the Vagus in *Notidanus griseus*. Even if it be proved that Gegenbaur is wrong, he did a great service in helping to abolish the old hard-and-fast conception of the numerical arrangement of the cranial nerves.

In 1877 Balfour (3) changed the whole outlook of neurologists by insisting upon the importance of embryological data. Arguing from these, and from the conditions then known in *Amphioxus*, he proved that the cranial and spinal nerves were not homodynamous, but that they had become differentiated from one another at a stage when only mixed motor and sensory posterior roots were present.

By the combination of physiological, histological, and anatomical methods, Gaskell (12) in 1886 laid a scientific foundation for the nerve component theory. Gaskell made mistakes in his deductions, probably because he worked on Mammals, but his methods were correct, and all work has since been done on lines laid down by him. By histological methods Gaskell distinguished the characters of fibres, and by dissections and experiments he also determined their course and function. Hence he was able to state (12) that "nerves which supply vascular and visceral systems have certain common histological characters, while nerves of the same function have also a well-defined anatomical course." This is the statement of an intellectual revolution as regards neurology. But Gaskell did not content himself with the external relations of nerves only: he likewise inquired into their origin in the central nervous system, at least with regard to spinal nerves, and discovered that the external origin from the spinal cord may be unimportant compared with the internal origin. As a result of his observations, Gaskell divided his afferent and efferent nerve fibres into somatic and splanchnic respectively, so that in a typical spinal segment there were four components.

Gaskell, like his contemporaries Goronowitsch and Stannius, considered that the cranial nerves were homodynamous with the present form of the spinal nerves, and that the spinal nerves in their present conditions were primitive. He therefore attempted to conform the cranial nerves with the spinal nerves. He says: "The cranial nerves, as a whole, are founded on the same plan as the spinal . . . . it is clear that no correspondence exists between each of the so-called cranial nerves and such a perfect spinal nerve as is met with in the thoracic region; in order to obtain a cranial segment comparable to any of the thoracic segments, parts of different cranial nerves must be pieced together, just as in the cranial region the first cranial nerve segment, for instance, is not complete without taking into account that part of the spinal accessory and of the ascending roots of the Trigeminal and the Vagus which belong to that segment." Gaskell did not attempt to homologise the nerves of special sense, as they were all considered 'peculiar.'

The Oculo-motor, Abducens, and Patheticus were regarded as comparable with a complete spinal nerve by the addition of efferent visceral (sympathetic) fibres, and what Gaskell considered the remnants of sensory ganglia and roots.

It is important to notice that Gaskell considered the Sympathetic as an integral portion of the nervous system, not as anatomically and physiologically distinct from the so-called 'central nervous system.'

Gaskell made two mistakes; (1) he did not sufficiently realise the qualitative differences between nerves. Thus, he classed all splanchnic nerves together, whether they supplied taste-buds or the general visceral surfaces. (2) He neglected the origin of the nerves in the brain. The former mistake was made, doubtless, because he did not work on a low vertebrate type; but it is serious, for only by an understanding of the various types of somatic and splanchnic fibres (sensory) is it possible to appreciate the great modifications and specialisations of the cranial nerves and the evolution of the brain.

In 1895 Strong (37), working along Gaskell's lines on the cranial nerves of Amphibia, divided the nerves into the following components:—

- Somatic.
  - A. Sensory.
    - 1. General Cutaneous.
    - 2. Special Cutaneous or Lateralis.
  - B. Motor.
- Splanchnic.
  - A. Sensory—Communis (end-bud nerve fibres).
  - B. Motor.

"The somatic sensory system is generally the means by which stimuli are received from the external environment, and gives rise to reflexes which directly affect the animal's relation to its environment. In man, it usually gives rise to sensations and conscious reactions. On the contrary, the stimuli received by means of the splanchnic sensory system give rise to reflexes which affect the organic activities of nutrition, respiration, circulation, and do not commonly produce sensations and voluntary movements" (21).

In 1899 Herrick published his paper on *Menidia.* His methods of work were similar to those of Strong, and his results were similar but more certain, more wide-reaching. Hence he is able to make statements while Strong could only make suggestions.

Since that date Herrick (14) and Cole (8) have worked on *Gadus*, Cole (10) on *Pleuronectes*, Johnston (29) on *Petromyzon*, and Strong (39) on *Squalus acanthias*, etc. All these studies have confirmed Strong's original work on Amphibia, so that the nerve component theory is no longer a theory but an acknowledged fact. The publication of most importance since Herrick's *Menidia* has been that of Johnston, who has showed the relationship of the acustico-lateralis to the general cutaneous system. It now remains to find the origin of the communis system from the general splanchnic system, or the latter from the former, and to find the cause of the separation of the sympathetic (afferent and efferent general splanchnic) from the so-called central nervous system.

In the following pages the sensory splanchnic system is subdivided into (1) communis or end-bud; (2) general sensory splanchnic, which is distributed to the viscera. Cole (10), however, uses the term 'somatic' for the end-bud fibres because they terminate in the skin, but he is hardly justified in doing so as long as the end-bud fibres and the general sensory splanchnic have a common origin in the brain. Also he says: "I do not consider the lateral line system of nerves to fall within the definition of somatic sensory nerves," but he can now hardly hold this opinion after reading Johnston's paper on *Petromyzon* (20).

At present we are not in a position to determine the nature of the fibres which supply the heat, cold, pressure, and pain endings of Mammalia, but their terminals in the skin and their physiology seem to indicate that they are specialisations of the general cutaneous system.

THE SOMATIC SENSORY SYSTEM.

A. The General Cutaneous.

The general cutaneous system consists of afferent sensory fibres, usually of small calibre. The centres in the central nervous system are of great extent. The nucleus in the brain sends out fibres into the 'spinal V tract,' which in its turn is continuous with the dorsal tract of the spinal cord. These three parts occur in all Vertebrates, but in some there are additional special collections of cells, for example, groups of cells accompanying the spinal Vth tract in *Petromyzon*, and the tuberculum acusticum in the region of the Xth and Vth nerves in *Acipenser*, *Petromyzon*, and *Scyllium*.

The general cutaneous fibres occur in the Vth and Xth cranial nerves only, and in all the spinal nerves, the afferent or dorsal roots of the latter containing chiefly general cutaneous fibres, the few remaining fibres being splanchnic or visceral. The general cutaneous fibres innervate the skin only by means of undifferentiated endings.

The majority of the cranial cutaneous fibres occur in the Vth nerve, part of these terminating in the chief trigeminal nucleus, "while a large part pass caudad as the spinal Vth tract, to terminate, after receiving the general cutaneous components of the Xth, in the nucleus funiculus of the spinal cord." Some general cutaneous fibres are said to occur in the IXth in Selachians, *Chimaera*, and *Acipenser*, but this has hardly yet been definitely demonstrated. Most of the general cutaneous fibres arise from the Gasserian ganglion, the remainder from the Jugular ganglion.

This system has undergone less change in the head than any other, and is particularly nearly related to its representative in the spinal cord. If Miss Platt (35) is right in stating that the IIIrd nerve has both sensory and motor elements in some of the lower forms, it is probable that the sensory element here is general cutaneous also.

B. The Acustico-lateralis.

The nerve fibres of the acustico-lateralis system constitute the pre- and post-auditory lateral line roots and the roots of the VIIIth nerve. These fibres pass out in the Xth and VIIIth nerves, and in the ventral and lateral branches of the VIIth, to innervate genetically-related special sense organs in the skin, such as pit and canal organs, Savi's vesicles, the ampullæ of Lorenzini, and the ampullæ of the internal ear. Strong, in his paper on *Squalus acanthias* (39), has proved definitely that the ampullæ of Lorenzini are supplied by acustico-lateralis fibres.

These fibres, which have large and deeply staining medullary sheaths, terminate in the brain, chiefly in the tuberculum acusticum, but also partly in the cerebellum. Of these centres the former is by far the more general and important. Johnston has proposed to give it the general name of 'lobus linæ lateralis.' This nomenclature would be very useful, as the confusion of terms is great; thus in *Acipenser* the lobus trigeminus is the lobus linæ lateralis, and this also appears to be the case in Elasmobranchs, while the lobus trigeminus of Teleosts is the lobus facialis (communis). The centre shows great variability of size, especially among the Rays and Skates, where the size of the centre follows to a nicety the degree of complication of the lateral line system and mucous canals.

Johnston (19) has shown the close histological relationship of the acusticum and cerebellum; for instance, the latter contains typical acustico-lateralis cells, and the former has Purkinje cells, which are characteristic of the cerebellum throughout the vertebrate series. The cerebellum is, he considers, a derivative of the rostral end of the acusticum. It is interesting and important to know that in *Petromyzon* the general cutaneous centres, cerebullum, and acusticum are so bound up with one another that they can hardly be separated. In the higher Vertebrates, most physiologists consider that the cerebellum is the part of the brain most intimately related to the ear, a sense organ which we now know to be a specialised portion of the lateral line system.

There are many who still regard the acustico-lateralis as a system standing by itself, because (1) the lateralis sense organs are primarily developed on the head, and only secondarily spread to the body; (2) there are cranial but no spinal centres for this system. Some have gone so far as to say that it is impossible to derive the acustico-lateralis from any other system, and that it is a system *sui generis.* This position was strengthened by Cole's paper (7) on the archaic form *Chimaera*, in which the lateralis system is comparatively little developed, and at the same time the acustico-lateralis fibres are more distinct from the other components than in any other known type. It was generally deduced from these facts that the acustico-lateralis system of *Chimaera* was in an early stage of evolution. Strong was the first to suggest that the acustico-lateralis might be related to other systems, as he thought he had found a representative of this system in the anterior region of the spinal cord of the Amphibia; now, however, Johnston has shown that in *Petromyzon* the acusticum and cerebellum are united morphologically with the nucleus trigeminus, the nucleus spiralis, and the dorsal horns of the spinal cord. Johnston says that the cutaneous centres, end-bud centres excepted, have been developed from a common rudiment which is the direct continuation and equivalent of the dorsal horns of the cord. There are others who regard the lateral line system as an independent development, chiefly because the auditory organ, which they for an unknown cause regard as the primitive centre of the system, has caused numerous alterations in the arrangements of the nerves. It was Ayers (2) who made the discovery, and who demonstrated beyond doubt, that the acustic and lateralis systems are one, and that the ear is a very highly specialised part of the lateralis system. But he over-emphasised the auditory organ as the morphological centre of the system, whence probably arose the above mistake. Undoubtedly the auditory organ is a "neomorph interposed amongst the nerves and altering their primitive courses"; but because this is the case, it does not necessarily follow that the whole acustico-lateralis system is an independent development.

What has probably happened is, that some fibres of one of the more primitive nerve systems became modified into the lateral line system, at first in connection with the head. This may have occurred in one or more of the original nerves of the head; for convenience sake, the fibres came to have a common special centre in the brain, just as any other highly-developed sense, such as speech, etc. Then from this centre branches passed outwards, somewhat regardless, no doubt, of their original courses. As has been pointed out by Miss Platt, the intermediate course of a component is quite variable and largely unimportant as a guide to morphological relationships.

In ontogeny, and without doubt in phylogeny, the lateral line system originates in the head, thence spreading to the body, where the sense organs are segmentally arranged, but this segmental arrangement is now certainly known to be secondary.

Some have considered that the lateral line branches of the cranial nerves are equivalent to the lateral or medial rami of the spinal nerves. This, however, cannot be the case, as the lateral line branches are distinguished by their composition and centre of origin from the spinal lateral rami, the latter consisting of somatic motor and general cutaneous sensory fibres. Thus, Neal and Fürbringer consider that these median rami, when absent, have been supplanted by the r. lateralis vagi. Even, however, omitting the question of components, this certainly cannot be the case, for both sets occur in the bony fishes, and each innervates its respective organs.

Great variations occur in the degree of development of the lateral line system, the most extraordinary complications being found in the Rays and Skates. In Amphibia we get a very interesting intermediate condition. The lateral line system is present in the tadpole, but gradually disappears as the fish-like tadpole develops into an adult frog.

The cerebellum of Amphibia is small compared with that of fishes on the one hand, and that of the higher Vertebrates on the other. Its condition in Amphibia is transitory; it has lost its chief function with the disappearance of the lateral line organs, and has not yet acquired complicated relations with the highly specialised ear (balancing sense) and the centres and terminations connected with pressure and touch. It is in this system that we find the greatest differences between the higher and lower Vertebrates. In Fishes the system is enormous, extending from one end of the body to the other, and in some cases it has the most extraordinary complexity, while in the Amniota the whole system is only represented by the auditory nerve. On account of these variations, we see how branches, or even whole nerves, may be absent in the higher Vertebrates, which are present and important in the lower.

The following table by Strong will give an idea of the great atrophy of nerve components which takes place in the tadpole during its metamorphosis, part II. alone remaining in the adult Frog. At the same time by this table we can compare the condition of the lateral line system in Fishes and higher Vertebrates, for the former is very much like that of the tadpole before metamorphosis and the latter afterward.

Special Cutaneous or Lateral Line System of the Tadpole (38).

Lateral Line System	I. Pre-auditory, dorsal root VII.	(1) Dorsal division proceeding above trigeminus (gang. above Gass. gang.).	(*a*) Several small twigs, inside orbit (r. oticus, etc.). (*b*) Supra-orbital, r. ophth. superficialis VII. (*c*) Infra-orbital, r. buccalis VII.
		(2) Ventral division joining motor and fasciculus communis roots of VII, and thus forming Truncus hyomandibularis (gang. on this trunk and fused with ventral part of Gasserian).	R. mand. externus, which divides into several branches on lower jaw and side of head.
	II. Auditory.		
	III. Post-auditory. Most anterior (cephalic) and dorsal roots of IX and X.	Lateral nerve gang. in dorsal and proximal part of IX and X gang. complex.	Small temp. and r. lateralis.

Beard (5) has stated that the "lateral line has arisen solely by the extension and multiplication of the primitive branchial sense organs of the Vagus." Ewart and Mitchell (11) supported this conclusion in their work on *Læmargus*, and remark: "The condition in the adult thus seems to indicate that the lateral canal has arisen from the branchial sense organ above the first vagus cleft." Our knowledge of the branchial sense organs is, however, at present far too indefinite to allow of any generalisations.

It has been suggested that the eyes and olfactory organs, as well as the ear, are specialisations of the lateral line system. Thus Locy (23) showed that in the cephalic plate there were not only eyes, but a series of metamerically arranged accessory optic vesicles, which he tentatively suggests may be modified lateral line organs. There is considerable variety of opinion as to the nature and origin of the olfactory organs, but as yet no convincing evidence.

In connection with the lateral line system, it is necessary to discuss the nature of the nerve called by various authors (1) nervus lateralis accessorius, (2) nervus recurrens facialis, (3) nervus lateralis trigemini, (4) superficial lateral line. This nerve in all cases arises from two root complexes, that of the Vagus and that of the Facial. Hence it appears that the term nervus lateralis trigemini is incorrect. The branches from these complexes anastomose behind the cranium and run backwards together. The n. lateralis accessorius consists generally and chiefly of communis fibres, but occasionally general cutaneous fibres are present, and in rare cases a few acustico-lateralis elements. Thus in Siluroids only communis fibres are present, while in *Batrachus* most of the fibres are lateralis, a few being general cutaneous from the facial and vagus roots. In *Batrachus* the lateral elements come from the Facialis only. Owing to the absence of terminal buds along the course of the nerve, the communis fibres have gradually been replaced by lateralis and general cutaneous elements. The same change has taken place in *Protopterus*. Herrick considers it probable that in *Gadus* general cutaneous fibres enter the nervus accessorius lateralis from the Gasserian or Jugular ganglion.

The principal function of this nerve is to supply the terminal buds of the body, not the general cutaneous areas, which are supplied by general cutaneous fibres from the spinal nerves.

A good deal of confusion between the nervus accessorius and the nervus lateralis vagi has arisen, owing to the fact that in some cases, as in *Menidia* and *Amia*, the latter undoubtedly supplies some terminal buds. We know now, however, that although this is the case, these terminal buds are supplied not by lateralis, but by communis fibres, which have passed into the nervus lateralis vagi. These facts also doubtless "helped in spreading the idea that the terminal buds may have originated from the lateral line end-buds."

A nerve which has given rise to much discussion is the lateral line nerve of *Petromyzon*. Ransom and Thompson (36) stated that its main origin was from the dorsal rami of the Facial and Vagus nerves. They say: "We may perhaps regard the lateralis as a collective nerve, collecting the dorsal rami of the posterior spinal roots, and this collection system is continued as far forwards as the Facial and perhaps the Trigeminal nerves. . . . It seems natural to regard this lateralis as a relic of the extensive and irregular commissural system connecting the posterior roots of *Amphioxus*." This nerve in *Petromyzon* supplied certain irregularly-arranged sense organs which were supposed to be of the nature of end-buds. Johnston (20) has now shown, however, that contrary to general belief, and in spite of Cole's demonstration (9), there are lateral line organs present, and these are supplied by the nervus lateralis, which is here a true lateral line nerve.

The lateral line nerve of *Petromyzon* receives its fibres from the VII–X anastomosis, which consists almost entirely of lateral line components, and from the post-auditory lateral line root. These fibres have their central endings in the acusticum and cerebellum. The lateral line is represented by numerous pit organs, arranged much as in other fishes. There are also simple sense organs corresponding to the end-buds of the higher fishes, but they are not numerous, and the fasciculus communis is correspondingly small.

The anatomical unity of the acustico-lateralis and general cutaneous systems has been demonstrated by Johnston, but Parker, in the *American Naturalist* (32), has added interesting evidence of the physiological and histological similarity of the sense organs and cells of these two systems. Thus he points out the similarity of the hair cells of the acustico-lateralis organs and the tactile cells of some Invertebrates, and demonstrates how these tactile cells have been modified to function as parts of the organs of hearing and equilibration.[1]

THE SPLANCHNIC SENSORY COMPONENTS.

The splanchnic sensory fibres are divided into two groups: (1) fibres supplying specialised nerve-endings on somatic surfaces, such as taste-buds, teeth-buds, and terminal- or end-buds;

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[1] Prof. Parker of Harvard informs me that he has experimental proof that, at any rate in some cases, the lateral line organs perceive sounds of very low vibration. His experiments show that physiologically the acustic and lateralis systems are one.

(2) fibres having no specialised endings, distributed to visceral surfaces—the afferent sympathetic fibres.

There has been some confusion of nomenclature in this group of components. Thus, Strong defines communis components as the fine fibres which innervate terminal-buds and end centrally in the lobus trigeminus. Johnston and Cole (?) also use the term in this sense. Herrick, however, has a broader definition, including under the term 'communis' the sensory cranial nerves supplying visceral surfaces, taste-buds, teeth-buds and terminal-buds of the outer surface of the body which do not belong to the lateral line system, together with their ganglia, root fibres, peripheral end organs, and terminal nuclei in the medulla oblongata.

In this paper the communis is used solely in the more limited sense of fibres to end-buds only. It seems wiser to continually bear in mind the division of the splanchnic sensory components into two great parts, which, although closely united in their central origin, appear unrelated in their terminal relations.

The splanchnic sensory fibres are generally of small calibre. They terminate centrally in the lobus vagi and lobus trigemini, and the fibres may enter the former directly by the vagus roots, or indirectly through the fasciculus communis from the VIIth and IXth nerves. In Fishes the former condition is the more usual, only a few fibres passing by means of the fasciculus communis to the lobus vagi, but where the end-bud system is well-developed, the pre-vagal portion of the fasciculus communis becomes much enlarged, and is known as the lobus trigemini. In all cases the post-vagal portion of the fasciculus communis is feebly developed and its relations obscure.

The homologies with higher animals are fairly clear. Strong has proved that the fasciculus communis with the lobus vagi and the vagal roots is, as a whole, homologous with the fasciculus communis of Amphibia, and with the fasciculus solitarius of Birds and Mammals. With the fasciculus solitarius must be included the combined IXth and Xth sensory nucleus of Mammals, for the latter is to be regarded as a specialised portion of the spinal nucleus of the Vagus, or of the terminal nucleus of the fasciculus solitarius, and is therefore included in the lobus vagi of Fishes. According to Van Gehuchten, however, the dorsal root of Vagus of Mammals is motor, so that the sensory part of the lobus vagi is represented in Mammals only by the spinal nucleus of the Vagus. This spinal nucleus is very diffuse in Amphibia, being a representative of a part of the hypertrophied lobus vagi, or of both lobus vagi and lobus trigemini of Fishes. It has been suggested that the scattered cells found along the spinal portion of the fasciculus communis represent the original spinal nucleus, which has not yet been completely absorbed into the lobus vagi. The Amphibian is, in this particular, more primitive than the fish, because in the fish the end-bud system is very highly specialised.

Splanchnic sensory fibres pass from the visceral centres in the brain to supply the terminal buds all over the body, for although we find that visceral centres are present in the spinal cord and in parts well developed, these cord centres never supply end-buds. On tracing the lobus vagi backwards, it is found to pass through the commissura infima Halleri into the intermediate zone, where there is a great development of large cells. In this region in Fishes we find the paracentral nucleus and in Mammals the lateral cornu and Clarke's column, both of which are associated with visceral sensory nerves. In Fishes the intermediate zone is very large compared with the dorsal and ventral cornua, an obvious result of the fact that the visceral nerves in connection with the end-buds are very important in these Vertebrata. We thus see that the cranial splanchnic centres are one with certain spinal centres.

Onuf and Collins (31) regard the paracentral nucleus as a motor splanchnic centre. The importance of these facts is in showing that although the special splanchnic system is in the present forms associated with the brain, it is there only as a specialised component which is also represented in the spinal neuromeres.

Johnston (19) denies the presence of visceral sensory fibres in the spinal nerves. "No sensory fibres of the spinal nerves supply visceral structures. We know of no sensory fibres entering the spinal cord from the sympathetic system."

Kölliker says much the same, but Onuf and Collins have ound degenerations which demonstrate without doubt that sensory nerves run from the sympathetic ganglia into the dorsa roots. Such a connection as this is also indicated by th embryological work of Paterson (34). Physiological reflexe also clearly show the presence of visceral sensory fibres in th cerebro-spinal system. Herrick says: "It is undoubtedly tru that this spinal visceral sensory system is very small, and that it is not present in all of the spinal segments is very probable, for, as we have seen, the functions of this system have been largely usurped by the cranial visceral system of the vagus." It is obvious that these spinal viscera centres, although continuous with the visceral brain centres have a different function, for they are connected with the sympathetic system only.

Herrick considers that the special splanchnic system is primitively viscero-sensory, and that its connection with the terminal buds, which he says are probably ectodermal in origin is secondary. He seems to think that the visceral system, as represented in the cord with its purely visceral connections represents the primitive state. It is to be noted that no spinal nerves ever terminate in end-buds. Cole, in his reply to Herrick suggests that the special splanchnic fibres arose as a cutaneous system in connection with the gill clefts. Now, according to Dohrn and most anatomists, the mouth is a modified gill cleft; hence we can see that these cutaneous terminals may have invaded the mouth in the same way as the teeth have done. But to carry the idea further, we must imagine that these special nerve endings migrated further into visceral areas and there reverted to the simple condition without special nerve endings, the form in which they must first have appeared in the skin. We find it impossible by any mental process to clearly imagine the whole of the afferent splanchnic system originating from a common ancestral form, and yet its existence as a separate and clearly-defined cranio-spinal system cannot be doubted. The nature of end-buds has lately been demonstrated by Herrick, who has shown that the end or terminal buds give rise to the sensation of taste, and are identical in function and structure with the taste buds of the mouth; therefore, physiologically, the end-buds are visceral in function. This being the case, it is obvious that there should be a common centre in the brain for the end-bud fibres and the general sensory splanchnic fibres, for they have to act in unison. The taste- and terminal- buds probably originated in the ectoderm of the mouth, and thence the latter spread to all parts of the body, a process just the reverse of that which has occurred with the teeth. The question now is, how did the taste- and end- buds become supplied with splanchnic fibres, a visceral brain centre being taken for granted on physiological grounds? May it not be suggested that with the reduction of the ventral somatic musculature in the head, and the consequent reduction of somatic afferent as well as efferent nerves, the place of the former was taken by splanchnic afferent in sense endings as well as in muscle endings? This curious connection being established on the head, would have continued when the terminal buds began to migrate on to the body, for there is no doubt that the terminal buds have invaded the trunk from the head like the acustico-lateralis system.

The special splanchnic sensory fibres occur in the Vagus, Glosso-pharyngeus and Facialis. The ganglia are the whole of the ganglion of the Glosso-pharyngeus, the geniculate ganglion of the Facialis and the branchio-visceral ganglion of the Vagus.

The Sympathetic System, including the General Afferent Splanchnic Fibres and the Efferent Splanchnic Fibres.

Paterson (34) says: "It may be pointed out that there are strong grounds—embryological, histological and physiological—for drawing a sharp distinction between the sympathetic and cerebro-spinal nervous system." He is supported in this point of view by many others. The evidence of the last few years, however, has been to modify, if not to abolish, this 'sharp distinction.' Embryologically we now know that these systems are one. A physiological distinction undoubtedly exists between sympathetic and 'central ganglia,' the former being trophic only, never reflex; but this is merely due to the lack of necessary anatomical arrangements. Both cells and fibres of the sympathetic are characteristic, the latter being non-medullated and the former of a characteristic shape. Ramage states that in Birds the difference between cranio-spinal and sympathetic cells is 'very evident.' Looked at from the point of view of the nerve component theory, the histological differentiation is only to be expected. Do we not find it to a large degree in all other systems? The differences of the cells is peculiarly interesting. With differences in fibres we might hope to find differentiations in cells, but at present this has not been demonstrated, except here and in the acustico-lateralis brain centres. It is to be noticed that the cell differences occur only in the cells in the sympathetic ganglia, which are chiefly in connection with afferent fibres.

Balfour (4), in 1878, and Schenk, in 1879, suggested that the sympathetic cells developed from germ cells possessing a motile power, which wandered from the spinal ganglia. Gaskell (12) accepted the supposition, and added that the sympathetic was the result of an outgrowth from the central nervous system of the splanchnic ganglionated efferent fibres. In 1890 Paterson (34) stated that the sympathetic develops *in loco* from the mesoblast, and that the connection with the spinal nerves is secondary. He modified Gaskell's statement, saying that some, but not all, of the splanchnic fibres join the sympathetic. Thus, in the anterior part of the thorax, all the splanchnic fibres appear to enter the sympathetic, but in the neck there is no connection. In 1891 His, and in 1896 Onody, furnished evidence which seems strongly in favour of the supposition that those cells which are the germ cells of the sympathetic do not develop *in loco.*, *i.e.* from the surrounding mesoblastic cells, but in the way suggested by Balfour and Schenk.

The sympathetic may thus be defined: "It consists of (1) a portion of the splanchnic sensory system concerned with vague or organic feelings, and seldom or never gives rise to immediate reflexes directed towards the environment" (21), and (2) the entire vaso-motor system. The afferent sympathetic fibres have their cells of origin in the sympathetic ganglia, and send processes into the cord by the dorsal roots; these nerve processes anastomose around nerve cells in the region of Clarke's column, either in their own or more anterior or posterior segments. The efferent sympathetic fibres have their cells of origin in the cord, also in the region of Clarke's column.

The outflow of the visceral nerves from the central nervous system into the sympathetic takes place only by means of the white rami communicantes, *i.e.* the rami viscerales. These white rami communicantes are formed by an outflow of medullated fibres from both anterior and posterior roots of the spinal nerves, "which medullated nerves pass not only into their metameric sympathetic (lateral) ganglia, but also form three main streams —upward into the cervical ganglia, down into the lumbar and sacral ganglia, and outwards into the collateral (pre-vertebral) ganglia" (12).

The brain centres are perhaps funiculi cuneati and Deiter's nucleus, which are continuous with the region of Clarke's column of the cord; the fibres occur in the roots of the Facialis, Glossopharyngeus and Vagus, and reach their final distribution by way of the visceral rami of the cranial nerves. It will be remembered that usually the splanchnic centre is greater in the brain than in the cord; this is especially the case where end-buds are found. But "in *Petromyzon*, where the end-buds are few, and the splanchnic fibres chiefly innervate the visceral area, we find that the centre in the medulla is very small in its rostral part, is largest near the commissure, and is larger in the cord than in the other Vertebrates" (20).

"It is now generally believed that all the non-striated muscular tissue, namely, that of the intestinal canal and of the gland-ducts in connection with it, the smooth muscle of the urogenital system, the smooth muscle found in the skin, the eye, and all vessels, receives its nerve supply from sympathetic neurons" (18). Glandular tissue is supplied with sympathetic fibres.

In *Ammocœtes* we find the sympathetic is in its most primitive condition, for in *Amphioxus* there is as yet no trace of it. Julin says: "La disposition du système nerveux sympathetique realisée chez *l'Ammocœtes* est une disposition primordiale." And in defining the condition in this type, he says: "C'est que toujours il y a au moins une paire de ganglions correspondant à chaque paire de nerfs spinaux tant dorsaux que ventraux." . . . "Il n'y a pas seulement que les nerfs spinaux dorsaux qui fournissent des rameux sympathetiques en relation avec des ganglions, mais aussi les nerfs spinaux d'un corda sympathetique unissant tous les ganglions d'un même côte. Les elements nerveux moteurs du sympathetique chez *l'Ammocœtes* sont distincts des elements nerveux sensibles du sympathetique comme cela a lieu pour les nerfs spinaux."

The migration of the sympathetic must have occurred very early in the history of Vertebrates, for the relation of the cranial roots to the sympathetic ganglia is much the same as in the case of the spinal roots, although in the case of the head the fusions and divisions are more variable and complicated. For example, in *Menidia* the 'head part' of the sympathetic contains six important ganglia, which are related to the roots of the X, IX, VII, V, III nerves. It is interesting to note that the important ganglia are clearly related to nerves (except III) which resemble spinal nerves.

Looked at from the embryological, histological, and physiological points of view, we must agree with Ransom and Thompson (36) that "the leading fact of the sympathetic is the metameric outflow of visceral fibres." Why this outflow should have taken place we do not know; it may be due to the physiological need of ganglion cells to be nearer their respective distribution areas, or it may be due to the general tendency by which similar cells gather into ganglia or centres.

We must regard the sympathetic as a system composed of two splanchnic components, motor and sensory, which has been evolved to supply the needs of a complex visceral and vascular system. It is closely connected both physiologically and anatomically with the cerebro-spinal system, and cannot logically be separated from the latter in any of our neurological conceptions.

THE MOTOR COMPONENTS.

The motor or efferent and secretory components are two—somatic and splanchnic.

The centres of the somatic motor fibres are almost co-extensive in length with the cerebro-spinal nervous system. The nucleus of the somatic motor fasciculus lies not far from the anterior end of the brain axis in the region of the chiasma, hence the fibres which originate from this nucleus pass ventrally beyond the nucleus of the third nerve and posteriorly into the motor fasciculus, which in its turn passes without any sudden demarcation into the motor V column, the ventral horn of the spinal cord. The fibres form all the motor components of nerves III, IV, VI, XII, and most of the motor components of the ventral branches of the spinal nerves.

The presence of the nucleus and tract, rostral to the first somatic motor nerve, is probably connected with the former existence of a somatic nerve rostral to III. This nerve would probably correspond to the anterior head cavity of Platt. In the head there has been a great reduction of ventral somatic musculature, and hence a reduction of the somatic motor nerves. Thus, in no cranial nerve do we find a ventral branch which can be compared with that of a spinal nerve. It must be noted that nerve XII really supplies somatic musculature which has encroached upon the head in the posterior regions. The somatic motor elements of the cord far exceed in amount the splanchnic motor except in *Petromyzon*, and, perhaps, *Mustelus*, where conditions are primitive, and where as yet there has not been a centralisation of the splanchnic motor centres in the brain.

The splanchnic motor centres of the brain are the nuclei of origin of the motor elements of nerves X, IX, VII, V. This centre on passing out of the medulla becomes much smaller, but is obviously continued in the cord into a region lateral to the ventral horn. In the cord it is distinguished from the somatic motor more or less clearly in different species. Usually the component is small in the cord, distinguished with difficulty, and is in close association with the afferent part of the sympathetic system. It is generally so small that its very existence was at one time doubted, but in *Petromyzon* the somatic and splanchnic motor columns are distinct in position and have well-defined histological characters.

Johnston, in his paper on the brain of *Petromyzon*, says: "The visceral motor and somatic motor nuclei of the medulla are imperfectly differentiated"; thus it appears that in the brain the differentiation of these two systems is very slight compared with the condition in higher forms. In *Petromyzon* we get the characteristic differences in the cord, but in the higher forms in the brain. The same seems to be true of *Mustelus*.

The splanchnic motor nucleus ends quite abruptly with the nucleus of the motor V, although it primitively gave rise to one or two pairs of nerves rostral to V, of which the motor components of the ophthalmicus profundus V is found occasionally during development.

The splanchnic fibres constituting the motor components of V, VII, IX, and X supply the splanchnic musculature of the branchial, hyoid, mandibular and labial cartilages.

It may be noticed here that although the branchial muscles are splanchnic in origin and supplied by splanchnic fibres, yet they are striped, not unstriped muscles. This is an instance how physiological necessity may modify the character of a tissue; a parallel case is found in the mammalian œsophagus, which, although of splanchnic origin, is yet largely supplied by striped muscle tissue. Generally speaking the splanchnic components, both motor and sensory, deal only with the 'internal and vegetative' activities of the organism; but to this the branchial region and the end-bud system are exceptions.

THE NERVES OF SPECIAL SENSE.

The special sense organs are the olfactory, optic, and the auditory. For a long time all were put on one side in any consideration of nerves and organs as peculiar and distinct, but the barrier has been utterly broken down as far as the auditory organ is concerned. Ayers (2) has proved most conclusively that the auditory organ belongs to the lateralis system, and it has now been shown (1) that the auditory nerves contain fibres which belong to the acustico-lateralis system; (2) that the acustico-lateralis system is only a specialised part of the general cutaneous system; therefore the auditory nerve may be regarded as afferent somatic in origin. An effort was made by Blaue in 1884 to show that the olfactory buds were derived from lateral line buds, but this seems to have been disproved by Madrid Moreno in 1886.

Marshall showed that the olfactory nerves arose like a typical cranial nerve, and MacClure states that they bear a normal relation to their encephalomere. These results suggest that the olfactory nerve is, at least in its method of origin, homologous with any ordinary segmental nerve. It has been recently stated that we must return to the original conception of the olfactory as a nerve not comparable with a typical segmental nerve.

A lateral line origin for the eye also has been suggested tentatively by Locy (23). The one fact (?) we have which brings the optic nerve into line with the others is the observation that the optic fibres grow back into the brain from the retina, along the optic stalk, and do not originate from the brain. MacClure says that the second encephalomere has no nerve in connection with it, but that the optic vesicle is just opposite. May we not imagine that this relative position of the two bodies may indicate a former connection?

The present form of the eye probably very early replaced the pineal (paired) eye. The latter eye may be perhaps related to the eye spot of *Amphioxus*, but certainly not to the normal 'vertebrate' eye. In the Invertebrata (ex. Leech) the eye spots are specialised cutaneous sense organs of touch and pressure, and we find the same phenomena again in the shells of *Chiton*. If an eye may be evolved from a more generalised sense organ in Invertebrates, it seems possible that a similar evolution may also occur in the vertebrate series. What that primitive sense organ may have been we cannot say—perhaps a branchial sense organ. Probably also we may conjecture that the optic fibres were differentiated from primitive afferent somatic fibres.

THE NUMERICAL NERVES IN THEIR RELATION TO THE COMPONENTS, AND THEIR HOMOLOGIES WITH ONE ANOTHER.

It has been stated above that each system may be defined by its origin and termination, where origin means internal origin in the brain, and termination the final relation of the nerve fibrillæ to endings in organs or tissues, these endings having each a definite physiological function. The intermediate course of the nerves or fibres of each system varies greatly in different natural orders, sub-orders, species, individuals, and even on opposite sides of the same individual. There are certain broad similarities in the arrangement of the components throughout the Vertebrata, but the variations are enormous. Of the variations the most important are those due to the suppression of organs, as in the case of the lateral line system. The relation of the components to the nerves is approximately thus—general cutaneous fibres occur in nerves X and V, afferent splanchnic (?) in nerves VII, IX, X, and acustico-lateralis fibres in the ramus lateralis vagi, in the auditory nerve, and in the ventral lateralis facialis.

Nerves I and II are probably somatic in origin, but evidence up to the present has been contradictory. Nerves III, IV, VI consist of somatic motor fibres only in the adult of all forms, but in embryonic stages afferent fibres are present for a short time. Nerve V varies considerably in different classes of Vertebrata.

Nerve VII. By all zoologists the palatine branch of VII is considered to be represented by the great superficial petrosal. In this case there is a considerable change of components, the former consisting of communis fibres only, the latter apparently of both somatic motor and general cutaneous. The ramus hyomandibularis, which in Fishes consists of motor, communis and lateralis fibres, is in Mammalia wholly (?) motor to supply the hyoid muscle, posterior belly of the digastric and the stapedius.

The Chorda tympani has given rise to a great deal of discussion. Many authors have considered that the Chorda of Mammals is the representative of the pre-branchialis VII, on the grounds that the Chorda of Mammals is pre-spiracular in origin, only later becoming post-spiracular. In *Raja* are found pre-trematic, post-trematic VII, and Chorda tympani; in *Chimaera* the r. pre-trematic VII = Chorda tympani; in yet another case, *Gadus*, the Chorda has fused with r. mandibularis V. It is thus obvious that the exact nature of the Chorda is not yet determined in Fishes, so that its homologue in Mammals must still remain uncertain. Nerve VIII always consists of lateralis fibres only, but varies much in size in the different groups.

Nerves IX and X. Shore (37) considered that the branchial nerves were formed by a separation of the splanchnic rami of some of the anterior spinal nerves from their corresponding somatic rami. Gaskell also believes that the Vagus contains the visceral but not the somatic elements of a spinal nerve, and is a compound, not of several complete segmental nerves but of the visceral components of the anterior spinal nerves, the corresponding somatic components of which remained separate.

He is supported by Herrick, who finds that the branchial fibres are communis or visceral, only a small portion, a dorsal branch of X, being somatic. Certainly the branchial muscles are visceral. On the disappearance of the branchiæ, these nerves became reduced, the IXth very much, but not so the Xth, which is even more extensive in Mammals than in Fishes, the small branches to the viscera assuming a great part in the complex mammalian anatomy.

The XIth and XIIth nerves are true spinal nerves in general relationships, but they are extremely variable in the nature of their components. This is due to the tendency to reduction in spino-occipital nerves. To quote Furbinger: "the reduction from before backwards, which was observed in the spino-occipital nerves of the Ichthyopsida, continues progressively as we ascend the taxonomic series, so that the general rule may be laid down that among adults of almost every class of Vertebrates, the more primitive forms are characterised by more, the higher forms by fewer, of the spino-occipital nerves. The embryology, in most cases where it is known, recapitulates more or less completely the steps in reduction. The higher Mammals have lost from five to six of the first spinal metameres, as compared with the lower Selachians." It is obvious, therefore, that the hypo-glossal and spinal occipital of one Vertebrate may not be the true homologue of the nerves of the same name of another.

Side by side with this tendency towards the reduction of nerves there is also a reduction of the dorsal or sensory elements in this region, the reduction taking place on account of the usurpation of the Vagus. An interesting intermediate condition has been found, by Pinkus, in a few Fishes; two dorsal roots, each with a ganglion, persist in *Protopterus*, and the same is true of *Polypterus* and some Elasmobranchs.

The great changes in nerves and their components from the Fishes to the Mammals are obviously due to—

(1) Reduction and disappearance of the gills.

(2) Reduction of lateralis and communis systems when life in air is substituted for life in water.

(3) Increasing specialisation of muscles, glands, and of cutaneous senses, such as heat, cold, etc.

In the accompanying figures (1, 2) the condition of nerves in the higher and lower Vertebrates may be compared. In the former the results are proximate and unsatisfactory, since in Mammals very little has been done from the component point of view.

CONDITION OF THE NERVES IN *AMPHIOXUS* AND THE NATURE OF A TYPICAL SPINAL AND BRANCHIOMERIC NERVE.

Hatschek has analysed the spinal nerves of *Amphioxus* thus: (1) a dorsal root consisting of a dorsal and a ventral branch, the former having only sensory components, the latter having chiefly sensory but also a few splanchnic motor fibres; (2) a ventral root, consisting of many branches to the somatic musculature. He considers that the spinal nerves of *Amphioxus* are the most primitive known as regards their anatomy and components, and he believes that it is the cranial nerves of higher Vertebrates which most nearly approach this condition, the simplicity of the spinal nerves being the result of reduction from a former more complex condition.

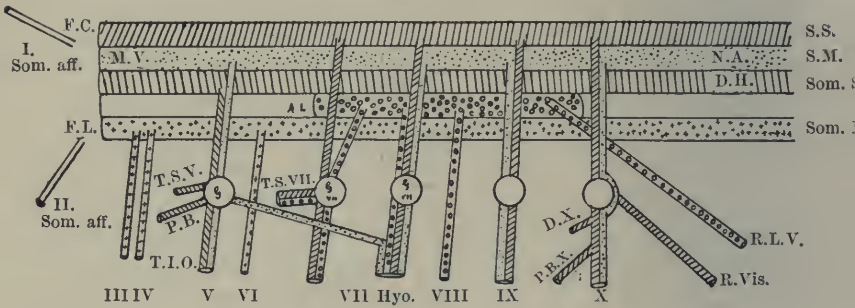

FIG. 1.

Sir Charles Bell, in 1824, separated a spinal nerve into two parts, a dorsal afferent or sensory ganglionated root and a ventral efferent or motor non-ganglionated root. This was both a physiological and an anatomical distinction.

Gaskell (12) gave the following definition of a complete segmental nerve :—

(1) Posterior root of afferent fibres, both somatic and splanchnic, the ganglion of which is stationary in

position and is always situated near the entrance of the fibres into the central nervous system.

(2) Anterior root of—

(I.) Efferent splanchnic and somatic fibres.

(II.) Efferent ganglionated splanchnic fibres of very fine calibre, the ganglion of which is vagrant and has travelled a variable distance from the central nervous system.

Herrick's (1891) view of a typical spinal nerve is as follows:—

Dorsal root, fine fibres.

Ventral root, coarse fibres.

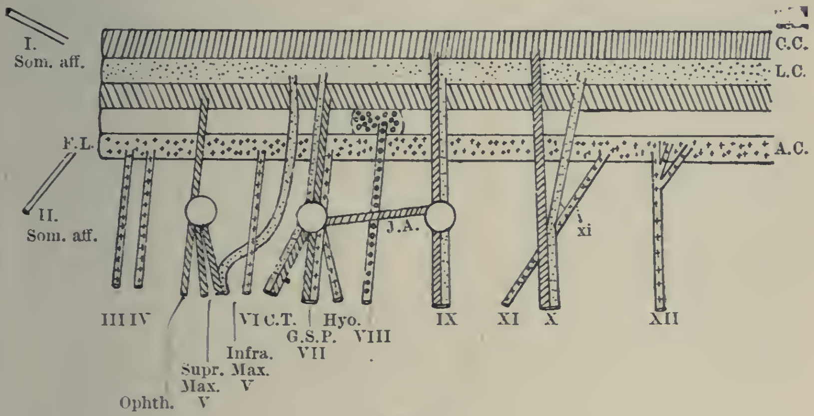

FIG. 2.

From the ganglion—

A. Two minute dorsal rami, the ramus communicans of somatic fibres passing cephalad, the ramus spinosus of splanchnic and somatic fibres passing caudad.

B. Median-sized medial rami, of somatic motor and somatic (?) sensory fibres.

C. Large ventral ramus of somatic fibres.

D. Nervus communicans or nervus visceralis, of splanchnic motor or sensory fibres.

There are a few splanchnic motor fibres in the n. spinous and medial ramus, which are chiefly vaso-motor and excito-glandular.

Ramon y Cajal has made a most important addition to our knowledge of spinal nerves by discovering that there are motor fibres in the dorsal root in all cases.

In *Amphioxus* we find both dorsal and ventral roots, which alternate, the former being intersomatic. The ventral roots are compound, and never unite with the dorsal to form a typical spinal nerve. The dorsal roots have dorsal and ventral branches, and are both sensory and motor in function. This condition is most nearly retained in the spinal cord of Cyclostomes, where there are alternate dorsal and ventral roots which do not unite (*Petromyzon*). In some regions there are two anterior roots to one posterior, a fact of interest as tending toward the condition found in *Amphioxus.* Balfour (4) states that in Selachian embryos the dorsal and ventral roots alternate, the former being intersomatic. Miss Platt (35) states that the dorsal roots originate in the concavity, but MacClure (24, 25), Marshall (27), Orr, Bérèneck, and Waters (40) deny such an origin.

The points of agreement between the cranial nerves of Vertebrates and the spinal nerves of *Amphioxus* are as follows:—Both have (1) dorsal branches; (2) all four sets of components; (3) the sensory ganglion more superficial than the vertebrate spinal ganglia; (4) a connection with the epidermis.

It seems probable that both cranial and spinal nerves of the higher Vertebrata have been differentiated along two lines from the condition in *Amphioxus*, the cranial nerves having a tendency to retain the primitive condition, at the same time being greatly modified by an increasing complexity of sense organs, the presence of gill arches, the neo-mouth, and the tendency to invade segments both posterior and anterior to their own. The spinal nerves have degenerated owing to the usurpation of a part of their functions by the cranial nerves. The 'head' of *Amphioxus* is probably only equivalent to a few, or even one only, of the anterior head segments of the higher Vertebrata.

As the head has been greatly modified by the branchial arches, we should therefore expect to find that in the higher forms those nerves which supplied branchial arches would be modified along definite lines, and this is certainly the case. Herrick gives the following analysis of a branchial nerve, the analysis being founded upon the post-optic (*i.e.* the more typical) branchiomeres.

1. Dorsal branch—general cutaneous and a few visceral fibres.
2. Palatine—visceral sensory components.
3. Pre-trematic (or branchial)—communis fibres.
4. Post-trematic—visceral motor and sensory components.

We know that V, VII, as well as IX, X, are primitively nerves supplying visceral arches, hence they must be modified branchiomeric nerves. This is obvious upon analysis of the branchiomeric nerve in the trigeminal segment, for example.

1. Dorsal—ramus ophthalmicus superficialis V (?), to which are added communis and lateralis components.

2. Palatine—none, being replaced by the forward extension of the ramus palatinus VII.

3. Pre-trematic—r. maxillaris, general cutaneous and communis fibres, but the latter come from the geniculate ganglion, and are therefore not truly trigeminal.

4. Post-trematic—r. mandibularis V, splanchnic motor and general cutaneous components.

It is stated above that the cranial nerves approached more nearly to a primitive segmental nerve, as represented in *Amphioxus*, than to a spinal nerve; and yet the present form of the cranial nerves has been greatly modified, owing to the influence of the branchial arches and gills. We may therefore conclude that the primitive segmental nerve gave rise directly to the spinal nerves, and indirectly, by way of a branchiomeric nerve, to the principal cranial nerves.

Nerves XI, XII are spinal and not branchiomeric in character. It is as yet impossible to state whether the third, fourth and sixth nerves at one time supplied certain pre-oral gill clefts, as has been suggested. Some think the olfactory organ is a modified gill cleft, in which case the olfactory nerve would be the remnant of a very anterior branchiomeric nerve. Nerve VIII must be regarded as a specialised portion of one nerve, or as a result of the coalescence of branches of several nerves. Of II we know nothing.

SEGMENTATION OF THE HEAD.

The questions which we have to consider concerning the nature of the head may best be expressed in Neal's words (10): "Was the vertebrate head like the trunk, primitively segmented?

if so, were these segments serially homologous with those of the trunk? and how many have entered into the composition of the head?" The first who attempted answers to this question said: "Yes, the head is segmented because the skull is segmented, and since the latter consists of three coalesced vertebræ, the brain must have two pairs of nerves." On these grounds the twelve pairs of cranial nerves were divided into two groups as follows. The first consisted of III, IV, V, VI and VII; of these III, IV, VI, VII, and the motor root of V made the complete motor root, while the sensory root of V made the complete sensory root. The second consisted of IX, X, XII and the anterior root of XI; of these IX, X, and the anterior root of XI made the complete sensory root, the motor consisting of XII only. This conception of the cranial nerves had no longer any support when the vertebral theory of the skull was discarded.

In 1849 Stannius tried to find the number of segments in the head by the study of the nerves. His method of reasoning was as follows:—As the cranial nerves are homodynamous with the present form of spinal nerves, it must be possible to find the number of complete nerves amongst the cranial nerves, for each spinal nerve consists of a motor and a sensory root with a ganglion on the latter. Stannius arranged the branches of V, VII, IX, and X so as to make each nerve conform to his idea of a typical spinal nerve. He omitted the nerves of special sense as they were considered *sui generis*, quite unrelated to any other nerves in the body. The nerves to the eye-muscles were also omitted, as they had no relation to any sensory nerves, and were therefore also unique.

Stannius was mistaken in taking it for granted that the present form of the spinal nerves is primitive, and in disregarding the origin in brain and cord, but he did pioneer work in showing that the metamerism of the head could probably be deduced from the condition of the brain and nerves, his idea being that the brain, rather than the cranium, was primarily metamerically segmented.

Balfour, in studying the segmentation of the head, introduced two new factors, visceral arches and head somites. According to him the changes undergone by nerves in relation to the organs they supply is so great that only in a very undifferentiated portion of the brain would they give reliable evidence. He accepted Gegenbaur's statement that there are five segments in the vagus region, but adds, that from the condition in *Notidanus cinereus, N. griseus* and *Scyllium*, we may conclude that other segments were once present.

He considered that VII and VIII belong to the same segment. He says: "The nerves indicate seven cranial segments, or if the nerves of the eye-muscles be included, at least eight segments; but to these must be added a number of segments now lost, but which once existed behind the last of those at present remaining." He concluded that there was one pre-oral and seven post-oral segments.

Marshall also worked on this principle, but he added a new cranial nerve, the olfactory, and homologised the nasal sac with a gill cleft.

Hatschek worked along similar lines, but the foundation of his arguments was the primitive character of the cranial nerves as compared with the spinal, the cranial nerves more nearly resembling those of *Amphioxus*, which he considered primitive, not degenerate.

The question of gill clefts and arches has always taken a prominent part in the determination of the segmentation of the head. Thus Gegenbaur, from his study of the compound nature of the tenth nerve of *Notidanus griseus*, came to the conclusion that the brain is comparable to a portion of the spinal cord, which has at least as many vertebral segments as there are gill pouches. Marshall and Balfour also considered that branchiomerism and metamerism coincided, a supposition contradicted by Van Wijhe, but lately supported and demonstrated by Neal.

We must expect the anterior region of the body to differ from the posterior, for even in the Protozoa the anterior region of the cell may differ in its anatomy and physiology from the posterior. When animals became segmented the difference was evidenced by the distinct nature of the first segment, which, even at the beginning, could not be homologised with the following segments. Ascending the animal series we find an increasing number of the succeeding segments tending to coalesce with the first segment. Here the question arises, how many of their original characteristics do these coalesced segments retain? The answer will vary in every species, but generally it will depend upon two factors, the degree of specialisation of the anterior region and the length of time since coalescence took place. *Amphioxus*, as the simplest Chordate known, must serve as the basis from which we may argue as to the probable number of fundamentally-modified segments in the ancestral Chordate. But the exact number of segments in the 'head' of *Amphioxus* is as yet undetermined; perhaps there are two, certainly not many. As there is no doubt about the segmented condition of the posterior portion of the vertebrate head, many anatomists have considered that the latter is homologous with the 'head' of *Amphioxus*, plus an indefinite number of body segments.

Many morphologists have doubts as to the segmented nature of the pre-otic region. The evidence for this region is increasing: thus, the presence of certain rudimentary structures has strongly supported the segmental theory of the pro-otic segments. It is possible that the accessory olfactory nerves described by Pinkus and Locy belong to two of the segments which enter into the primary forebrain, while the *N. thalmicus* of Platt belongs to the mid-brain. Evidence of its segmentation depends chiefly, however, upon the presence of transient somites and theoretical gill arches. Dohrn, who went to great extremes, found so many myotomes that he identified nasal sac, lens, hypophysis, mouth, thyroid, auditory sac, etc, as modified gill clefts. He finds twelve to fifteen segments in the anterior head region. This is a great increase on Van Wijhe, who gives four, while Rabl considers that there is no mesodermal segmentation in this region.

In the pre-oral portion of the head, the encephalomeres are certainly absent, although some observers seem certain of their existence. Allis (1) says: "There are thus two pre-oral arches indicated in the embryos of *Mustelus*. In each arch there are, according to Gegenbaur, remnants of the cartilages of the arch, and I now further find not only muscles definitely related to one of the arches, but also nerves that certainly might be considered as the pre- and post-trematic branches of each arch."

The existence of a segmented condition of the brain has been known for some time. It was observed by Marshall, who attempted to discover a cranial nerve for each expansion of the neural tube, but it is Neal who has given to the neuromere theory its full significance. It has been observed that the spinal cord is divided into neuromeres, which are arranged segmentally, each having a definite relation to dorsal and ventral nerves and to the body segments. In the brain we first find a segmented condition, which later gives rise to a different one. The questions which arise are, which of these brain segmentations is the more primitive, and is either set of segments homologous with the neuromeres of the spinal cord? Also, can the existence of brain and spinal neuromeres be explained as the result of lateral pressure of the muscles of the somites? It seems undoubtedly to be the case that the encephalomeres or primitive neuromeres of the brain are the remains of a former, more complete, segmentation of the head, the encephalomeres persisting even when the nerves connected with them appear only transitorily or have disappeared permanently. We must be prepared to consider that there may have been encephalomeres which have entirely disappeared; in this case, however, it is frequently possible to correct dubious or wrong results by a careful comparison of encephalomeres and somites, the latter in some cases certainly persisting independently of the encephalomeres.

According to Neal the neuromeres of the hind brain are certainly of equal morphological value with those of the spinal cord, but so-called "neuromeres have been described which are not the morphological equivalent of the neuromeres of the trunk. These have been shown to differ from the typical neuromeres in shape, in structure, and in relation to the dorsal and ventral zones of the neural tube." Another difficulty of these so-called neuromeres is that they appear late and are secondary divisions of primary vesicles, and thus differ from the hind brain and spinal expansions. In attempting to explain this, Waters (40) says: "It seems not unreasonable to conjecture that the constrictions, being essentially primitive, and in a state of degeneration, have gradually been more and more crowded out by the specialising brain development, and hence appear at a much later period in the ontogeny than would be expected." This assumption is supported by no facts, and appears peculiarly objectionable, when we realise that these 'fore-brain neuromeres' are the fundaments of adult organs, and in this respect also differ from the typical hind-brain neuromeres and the expansion of the myelon. Herrick says, probably much more in accordance with facts: "If neuromeres once existed in the fore-brain, they would be visible only at an embryonic stage, and would be obscured by altered conditions, so that we may consider that the fore- and mid-brains of embryos are neuromeres, the remainder being represented by the divisions of the primitive hind-brain."

The neuromeres and somites show an exact numerical correspondence throughout the length of the embryo. "The serial alternation of myelomeres and somites evinces the metamerism of the former, while the exact numerical correspondence of the encephalomeres and head somites appears equally convincing evidence of the metameric value of encephalomeres. The somatic value of the post-otic head segments is indisputable, and the pre-otic somites, five in all, are also, in my opinion, homodynamous with trunk somites" (Neal). Miss Platt considers also that it is no longer possible to separate the pre- and post-otic segments.

In the trunk there are obvious metameric relations between neuromeres, nerves, and myelomeres, but in considering the cranial nerves it is necessary, as emphasised by Gaskell, to consider the central origin as well as the peripheral distribution. Thus Platt (35) says: "I find that the ganglion cells of cranial nerves enter into fibrillar relation with the neural tube at points quite widely separated from the encephalomeres from which the cells were proliferated, and also that in embryos of different Vertebrates the relations of the fibres of the same nerves to the encephalomeres are variable, not only in the case of ganglionated roots but also of medullary, as that of the Trigeminus, Abducens, Glosso-pharyngeus. It is obvious, then, that in the case of cranial nerves both the location of the kerne of the medullated roots and the regions of the proliferation of the ganglionic cells of ganglionated roots may be taken into consideration."

Herrick says, that while it is possible to establish a numerical correspondence of encephalomeres and somites, the nerve relations are not so clear. We find that encephalomeres II, III, VII are connected by ventral (motor) nerves with the first, second, and third somites of Van Wijhe. Such evidence of a want of segmental correspondence would seem at first sight to render untenable the assumption that encephalomeres have the same segmental value as myelomeres. Again, a want of correspondence of encephalomeres and visceral arches is shown by the fact that the dorsal motor fibres connected with encephalomeres II and V innervate two successive visceral arches.

It is, however, possible to explain these facts on the supposition that encephalomeres have disappeared and others have taken on their function. Thus encephalomere VII might become secondarily connected with somite III by ventral roots.

On the whole it seems reasonable to suppose that the head at first consisted of a number of segments, all of which, except the most anterior, were homodynamous with the primitive body segments. If we believe this, we must consider that the head of higher Vertebrata is equivalent to the head plus an indefinite number of segments in *Amphioxus*.

Julin, in his work on the brain of *Acipenser*, supports Hatschek's contention that we find in the whole body of *Amphioxus* an arrangement of nerves which occurs only in the head in the higher Vertebrata. In our primitive Vertebrate we should expect to find each brain segment, encephalomere, supplied with a typical primitive nerve, and although our present knowledge of brain development does not yet throw sufficient light on this point, we cannot but believe that the primitive vertebrate brain was divided into encephalomeres, and that these were definitely and regularly related to certain nerves and their origin, and thus, even now, throughout a large series of types, we find nerves VII, IX, X related to encephalomeres 4, 5, 6.

With our present knowledge we can say that probably the first nerves now connected with the encephalomeres are not of a typical composition, for the ontogenetic development of the brain has been so profoundly modified that we should expect to find many phylogenetic steps omitted or unrecognisable. The question of adult nerve components throws little or no light on the subject. Primitively we had without doubt alternate dorsal and ventral roots as in *Amphioxus.* An intermediate condition is found in the Cyclostomes; thus in *Myxine* there are several ventral roots to one dorsal. Of the components in *Amphioxus* we know nothing, but we know now those of the Cyclostomes, and the condition is extremely interesting. The components are divided into somatic and splanchnic, motor and sensory, but the two types of motor are not well differentiated, especially as regards their centre in the medulla (20). We find that the splanchnic sensory is differentiated only to a small degree, and that the somatic differentiations are so slight that their origin from a common somatic rudiment is undoubted and clear.

We must suppose that in *Amphioxus* the differentiation of components has not yet gone very far, the somatic motor and sensory being much more important than the splanchnic, which is probably only incipient. Primarily the whole nervous system was somatic, as at the time of origin of nerve cells, say in a Hydra-like form.

Looking at the central nervous system from another point of view, we may regard it as consisting of four long strands of somatic and splanchnic motor and sensory cells and fibres, which strands are segmented in the most primitive condition. This is probably the condition in *Amphioxus.* The differentiation has proceeded in two directions:—

(1) The splanchnic centres, both motor and sensory, have almost disappeared from the cord, as a great sensory centre has at the same time been evolved in the brain, into which most of the fibres enter. Many splanchnic nerve cells have migrated from the cord to become the sympathetic nervous system (sensory portion).

(2) The sensory somatic fibres have remained only general cutaneous in the cord, but in the brain have become differentiated as the acustico-lateralis, the separation of which from the general cutaneous is so distinct that not until we found a more primitive condition, as in *Petromyzon,* could we easily realise their common origin.

We now know that only one important difference exists between cranial and spinal nerves, *i.e.* in their method of origin.

In the process of development the cranial nerves acquire a connection with an epidermal sensory patch, but the spinal nerves do not. We must, I think, consider this as one of the relics of a primitive condition which the brain has retained and which the spinal cord has lost. Commenting on this phenomenon, Marshall (27) says: "All nerves originally must have been connected with the skin. May not this be the reason why each cranial nerve in turn becomes connected with it; the olfactory epithelium is but the remainder and specialised part of the original sensory epithelium, which probably practically covered the head." Strong's opinion (38) is that "if the homologies with Kupffer's results be correct, it is precisely the branchio-visceral ganglia of VII, IX, X (epibranchial ganglia), and special cutaneous ganglia, lateral line ganglia and ganglia of the nerves to end-buds also (perhaps), which arise from special epiblastic thickenings as opposed to those ganglia which belong to the cranial nerves with long trunk branches, in other words, those which have taken the place of certain portions of the spinal nerves. The ganglia of the cranial nerves which arise in connection with epiblastic thickenings are, therefore, the ganglia which the spinal nerves do not possess, having probably lost them. This would explain this difference in mode of origin of cranial and spinal ganglia."

After a consideration of the above facts, we must agree with Neal (30) that "the bounds between the head and the trunk in the Vertebrate series are not fixed; there is an unbroken continuity throughout the head and trunk of such essential components of metameres as neuromeres, somites, nerves, visceral arches, visceral clefts and aortic arches; this is evidence sufficient to warrant the general belief in the serial homology of the segments in these two regions." There may be some doubt concerning Neal's statement about the visceral arches; thus Kupffer says: "There enters into the composition of the cranial nerves two systems, the spinal and the branchial, the first is common to the head and trunk, the latter appears only in the head." From this it appears that Kupffer considers the visceral arches as head structures. The vertebrate head, even in its simplest form, is connected with the visceral arches, but in *Amphioxus* the visceral arches, even the first eight, are 'trunk,' not 'head,' structures. What appears to have happened is that as the anterior body segments coalesced with the primitive 'head' to form the vertebrate 'head,' the visceral arches lost their connection with the trunk and became 'head' structures.

The number of metameres has been differently computed. Neal gives the following as an average of results:—five pre-otic metameres, one otic and five post-otic cephalic metameres (*Squalus*). The post-otic are variable in number.

The more anterior metameres are far from complete. This would obviously be the case, as the anterior are the older and more modified, while the more posterior, being later additions, are the more complete. The factor of greatest importance in the modification of these somites is the disappearance or transformation of the visceral arches.

One of the most difficult nerves is the Vagus, in that embryological and adult data do not coincide. In its beginning the Vagus has a single ganglion, or, at most, two, and appears to be connected with only one neuromere, while in the adult condition the Vagus in all but the higher Vertebrata obviously consists of a number of nerves with a ganglion connected with each. Why is there this discrepancy, and how does it arise? The embryological condition has been generally overlooked, and the adult alone has served as a basis of Gegenbaur's theory of the segmentation of the head in this region. Since his paper on *N. griseus*, the Vagus has been considered a nerve compounded of from four to seven simple nerves. But reasoning from the embryological condition, what should we consider the nature of the Vagus? This determination is important, as it will considerably modify our idea of the number of neuromeres in the brain. The question is, what is the nature of the branchial ganglia of the Vagus; are they equivalent to one another, for example, or are they epibranchial ganglia which have become connected with the Vagus and its own proper ganglia? Undoubtedly the branches of the Vagus arose in connection with the visceral arches—but how? Each of the branchial arches may have been originally supplied by a branch of an occipital nerve. The neuromeres which have disappeared in this region of the head may have been those connected with the occipital nerves which sent branches to the branchial arches. On the disappearance of these spino-occipital nerves, their branches may have joined the orginal Vagus, taking with them the ganglia produced by the persistence in a changed form of the epibranchial ganglia, one of which occurred in relation with each branchial arch. If this were the case, the Vagus in origin is a single nerve, and hence in its development is connected only with one neuromere. If the complete Vagus is regarded as a single nerve, then visceral arches belonging to a series of segments are supplied by branches of a nerve of an anterior segment, just as the intestinal branch of the Vagus supplies certain segments which were formerly supplied by branches of spinal nerves belonging to these segments; but comparisons with the intestinal branch do not help to solve the problem of the branchial ganglia.

Ransom and Thompson state concerning *Petromyzon*, that the Vagus arises by four roots, exactly like the normal spinal posterior roots. These four unite, and from them proceed both dorsal and ventral rami exactly as in the case of a typical spinal nerve. This suggestion of an origin from a series of spinal nerves is partly confirmed by a segmental arrangement of the ganglion cells. If a similar condition occurs in the higher Fishes, the branchial ganglia of the Vagus are easily accounted for, but not the epibranchial ganglia, which undoubtedly enter into the formation of the Vagus. It may be that the remnants of the spinal and the epibranchial ganglia have fused. If this is the case it is difficult to see why the neuromeres did not persist with their ganglia.

GENERAL CONCLUSIONS.

1. According to the nerve component theory, the nerve fibres may be divided into two systems—somatic and splanchnic. Each of these is divided into motor and sensory. Somatic sensory is sub-divided into (*a*) general cutaneous, (*b*) acustico-lateralis; splanchnic sensory is sub-divided into (*a*) general splanchnic, *i.e.* the afferent sympathetic fibres, (*b*) the communis or end-bud system and taste buds.

2. The components are found in their most typical form in the Fishes and during the aquatic part of the life of Amphibia.

3. Whilst the Mammalia are lacking in the chief part of the acustico-lateralis system, and a large part of the communis, they are possessed of special endings for heat, cold, pressure and pain, the relation of which to the above systems has not yet been determined.

4. It is probable that ultimately the optic and olfactory nerves will be brought into line with the other nerves.

5. The sympathetic system is to be regarded as a derivative of the 'central nervous system.' It is composed of afferent and efferent splanchnic fibres, which are distinguished by their anatomical arrangement and histological characters from all other fibres in the body.

6. Our ultimate knowledge of the segmentation of the head must depend upon a combination of facts regarding neuromeres, somites, head cavities, the components of primitive nerves and the components and distribution of adult nerves.

7. A typical primitive nerve must have consisted of afferent and efferent somatic and splanchnic fibres, the former being more numerous and better differentiated than the latter. The sensory fibres, both splanchnic and somatic, are as yet unassociated with special sensory endings.

8. This typical primitive nerve is to be regarded as the common ancestor of spinal, branchiomeric, and special sense nerves.

9. The cranial nerves are a combination of spinal, branchiomeric, special sense and primitive nerves.

10. It is important to fully understand such types as *Amphioxus* and the Cyclostomes, for they are very near the beginning of the Vertebrate series, and, on the whole, are primitive rather than degenerate.

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DESCRIPTION OF FIGURES.

Fig. 1. A General Scheme of the Components in the lower Vertebrata.

Fig. 2. A General but incomplete Scheme of the Components in the Mammalia.

░	Splanchnic or visceral motor (S. M.).
◌	Acustico-lateralis (A. L.).
▦	Somatic motor (Som. M.).
▨	Splanchnic sensory (S. S.).
▧	Somatic sensory (Som. S.).

ABBREVIATIONS.

A.C.,	anterior cornu.
C.C.,	Clarke's column.
C.T.,	Chorda tympani.
D.X.,	dorsal branch of Vagus.
D.H.,	dorsal horn.
F.C.,	fasciculus communis.
F.L.,	fasciculus longitudinalis.
G.,	Gasserian ganglion.
G.S.P.,	great superficial petrosal.
G. VII.,	ganglion of VII.
Hyo.,	hyomandibular.
J.A.,	Jacobson's anastomosis.
L.C.,	lateral column.
M.V.,	motor V. tract.
N.A.,	nucleus ambiguus.
Ophth.,	ophthalmic.
P.B.,	pre-branchial or maxillary V.
P.B.X.,	pre-branchial of Vagus.
R.L.V.,	ramus lateralis vagi.
R. Vis.,	ramus visceralis.
Som. aff.,	somatic afferent.
T.I.O.,	infra - orbitalis with mandibular.
T.S. V., and *T.S. VII.*,	ophthalmicus superficialis V. and VII.

Journal of Anatomy and Physiology.

THE NATURE OF THE MAMMALIAN DIAPHRAGM AND PLEURAL CAVITIES.[1]

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(1) *The nature of the diaphragm.*—In three figures in the succeeding page (figs. 1, 2, 3) I have attempted to throw into a diagrammatic form the main results of an investigation into the nature and origin of the mammalian diaphragm and pleural cavities. In fig. 1 is represented the body cavity as seen in fishes and amphibians; it is seen to be divided into cardiac and abdominal compartments by the septum transversum (*g*). The lungs lie within the abdominal compartment. In fig. 2 the condition in birds is shown; there it will be seen that the greater part of the lung has become extruded from the abdominal cavity; the part that remains forms the most posterior of the four air sacs. In fig. 3 the mammalian arrangement of cavities is represented; the lungs are now seen to be completely extra-abdominal, and are separated from the abdominal cavity by part of the bounding wall of that cavity. Thus it will be seen that this investigation has led me to regard the lungs as we do the testicles, viz., as organs which have been extruded as herniæ from the abdominal cavity because of certain physiological conditions that became of functional importance in the course of evolution. Whereas the testicle, in its migration, passes through all three of the primary muscular layers of the hind part of the body-wall, the lung is produced within a space formed in the fore-part of the body-wall between the inner and middle of the three primary

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[1] Read before the Anatomical Society of Great Britain and Ireland, Nov. 1904.

layers. In short, the mammalian pleural spaces are new cavities formed within the body-wall, and the diaphragm is a part of the body-wall which has been depressed within the body cavity by the extra-abdominal development and growth of the lungs. The pleuro-peritoneal opening and internal abdominal ring are corresponding structures; the testis escapes from the abdominal cavity by the one, the lung escapes by the other.

(2) *The relationships of the mammalian diaphragm to the pericardium and roots of the lungs.*—The intimate structural and functional relationships which exist between the central tendon, the pericardium, and roots of the lungs, require close consideration in seeking to trace the origin of the diaphragm. These relationships are represented in fig. 4. In man and the great anthropoid apes the pericardium is intimately bound to the central tendon of the diaphragm, and in all mammals the pericardium is closely and strongly bound to the roots of the lungs. The crura of the diaphragm (fig. 4) with the fibres from the

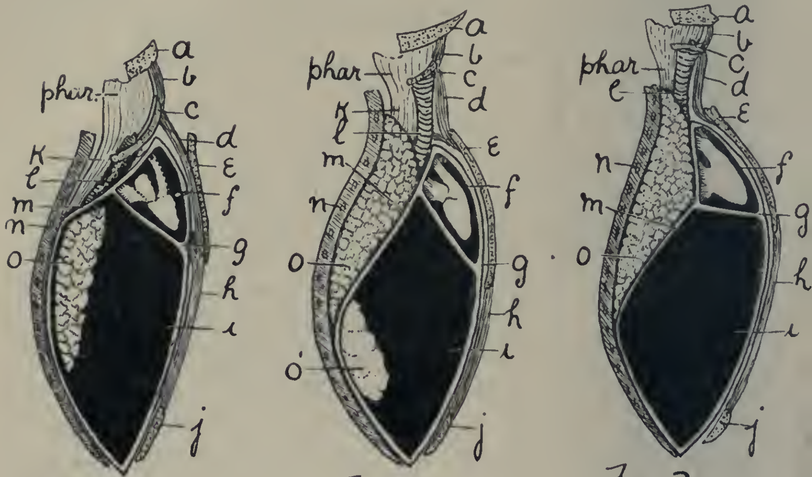

Fig. 1 Fig. 2 Fig. 3

Figs. 1, 2, 3.—Diagrams illustrating the origin of the diaphragm and pleural cavities. Fig. 1, the amphibian body-cavities; fig. 2, the corresponding cavities in a bird; fig. 3, in a mammal. *a*, mandible; *b*, genio-hyoid; *c*, hyoid; *d*, sterno-hyoid; *e*, sternum; *f*, pericardium; *g*, septum transversum; *h*, rectus abdominis; *i*, abdominal cavity; *j*, pubis; *k*, œsophagus; *l*, trachea; *m*, cervical limiting membrane of abdominal cavity; *n*, dorsal wall of body; *o*, lung; *o′*, air-sac.

arcuate ligaments—which I shall name in this paper the spinal part of the diaphragm—ascend in a more or less vertical direction to end in the central tendon, while the sterno-costal fibres (sterno-costal part) pass upwards and backwards to the same insertion. One infers from the anatomical arrangement of parts, that on inspiration the central tendon, pericardium, and heart and roots of the lungs must move in a downward and forward direction (*i.e.* towards the umbilicus). The examination of the living by means of X-rays reveals the inspiratory movement of the heart in a forward and downward direction, the extent of

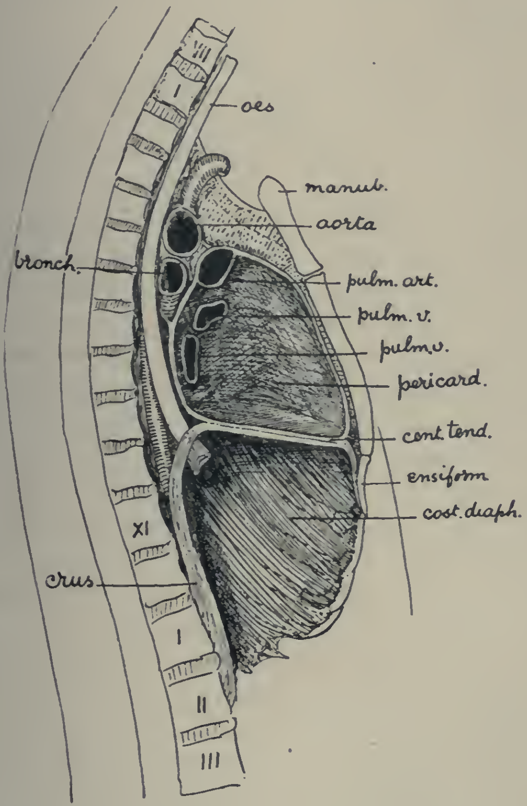

Fig. 4.—Mesial section of a thorax in which the heart and abdominal viscera have been removed. The crus of the diaphragm is seen to ascend to the central tendon, while the fibres which arise from the ribs pass upwards and backwards. The sternal fibres are vertical in position.

the movement varying with the type of respiration in the individual examined and the vigour of the inspiratory effort.[1,2] The curvature of the diaphragm remains practically unaltered during inspiration[3] (1) (4). Formerly it was believed that the central tendon, the heart, and roots of the lungs were practically stationary, and that the curvature of the diaphragm was flattened during inspiration.

(3) *The relationship of the diaphragm to the liver and abdominal cavity.*—The diaphragm, when present, bears a constant relationship to the liver and abdominal cavity throughout the vertebrate series. It invariably forms a hood for the liver, possessing thus the power of compressing the hepatic substance and forcing the hepatic blood into the pericardial cavity. At the same time the diaphragm compresses all the abdominal contents, and thus maintains the portal and hepatic circulation. In the course of this paper evidence will be produced to show that the diaphragm appears, not as a muscle which acts on the lungs, but as a muscle which compresses the abdominal contents, and regulates the tension within the abdominal cavity. While the relationship of the diaphragm to the lungs varies, its connection with the liver and abdominal contents remains absolutely constant throughout the vertebrate series.

(4) *Connection of the diaphragm with the pulmonary roots.*—The structural and functional relationship of the diaphragm to the roots of the lungs is one of primary importance. Why should the pulmonary roots undergo a respiratory movement? In fig. 5 the inspiratory movement of a human lung as seen in profile is diagrammatised; in the figure it will be seen that the apex of the lung—that part which lies anterior to the neck of the first rib—is represented as the fixed point from which the expansion of the lung takes place in a forward and downward direction.[4] The root of the lung and heart participate in this

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[1] Grönroos, H., *Das centrum tendineum und die respiratorische verschiebung des Zwerchfells*, Bd. xiii. 1897, p. 536.

[2] Keith, A., "The Nature and Anatomy of Glenard's Disease," *Lancet*, March 7, 1903.

[3] Dally, "On the Use of the Roentgen Rays in the Diagnosis of Pulmonary Disease," *Lancet*, June 27, 1903.

[4] For fuller details of this movement see *Proc. Anat. Soc. Great Britain and Ireland*, May 1903. See also, *Die Formen des Menschlichen Körpers und die Formänderungen bei der Athmung*, by C. Hasse, Jena, 1888–1890.

movement; the movement of the root is necessary for a proper expansion of the apical and dorsal part of the lung.

The close connection between the central tendon of the diaphragm, pericardium, and roots of the lungs, seen in man and the great anthropoids, is undoubtedly due to a reversion to a more primitive condition, for in the typical mammal their connection is much less intimate.[1] In a typical mammal, such as the monkey or rabbit, the movement of the pulmonary root is relatively slight, because the part of the lung above the

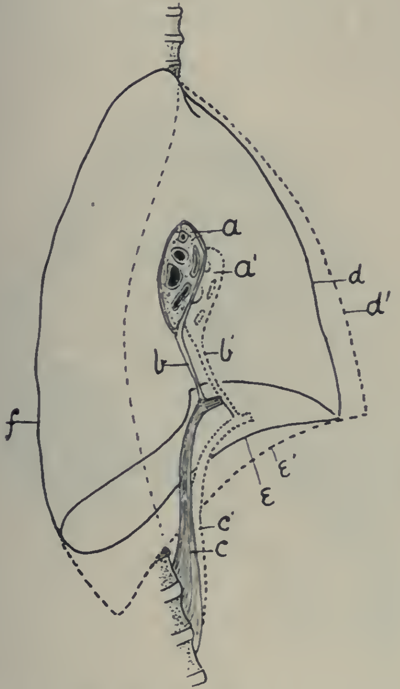

FIG. 5.—A diagram of the mediastinal aspect of the left lung, showing the respiratory movements and relationship of the crus to the root of the lung. *a*, root of the lung in expiration; *a'*, in inspiration; *b,b'*, dorsal wall of pericardium; *c,c'*, crus of the diaphragm; *d,d'*, anterior border of the lung during expiration and inspiration; *e,e'*, diaphragmatic border during expiration and inspiration; *f*, the posterior or dorsal border during expiration and inspiration.

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[1] See "Die Grenzlinien der Pleuralsäcke und die Lagerung des Herzens bei Primaten, inbesondere bei den Anthropoiden," by G. Ruge, *Morph. Jahrb.*, 1893, Bd. xix. pp. 149–249.

pulmonary root is relatively small (fig. 6). The azygos lobe of the right lung expands between the central tendon and pericardium; the entrance to the subpericardiac space, in which the azygos lobe is contained, is seen in fig. 6, between the œsophagus and inferior vena cava, and below the root of the lung. The descent of the diaphragm, which in man is followed by a movement of the heart and pulmonary roots, brings about a direct expansion of the azygos lobe in a typical mammal. The inferior cava is highly elastic to allow this expansion to take place; so is the dorsal mesentery of the thorax (see fig. 6).

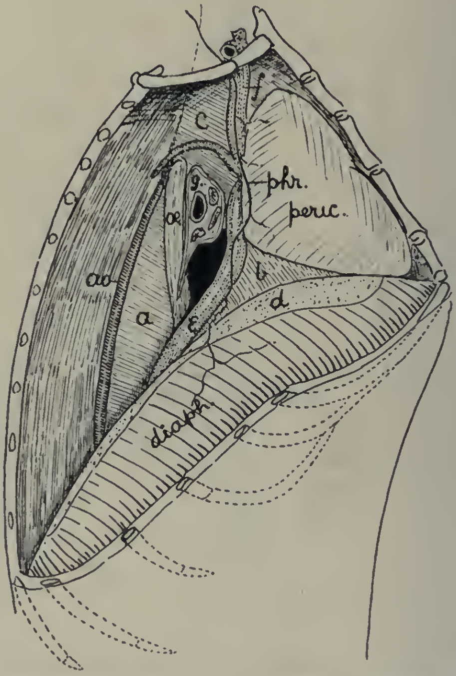

FIG. 6.—Right pleural cavity of a rabbit to show the relationship of the root of the lung to the diaphragm. *a*, dorsal mesentery of thorax; *b*, mesentery between pericardium and central tendon (*d*), forming right wall of subpericardiac space; *c*, on mesentery of thorax, above vena azygos major; *e*, inferior vena cava; *f*, superior vena cava; *g*, root of lung; *ao.*, aorta; *œ.*, œsophagus; *phr.*, phrenic nerve.

The close relationship which exists between the diaphragm and pulmonary roots suggested to me the possibility of the diaphragm having appeared first, not as a partition across the body cavity, but as muscular bands which acted directly on the roots of the lungs, moving them, during the inspiratory phase, in a forward and downward direction. To produce such a movement I postulated the existence of dorsal and ventral bands of musculature, which, rising from the dorsal and ventral walls of the body, ended directly on the pulmonary roots. Although this theory only proved partially true, it served me very well at the commencement of my investigation.

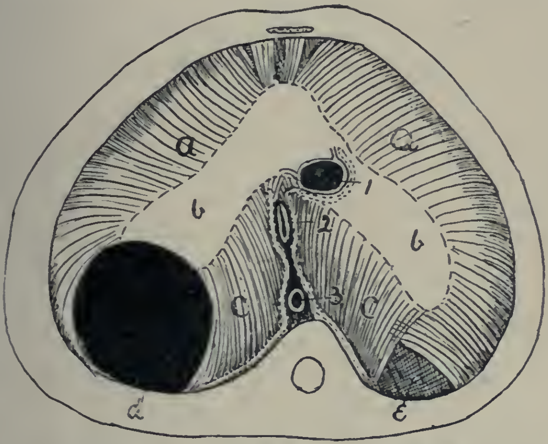

FIG. 7.—Thoracic aspect of the diaphragm of a child in which the left pleuro-peritoneal opening is widely patent. *a,a*, sterno-costal parts of diaphragm; *b*, central tendon; *c,c*, spinal parts; *d*, left pleuro-peritoneal opening; *e*, position of right opening (spino-costal hiatus). 1, inferior vena cava; 2, œsophagus; 3, aorta, between layers of mediastinal pleura (dorsal mesentery of thorax).

The diaphragm in cases where the pleuro-peritoneal openings remain unclosed.—Turning first to the diaphragm of infants, in which the communication between the pleural and peritoneal cavities has remained open owing to the presence of a diaphragmatic hernia,[1] I found clear evidence of such muscular bands as I had postulated (fig. 7). Each half of the diaphragm is seen to be composed of three parts—a ventral or sterno-

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[1] A summary of what is known of diaphragmatic hernia will be found in Dr J. W. Ballantyne's excellent *Manual of Antenatal Pathology*, vol. ii. p. 477 (1904). Dr Ballantyne, as is the case with all who have written on this subject, finds it difficult to explain the various forms of diaphragmatic hernia on the basis of our present knowledge of the origin and development of the diaphragm. By far the commonest form is that in which the hernia takes place

costal muscular part (fig. 5, *a*); a dorsal or spinal muscular part (*c*), and an intermediate tendinous part (*b*), which, as we have seen, is connected with the pulmonary roots through the intermediation of the pericardium. Examination of specimens, of such a nature as is represented in fig. 7, clearly show that the origin of the diaphragm must be sought for within the partition or mesentery which separates the right from the left half of the cœlom, for the diaphragm will be seen to lie between the pleuro-peritoneal cœlomic passages. One infers that the dorsal and ventral bands of the diaphragm have reached the roots of the lungs through the dorsal and ventral mesentery of the fore-gut—an inference which further inquiry will show to be only partially true.

Elementary parts of the diaphragm.—In the normal human diaphragm the spinal and sterno-costal muscular bands become more intimately blended than in any other mammal, and yet it is commonly possible to distinguish them. In fig. 7 the position of the right pleuro-peritoneal opening is indicated by a fibrous interval—the spino-costal hiatus. In fig. 8 two conditions of this hiatus are represented. On the left side there is a wide interval shown between the two muscular segments (*d*), for on the left side the spino-costal hiatus is commonly more extensive than on the right side. On the right side the hiatus is obliterated, owing to the complete approximation of the spinal and sterno-costal segments.

The condition of the spino-costal hiatus and the relationship of the spinal to the costal parts of the diaphragm in a typical mammal are shown in fig. 9. The arrows in that figure show the position of the spino-costal hiatus and the former site of the pleuro-peritoneal communication. As is seen to be the case in fig. 7, where the pleuro-peritoneal communication

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through a patent pleuro-peritoneal opening (the false hernia), but occasionally a part of the liver (such as was described in the rabbit by Professor Arthur Thomson in the *Proc. Anat. Soc.*, May 1901), and as occurs in the ox and sheep and human fœtus, or any other abdominal viscus, becomes herniated within the thorax by pushing in front of it a sac formed by an expansion from the diaphragm (true herniæ). The manner in which true herniæ are formed will be referred to later in this paper. The patency of the pleuro-peritoneal passage belongs to the same series of abnormalities as hare-lip, cleft palate, hypospadias, and *atresia ani*, all being more or less marked examples of reversion to a primitive stage of evolution.

persists, the spino-costal hiatus is bounded by all three parts of the diaphragm, the central tendon reaching the margin of the hiatus and completely separating the spinal from the costal muscular fibres. The assumption of the erect posture in man and the great anthropoids entailed extensive alterations in the mechanism of their respiration. In these alterations the origin of the spinal fibres of the diaphragm migrated outwards over the psoas and quadratus lumborum, the sheaths of which were thickened to form the arcuate ligaments. The quadratus lumborum, which in typical mammals forms merely a narrow series of muscular slips (fig. 9) undergoes a corresponding outward migration. There is also evidence that the origin of the costal fibres of the diaphragm has become approximated to the spinal origin, for occasionally the costal fibres in man do not extend beyond the eleventh rib. In man and the anthropoid

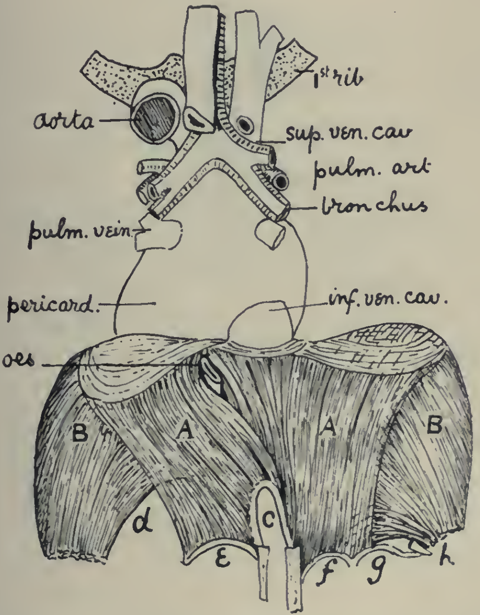

Fig. 8.—A dorsal view of the human diaphragm showing its connections with the pericardium and roots of the lungs. *A*, spinal part; *B*, sterno-costal part; *c*, aortic opening; *d*, spino-costal hiatus (position of pleuro-peritoneal opening); *e*, left internal arcuate ligament; *f*, right internal arcuate ligament; *g*, external arcuate ligament; *h*, twelfth rib.

apes the spinal and costal fibres overlap each other at their insertion to the central tendon (compare figs. 8 and 9).

The evidence derived from the phrenic nerve.—The nerve supply of the diaphragm, which has been very fully investigated by von Gössnitz,[1] also points to the fact that there are two distinct muscular elements in the diaphragm. The phrenic nerve, when it reaches the diaphragm (fig. 6) divides into a ventral division which supplies the sterno-costal part and a dorsal to the spinal part. In some animals, and occasionally in man, these two divisions separate before reaching the diaphragm. Further, the origin of the phrenic nerve from the 3rd, 4th, and 5th

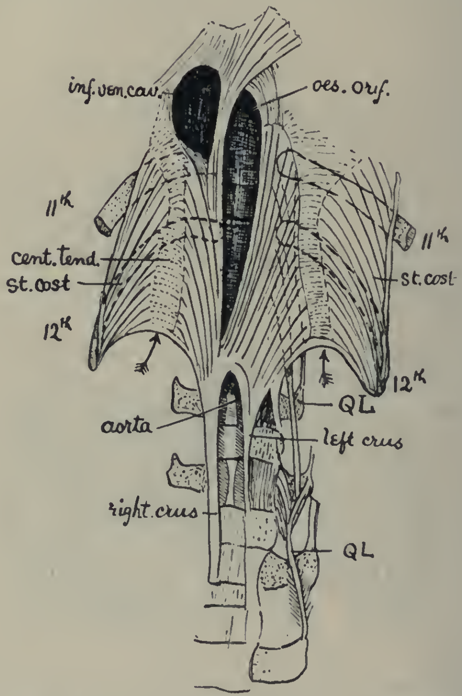

FIG. 9.—The spinal part of the diaphragm of a monkey (*Semnopithecus cinereus*) seen on its abdominal aspect. The arrow indicates the spino-costal hiatus, the position of the pleuro-peritoneal communication. Q.L., quadratus lumborum. Only part of the sterno-costal (*st.cost.*) segment is shown.

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[1] Gössnitz, Wolff. von, *Beitrag zur Diaphragmafrage*, 2 Taf. *Zoologische Forschungsreisen in Australien*, etc., von Richard Semon, Bd. iv. Lief. 3, pp. 205–262.

cervical segments, its passage on the lateral aspect of the jugular vein and duct of Cuvier, its supply to the pericardium and its distribution on the abdominal aspect of the diaphragm, all prove important clues in unravelling the origin of this muscle.

An examination of the anatomy of the diaphragm thus supported the theory I had formulated, viz., that the diaphragm arose probably as dorsal and ventral bands of musculature which acted on the roots of the lungs.

The amphibian diaphragm.—The search for such muscular structures amongst present-day birds and reptiles proved fruitless, as those familiar with their anatomy would expect. But it was quite otherwise when I commenced to study the Amphibia. My attention was naturally directed first to the condition in the African toad, Xenopus, and to the Surinam toad (*Pipa Americana*) in which Beddard[1] had described a structure which he regarded as homologous with the diaphragm of mammals. Mr Beddard supplied me with specimens to reinvestigate the anatomy of these toads. A lateral view of a partially dissected specimen of Xenopus is shown in fig. 10. The fore-limb has been removed and a part of the external oblique taken away to expose two muscles which exactly correspond to the muscular bands which I had postulated as the primitive form of the diaphragm. A dorsal muscular band (A, fig. 10) is seen to arise from the ilium, and, expanding as it passes forwards, ends on the œsophagus, over the root of the lung and on a fibrous expansion (cervical aponeurosis of the abdominal cavity) which covers the liver and is continuous with the pericardium (see fig. 11). It is this sheet which Beddard regarded as representative of the mammalian diaphragm. On the other hand, I regard it as representing only the spinal segment of the diaphragm. Its nerve arises from the brachial plexus (fig. 10) and passes down on the lateral aspect of the superior vena cava (duct of Cuvier).

The evolution of the dorsal part of the amphibian diaphragm (A, in fig. 10) can be traced; it is derived from the anterior

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[1] Beddard, F. E., "On Some Points in the Anatomy of *Pipa Americana*," *P.Z.S.*, Dec. 3, 1895; "The Diaphragm and Muscular Anatomy of Xenopus," *P.Z.S.*, Dec. 3, 1895.

(cervical) part of the transversalis. In *Rana esculenta* and *Rana temporaria*, as may be seen in the very exact work of

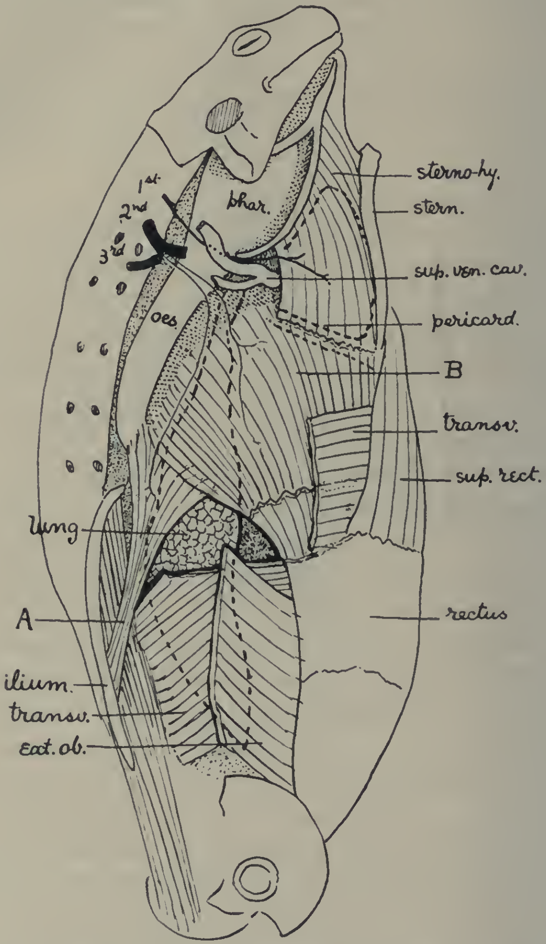

FIG. 10.—Lateral view of a partly dissected specimen of Xenopus. A, dorsal part of the amphibian diaphragm (anterior or cervical part of transversalis muscle); B, ventral part of amphibian diaphragm (deep rectus abdominis). Parts of the external oblique (*ext.ob.*) and transversalis muscles have been cut away. Parts of the lung and liver have been thus exposed. The outline of the pericardium is represented by a broken line beneath the sterno-hyoid and sterno-thyroid muscles. The 1st, 2nd, and 3rd spinal nerves are shown, and the two nerves which represent the phrenic.

Gaupp,[1] and as shown in fig. 12, the anterior fibres of the

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[1] *Anatomie des Frosches*, 3rd edition, 1896.

transversalis come from the costal process of the 4th vertebra and end on the œsophagus side of the pericardium and the root of the lung between these insertions. This part of the transversalis covers the lung (rather obscurely shown in fig. 12), and is already differentiated functionally from the rest of the transversalis. In Xenopus its insertion has migrated backwards to the ilium (fig. 10); in *Pipa Americana* it has migrated along the ilium and reached the femur (fig. 13). The primitive condition of this muscle can be seen in long-tailed amphibians (see fig. 28). Fibres of the human diaphragm have been seen to arise from the ilium.

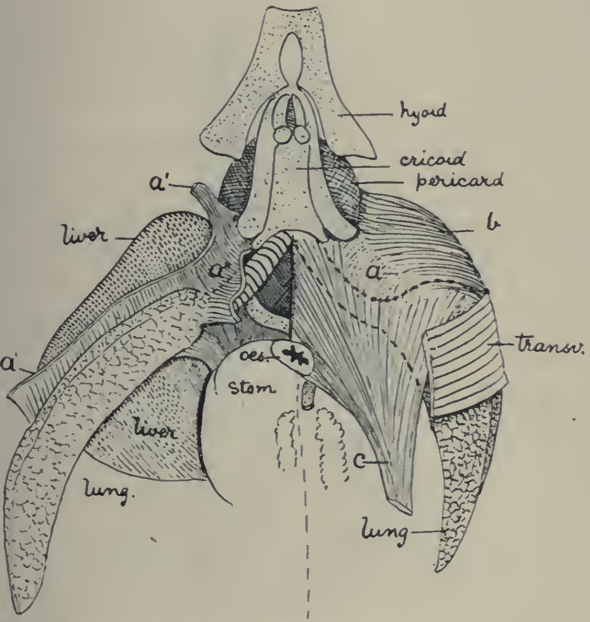

FIG. 11.—The connections of the dorsal part of the amphibian diaphragm (as seen in Xenopus) exposed by the removal of the spinal column, spinal muscles, and pharynx. A, aponeurosis of the cervical wall of the abdominal cavity; it is situated over the liver and represents the central tendon of the mammalian diaphragm; *a'*,*a'*,*a''*, parts of the cervical aponeurosis into which the dorsal and ventral parts of the amphibian diaphragm are inserted; *b*, ventral part of the amphibian diaphragm (rectus profoundus); *c*, dorsal part of the amphibian diaphragm. Between the cricoid and œsophagus (*œs.*) the dorsal mesentery is exposed.

The sterno-costal part of the mammalian diaphragm is represented in Xenopus by a part of the deep layer of the rectus abdominis muscle (B, fig. 10). Behind, it is continuous with the deeper fibres of the rectus abdominis; anteriorly it expands, and is inserted to the septum between the pericardium and abdominal cavity (amphibian septum transversum); to the cervical aponeurosis over the liver and to the root of the lung (figs. 10, 11, and 12). It will be thus seen that I regard the sterno-costal part of the diaphragm as a derivative of that segment of the rectus abdominis which lies immediately behind (caudad) the sterno-hyoid and sterno-thyroid segments of that

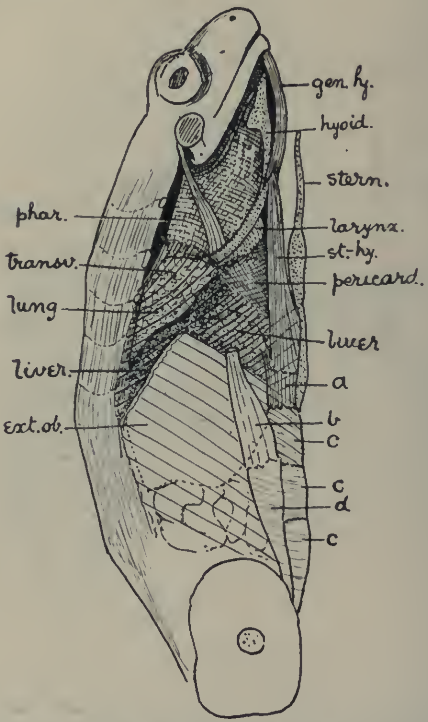

FIG. 12.—Lateral view of *Rana esculenta*, in which the fore-limb and shoulder girdle have been removed. *a*, the fourth segment of the rectus abdominis from which the ventral part of the diaphragm arises; *b*, pectoralis; *c*,*c*,*c*, mesial or deep rectus; *d*, lateral or superficial rectus. The vertebral or cervical part of the transversalis (*transv.*) is seen to end on the œsophagus and roots of the lungs; under it, rather obscurely shown in the figure, the lung is represented. Fibres of the transversalis are represented over the liver and ending on the ventral aspect of the rectus.

sheet. The origin of the diaphragm from this segment has been clearly stated by Gegenbaur and by Gössnitz.

The expansion of the fourth segment of the rectus abdominis to form the ventral (sterno-costal) part of the diaphragm can be followed step by step in amphibians. The primitive or urodelian condition of the fourth segment may be seen in *Rana esculenta* (see A, fig. 12, and B, fig. 14). The first segment forms the genio-hyoid, the second and third, the depressors of the hyoid (fig. 14). The fourth segment joins the hyoid segments to the rectus abdominis; some of its deep fibres may end on the pericardium. In long-tailed amphibians, the fourth segment lies on the deep aspect of the ventral part of the shoulder

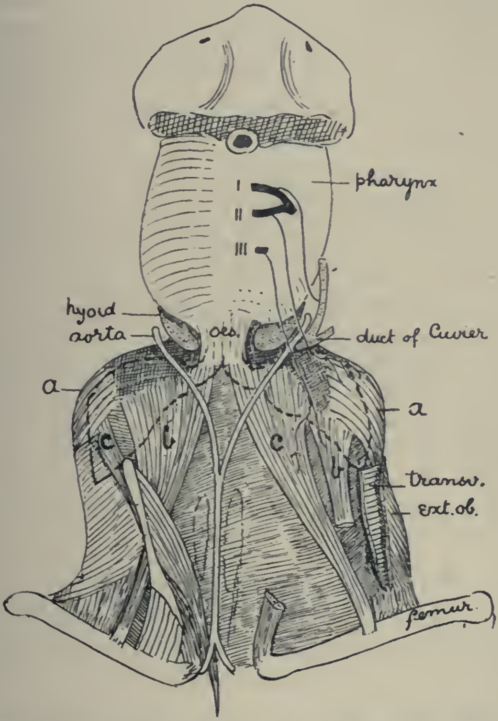

Fig. 13.—Dorsal view of the diaphragm of *Pipa americana*, obtained by removal of the spinal column. *a*, ventral part of diaphragm, derived from rectus abdominis; *b*,*c*, dorsal parts of the diaphragm, derived from transversalis. The part marked *c* arises from the ilium, as in Xenopus. The outlines of the lungs are shown by broken lines. The nerves to the diaphragm are shown to arise from the second and third spinal nerves.

girdle (see fig. 28); it is closely adherent to the septum transversum. In Amblyostoma, an abranchiate urodele, there are two parts of the fourth segment which end on the pericardium: (1) deep fibres which rise from the xiphisternum; (2) others of the deep fibres continuous with the rectus sheet. In Bombinator igneus the fibres of the fourth segment spread outwards, and at their proximal end find an insertion to the pericardium. In Xenopus and *Pipa*, as may be seen from figs. 10, 11, 13, the deep fibres of the fourth segment of the rectus have attained a wide insertion to the pericardium and cervical aponeurosis.

Thus the amphibian diaphragm is made up of three parts, a dorsal muscular part derived from the transversalis, a ventral part from the fourth segment of the rectus abdominis, a central part from the cervical aponeurosis of the abdomen.

It must not be supposed that I desire to trace the mammalian stock from such specialised amphibians as either Xenopus or *Pipa*; the great specialisation of the tail-less amphibians and their late appearance in the geological record exclude them from all speculations regarding the origin of the diaphragm. But with the long-tailed amphibians the case is quite otherwise; even in the absence of any geological record, their whole organisation points to their being a connecting link between the lowest and highest of vertebrate forms. In bringing forward the condition in Xenopus and *Pipa*, I merely wish to emphasise the point that in these forms, which have certainly been derived from long-tailed amphibians, a diaphragm has been evolved from the rectus abdominis and transversalis; and on the supposition that the mammalia have also been evolved from a primitive amphibian form (stegocephalia[1]), it is probable that the same elements which give rise to the diaphragm in the anura may also have become modified to form a corresponding structure in mammals.

The nerve supply of the fourth segment of the rectus abdominis in amphibians has many points in common with the nerve supply of the sterno-costal part of the diaphragm. In the first place, the phrenic nerves perforate the diaphragm,

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[1] See *Outlines of Vertebrate Palæontology*, by A. Smith Woodward, Cambridge, 1898.

commonly the tendinous part, and are distributed on its peritoneal aspect. In fig. 14 the nerve supply of the fourth segment of the rectus in *Rana esculenta* is represented. It arises from the second spinal nerve (see also fig. 15) and passes for some distance in common with the nerve which supplies the pectoral group of muscles (coraco-clavicular nerve of amphibians, anterior internal thoracic of mammals). It then perforates the cervical aponeurosis of the abdominal wall (central tendon), and forms a plexus on the deep or peritoneal aspect of the fourth segment. Gaupp notes the fact that in Amphibia the nerves to the rectus form a plexus on the deep aspect of the muscle. Each spinal nerve in the brachial plexus of urodeles sends a ventral branch to the deep aspect of the rectus abdominis.

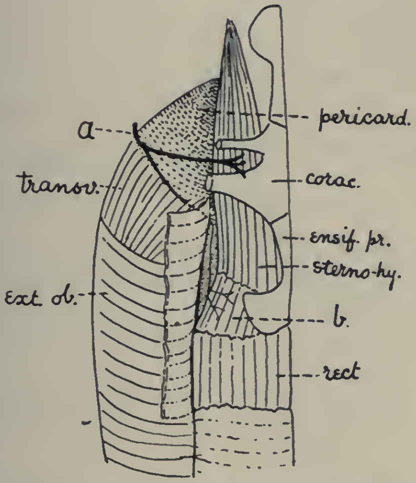

FIG. 14.—Right shoulder girdle and muscles of the right half of the body-wall of *Rana esculenta* (after Gaupp). *a*, branch from the second spinal nerve, giving off a nerve to the fourth segment of the rectus (*b*) and the coraco-clavicular branch to shoulder muscles. The part of the transversalis which passes on the ventral aspect of the rectus has been reflected. The part so reflected becomes the triangularis sterni in mammals. The part anterior to it, which ends on the aponeurosis and pericardium, becomes the dorsal part of the diaphragm.

Evidence derived from nerve supply.—In fig. 15 I have given a diagrammatic representation of the nerve supply of the various muscles derived from the ventral longitudinal (rectus) sheet in Xenopus. By the side of the diagram are placed the nerve supply as given by Gössnitz in his monograph cited on p. 252 of this article, for the corresponding muscles in man. From its nerve supply, Gössnitz infers (1) that the sternocostal part of the diaphragm is derived from the 3rd and 4th body segments, and the spinal part from the 4th and 5th; (2) that the phrenic nerve is in series with the hypoglossal (1st spinal nerve of amphibians) and with the ventral branches of other spinal nerves which supply the rectus abdominis muscle. The nerve supply of the parts of the rectus and transversalis sheet answer the conditions presupposed by Gössnitz. The nerve supply of the dorsal part arises behind that for the ventral part (see figs. 10 and 13). The subclavius muscle is probably a derivative of the sterno-coracoid muscle, which in turn is derived from the rectus sheet, probably from

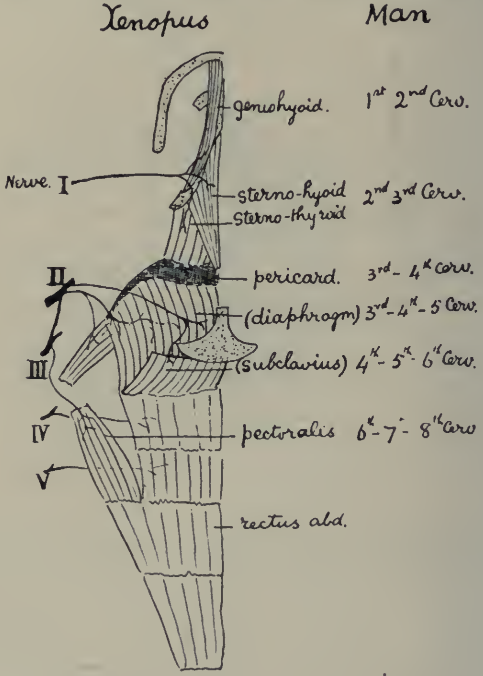

Fig. 15. Diagrammatic representation of the nerve supply of the muscles derived from the rectus sheet in Xenopus. The column to the right gives the nerve supply of the corresponding muscles in man, as stated by Gössnitz.

the same segment, or one just behind that which gives origin to the sterno-costal part of the diaphragm. But whereas the diaphragm springs from the deep layer of the rectus (rectus profundus), the sterno-coracoid springs from an intermediate layer, which lies superficial to the rectus profundus, but deep to the pectoral derivatives of the rectus sheet. The close union that exists between the phrenic and the nerve to the subclavius muscle points to their origin from the same segment.

There is a discrepancy which must be noted here. How did the two nerves to the diaphragm become united in the phrenic, and why is it, while the nerves to the transversalis sheet are invariably distributed on its outer or more superficial aspect, the nerve to the dorsal part of the diaphragm is distributed on the peritoneal aspect? Those difficulties will be again noted when discussing the development of the pleural cavities.

Corresponding points in the relationships of the amphibian and mammalian diaphragms.—If figs. 7 and 10 be compared, it will be seen that in their relationships to the heart, to the pericardium, to the duct of Cuvier, to the liver, and to the organs of digestion, the amphibian and mammalian diaphragms are in complete agreement. In both forms the cardiac structures are supra-diaphragmatic and the abdominal contents are infra-diaphragmatic. Both forms agree functionally, too, in this, that when they contract, they tend to enlarge the pericardial cavity and diminish or compress the abdominal, thus forcing the blood from the abdomen to the heart. Thus it will be seen that there is a very close resemblance between the diaphragm of amphibians and that of mammals, excepting in two very important points. In the first place, the diaphragm is supra-pulmonary in amphibians and infra-pulmonary in mammals; in the second, it is distinctly a muscle of expiration in amphibians and of inspiration in mammals. Supposing evolution to proceed without sudden breaks or jumps, but merely by a gradual development along definite physiological lines of progress, in what manner and under what conditions was it possible for the amphibian diaphragm to become gradually transformed into the mammalian type? It is impossible to conceive that the mammalian diaphragm arose from any structure or combination of structures found in extant birds or reptiles; and we are perforce driven back on the more primitive structures found in amphibians.

Primitive function of the diaphragm.—In one important function, however, the amphibian and mammalian diaphragms correspond. The researches of Dr Leonard Hill[1] have made manifest that the tone and contraction of the abdominal parietes, especially of the diaphragm, are the chief factors in regulating and maintaining the portal, hepatic, and abdominal venous circulation. The mammalian diaphragm is the chief agent in filling the heart. A glance at figs. 10, 11, 12, and 13 will show that this is not only the chief but the only function of the amphibian diaphragm; it is in connection with this circulatory function that the diaphragm came into being.

The septum transversum.—The amphibian diaphragm is functionally correlated with the septum transversum, the fibrous partition between the pericardial and abdominal cavities (fig. 1). Although the embryology and morphology of this structure have been discussed and described at great length, I do not remember any allusion to what ought to be the first subject of inquiry—what is it for? To see its primitive condition, one has to turn to its arrangement in fishes. Its condition and attachments in the dog-fish are shown in fig. 16. It forms a fibrous septum between the pericardial and abdominal cavities (see figs. 1, 2, 3), and is continuous with the strong fibrous membrane or aponeurosis which bounds these cavities in fishes. It serves the minor purposes of affording a fixed base or fulcrum for the cardiac pump; it also supplies an attachment for the liver and oviducts; but its main purpose is to separate two cavities in which the conditions of the circulation are in direct antagonism. The circulation within the abdominal cavity—at least, the venous circulation—is almost entirely dependent on the contraction of the muscles of its walls. The compression of the abdominal cavity, or a rise of pressure within it, must be attended by an enlargement of the pericardial cavity, or, at least, by a lower pressure than exists within the abdominal cavity, otherwise the heart could not be filled. When the rectus

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[1] "The Influence of Gravity on the Circulation," *Journ. of Physio.*, vol. xviii. p. 15, 1895; vol. xxi. p. 323, 1897.

abdominis of the dog-fish contracts (fig. 16) the abdominal cavity is compressed and the pericardial cavity enlarged, for it is inserted to the ventral part of the shoulder girdle (sternum), which is imbedded in the fibrous wall of the pericardium. On the other hand, when the sterno-hyoid contracts, water is drawn into the pharynx, the pericardium is compressed, the auricles emptied, and the gills repleted with blood. One must remember that the heart of the fish is purely a respiratory pump; it is relatively very small; systemic arterial and venous circulation depend chiefly on the movements of the body and of the gills. In amphibians, the septum transversum becomes less stout and is partly invaginated within the abdominal cavity; the abdominal aponeurosis, so strong in fishes, is in them well developed only in the dorsal and anterior (cervical) part of the abdominal cavity, where it provides an insertion for the diaphragm and links that muscle to the pericardium and septum transversum (figs. 10, 11, 12). By its attachment to the septum transversum and cervical abdominal aponeurosis, and by the arrangement of its fibres, the amphibian diaphragm is admirably adapted for filling the heart; in this respect it is the same functional structure as the mammalian diaphragm.

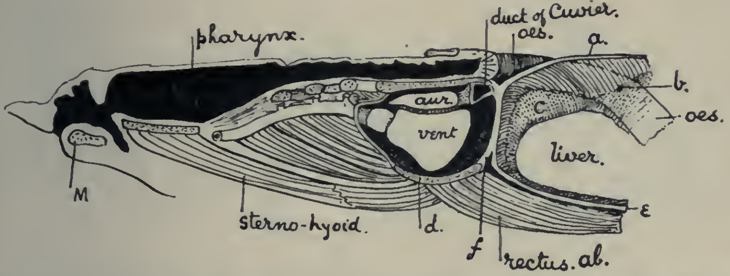

Fig. 16.—Section of the pharynx, pericardium, and anterior part of the abdominal cavity of a dog-fish. *a*, cervical aponeurosis of abdominal cavity; *b*, œsophagus perforating the cervical aponeurosis; *c*, mesentery attaching liver to septum transversum; *d*, ventral part of coracoids (sternum) embedded in pericardium; *e*, abdominal aponeurosis; *f*, septum transversum; M., mandible.

Assumption by the lungs of a supra-diaphragmatic position.—The amphibian diaphragm forms the dome-like cervical wall of the abdominal cavity, lying over and surrounding the lungs and other abdominal viscera. Before discussing the physiological factors which brought about the supra-diaphragmatic position of the mammalian lungs, it is necessary to give a brief description of the structural alterations involved in this transformation. First, there is the development of an apical part of the lung. In Amphibia the apex and root of the lung coincide (A, fig. 17). But in reptiles can be traced the gradual formation of a supra-radicular or apical part of the lung (B, fig. 17). The result is, that part of the lung now lies on the dorsal wall of the pericardium (B, fig. 17), carrying in front of it an expansion of the cervical aponeurosis of the abdominal cavity (s). In the figure the trachea is represented as separating the dorsal wall of the pericardium from the adjacent prolongation of the cervical aponeurosis: in reality these two laminæ become amalgamated. In mammals this can be more clearly seen to be the case (C, fig. 17). In reptiles, however, the cervical aponeurosis is carried forward as a whole; the entire amphibian diaphragm is evaginated in front of the lung; in mammals, on the other hand, the lungs carry only part of the diaphragm in front of them; they pierce the amphibian diaphragm, carrying over them a thin fibrous prolongation, part of which can be recognised as Sibson's fascia in the apex of

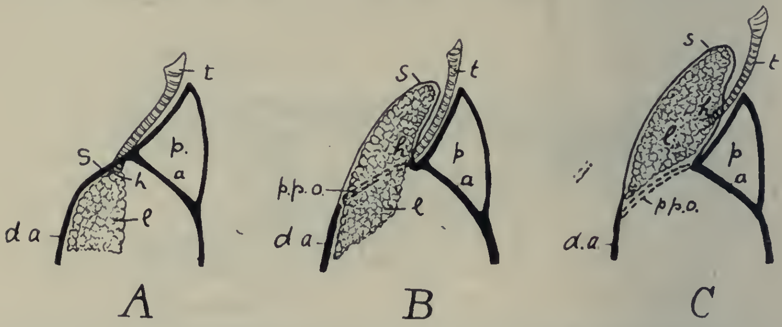

FIG. 17.—A. The relationship of the lung (*l.*) to the cervical aponeurosis (*d.a.*) of the abdomen and to the septum transversum (*a*) in amphibians. *h*, root of lung; *t*, trachea; *p*, pericardial cavity.

B. The relationship in reptiles. *p.p.o.*, pleuro-peritoneal communication in the cervical aponeurosis; *s.*, the prolongation of cervical aponeurosis carried on apex of lung. (See also figs. 20, 21.)

C. The relationship in mammals. *p.p.o.*, pleuro-peritoneal opening; *s.*, Sibson's fascia.

the fully-developed pleural cavity (C, *s*, fig. 17). The perforation made in the amphibian diaphragm by the extension of the lung is the pleuro-peritoneal opening; when this is closed, the mammalian diaphragm is complete. When the development of the pleural cavities and diaphragm in the human embryo are dealt with later in this article, it will be found that the structure named the septum transversum by His, is a complex structure made up of a ventral part, marked *f* in B, fig. 27, and which represents the piscian or amphibian septum transversum (*a*, in fig. 17); and a dorsal part, indicated by *b* in B, fig. 27, which represents the cervical aponeurosis of the amphibian diaphragm. It is within the dorsal part of the embryonic septum transversum that the pleural cavity is developed (see C, fig. 27).

The evolution of body-wall as an inspiratory mechanism.—In Amphibia the lungs are filled by means of the pharynx; in reptiles, birds, and mammals, the body-wall has become modified to form an inspiratory mechanism. How and when did the ribs and intercostal muscles assume a respiratory function? It is necessary to discuss this problem before dealing with the extrusion of the lungs from the abdominal cavity.

The evolution of ribs.—It is especially unfortunate that those who have sought for the origin of the mammalian mechanism of respiration have studied only the anatomy and respiratory movements in the tailless amphibia. In fig. 18 a transverse section of the body of *Rana temporaria* is shown; the middle of the three primary muscular layers of the body-wall—the internal oblique is absent, yet in its tadpole stage[1] and in the long-tailed amphibians this layer is present. In the abranchiate urodeles the middle layer is bilaminar. The ribs, too, have become fused with the transverse process in the Anura. Hence in the tailless amphibia all means for enlarging the dimensions of the body cavity are irretrievably lost; the basis out of which ribs and intercostal muscles are evolved has almost disappeared. The body musculature of the frog can only compress the abdominal contents. Further, it is inconceivable that either of the two kinds of respiratory movements

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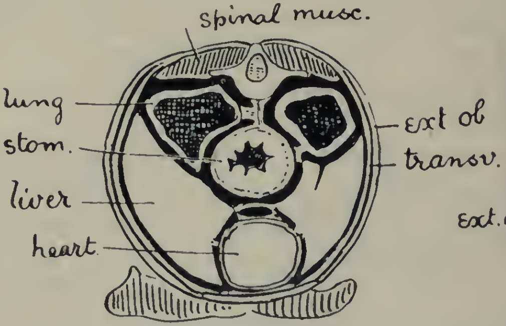
[1] Goette, A., "Entwickelungsgeschichte der Unke" (Bombinator igneus), Leipzig, 1874.

of the frog—neither those connected with filling and emptying the lungs (inspiration and expiration) or those connected with the pulmonary circulation and the filling of the heart—the oscillatory movements which take place when the lungs are full and the glottis closed—could be transformed into the mammalian type of respiratory movement.

Although the respiratory movements of the long-tailed Amphibia are of the two kinds just described in the Anura, yet their body-walls possess certain structural and functional characters which clearly foreshadow features in the body-wall of the higher vertebrate types (fig. 19). The functional character alluded to is the power not only to contract but also to expand their abdominal wall; the structural characters are the presence of ribs and intercostal muscles.



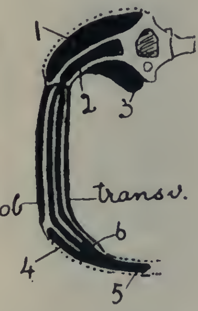


Fig. 18.—Transverse section of the body of *Rana temporaria*, to show the position and relations of the lungs and the structure of the body-wall.

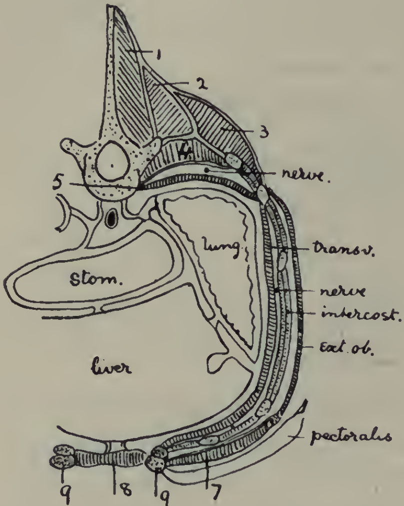
Fig. 19.—A diagrammatic section of the musculature of the body-wall of a tailed amphibian (*Ambylostoma tenebrosum*). The wall is seen to be made up of dorsal, lateral, and ventral segments. The outer layer of the lateral wall is formed by the external oblique; the inner layer by the transversalis; the middle layer (internal oblique—intercostals) is bilaminar. The ventral part is made up of the rectus abdominus, which is unilaminar (5) near the middle line, but becomes bilaminar as it approaches the lateral wall, the deeper part (6) becoming continuous with the internal oblique, and the more superficial (4) ends at the external oblique. In the dorsal part three layers may be distinguished—a middle layer (2) (intercostal, intertransverse), supra-vertebral layer (1), and sub-vertebral layer (3). The spinal nerves lie between the middle and inner layers of musculature.

In fig. 19 a transverse section of the body-wall of a long-tailed amphibian is represented. Three muscular layers are present, but the middle one, or internal oblique, is the primary one of the three; the transversalis and external oblique layers are derived from it in the course of development. The middle layer is not only the primary layer of the three, but is especially important in connection with the mechanism of respiration, for within it the ribs are evolved, and out of it the intercostal muscles and internal oblique are developed. As the middle layer is traced towards the mid-dorsal line, it is seen to become continuous with the intercostal and dorsal inter-transverse muscles (2, fig. 19), while as it approaches the median ventral line, it becomes continuous with the ventral longitudinal sheet, or, to be more accurate, with the deeper layer of that sheet. In tailed amphibians the ribs extend some way into the middle layer, the upper part of which thus becomes intercostal. Already the intercostal part shows division into external and internal layers. The external layer (3, fig. 19) can pull the ribs forwards until they project outwards at right angles to the spine; the internal intercostals can pull them backwards until they form an acute angle with the spine. By this movement the transverse diameter of the body cavity is increased and diminished.

Yet in the tailed amphibians neither the ribs nor intercostal muscles are used for the purpose of filling the lung with air, that is to say, they are not yet respiratory in function. The lungs are repleted by the swallowing action of the pharynx. Apparently they (the ribs and intercostal muscles of amphibians) are for regulating the tension within the abdomen; when the ribs are drawn forwards the size of the abdominal space is increased and the tension within it lowered; when drawn backwards, the space is diminished and the tension lowered. The tension within the abdominal cavity regulates the venous circulation and the filling of the heart. The ribs and intercostal muscles, then, like the diaphragm, were evolved first, not in connection with the mechanism of respiration, but with that of the circulation.

The abdominal ribs—such as are seen in crocodiles, in Hatteria, and especially in extinct reptiles, but not in extinct Amphibia, serve the same purpose as the primitive ribs. When the rectus abdominis contracts, they assume a more transverse direction, thus increasing the transverse diameter of the abdominal cavity. It is highly probable that the costal cartilages first appeared in this manner; in the reptilia true cartilages are only formed in the deeper of the two layers of the rectus muscle.

Already in the Amphibia of the Carboniferous and Permian periods the ribs have assumed such a length that one may safely infer they not only regulated the tension within the abdominal cavity, but by their forward movement possessed the power of dilating the body cavity and filling the lung with air at the same time, thus replacing the pharyngeal pump.



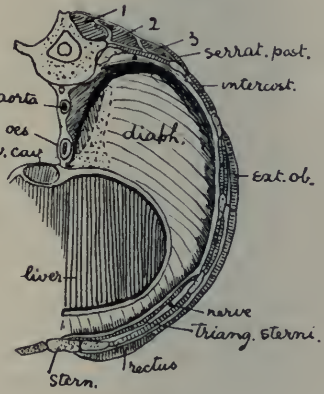


FIG. 20.—Section of the body of a lizard showing the arrangement of the muscles in the thoracic region.

FIG. 21.—Section of the body of a human fœtus to show the arrangement of muscles.

Outer layer—1. Multifidus spinæ; 2. longissimus dorsi; 3. iliocostalis; *ext.ob.*, external oblique; Z, superficial rectus.

Middle layer—4. Intertransverse and quadratus lumborum; intercostals and interchondrals.

Inner layer— 5. Long internal intercostals; triangularis sterni, transversalis.

The structure of the body-wall in reptiles, birds, and mammals, shows that in each case it is derived from the trilaminar arrangement seen in tailed amphibians. The nerves invariably run between the inner and middle layers; the musculature which lies deep to the nerves of the body-wall in any vertebrate, may be safely regarded as being parts of that sheet in which the transversalis muscle is developed.

TABLE *showing the corresponding groups of muscles of the body-wall in a tailed amphibian, lizard, and mammal*—(see figs. 19, 20, 21).

I. In dorsal part of body-wall.

	AMPHIBIAN. (Fig. 19.)	LIZARD. (Fig. 20.)	MAMMAL. (Fig. 21.)
A.	Supra-spinal layer (1)	Multifidus spinæ (1) Longissimus dorsi (2) Ilio costalis (3)	Multifidus spinæ (1) Longissimus dorsi (2) Ilio costalis (3)
B.	Middle layer (2) Inter-transverse (dorsal) Intercostal	Dorsal inter-transverse (4) Intercostal in dorsal wall of body Quadratus lumborum	Dorsal inter-transverse Intercostals in dorsal wall of thorax Levatores costarum
C.	Subvertebral layer (3) Centro-transverse Ventral inter-transverse Costo-transverse	Centro-transverse Ventral inter-transverse Long internal intercostals (5)	Longus colli Ventral inter-transverse Subcostals

II. In lateral part of body-wall.

A.	External oblique	External oblique	External oblique Posterior serrate
B.	Internal oblique (bilaminar)	External intercostals Internal intercostals Internal oblique (bilaminar in some)	External intercostals Internal intercostals Internal oblique
C.	Transversalis	Transversalis	Transversalis Triangularis sterni Subcostal

III. In ventral part of body-wall.

A.	Mesial part of rectus (5)	Mesial part of rectus (8)	Absent
B.	Superficial part of rectus (4)	Superficial rectus abdominis	Rectus abdominis (atrophied in man over upper costal cartilages)
C.	Deep part of rectus (6)	Interchondrals	Interchondrals

It is a remarkable fact that in typical tailed Amphibia such as *Necturus maculatus* the first intermuscular septum which extends completely to the median ventral line is that behind the seventh segment of the rectus abdominis. It is in this septum that the first complete or sternal rib is developed in typical reptiles and mammals.

The respiratory mechanism of typical reptilia.—When the body-wall of a lizard-like reptile (see fig. 22) is compared with that of a tailed amphibian, the following are seen to be chief modifications: (1) The ribs are no longer confined to dorsal wall of the body; they grow forwards within the middle of the three primary muscular layers on the lateral aspect of the body; they are contiguous with cartilages developed in the deeper of the two layers of the rectus abdominis. (2) The sternum is enlarged, and forms a fulcrum for the costal cartilages. The reptilian parasternum probably arises by the union of cartilages developed in the mesial part of the rectus sheet, but there is no evidence that this is the case in mammals. (3) The middle primary muscular layer becomes the intercostal sheet. (4) The costal cartilages lie in the intersepta of the deep sheet of the rectus abdominis. (5) The apical parts of the lung have grown forwards over the dorsal aspect of the pericardium, pushing in front of them the cervical dome of the abdominal aponeurosis (fig. 22). (6) Short ribs (cervical) lie over and distend the apex of the lung. (7) The cervical part of the trunk is increased in length, the head and pharynx being thus carried away from the heart and lungs.

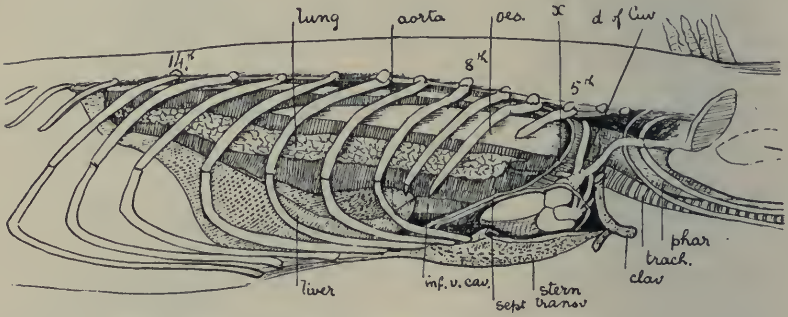


Fig. 22.—Lateral view of a partially dissected reptile—Iguanodon (sp. ?). The lung is represented in a collapsed condition. It is attached to the ventral mesentery between the œsophagus and liver. x, the cervical aponeurosis of the abdomen, which corresponds to part of the central tendon of the mammalian diaphragm.

As far as their respiratory structures are concerned, a typical reptile such as Iguanodon (fig. 22) is simply an amphibian form in which the costal mechanism, which in Amphibia regulates the intra-abdominal tension, has become the agent, not only for regulating the tension, but also for actively expanding the abdominal cavity and thus filling the lungs. In Iguanodon as in Necturus (a tailed amphibian), the lungs lie in the abdominal cavity (see figs. 22 and 27); their attachments to the mesentery are similar; in both the pulmonary artery has to perforate the cervical aponeurosis of the abdomen to reach the lung (fig. 22). But whereas in Necturus there is a diaphragm which covers the apical part of the lung and can only empty it of air and blood, in Iguanodon there are three cervical ribs which can both expand and compress the apex of the lung and thus completely remove the necessity for any form of diaphragm. These two forms also differ in this important point: when the amphibian pumps air into its lung by its pharynx, the positive pressure which is thereby created in the lung tends to force out the pulmonary blood from the lung; in the lizard a negative pressure is produced in the lung by its costal mechanism, and thereby not only air, but also blood is sucked into the lung. In this respect the reptilian is a higher mechanism than the amphibian; for in an ideal respiratory mechanism the act which replenishes the pulmonary air also repletes the lung with impure blood.

In one point, however, the reptile retains one part of the amphibian mechanism, namely, the pharyngeal oscillatory movements. As Paul Bert[1] showed, the respiratory pause occurs in Reptiles as in Amphibia when the lungs are full. During the inspiratory pause, in both of these forms, certain oscillatory movements of the pharynx then occur which, by altering the tension within the lungs, regulate the flow of blood through them.

Functional reptilian diaphragms.—There are two groups of reptiles, however, which possess diaphragms, not of the mammalian or avian type, but whose origins must be sought for at the same source, viz., in the primitive amphibian diaphragm. The diaphragm of crocodiles is shown in fig. 23. In that animal the lungs occupy relatively the same position as in birds; they lie dorsal to the heart and liver, but there is no septum between them: the lungs of the crocodile lie in forward extensions of the abdominal cavity. The whole amphibian diaphragm is carried forwards during development of the lungs. When the three primary muscular layers are removed, as in fig. 23, a sub-peritoneal sheet of muscle is seen to arise from

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[1] Bert, P., "Des mouvements respiratoires chez les Batraciens et les Reptiles," *Journ. de l'Anat. et Physio.*, T. vi., 1869.

the pubis and ilium and to pass forward to be inserted to the pericardium and to the lateral aspect of the stomach and liver. Its action, clearly, is to draw backwards the stomach, liver and pericardium, and thus directly increase the pulmonary space in the anterior part of the trunk. Functionally it serves the same purpose as the mammalian diaphragm.

The nerve supply shows the origin and nature of the crocodilian diaphragm. It is part of the rectus profundus; so is the sterno-costal part of the mammalian diaphragm; but while the mammalian structure springs from the anterior or cervical part of that muscle, the crocodilian arises from the posterior or pubic part. In fig. 23 the nerve to the crocodilian diaphragm is shown, and in fig. 24 the nerve supply to the corresponding part of the rectus abdominis of a lizard. The last nerve to the body-wall of the lizard takes a peculiar course quite different to the other nerves (see fig. 22), and ends in the deep surface of the posterior end of the rectus. The nerve to the crocodilian diaphragm is clearly the last body-wall nerve; in its course it resembles that of lizards. Clearly the diaphragm of crocodiles, although derived from the same sheet as the sterno-costal part of the mammalian diaphragm, is a structure which has been evolved independently of the mammalian diaphragm.

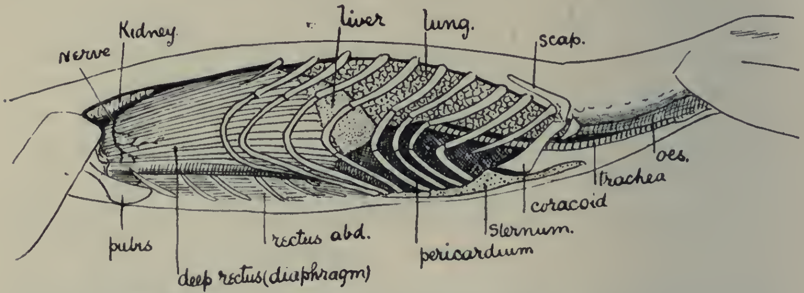

Fig. 23.—Lateral view of a young crocodile from which the three primary layers of muscles have been removed to expose the deep rectus (diaphragm).

On the other hand, those most primitive reptilian types, the tortoises or turtles, possess a diaphragm which, like the mammalian, can be traced to the amphibian diaphragm. The diaphragm of the tortoise forms a muscular partition on each side of the anterior opening of the carapace between the muscles of the shoulder girdle in front and the visceral contents of the abdominal cavity behind. When viewed on its posterior aspect in the expiratory condition, the diaphragm projects as a right and left dome within the cavity of the carapace. On inspiration, the domes become flattened, the intra-abdominal space being enlarged and the lungs filled. As in the mammalian diaphragm, there are two parts: a small dorsal part which is probably part of the transversalis muscle, and a ventral part passing from a rib to the ventral end of the coracoid, and which, from its nerve supply, I believe to have arisen from the rectus profundus.[1]

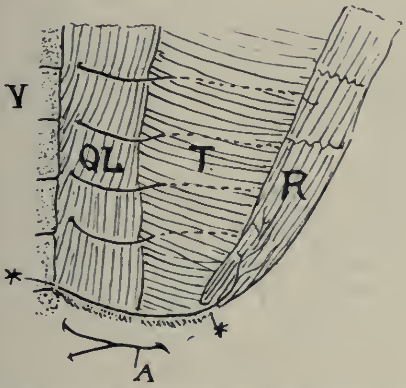

FIG. 24.—Posterior part of the abdominal wall of a lizard exposed on its deep aspect. Q.L., quadratus lumborum ; T., transversalis ; R., rectus abdominus ; A., anterior crural nerve. The course of the lumbar nerves is shown ; asterisks mark the nerve to the deep part of the rectus.

The diaphragm of birds.—A study of the respiratory mechanism in birds assists one, I think, to form a conception of the manner in which the diaphragm and pleural cavities arose in mammals. In fig. 2, and again in B, fig. 17, I have represented the avian position of the lungs ; they are not intra-abdominal, as in all reptiles—with the doubtful exception of

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[1] Messrs Weir Mitchell and G. R. Moorhouse (*Smithsonian Contributions*, vol. xiii., 1863) ascribe the chief inspiratory power to the transversalis muscles which form domes over the apertures of the carapace at which the hind limbs project. Their observations were made on the snapping turtle, mine on two species of tortoise. In the tortoise the pelvic part of the transversalis is expiratory.

Chelonia,—but extra-abdominal, being outside the cervical aponeurosis of the abdomen—with the exception of their posterior ends, which are dilated to form the abdominal air sacs. Yet when the lungs appear in embryo chicks,[1] they are clearly intra-abdominal in position. Yet from the description of their development given by Butler,[2] and from an examination of the adult condition, it is evident that in the course of their development the avian lungs have grown through the cervical aponeurosis of the abdomen and formed for themselves a space in the body-wall.

In fig. 25 is shown a section across the thoracic region of a pigeon's body. The lungs are separated from the liver by a fibrous septum or diaphragm. Into this septum or diaphragm, as Butler demonstrated in the developing duck, air-sacs are developed, and by these the septum is divided into two layers—dorsal or pulmonary, and a ventral or abdominal (fig. 25). One has only to look at the relationships of the avian diaphragm to the liver and to the pericardium to see that it represents the cervical aponeurosis of the amphibian abdomen. Were one to pluck out the lungs from the thorax, in such a specimen as is shown in fig. 25, and replace the avian diaphragm against the dorsal wall of the thorax, the tri-laminar body-wall of amphibia would be obtained. The avian diaphragm, then, is the cervical aponeurosis of the amphibia, which, with the inner layer of muscles, has been separated from the middle (intercostal) and outer layers of the body-wall by the development of the lung. But the muscular element belongs, not to the cervical, but dorsal part of the transveralis sheet.

As is shown in fig. 25, the muscular fibres of the avian diaphragm form part of the pulmonary layer. The muscular part of the diaphragm is supplied by intercostal nerves, for although a phrenic nerve is present, at least in the ostrich, it ends merely in the pericardium and fibrous tissue of the diaphragm. The muscular slips of the diaphragm lie internal to the intercostal nerves, and therefore belong to the transversalis

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[1] Ravn, E., "Die Bildung des septum transversum bei Hühnerembryo," *Archiv für Anat. und Entwickel.*, 1896, p. 157.

[2] Butler, G. W., "On the Subdivision of the Body-cavity in Lizards, Crocodiles, and Birds," *P.Z.S.*, 1889, p. 452.

sheet, and probably represent the triangularis sterni of mammals. Although the muscular fibres are of different origin to those of the mammalian diaphragm and different in action, yet the fibrous substance of the avian diaphragm is derived, just as in the mammalian, from the cervical aponeurosis of the amphibian abdomen. Bertilli observed that the pleural cavities were gradually obliterated in embryo chicks, the obliteration commmencing about the fourteenth day by the fusion of the parietal and visceral layers of the pleura.

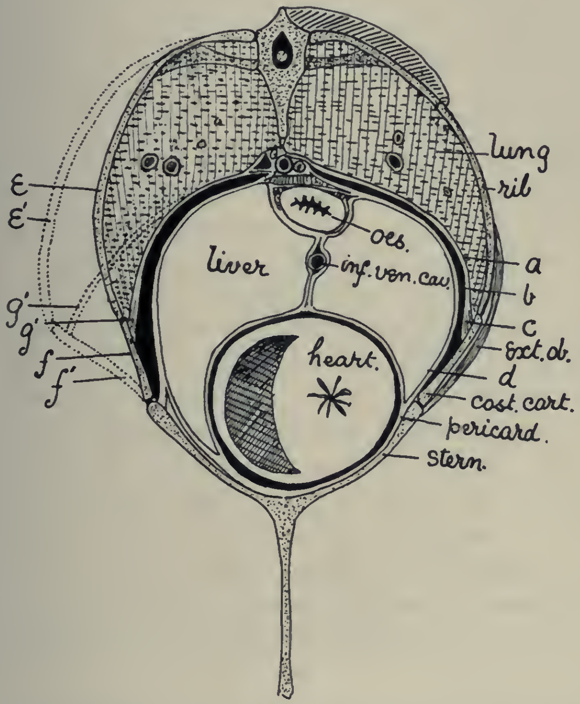

Fig. 25.—Section across the body-wall of a pigeon to show the relations of the avian diaphragm and of the lungs. The section also passes across the pericardium. *a*, pulmonary layer of diaphragm ; *b*, air-sac ; *c*, muscular part of diaphragm ; *d*, abdominal layer of diaphragm ; *c*, position of rib in expiration ; *ε′*, position of rib in extreme inspiration ; *f*, sternal rib in expiration ; *f′*, in extreme inspiration ; *g*,*g′*, pulmonary diaphragm in expiration and inspiration.

Functional advantages of the supra-diaphragmatic position of the lungs.—The functional gain which results from the extrusion of the lungs from the abdominal cavity and their lodgment in a separate compartment of the body are best appreciated by observing the conditions of the pulmonary circulation in the reptilia. In the Iguanodon, for instance, the lung is subjected to the same pressure as the abdominal viscera; the inspiratory expansion of the body-wall not only dilates the lungs and the pulmonary vessels, but also the venous channels and spaces of the abdominal cavity; those within the liver are especially dilated. The moment the lungs are filled, the larynx of the lizard is closed, thus locking the air up within the lungs. The inspiratory muscles cease to contract; the body-wall compresses the abdominal cavity, forcing the blood within it and within the lungs and liver forwards to the pericardium, thus filling the heart. The oscillatory movements of the pharynx take place during the inspiratory phase, with the result, I believe, of causing slight alterations in pressure within the lungs, enough to regulate and assist the pulmonary circulation.

With the extrusion of the lungs from the abdominal cavity and their lodgment in a separate compartment of the body cavity, the negative pressure produced by the inspiratory act is confined to the lungs—at least in mammals, for in birds this end is not completely attained. Not only is the negative pressure confined to the lungs, whereby their chambers are filled with air and their capillaries and veins with blood, but the descent of the diaphragm compresses the abdominal viscera, emptying the blood from the abdominal cavity into the heart. Thus the inspiratory movement of the mammal fills the vessels of the lungs and empties those of the abdomen; in the lizard both are filled together, both are emptied together. With the evolution of the separate pulmonary cavity in birds and reptiles, other changes are correlated: (1) the respiratory pause takes place at the end of the expiratory movement; (2) the heart becomes completely divided into right and left chambers; (3) the venous valves at the entrance to the right auricles atrophy.

Differentiation of the lung into saccular and pulmonary parts.—In most reptilia the lung shows a differentiation into two parts—a posterior, thin-walled, non-respiratory part, which may be termed saccular (see A, fig. 26), and an anterior pulmonary part, grouped in front of and round the hilum of the lung. The thin-walled part, being by far the most easily distended, expands much more than the pulmonary part during inspiration. Hence the foul air in the pulmonary tissue is drawn back into the saccular part, bringing the fresh air through the bronchus to the pulmonary tissue. On expiration it is the saccular part that collapses, the foul air being thus driven out. In birds this differentiation is complete; the saccular part forms the air-sacs of the lungs; the saccular part alone expands during inspiration. Thus in inspiration the foul air is drawn into the sacs and the lungs replenished with fresh air. In a smoky atmosphere, I found that pigeons drew no soot within their air-sacs, yet the lungs were laden. In mammals the saccular and pulmonary parts of the lungs are combined, the infundibula representing the saccular part. On inspiration the infundibula expand; it is highly doubtful if the alveoli undergo any enlargement. There is evidence that the saccular and pulmonary parts of the mammalian lung were at one time distinctly separated.

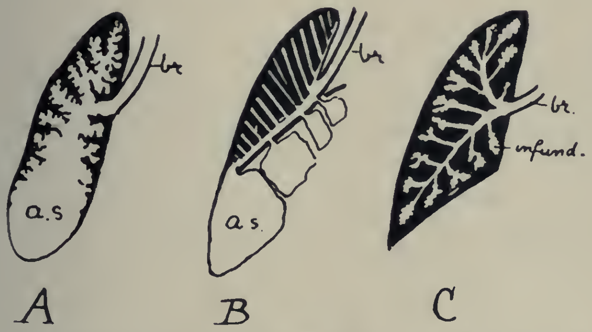

Fig. 26.—A. Diagram showing the differentiation of the lung of the tortoise into pulmonary and saccular parts. *br.*, bronchus; *a.s.*, saccular part.
B. Diagram of the bird's lung. *br.*, bronchus; *a.s.*, air-sac.
C. Diagram of the mammalian lung.

Manner in which the lungs became supra-diaphragmatic.—A study of the respiratory mechanism in birds gives a clue, I think, to the manner in which the lungs became extruded from the abdominal cavity. A glance at fig. 25 will show that the lungs of birds are very slightly, or not at all, expanded during inspiration; the expansion only affects the air-sacs; the most posterior or abdominal are those which expand most, and these are known to be produced from and represent the most posterior part of the lung. The differentiation of the lung into pulmonary and saccular parts, which is complete in the bird, can be seen in progress in various members of the reptilia. As Gegenbaur expresses the matter—"There is a tendency to the aggregation of the proper pulmonary tissue round the hilum of the lung in the reptilian lung." The posterior part of the Chelonian lung is really an air receptaculum; such is also the case in serpents. The receptacular parts, like the air-sacs of birds, are supplied direct from the aorta—not from the pulmonary vessels. They are not directly concerned with the oxygenation of the blood.

Were, then, the pulmonary part of the lung produced through the cervical aponeurosis into a new chamber, while the receptacular part remained within the abdomen, respiration of such a type as is seen in the bird would be set up in mammals (see fig. 2). Instead of remaining stationary during respiration, one can conceive that the pulmonary part might also undergo a direct inspiratory expansion, with the result that the saccular part within the abdomen would atrophy, while a substitute for the saccular part might arise by the development of infundibula.

The distribution of the bronchial arteries in the mammalian lung offers evidence in favour of the theory I advance of the manner in which the lungs were extruded from the abdominal cavity. If a successful injection of these vessels is obtained, then a rich and elaborate plexus of bronchial arteries will be found on the diaphragmatic and mediastinal surfaces of the lungs, and nowhere else in the subpleural tissue. They are found in the exact position where the air sacs are given off in birds, and point to the fact that a saccular part did at one time exist in the mammalian lung.

The evidence of development.—Turning to the development of the mammalian pleural cavities, ample evidence is to be found of the theory which is here advanced as to the origin of the diaphragm. It is first necessary to clear up the nature of a certain fold which has been accurately described by many authors, especially by Lockwood,[1] Mall,[2] Piper,[3] and Broman,[4] and by all of them, with the exception of the last-named, has been regarded as the part of the diaphragm first formed. The fold referred to is shown in B, fig. 27, where it (*c*) is shown passing from the liver (*e*) below, to the anterior end of the Wolffian body above, with its fixed border attached to the septum transversum (*b*). It lies on the lateral surface of the developing lung, the posterior end of which is seen to project within the abdominal cavity, at the point which will become the pleuro-peritoneal opening (B, fig. 27). To this fold Lockwood gave the name of dorsal diaphragm; embryologists generally give it the name of pleuro-peritoneal membrane, and regard it as the basis of the diaphragm. Broman rightly observed that it had no part in the formation of the diaphragm.

The nature of this fold can be seen in the tailed amphibians (fig. 28). At the point where the amphibian lung appears within the abdominal cavity, there is a crescentic peritoneal fold answering in its shape, in its relationships and attachments, to the crescentic fold of the human embryo (fig. 27). Ventrally it is attached to the liver and inferior vena cava; dorsally to the anterior end of the Wolffian body; its free border looks backwards and lies on the lung; its fixed border is attached to the cervical aponeurosis, over which lies the transversalis (or spinal) part of the amphibian diaphragm. In the female this fold serves as the mesosalpinx or mesentery of the oviduct. The presence of this fold in the human embryo, presuming my identification to be correct, serves as a further proof that the origin of the mammalian diaphragm has to be looked for in that of the tailed amphibia.

When the lung appears in the human embryo it lies within the abdominal cavity and encircled laterally by a semilunar or crescentic fold of peritoneum, just as in the developing amphibian (B, fig. 27; fig. 28). But whereas in the amphibians

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[1] I am very greatly indebted to Mr Lockwood. He placed freely at my disposal his large collection of prepared embryoes. See his paper, "The Development of the Pericardium, Diaphragm, and Great Veins," *Phil. Trans.*, 1888.

[2] *Bull. Johns Hopkins Hosp.*, vol. xii. Nos. 121–123, pp. 158–171.

[3] *Anat. Anz.*, Bd. xxi. 1903, p. 531.

[4] *Verhand. Anat. Gesellsch.*, 1902, p. 9.

the lungs grow backwards into the abdominal cavity, attached to the mesentery between the aorta and œsophagus above and the liver and stomach below, in the human embryo they bud forwards and outwards into the mass of tissue which constitutes the dorsal part of the septum transversum of the human embryo.

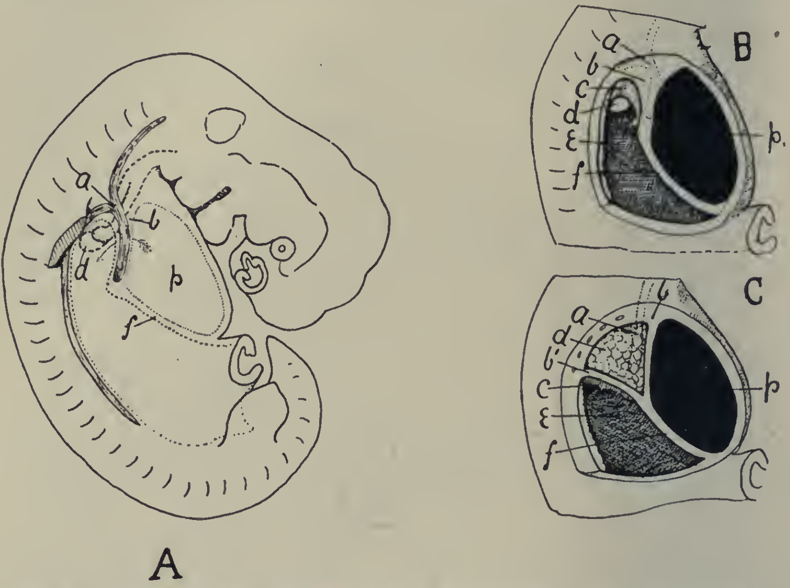


Fig. 27.—Figures showing the position and development of the diaphragm and pleural cavity in the human embryo.

A. Lateral view of a human embryo in the fifth week of development showing the duct of Cuvier (*a*) lying in the body-wall and entering the dorsal part of the septum transversum (*b*). *f*, ventral part of septum transversum; *d*, lung; *p*, pericardium. (After His.)

B. Part of the lateral wall of a human embryo in the fifth week of development, cut away to expose the semilunar or Wolffian fold (*c*) lying on the lateral aspect of the lung (*d*), attached ventrally to the liver (*e*), dorsally to the Wolffian body, and in front to the dorsal part of the septum transversum (*b*). *p*, pericardial cavity; *a*, duct of Cuvier; *f*, ventral part of septum transversum. (After Piper.)

C. Section of the lateral wall of the human embryonic thorax at a later stage of development, showing the growth of the pleural cavity within the dorsal part of the septum transversum, which is thus apparently divided into the dorsal wall of the pericardium (*b*) and diaphragm (b^1). *a*, position of duct of Cuvier; *c*, the Wolffian fold; *e*, liver; *f*, ventral part of septum transversum (central tendon and diaphragmatic wall of pericardium). (After Mall.)

Now, it has been shown that the septum transversum of the human embryo consists of two parts: (1) A ventral part (B, *f*, fig. 27) representing the whole septum transversum of fishes and amphibia (A, *a*, fig. 17), and (2) a dorsal part (B, *b*, fig. 27), which is made up by a fusion of the amphibian cervical aponeurosis with the dorsal wall of the pericardium (B, C, fig. 17). The duct of Cuvier becomes included in the dorsal part of the septum transversum of the mammalian embryo (B, fig. 27). The forward growth of the developing lung, its excavation of the

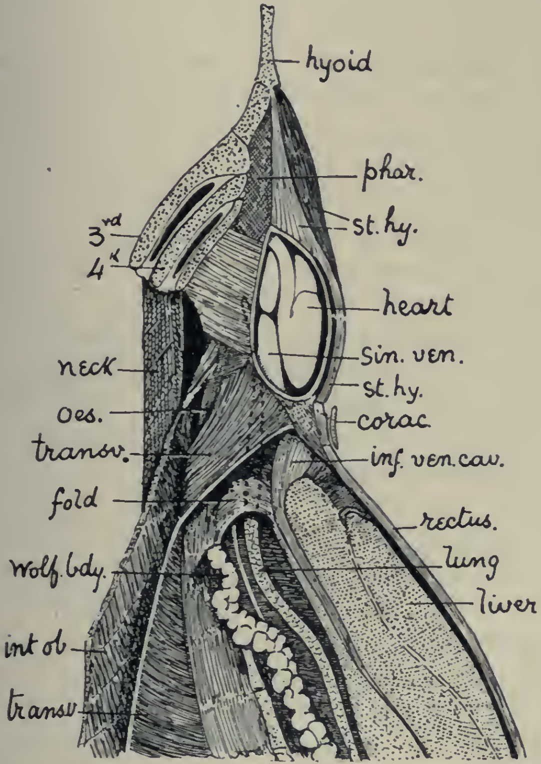


FIG. 28.—Right half of the abdominal cavity of a tailed amphibian (*Necturus maculatus*) laid open, showing the semilunar or Wolffian fold on the lateral aspect of the root of the lung. The cartilages of the 3rd and 4th visceral arches are shown. The internal oblique is thrown back and partly cut away. The cut edge of the left rectus abdominus is shown; also that part of the transversalis which forms the dorsal segment of the amphibian diaphragm. The lung is attached to the mesentery between the aorta above and liver below. The position of the trachea is shown by stippled lines.

dorsal part of the septum transversum, its cleavage of that mass into two layers—a pericardial or pleuro-pericardial, and a diaphragmatic or pleuro-peritoneal—represents the extrusion of the mammalian lung through the amphibian diaphragm and its expansion between the inner and middle of the three primary muscular layers of the body-wall. As the pleural cavities expand and grow they push beneath them the amphibian diaphragm, which thus assumes its intra-abdominal position. The cervical and dorsal regions of the spine undergo a rapid elongation; the neck is produced, carrying the head and pharynx away from the heart and liver. The lungs are, as it were, wedged in between the neck and the abdominal cavity. The œsophagus and its mesentery are elongated. In short, the appearances presented by the development of the lungs, pleural cavity, and diaphragm in a human embryo support the theory I advance—that the mammalian diaphragm is the cervical wall or diaphragm of the amphibian abdominal cavity, which is perforated and displaced during the development and growth of the lungs. The point of perforation becomes the pleuro-peritoneal opening.

A clearer conception of the formation of the pleural cavity as an excavation within the body-wall is given by a transverse section of the thoracic region of a mammalian embryo (fig. 29). In such a section the lungs are seen to bud out from the mesentery of the fore-gut (A) at the point where the mesentery is adherent to the dorsal wall of the pericardium. The arrows show the direction in which the lungs grow out into the body-wall separating the pericardium and diaphragm from the thoracic wall.

One important point, which still remains to be explained, will be best understood by a reference to fig. 7, p. 249, and fig. 10, p. 254. In fig. 5 it is shown that the mammalian diaphragm forms the *mesial* boundary of the pleuro-peritoneal opening. The two parts of the amphibian diaphragm, on the other hand, meet on the lateral boundary of the cœlom. But it will be seen from figs. 10, 11, and 12 that already the dorsal part of the amphibian diaphragm is attached to the œsophagus, and I conceive it probable that in the ancestry of the mammalia the whole insertion of the dorsal part of the amphibian diaphragm was transferred to the mesentery of the fore-gut, and within that structure reached the pericardium, not on the lateral aspect of the lungs, but on their mesial aspects. Such a migration of the dorsal part of the diaphragm may be assumed, for in the amphibia the origin and insertion of the dorsal part of the amphibian diaphragm are exceedingly liable to variation.

Summary.—(1) There is a cervical diaphragm in amphibia composed of three elements: (*a*) a ventral muscular element derived from the fourth segment of the rectus sheet; (*b*) a dorsal element derived from the cervical part of the transversalis sheet; (*c*) the cervical part of the abdominal aponeurosis. The mammalian diaphragm is the same structure, similar in composition and similar in its nerve supply.

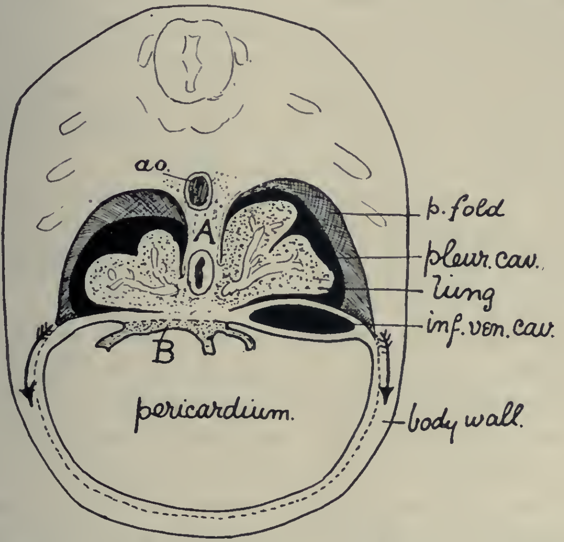


FIG. 29.—Section of rabbit embryo (after Lockwood). The lungs are seen growing outwards from the mesentery of the foregut (A, which is placed above the œsophagus and below the aorta). B, attachment of left auricle to dorsal wall of pericardium. Behind the lungs is seen the abdominal cavity; the folds bounding the pleuro-peritoneal opening on each side are the crescentic or Wolffian folds (p. fold).

(2) In amphibians and mammals alike the diaphragm forms the anterior or cervical wall of the abdominal cavity, and is designed to assist the venous circulation of that cavity, and to

fill the heart with blood. This is the primary function of the diaphragm.

(3) In mammals the lung is evaginated from the abdominal cavity through the cervical wall or diaphragm, which structure thus becomes infra-pulmonary and inspiratory in function. The two pleuro-peritoneal openings mark the points of perforation.

(4) The ribs and costal cartilages are developed at first to regulate abdominal tension; the intercostal sheet (middle primary muscular layer of the body-wall) to compress the abdominal viscera and assist venous circulation. By the elongation of the ribs within the intercostal sheet in certain of the early forms of amphibia, the middle layer of the body-wall became inspiratory in function. The outer and inner primary layers (external oblique and transversalis) retained their expiratory action in the mammalian stock.

(5) The structure described by Lockwood as the dorsal diaphragm, and by other embryologists as the pleuro-peritoneal membrane, is merely a crescentic fold of peritoneum, forming part of the genital mesentery.

(6) The respiratory systems of reptiles and mammals have arisen independently from an amphibian stock, but that of birds is more nearly related to the mammalian than to the reptilian form. In reptiles the whole amphibian diaphragm is carried forwards on the apex of the lung; its muscular elements vanish; in birds it is perforated, but the cervical muscular elements are lost and replaced by muscles derived from thoracic segments; in mammals the amphibian diaphragm is perforated and retained in entirety.

(7) The formation of a neck and the excavation of a pleural cavity in the body-wall anterior to the abdominal cavity have widely separated the head and pharynx from the abdominal cavity. The heart and liver and abdominal contents retain their embryonic relationships to the umbilicus; on the other hand, the cervical and anterior dorsal segments of the body-wall undergo an enormous elongation, and carry the head and pharynx forwards. It is not the heart and liver which migrate, but the body-wall.

DISSOCIATION IN CERTAIN VITAL PHENOMENA.

By ANDERSON M'KENDRICK, M.B., *Captain I.M.S.*

THAT the theory of chemical dissociation has so far played so small a part in the explanation of the chemical processes occurring in living matter, whilst nervous action, in the physiology of muscle and nerve, has been assumed to be closely associated with electrical phenomena, is a statement that cannot fail to arrest the attention. In the laboratory of living matter we find synthetical and analytical processes occurring that can only be imperfectly imitated *in vitro* by the action of powerful chemical substances and by high temperatures. And yet physiologists have not adequately realised the peculiar and potent physico-chemical conditions in which chemical phenomena occur in living tissues. Thus common salt, the most widely distributed salt in the animal fluids, is known to be built up of two of the most powerful anionic and kationic elements, but that it exists in the blood in such a dilution as to be almost completely dissociated has been disregarded. During the last few years, however, physiologists, both at home and abroad, and notably Loeb and his followers, have attempted to offer explanations of various phenomena on the basis of the action of ions.

To explain many phenomena, resort has been had to the supposed action of enzymes or ferments, and the problem has not been simplified by attributing a newly discovered action to the activity of another hypothetical enzyme. That a chemical action, occurring in physiological conditions, has a possible reverse action, and that varying conditions of acidity or alkalinity may determine those actions in one direction or the other, are views that have not yet taken hold of the minds of physiologists. The laws regulating and underlying chemical actions in living matter have not yet been fully recognised. For example, in connection with the assimilation of proteid, we know that proteid, at the end of its metabolic progress through the body, becomes proteid, carbohydrate, whatever may be its transformations, is at the end carbo-hydrate, and fat remains fat.

I propose, in this discussion, to deal principally with carbohydrates, but I venture to think that any principles I may be able to establish will apply to the career of the other proximate principles.

It is admitted that dissociation occurs in many physiological processes, as, for example, in the phenomena manifested by hæmoglobin as the oxygen carrier. It is only by assuming dissociation that we can comprehend the potency of chemical change in many physiological actions. It is important to look for such dissociation phenomena in those organs in which we have been accustomed to recognise a special kind of vital activity, as in the secretory glands, which we associate with enzyme-like action. Enzymes are presumed to produce active metabolisms, but if so, and if they exist, as is asserted, in the tissues generally, it is difficult to understand how damage to the tissues, in ordinary circumstances, does not occur. To account for this, physiological chemists have been driven to the assumption of the existence of antagonists to enzyme action, anti-bodies as they are called, such as anti-pepsin, etc.

Dissociation requires the concurrence of certain factors. If dissociation means, as it does, the splitting up of a complex body with two simpler ones, we must recognise the existence of the two components. If we admit the formation of the one, we must also admit the existence of the other. If water may be dissociated into H and OH, then if a complex organic body $x\ y$ is dissociated, x and y are both formed. Suppose that pepsin is formed from pepsinogen, and that the latter is formed in the secreting cell of a peptic gland. If pepsin is formed from pepsinogen by a dissociative process, and the pepsin excreted, the complement of pepsin must be left behind. Similarly, if amylopsin is formed from a precursor in the cells of the pancreas, its complement must remain behind, and it must be accounted for.

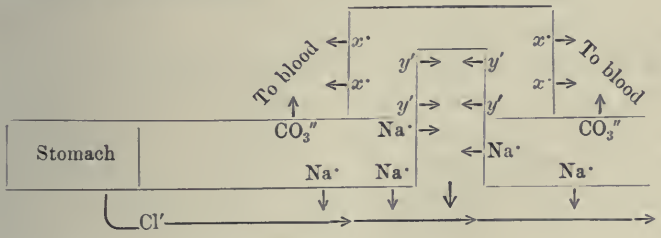
Consider next the fact that from the lower to the upper end of the alimentary canal we have the following series of reactions:

alkaline (great intestine), acid (lower part of small intestine), alkaline (upper part of small intestine), acid (stomach), alkaline or nearly neutral (saliva). It is known that the alkaline secretion of the small intestine is called forth by the acid secretion of the stomach, and an effective stimulant to the flow of acid gastric juice is the saliva. The formation of an alkaline or faintly neutral saliva in the mouth is a somewhat difficult problem, because it is not easy to see what determines its reaction.

The view I venture to propose is that these reactions are due to the activity of free ions, and that these ions attract from the secretory tissues ions of an opposite character. If we assume that the pancreatic enzymes are anionic, as I shall try to establish, they are drawn into the bowel from a considerable distance, and they would be only feebly attracted, as compared with such dissociated elements as Na or Cl.

The acid gastric juice, according to my view, attracts the kation Na from the intestinal wall, and consequently from the duodenum and the duodenal end of the pancreatic duct. Thus there will be a flow of kation in the pancreatic duct. This kationic flow will attract from the more distant pancreas an anionic flow. In other words, secretion will take place as two operations: (1) The chemiotactic attraction of the acid duodenal content drawing down the alkali from the intestinal and neighbouring duct cells; and (2) this alkali attracting an acid flow from the pancreas proper.

Let $x^{\cdot} y' =$ the zymogen



Thus there passes into the bowel (1) Na·
(2) y' enzyme;
and there passes into the blood stream (1) CO_3''
(2) $x^{\cdot}$ complement.

Let us now follow the amylopsin and ascertain what happens to it. Set free by the alkali of the pancreatic juice, it passes into the bowel, and it is not interfered with by the Na, which is attracted to a more powerful neighbour. By the action of the amylopsin starch is converted into sugar, or, as I prefer to express it, into starch plus amylopsin, so that we may regard starch as sugar minus water plus amylopsin. It is not necessary to suppose that amylopsin becomes actually attached to the starch, but, if I may be allowed to use the expression, sugar is amylopsinised starch. That this occurs best in faintly acid medium, there is reason to believe, and for the following reasons:—

(1) Starch may be converted into sugar in a test tube by the action of a weak acid.

(2) It is said that the ptyalin of the saliva works 4·75 times better in a $\frac{1}{1000}$ per cent. solution of hydrochloric acid than in a neutral solution; and that amylopsin works best in a 0·01 per cent. solution of hydrochloric acid.

If acids are freely given in the food there may be a temporary glycosuria showing the excessive formation of sugar in these conditions.

The hydrolysed starch, or, as we might put it, amylopsinised starch, is taken into the mesenteric veins and passes to the liver in the portal vein. Here it meets with blood returned from the pancreas, which contains the amylopsin complement. The fluid is faintly alkaline. It would then seem probable that a reverse action takes place, the antagonistic complement undoing the work which the amylopsin had performed on the starch in the bowel. The effect of the amylopsin is removed.

This view may explain the following experimental facts:—

(1) It is well known that extirpation of the pancreas is followed by a hypersaccharine condition of the blood or glycosuria. After removal of the pancreas there could be no dissociation, and so there would be no complement absorbed into the blood by which the sugar formed by ptyalin could be reconverted into glycogen. Consequently glycogen would not be stored in the liver, but there would be abundance of carbohydrate in the blood in the form of sugar.

(2) It is known that ligature of the pancreatic duct does not

cause glycosuria. It would not prevent the dissociation process, and the dissociated kations and anions, that is, the amylopsin and its complement, would both be returned to the blood stream. Chemical dissociation processes, if they happen frequently, may acquire a kind of habit, and thus they may be repeated although the conditions in which they first occurred may be much modified.

(3) In the normal digestive process, dissociation is one of the most evident phenomena. The anionic portion of the zymogen passes into the bowel, while the kationic portion passes into the blood stream. It would thus appear that the dissociated kationic complement is a potent factor which acts on the absorbed sugar, converting it, for a time at least, into glycogen.

It is well known that glycogen is formed after the subcutaneous injection of dextrose and levulose, just as if those sugars had been absorbed from the alimentary canal, but if dextrin is injected subcutaneously, it is excreted by the kidneys. This appears to show that no anionic action has taken place, and that very little dissociated zymogen exists in the blood. On the other hand, the constant passage of carbonic acid into the blood, whilst altering the $\frac{Na_2CO_3}{NaHCO_3}$ quotient to a marked extent, will, in addition, prevent the separation in the free state of a kationic complement in venous blood. Slight excess, indeed, may favour an anionic formation of glucose. It may at least be said that no sugar will be converted into glycogen in venous blood, while it may be in arterial blood, a view of considerable importance in relation to metabolism. If the zymogen remain undissociated, then any sugar absorbed would be unaltered. On the other hand, if excess of acid be given in the diet, then the kation would be fixed by the acid, and glycosuria would occur.

The subject may be looked at from another point of view. Carbonic anhydride is anionic. As I have already stated, this permits of anionic reaction, and by binding up any kation the latter becomes ineffective. Thus one would expect to find in venous blood a tendency to anionic action. This is supported by the fact of the absence of glycogen and other products of kationic action. In arterial blood, on the other hand, this tendency would be less, and in certain conditions would be absent. This suggests an explanation of the "delayers of blood coagulation," and the fact that venous blood which contains more kations, and coagulates less readily than arterial points to thrombin (the blood-enzyme), being opposed in action to the digestive enzymes, and therefore kationic. It is known that coagulation is retarded by diastase. When it is desired to cause coagulation in the sac of an aneurism by passing into it a continuous current, it is the kathode that is inserted into the sac. Thrombin, being kationic, will act best in the presence of kations. Oxidation is really the addition of a positive charge or the removal of a negative charge. Such kations as H, Na, etc., carry positive charges, while anions carry negative charges. From this point of view oxidation must mean the raising of the power of the blood to counteract the carbonic acid, so that any kation factor in it is left free to act. Reduction must be the converse, namely, a diminution in the positive, or an increase in the negative charges. This again explains why sugar has the power of reduction. It does so because it has in it a readily available anionic factor, which in starch is locked up within the molecule.

Thus sugar (and if the digestive parallel holds good, peptones and albumoses) has an anionic tendency, and from the foregoing argument should thus prevent coagulation, the kationic thrombin being in all likelihood fixed by the anionic factor which sugar is so ready to give up. This view is supported by the fact that sugar does delay or arrest coagulation. Blood lightly laden with anionic CO_2 might allow of kationic action, but if heavily laden it certainly would not. The influence of Ca would be to attach itself to any CO_2 which might be free, and thus allow of the action of the kationic thrombin.

This may be illustrated by a reference to scurvy. In this disease the alkalinity of the blood is diminished, the CO_2 is in a less fixed condition, and therefore no kation can remain free to act. From this follows the long train of symptoms due to loss of coagulability.

Coagulation would thus appear to be due to the action of a kationic thrombin, and would occur only under such conditions as would permit of the free action of the thrombin, such as oxidation, presence of excess of Ca (Ca has more affinity for

CO_2 than the alkalies Na and K, because its carbonates are insoluble, a fact of physical chemistry). I venture to think that the above view will account for the action of all the substances which have been used, as controllers of the coagulation process.

Thus the whole system of metabolism resolves itself into a question of electric potential. Oxidation in tissues is the assumption of a positive charge. Katabolism, with its resultant change of reaction (such as the formation of CO_2 or sarcolactic acid), is then the giving off a positive charge, that is to say, it is a process of reduction.

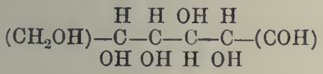
Kationic action seems to have the power of fixing such substances as albumen, by giving to them a positive charge. Anionic action, on the other hand, seems to result in fluidity, and the giving up of positive ions.

In the early part of my paper I made the statement that

$$\begin{aligned} \text{amylopsin} + \text{starch} &= \text{sugar}; \\ \text{or} &= \text{starch} + \text{anion}. \end{aligned}$$

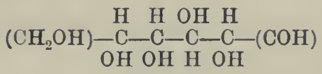
This seemed improbable, but in the light of the previous argument as to oxidation, the principle at once reveals itself. The formation of the starch + ion means that the starch in becoming sugar has acquired a negative potentiality (at the same time taking up of OH' and $H^{\cdot}-$), while by a converse action (namely the handing to it of a kationic factor) the sugar will give up its recently acquired negative characteristic (at the same time relinquishing HOH).

Let us examine this chemically:



$$(CH_2OH)-\underset{OH}{\overset{H}{C}}-\underset{OH}{\overset{H}{C}}-\underset{H}{\overset{OH}{C}}-\underset{OH}{\overset{H}{C}}-(COH)$$

B (Glucose) A



$$(CH_2OH)-\underset{OH}{\overset{H}{C}}-\underset{OH}{\overset{H}{C}}-\underset{H}{\overset{OH}{C}}-\underset{OH}{\overset{H}{C}}-(COH)$$

B (Glucose) A

The glucose formula has been proved to have an aldehyde end A and an alcohol end B. All aldehydes reduce Fehling's solution, just as sugar does.

There are in organic chemistry compounds called acetals, which are formed by the conjunction of an aldehyde with an alcohol. (Acetal $CH_3CH<\begin{smallmatrix}(OC_2H_5)\\(OC_2H_5)\end{smallmatrix}$ with the elimination of one H_2O.) These are broken up by the action of dilute acids into the aldehyde and the alcohol respectively. These acetals, unless thus split up, have no aldehyde-reducing effect on copper or salts of similar metals. Now, as sugar peculiarly satisfies this acetalic conjunction by having an aldehyde group at one end and an alcohol group at the other, the limit to its conjunctions would be infinity, and under suitable conditions this might be brought about. But we must note that the slight acidifying does not mean combination of the acid with either aldehyde or alcoholic group. A ferment, in performing the same duty, need not attach itself, but may still remain free to act, whilst by breaking up those special bonds it confers on the combined group a reducing or anionic potentiality which was previously locked up within it.

The meeting of glucose with a kationic agency may have a converse action. Hydrogen phosphite (PH_3) is used to bring about acetal formation.

That prototypes of peptones are in similar chain-like forms seems probable for the following reasons :—

E. Fischer has prepared synthetically glycyl compounds in series, up to four glycyls.

$$C_2H_5Ca \mid NHCH_2CO \mid NHCH_2CO \mid NHCH_2CO \mid NHCH_2CO \mid OC_2H_5$$

The glycyl and its multiples all give the biuret reaction. It is interesting to compare with this a substance called amido-acetal $NH_2CH_2CH(OC_2H_5)_2$ formed from acetaldehyde, and which, with the addition of an acid, splits into amido-acetaldehyde and alcohol NH_2CH_2COH and $2C_2H_5OH$. The junction here is aldehyde to alcohol. Fischer in his glycyl-derivatives has obtained an aldehyde to amide-junction. He states that glycylglycyl $NH_2CH_2CO \mid NHCH_2COOH$ is very similar to peptone in all its reactions. Thus in the prototypes of peptones, and also in polyoses, it seems as if there existed a quasi-polymerisation of peptone and monose, a forming of long chain-like molecules, which, by virtue of the peculiar qualities of their "ends," may do so on to infinity. It is a very significant fact that both starches and albumens are colloidal, and that solutions of them have high surface tensions. To break up those chains demands no loss on the part of the active agency, and this agency is in both cases anionic.

This conception of peptonisation as the breaking of the chain into its units is not hard to grasp, and that little is required to let the fragments recombine is quite conceivable. The splitting results in the formation of small molecules, such as may pass more easily through living animal membranes, and which will not hinder the blood-stream. We must remember in relation to this what I have said with regard to the coagulative power of thrombin—a kation. Coagulation with respect to proteids may be said to be the kationic action of building up or chain-forming, and digestion the breaking down of those chains, or liquefaction by a splitting up of the complex molecule. That kations and anions have these peculiar respective powers is a function of the substances on which they act—their power of chain-forming *ad infinitum*.

That anions are responsible for the breaking up of proteids and carbohydrates can, I think, be proved by experiments which have been done on muscle and nerve. For muscular contraction is believed by all to be primarily coagulative and ultimately destructive, and results in the splitting up of glycogen, and the proteid called inogen, into CO_2, sarcolactic acid, urea or its precursors. The first two are formed from glycogen by way of sugar, and the latter from the proteids by way of peptones. Glycogen disappears. That a nervous impulse in a motor nerve flows centrifugally we know, and that we can by sending electric current in a similar direction (positive to negative towards the muscle) produce a contraction, seems to show that the downward travelling kation is responsible for that peculiar contractile effect. Now, a nerve has the property of conductivity—which if the substance of the nerve be considered as a fluid containing chemical substances means that it is in a state of ionisation.

Again in electrotonic experiments it has been shown that with descending currents there is a descending katelectrotonic current beyond the kathode—and that after the current has ceased, there is a so-called demarcation current in the opposite direction. This katelectrotonic current in which kations are travelling towards the muscle causes hyper-excitability, and, on opening, tetanus occurs if the galvanic current be strong enough (Ritter's tetanus). The kation seems here to be the effective factor, or the contraction is due to some condition proceeding from the positive pole. But during rest, and after contraction is over, a spring back takes place, and there is a current opposite in direction, the anions this time approaching the muscle. This is the katabolic current, the current causing the muscle destruction. The history of a contraction seems then to be the sudden kationisation of the ionised proteid, with some tendency towards coagulation, and a consequent spring back during which anions descend and split up the "coagulum," and proceed to the farther effect of katabolite formation. To trace out and explain the many phenomena of electrotonus and demarcation currents is beyond the scope of this paper, but a study of them on the lines which I have indicated will best illustrate the idea of this paper arrived at from an entirely different standpoint, namely that coagulation, in its widest sense, is the result of kationic action, and that breaking up (peptonisation, glucosation, etc.) is the result of anionic action.

The application of this view to bacteriology is of extreme interest. The organism, in the same manner as the gland cell, has its kationic (or coagulative) and anionic (or liquefactive) secretions. Its pathological effect will depend, firstly, on the relative strength of kation and anion, and, secondly, on the "reaction" of the tissue in which it lodges. If this reaction be alkaline there will be local coagulation and circulating anions, if, on the other hand, it be acid, then there will be local liquefaction and circulating kations. The typhoid bacillus is known to be confined to the acid parts of the intestine, and it passes agglutinins into the circulation.

OBSERVATIONS ON THE LUMBAR ARTERIES. By

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The lumbar arteries are obviously somatic segmental branches of the abdominal aorta; they correspond to the intercostal branches of the thoracic aorta.

In each segment a pair of arteries (*right* and *left*) is given off; and since they usually include four or five pairs, four or five segments are accordingly represented. In any particular segment the opposite vessels of the corresponding pair of arteries may arise separately from the aorta, not uncommonly at different levels; or, on the other hand, the two opposite vessels may, by fusion of their origins, arise by a common stem. The lowest of the lumbar arteries, however, is frequently described as springing, not from the aorta direct, but from the so-called direct continuation of the aorta (caudal aorta), viz., the middle sacral artery.

Professor Thane,[1] in describing the distribution of the middle sacral artery, states that "the middle sacral artery often gives off on each side a considerable branch (*lowest lumbar artery*), which passes backwards on the fifth lumbar vertebra"; and apparently this statement is endorsed by most writers.[2]

I very much doubt, however, whether the lowest lumbar artery is ever a branch of the middle sacral artery; on the contrary, the latter vessel is not uncommonly a branch of one or both of the lowest pair of lumbar arteries.

The middle sacral artery may arise from either the right or

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[1] *Quain's Anatomy*, 10th edition, vol. ii. part ii. p. 469.

[2] Macalister, *Text-Book of Human Anatomy*, 1889, p. 428; Cleland and Mackay, *Human Anatomy*, 1896, p. 448; Walsham, *Treatise on Human Anatomy*, 3rd edition, edited by Henry Morris, F.R.C.S., p. 584; Young and Robinson, *Text-Book of Anatomy*, edited by D. J. Cunningham, F.R.S., etc., 1902, p. 795; Levi, G., "Morphologia delle arterie iliache," *Archivio Italiano di Anatomia e di Embryologia*, vol. i. p. 297; Spalteholz (W.), *Handatlas der Anatomie des Menschen*, 1899, Zweiter Band, p. 430, fig. 471; Henle, *Handbuch der systematischen Anatomie*, iii. p. 202; Sappey, *Traité d'Anatomie*, Tome ii. p. 560; Testut, *Traité d'Anatomie Humaine*, vol. i. p. 1018.

left lowest lumbar artery, or it may arise from a common stem or axis of the lowest pair of lumbar arteries.

From a purely descriptive point of view it is perhaps of little importance whether one regards the lowest lumbar artery or arteries as arising from the middle sacral artery, or the reverse, but obviously it has a direct bearing on the question of the morphology of the last-named vessel.

The fact that somatic segmental branches, corresponding to the lumbar arteries of the abdominal aorta or the intercostal arteries of the thoracic aorta, arise from the middle sacral artery may be regarded as evidence in favour of the primitive aortic nature of the middle sacral artery.

If the middle sacral artery represented any part of the primitive dorsal aorta, then in all probability one or more of the lower lumbar arteries would be found not unfrequently to arise from it.

I think it has been shown[1] that the middle sacral artery does not represent any part of the primitive dorsal aorta.

The fact that the middle sacral artery is not formed by the primitive dorsal aorta, and cannot be regarded as a direct continuation of it, is further pointed out by my friend and former colleague Prof. Arthur Robinson and myself in a preliminary communication, "On the Development and Morphology of the Tail." The communication was read in the Anatomical Section of the British Medical Association at its recent meeting in Oxford (July 1904), and has not yet been published in full.[2] I may be permitted to make some observations dealing with the development and nature of the middle sacral artery:

"The middle sacral artery is formed by two arteries in the tail prolonged backwards into the growing appendage from the dorsal portions of the primitive aorta. The two primitive

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[1] Young, "On the Termination of the Mammalian Aorta," *Studies in Anatomy from the Anatomical Department of the Owens College, Manchester*, vol. i. p. 209; Young and Robinson, "The Development and Morphology of the Vascular System of Mammals," *Proc. Roy. Soc. London*, 1898, vol. lxii. p. 350, and *Studies in Anatomy, Owens College, Manchester*, vol. ii. p. i; Keith (Arthur), *Human Embryology and Morphology*, 1902, p. 246.

[2] This paper has since been published. See *British Medical Journal*, No. 2290, Nov. 19, 1904, pp. 1384–1391.

vessels are both segmental arteries, and they fuse into a single median caudal artery, which lies ventral to the vertebral column. When the fusion of the primitive vessels has occurred, the single resulting trunk (middle sacral artery) may spring from the dorsal aspect of the aorta, a little in front of its bifurcation from a trunk or axis common to it and the last pair of lumbar arteries, or from the lowest lumbar artery of one side, and all the intermediate stages between the two extreme conditions are frequently met with."

I venture to suggest, therefore, that when the middle sacral artery appears to give off either one or both of the lowest lumbar arteries, it is, as a matter of fact, just the opposite—the middle sacral artery, arising from one or both of the lowest lumbar arteries.

Apart from the conclusions arrived at from developmental and morphological considerations, some cases have recently come under my notice in the Anatomical Rooms at the Owens College in Manchester which bear directly on the question, and accordingly I have thought it advisable to record these cases.

In one case (fig. 1) the lowest lumbar artery on each side arose separately from the aorta above the usual level of origin of the middle sacral artery, and this latter trunk was clearly a branch of the right lowest lumbar artery.

FIG. 1.—The lower end of the aorta (seen from behind). Showing the origins of the lowest lumbar arteries (from the aorta) and the middle sacral rising from the right lowest lumbar artery.

In another case (fig. 2), whilst the right lowest lumbar artery arose from the aorta, well above its bifurcation, the left lowest lumbar artery arose from the commencement of the left common iliac, and the middle sacral artery arose so close to the origin of the left lowest lumbar artery that it was difficult to determine whether it was a branch of the lumbar artery or arose with it by a common trunk from the left common iliac artery.

Fig. 2.—Lower end of the aorta (seen from behind). The right lowest lumbar artery arising from the aorta, the left lowest lumbar arising from the left common iliac artery, and apparently giving off the middle sacral artery.

In a third case (fig. 3) the arrangement was of peculiar interest. There was a single trunk arising just above the bifurcation of the aorta, and it appeared to be continued as the right lowest lumbar artery. Just after its origin a common trunk was given off to the left side, which soon divided into the left lowest lumbar artery and the middle sacral artery. This may be explained in different ways:

Fig. 3.—Lower part of the aorta (seen from behind). Unusual arrangement of the origins of the lowest lumbar arteries and the middle sacral.

(*a*) One might regard the original trunk as the middle sacral artery, giving off the two lowest lumbar arteries.

(*b*) The two lowest lumbar arteries might be regarded as arising from a common trunk, the middle sacral taking origin from the left lowest lumbar artery.

(*c*) The right lowest lumbar artery and the middle sacral artery might be regarded as arising by a single trunk; the left lowest lumbar artery arises from the middle sacral.

The next two cases (figs. 4 and 5) are of special interest in connection with a class of cases in which the middle sacral artery springs from a trunk or axis common to it and the last pair of lumbar arteries.

It is not uncommon to find that the lowest pair of lumbar arteries arise by a common trunk, whilst the middle sacral artery arises in the usual manner., *i.e.*, from the dorsal aspect of the aorta, a little in front of its bifurcation (see fig 4). I have not kept this specimen, but it is figured also by Dr Levi.[1]

In other cases, however (fig. 5), in which the lowest pair of lumbar arteries arise by a common stem, the middle sacral artery takes origin at a higher level than usual, and it may arise from the common stem of origin with the last pair of lumbar arteries (see fig. 5).

FIG. 4.—Lower part of the abdominal aorta (from behind). The lowest pair of lumbar arteries arising by a common trunk, the middle sacral artery arising normally.

FIG. 5.—Lower part of the abdominal aorta (from behind). Showing the lowest pair of lumbar arteries and the middle sacral artery arising, higher than usual, from the common stem of the two lowest lumbar arteries.

Obviously if the common stem is part of the conjoined lowest lumbar arteries, then one could not regard these other vessels as being given off from the middle sacral artery. But this is precisely the arrangement which has given rise to the view that the middle sacral often gives off on each side a considerable branch (*lowest lumbar artery*).

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[1] *Loc. cit.*, *Archivio Italiano di Anatomia e di Embryologia*, vol. i. p. 295, fig. 18.

The last specimen (fig. 6) which I wish to record is a preparation of considerable interest as showing the general characters of the origins of the lumbar arteries, and, like the preceding case shown in fig. 5, it suggests that the middle sacral artery is simply a branch or part of the common stem of origin of the last pair of lumbar arteries.

Some years ago I made some observations on the abnormalities of the middle sacral artery,[1] and in referring to the anomalies of distribution of the middle sacral artery, stated that "the lowest lumbar arteries arise in many instances rather in common with the middle sacral than from it, and it is not possible to say which trunk arises from the other, whilst in other cases it is clear that the middle sacral itself arises from one of the lower lumbars."

1st lumbar arteries, arising separately and at different levels.

2nd pair of lumbar arteries, origins closer and at same level.

3rd pair of lumbar arteries, origins closely approximated, foreshadowing a common stem.

4th pair of lumbar arteries, arising by a common trunk.

5th pair, also arising by a common trunk; the middle sacral artery arises from the trunk common to the last pair of lumbar arteries.

FIG. 6.—Lower part of the aorta (seen from behind). Showing the origins of the lumbar and middle sacral arteries.

In view of the cases recorded now, and in view also of the further study of the development and morphology of the middle sacral artery, I think that in this paragraph the word "not" must be *deleted*.

[1] *Journ. Anat. and Physiology*, vol. xxxi. p. 169.

THE SMALL OR SUPERFICIAL THYRO-ARYTENOIDEUS MUSCLE.

By R. B. SEYMOUR SEWELL, B.A., *Christ's College, Cambridge; Fellow of the Anthropological Institute of Great Britain and Ireland.*

Historical.—This little muscle has been described by several anatomists, among whom one may make mention of Santorini (1). This observer gave to it the name of the superior thyro-arytenoideus muscle. I have not, however, been able to obtain his original description.

Soemmerring (2) also called attention to the presence of this muscle in the human larynx under the name of thyro-arytenoideus minor; he also refers to the atlas compiled by Albinus (3), in which the muscle is correctly represented.

Frequency of Occurrence.—Most previous observers agree in stating that the muscle is frequently absent. I have, however, examined 37 larynxes, and have only found 4 cases in which it was not present:

Larynx No. 14. Right side.
15. Right side.
Larynx No. 16. Right side.
22. Left side.

(In 5 cases one side of the larynx had been already dissected, so that it was impossible to tell whether the muscle had originally been present or not.)

We see accordingly that it is present in 65 out of 69 cases, or in a percentage of 93 per cent. The muscle is exceedingly variable in the general arrangement of its fibres, and one is able to distinguish four chief types.

Type 1.—The most common arrangement found is that in which the muscle forms a narrow fleshy fascicle arising from the deep aspect of the ala of the thyroid cartilage close to the notch and above the origin of the thyro-arytenoideus externus muscle.

From this point the muscle passes downwards in a slight curve, the concavity of which is directed downwards and forwards, and is inserted into the lateral border of the arytenoid cartilage immediately above the insertion of the crico-arytenoideus lateralis muscle. In Poirier's figure (iv.) the concavity is represented in the reverse direction, looking upwards and backwards.

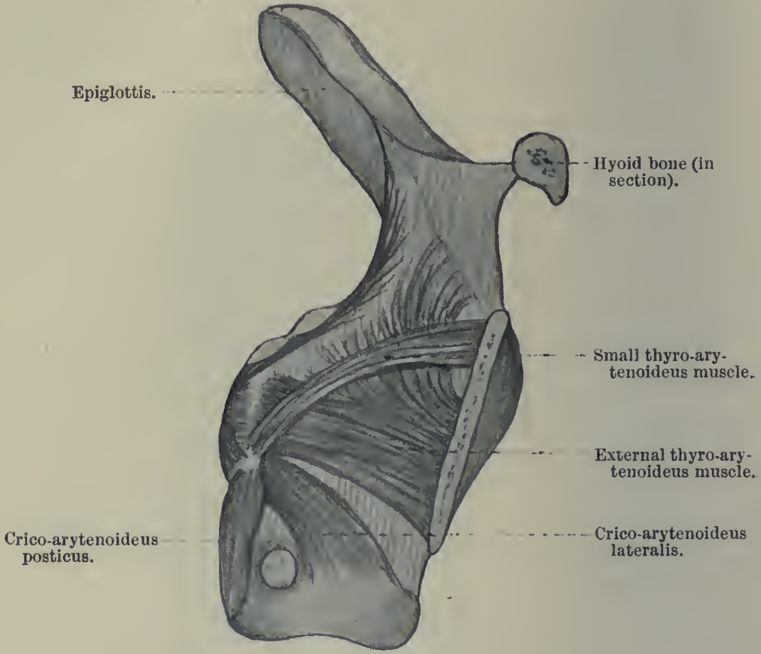

Fig. 1.—Diagram showing the arrangement of the muscular fibres in Type 1.

I have found this type of arrangement to be present in 32 cases, viz. :—

Larynx No. 1. Left side.
2. Left side.
5. Right side.
8. Right side.
Left side.
9. Left side.
10. Right side.
Left side.
13. Right side.
15. Left side.
16. Left side.

Larynx No. 17. Left side.
20. Right side.
23. Right side.
24. Left side.
25. Right side.
Left side.
26. Left side.
27. Right side.
Left side.
28. Right side.
Left side.

Larynx No. 30. Right side.
31. Left side.
32. Right side.
Left side.
33. Right side.
Larynx No. 33. Left side.
34. Right side.
Left side.
35. Right side.
Left side.

In several cases the fibres presented slightly different arrangements from the above; in 3 specimens the muscle was separated into two delaminations, a superficial and a deep.

The *superficial* fibres followed the usual course, and crossed superficial to the fibres of the thyro-arytenoideus externus muscle.

The *deep fibres* were interlaced with the fasciculi of this muscle.

Such a condition was present in the muscle in—

Larynx No. 4. Left side.
17. Right side.
Larynx No. 31. Right side.

In one instance—in larynx No. 4, right side—the whole mass of the muscle ran deeply to the thyro-arytenoideus muscle: the fibres described a somewhat *s*-shaped course; arising from the ala of the thyroid cartilage they at first passed backwards, then curving downwards they passed under cover of the thyro-arytenoideus externus, and finally curved backwards again to be inserted into the arytenoid cartilage between the thyro-arytenoideus internus and externus.

Type 2.—The muscle arises from the ala of the thyroid cartilage close to the upper border. From this origin the fibres curve backwards and downwards. Some are inserted into the side of the arytenoid cartilage; the rest of the fleshy fasciculi, however, curve forwards again and become inseparably blended with the fasciculi of the thyro-arytenoideus externus muscle.

Such a condition I found to be present in 13 cases:

Larynx No. 2. Right side.
6. Right side.
9. Right side.
11. Right side.
Left side.
12. Right side.
14. Left side.
Larynx No. 18. Left side.
20. Left side.
21. Right side.
24. Right side.
30. Left side.
36. Right side.

In one example—larynx 18, right side—the muscle was very small, and all the fibres curved round to join the thyro-arytenoideus externus, none being inserted into the arytenoid cartilage.

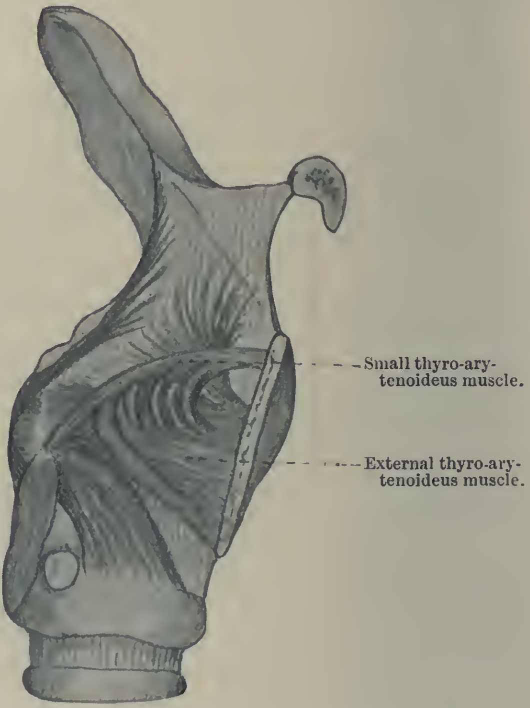

FIG. 2.—Diagram showing the arrangement of the muscular fibres in Type 2.

Type 3.—The muscle consists of two distinct sets of fibres. *The superficial set* arises in the usual manner from the thyroid cartilage, and is inserted into the arytenoid cartilage. *The deep set* of fibres arises from the side of the epiglottis above the thyroid: running downwards and backwards, they cross the saccule of the larynx, and then join the superficial set, lying deeper, however, and at a somewhat higher level; finally they are inserted into the side of the arytenoid cartilage with the superficial fibres. In some cases some of the fibres are attached above to the false vocal cords.

This condition was found to occur in 8 cases:

Larynx No. 1. Right side.
3. Left side.
5. Left side.
6. Left side.
Larynx No. 7. Right side.
12. Left side.
19. Left side.
37. Right side.

In one instance—larynx No. 7, left side—the superficial set of fibres was not present, the muscle being represented solely by a bundle of fibres, which were attached by a small delicate tendon to the arytenoid cartilage and which passed upwards and forwards over the saccule to be attached to the side of the epiglottis.

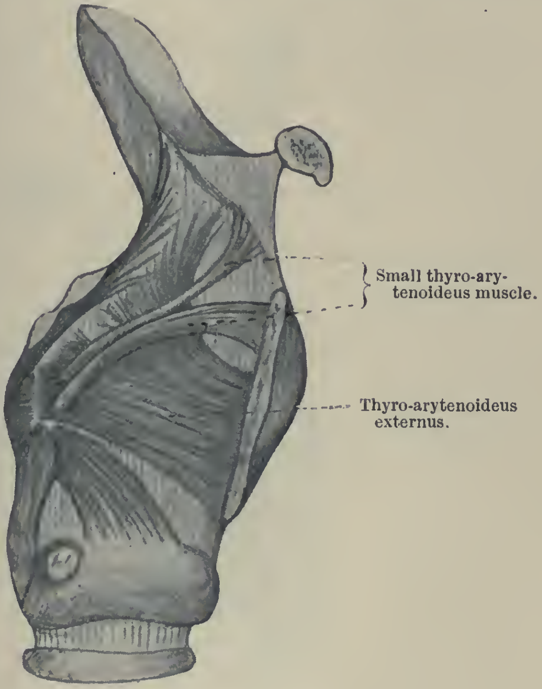

Fig. 3.—Diagram showing the arrangement of the muscular fibres in Type 3.

Type 4.—The muscle was attached posteriorly by a thin flattened tendon to the side of the arytenoid cartilage; anteriorly the fibres curved upwards and forwards, and, spreading out in a fan-shaped manner, blended with the fasciculi of the thyro-arytenoideus externus muscle.

Such a condition is comparatively uncommon, and I have only found it present in three cases:

Larnyx No. 3. Right side.	Larnyx No. 23. Left side.
22. Right side.	

In one larynx—No. 29—the muscles on both sides presented an arrangement differing slightly from the above, in that, whilst most of the fibres curved upwards and forwards, and became blended with the thyro-arytenoideus externus muscle, some of them curved upwards again, and either became attached to the epiglottis or were lost on the side of the larynx.

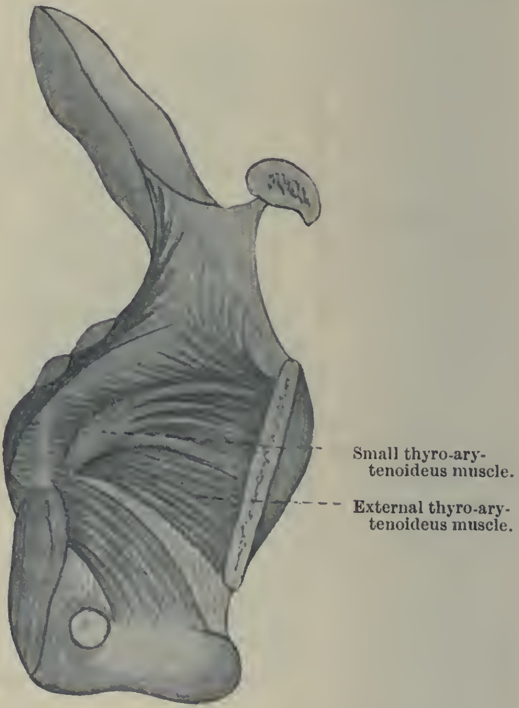

Fig. 4.—Diagram showing the arrangement of the muscular fibres in Type 4.

Size.—In size the muscle is found to vary very considerably. In the majority of cases the muscle is small, though well defined, but in nearly 30 per cent. of the cases examined it was well developed, and in a few specimens it measured as much as 6 mm. across.

The *nerve supply* of this little muscle is derived from a branch of the recurrent laryngeal nerve. This enters the larynx between the ala of the thyroid and the cricoid cartilages; anteriorly it gives off a large branch, which enters the thyro-arytenoideus muscle and supplies it. The remaining portion of the nerve runs upwards and forwards in the same direction as the thyro-arytenoideus parvus, but at a slightly lower level, and gives off two or three delicate twigs to this muscle, which enter it on its deep aspect near the lower border about the middle of its length.

AUTHORS CITED IN THE TEXT.

(1) Santorini, *Observationes Anatomica Venet.*, 1724, iv. p. 106.
(2) Soemmerring, *De Corporis Humani Fabrica*, Tome iii.
(3) Albinus, *Tabulæ Sceleti et Musculorum Corporis Hominis.*
(4) Poirier et Charpy, *Traité d'Anatomie Humaine*, Tome iv. p. 441.

Another description is given by Malgaigne, "Nouvelle théorie de la voix," in the *Archives générales de Médecine*, 1831, xxv. 212, but it does not accord with the forms which I have enumerated above.

THE MYOLOGY OF THE HIND LIMB OF THE MARSUPIAL MOLE (NOTORYCTES TYPHLOPS).

By Peter Thompson, M.D., *Lecturer on Anatomy, Middlesex Hospital*, and W. T. Hillier, M.R.C.S., L.R.C.P., *Middlesex Hospital*. (Plates XXXVIII and XXXIX.)

The observations of Stirling (15 and 16), Gadow (7), Wilson (17), Elliot-Smith (14), and others have already made us fairly well acquainted with the habits and structure of this rare member of the marsupialia. There are, however, certain parts still remaining to be described, and this contribution to the limb myology will, it is hoped, furnish additional evidence of the nature of the relationships existing between the Marsupial Mole and other more or less allied forms. Undoubtedly, from the myological standpoint, the preponderant type is marsupial, though there are certain peculiarities, for a structural resemblance to which, it is necessary to search outside the limits of the marsupialia. These, for the most part, appear to be common to animals with similar skeletal arrangements to those of the mole, as, for example, the edentates, in which there is a corresponding ankylosis of the hip-girdle with the vertebral column, and in a less degree to others whose limbs have undergone functional modifications in association with fossorial habits.

It is to Professor J. T. Wilson of Sydney (17) that we are indebted for a most detailed account of the muscles of the fore-limb, which he published, along with certain other notes, in 1894. In this account he endeavoured not only to give a descriptive view of the arrangement of the individual muscles of the limb, but to provide also for a morphological comparison between them and the corresponding muscles of other animals. The result was a most careful, and indeed almost exhaustive, survey of the myology of the marsupialia and some other forms. This section of his work, however, did not deal with the myology of the hind limb, and, as far as we can ascertain, no account of this has, up to the present, been published.

When, therefore, a specimen, in a fairly good state of preservation, was received by one of us (W. T. H.) direct from the Northern Territory of South Australia, we took the opportunity of examining the muscles of the hind limbs. Since these observations were completed we have been fortunate, through the kindness of Professor Stewart, in being able to revise the work on another specimen from the stores of the Museum of the Royal College of Surgeons; and for a third specimen we are greatly indebted to Dr W. E. Hoyle, Curator of the Manchester Museum. Further, we have to thank Mr R. H. Burne, of the Royal College of Surgeons, for the loan of several water-colour drawings of dissections of Notoryctes prepared by him for the Museum.

Ecto-gluteus (*gluteus maximus*) *and tensor fasciæ femoris.*—A single muscle, triangular in form and comparatively thin, arises by its base from the fused metapophysial elements of the sacral vertebræ, and is inserted by a narrow tendon into the outer and anterior part of the great trochanter, giving off an expansion also into the fascia of the thigh. Although there is no evident division into two parts, it is probable that the muscle represents both the ecto-gluteus and the tensor fasciæ femoris. In Trichosurus a somewhat similar arrangement is found, and the anterior part is identified by receiving a branch from the superior gluteal nerve. The fusion of these two muscles is a frequent occurrence in marsupials. Cunningham describes such an arrangement in Cuscus (3), Young in Koala (19), and Maccormick in Dasyurus (9). On the other hand, it is interesting to note that in some of the edentata, according to Windle and Parsons (18), the tensor fasciæ femoris is inseparable from the sartorius.

Femoro-coccygeus.[1]—This muscle is very closely associated with the foregoing in many animals, but in Notoryctes the primitive connection is somewhat obscured by the extension forwards of the biceps femoris, so that the femoro-coccygeus lies completely concealed by it. When, therefore, the biceps is reflected the femoro-coccygeus is seen to arise from the ischial tuberosity. It runs down the back of the thigh, grooving the posterior surface of the shaft of the femur, and is finally inserted

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[1] We have in this paper adopted the nomenclature used in Broun's *Thier-Reichs*.

into the prominent bony projection on the outer side of the posterior end of the patella. At its insertion it lies deep to the biceps and the vastus externus.

In other marsupials, viz., Trichosurus and Dasyurus, the ecto-gluteus, tensor fasciæ femoris, and femoro-coccygeus lie in one and the same plane, more or less fused together, and the femoro-coccygeus is that part of the sheet which lies caudal to the ecto-gluteus and extends backwards as far as the biceps femoris. In Notoryctes the origin of the biceps femoris, and indeed the whole muscle is so strongly developed that, as stated above, the femoro-coccygeus is completely hidden by it.

In Sarcophilus also, Macalister (8) found the agitator caudæ, *i.e.* femoro-coccygeus, separate from the gluteus maximus, but the more prevalent arrangement in marsupials is the one in which the two muscles are inseparably connected.

Meso-gluteus (gluteus medius), ento-gluteus (gluteus minimus), and pyriformis.—It is interesting to find that, as in the edentata, there is an imperfect differentiation of these three muscles. In two specimens of Notoryctes, the gluteus minimus could not be recognised as a separate muscle, but in the third specimen, a gluteus minimus was quite distinct.

The gluteus medius arises as a thick mass from the hollow immediately above the ilium, *i.e.* from the under surface of the fused metapophyses and from the outer surface of the ankylosed traverse processes of the sacral vertebræ. The muscle is to a large extent covered by the gluteus maximus, but a small portion appears superficially between the posterior edge of the sartorius, the inferior edge of the gluteus maximus, and the upper edge of the vastus externus. The muscle is inserted by a short tendon into the outer part of the great trochanter, near the summit. The mass is distinctly bilaminar, thus resembling the corresponding muscles in Thylacine (3), and the Koala (19). In the limb in which the gluteus minimus was differentiated, the fibres lay in contact with the capsule of the hip-joint, and were inserted into the great trochanter close to the gluteus medius. If this differentiation of the gluteus minimus is unusual, as it appears to be, in Notoryctes, then the number of gluteal muscles is not so complete in this animal as that found in many other marsupials, in which the three glutei, and often a fourth, can be observed without difficulty. The gluteus quartus, moreover, was not found in any of the limbs we dissected. According to Macalister (8), the gluteus medius and minimus are hardly separable in the Wombat and Sarcophilus.

The pyriformis was not present as an independent muscle. It is absent also in Erinaceus, Myogale, Talpa, and Condylura among insectivores (4). It is present in Thylacine (3), Cuscus (3), and Dasyurus (9), and probably most marsupials, though Macalister states that it is indistinguishable as a separate muscle in Phalangista (8).

In Notoryctes a conspicuous feature of the sacrum is the great development and coalescence of the metapophysial elements and traverse processes of its constituent vertebræ, and the fusion of the ilia and ischia with the anterior and posterior extremities respectively of the metapophysial mass. This leads to a reduction in the size of the great sacro-sciatic foramen, the small size of which may account not only for the failure of the extension inwards of the intrapelvic portion of the pyriformis, but also for the entire absence of any differentiation from the meso-gluteal mass of the extrapelvic portion of the muscle.

In Echidna, Mivart (10) found the pyriformis arising from the transverse processes of five caudal vertebræ. The great sciatic nerve, however, passed out superficially to it, instead of the muscle being superficial to the nerve. This muscle may, however, represent the caudo-femoralis described later.

Obturator internus and gemelli.—These muscles have been regarded by some writers as a single mass consisting of two bellies—one the intrapelvic belly, which represents the obturator internus; the other the extrapelvic belly, which represents the obturator internus and the two gemelli. As already pointed out above, the ischium in Notoryctes is ankylosed to the sacrum, and in consequence it is not surprising to find that the muscles do not exhibit the usual mammalian arrangement. Indeed, the obturator internus is entirely unrepresented as a separate muscle emerging from the pelvis, and the same reasons which have been advanced to account for the absence of the pyriformis may perhaps explain the failure in development of an intrapelvic belly in this case. There are, however, two small extrapelvic muscles which represent the gemelli, which arise deeply from the ischium above the acetabular cavity and pass to be inserted into the inner and top side of the great trochanter, though before dissection they appeared to form a single muscle. It is interesting and significant, in connection with the arrangement, to find that Windle and Parsons (18) describe the same disposition throughout the edentata, with the exception of the Orycteropodidæ, in which the typical Mammalian arrangement occurs. Now in all edentates, except Orycteropus, the ischia unite with the vertebral column (Flower).

But Notoryctes is not peculiar amongst marsupials in not possessing an obturator internus, for Macalister (8) records its absence in the Wombat and Sarcophilus. The gemelli, on the other hand, are strongly developed in most marsupials, but in Halmaturus (2) they are said to be absent. Both the gemelli and also the obturator internus are absent in Echidna (10).

Obturator externus.—A well-developed fan-shaped muscle which arises from the outer surface of the ischium below and behind the acetabulum. It is inserted by a comparatively broad tendon into the back of the great trochanter, covering the small trochanter near its termination. Its deep surface is in relation with the capsule of the hip-joint, and its lower border is in contact with the caudo-femoralis.

As a differentiation of the obturator externus, the obturator intermedius is found in certain insectivores, and a corresponding muscle is present in the monotremes. Leche (2) has observed the muscle in Didelphys, amongst marsupials; but although careful search was made for the muscle in Notoryctes, it was not found.

In describing the next muscle reference is made to the occasional fusion of the quadratus femoris with the obturator externus in some animals, and it seems quite possible that in Notoryctes, in which a separate quadratus femoris is not present, such a fusion may have occurred.

Caudo-femoralis.—A glance at the literature of the caudo-femoralis shows how frequently this muscle has been described as the quadratus femoris. With one or two exceptions, its arrangement in marsupials, however, is so characteristic, and its relations so constant, that a short description may perhaps with advantage precede the description of the muscle in Notoryctes.

In Cuscus (3), Thylacine (3), and Myrmecobius (2), the muscle arises, either from the vertebral column, the great sacro-sciatic ligament, or the ischial tuberosity, and is inserted for a variable distance along the back of the femur, reaching, in the case of Myrmecobius, as far down as the internal condyle. In all these animals the muscle is covered by the ecto-gluteus, femoro-coccygeus, and biceps, and the great sciatic nerve runs superficial to it, giving off a branch to the muscle on its way down. When the muscle takes origin from the tuber ischii, it is perhaps not surprising that it should have been so frequently described as quadratus femoris.

Whatever may be the morphological significance of the caudo-femoralis, it is well known that in the marsupials mentioned above a second muscle is present arising from the ischial tuberosity and passing to be attached to the femur, which is innervated by the obturator nerve and described under the name of quadratus femoris.

In these marsupials, therefore, it is clear that there are two muscles, one associated with the hamstring group, innervated by the great sciatic nerve and named the caudo-femoralis, and the other associated with the obturator externus, sometimes the adductor magnus, and innervated by the obturator nerve.

In Notoryctes only one of these two muscles is present, the caudo-femoralis. It arises from the pelvis just in front of the ischial tuberosity, and is inserted into the posterior aspect of the shaft of the femur, external to the insertion of the pectineus, reaching for a considerable distance down towards the lower end of the bone; so obliquely are the fibres of the muscle directed that they run almost parallel with its shaft. The quadratus femoris in the case of Notoryctes is not present as a distinct muscle. It may, however, be fused with the obturator externus, which lies immediately ventral to the caudo-femoralis. That this fusion is not improbable is supported by the observations of Windle and Parsons (18) in the Manidæ, in which the fusion of the two muscles in question has been frequently noticed.

What, therefore, is the morphology of the caudo-femoralis? Cunningham (3) and Maccormick (9) refer to the muscle in marsupials under the name of ischio-femoralis. The former, in describing the muscle in the *Challenger* reports, says "that the muscle is liable to be confused with the quadratus femoris, but it lies in quite a different plane, being superficial to the gemelli, true quadratus, and adductor mass. It must, therefore, be regarded as a separate muscle, the morphology of which is by no means certain." We feel, too, that the question is one of great difficulty, and at present we are not prepared to commit ourselves to a definite statement of opinion, but we venture to suggest that the caudo-femoralis is the homologue of the human quadratus femoris. The transference of the attachment of the proximal end of the muscle from caudal vertebræ to the great sacro-sciatic ligament, and from the sacro-sciatic ligament to the ischial tuberosity, is clearly illustrated by the study of the origin in Trichosurus, Koala, and Dasyurus. The insertion of the caudo-femoralis is invariably into the posterior aspect of the femur; and whilst in Dasyurus it reaches as far down as the internal condyle, in the Koala the insertion is confined to the posterior border of the great trochanter. If this view is tenable, then we must admit that the second muscle, described in marsupials under the name of quadratus femoris, has in man either disappeared or fused with the obturator externus. The results of Professor Macalister's dissections of two specimens of Sarcophilus are also suggestive in connection with this point. In one the quadratus femoris exhibited the usual mammalian arrangement, whilst in the other "it was very remarkable, arising from the transverse process of the first caudal vertebra, from the tuber ischii, and a tendinous band which passed from the one to the other." There seems little doubt that the latter is the representative of the ischio-femoralis described by Maccormick and Cunningham, and the caudo-femoralis so-called in this paper.

THE HAMSTRING MUSCLES.

Biceps.—This muscle and the femoro-coccygeus are very intimately connected at their origins, but towards their insertion the two are easily separated. The biceps is a powerful muscle, and arises from the ischial tuberosity immediately behind the gluteus maximus, lying between the vastus externus and the other hamstrings. It passes downwards towards the knee, and is inserted into the outer side of the patella and the tubercle of the tibia, along with and immediately below the vastus externus and the sartorius.

Bicipiti accessorius.—Tenuissimus.—This muscle is very closely associated with the former at its origin. It is a narrow, ribbon-like muscle which arises from the ischium ventral to the gluteus maximus and biceps, and above and in front of the semitendinosus. As it passes downwards it lies superficial to the caudo-femoralis and semitendinosus, and then on the outer side of the gastrocnemius, finally ending in a thin fascial sheet which is continued down the back of the leg as far as the calcaneal spur to form a sheath for the tendo Achillis. The fascia can be distinctly traced on to the outer side of the foot, so that the tenuissimus in Notoryctes forms a distinct "ischio-pedal" muscle.

Parsons (12) has already drawn attention to, and explained the reason of, the special development of this sheath in the ungulates, and it is interesting to find that a clearly-defined sheath, in this case prolonged from an independent muscle—the tenuissimus—should occur in a member of a group so widely separated from the ungulates. Notoryctes, though essentially a burrowing animal like other moles, differs from them in not usually forming a permanent burrow. The functions of the hind limb are largely to push the body onwards, using the feet as a *point d'appui*, and to throw back the sand, in which it is almost constantly working, whilst the fore-claws work under the body. A most important part of the whole movement of progression will necessarily be extension of the ankle-joint, and the tenuissimus and its fascial prolongation will help considerably in this movement.

The tenuissimus appears to be only occasionally present in marsupials. Macalister (8) records its presence in Sarcophilus, in which animal it is the longest muscle of the body.

Semitendinosus.—The semitendinosus arises from the ascending ramus of the ischium immediately in front of the ischial tuberosity, and is inserted into the inner surface of the shaft of the tibia about its middle third. Near its insertion the muscle tends to be divided into two parts. There is no tendinous intersection in its substance, and in connection with this point Cunningham (3) says that it is a rare occurrence to find such in the semitendinosus of a marsupial, though he has noticed it in Thylacine. Maccormick (9) records a tendinous intersection in the semitendinosus of Dasyurus, and we have recently observed it in Trichosurus.

Semimembranosus.—This is a well-developed muscle, and separates readily from the other hamstrings. If viewed from the dorsal aspect it is situated ventral to the semitendinosus and the tenuissimus, and arises from the hinder end of the ischium immediately below these muscles. The fibres form a mass which near its commencement is rounded in transverse section, but towards its insertion it becomes flattened and is attached by a rather broad tendon into the inner surface of the shaft of the tibia, anterior to the insertion of the semitendinosus and under cover of the gracilis.

Presemimembranosus.—In Notoryctes (and also in Trichosurus) this muscle is separated from the semimembranosus right from origin to insertion. It arises from the ischium close to the origin of the semimembranosus and the adductor mass, and passing downwards in close contiguity to the caudo-femoralis it is inserted into the internal condyle of the femur. Unfortunately a separate nerve-supply to this muscle was not obtained; but in Trichosurus, in which a dissection of the muscles of the hind limb was carried out simultaneously with that of Notoryctes, there was no doubt that the corresponding muscle received its nerve-supply from the great sciatic nerve.

MUSCLES ON THE ANTERIOR AND INNER ASPECTS OF THE THIGH.

Sartorius (*ilio-tibialis*) arises from the anterior end of the bony ridge formed by the fused metapophysial elements immediately opposite to the fourth lumbar vertebra. The muscle is directed forwards, outwards, and slightly downwards, and ends in a narrow tendon, which, passing over the patella, is attached to the front and outer aspect of the tubercle of the tibia. It is a thick, powerful muscle, and acts as an extensor of the knee-joint, and a flexor of the thigh. In Trichosurus, on the other hand, the muscle is very thin and ill-defined.

QUADRICEPS EXTENSOR CRURIS.

I. *Quadricipitis centralis* (*rectus femoris*).—A well-developed muscle, lying beneath the sartorius, and covered at its distal part by the junction of the vasti, which arises from a well-marked tubercle immediately dorsal to the acetabular cavity. The origin is broad, and although two heads are not obvious before dissection, they can be separated with a little trouble. These, corresponding to the straight and reflected heads of the muscle, lie very close together, and quickly unite, so that the point of the knife can scarcely be introduced into the interval between them without breaking down some muscular fibres. On separating the two vasti the rectus is seen to end in a slender tendon which is inserted conjointly with the other segments of the extensor mass into the summit of the patella. Only one head is present in Macropus and Didelphys (2), and Windle and Parsons (18) describe the usual origin in edentates as a broad head which represents the acetabular and iliac heads of the muscle in man. On the other hand, Young (19) describes a double origin to the muscle in the Koala.

II. *Quadricipitis lateralis* (*vastus externus*).—This muscle is very large in proportion to the mesialis (vastus internus), and lies immediately anterior to the biceps and femoro-coccygeus, the latter muscle lying in a groove on its posterior border. It arises from the whole length of the outer aspect of the shaft of the femur below the insertion of the ecto-gluteus, and, meeting the mesialis over the rectus femoris (centralis), joins the common tendon of insertion.

III. *Quadricipitis mesialis* (*vastus internus*) is the portion of the muscle lying to the inner side of the rectus femoris. It arises from the inner aspect of the shaft of the femur and is inserted into the common extensor tendon. Near its insertion it is grooved by the adductor longus.

IV. *Quadricipitis profundus* (*crureus*).—This muscle and the subcrureus are not distinguishable as separate factors in the mass, but form a thick bed under the rectus, continuous with the vasti. Subcrurales have been noted in Dasyurus and Didelphys (2). The insertion of the common extensor mass takes place into the front part of the patella and into the tubercle of the tibia below. In the Koala (19) there is no patellar ossification, and the broad tendon of insertion is inserted directly into the upper extremity of the tibia.

Psoas parvus and psoas magnus.—Although in most marsupials the psoas parvus is a larger muscle than the psoas magnus, in Notoryctes the reverse is the case.

The *Psoas parvus* takes origin by a tendon from the transverse process of the second lumbar vertebra, and is inserted by a tendon into the ilio-pectineal eminence. The upper half of the muscle forms a fusiform belly, and the lower half is a fine slender tendon. In Trichosurus, too, the psoas parvus is smaller than the psoas magnus, whilst in monotremes the muscle is very large.

The *Psoas magnus* arises from the sides of the last dorsal and all four lumbar vertebræ. It passes vertically downwards as a muscular mass, flattened from side to side, and, crossing the front of the capsule of the hip-joint, is inserted into the trochanter minor.

Iliacus.—This muscle arises from the whole of the inner surface of the ilium, and is inserted by a short tendon into the small trochanter independently of and immediately external to the insertion of the psoas.

Adductor cruris (*gracilis*).—This is a broad, flat, well-developed muscle, lying in a plane superficial to the semimembranosus and the adductor longus, and arising from the hindmost part of the symphysis pubis and from the sub-pubic margin below. As it runs outwards it broadens out somewhat, and is inserted into the tibia near the upper end of the bone, giving off an expansion to the fascia of the leg over the tibialis anticus.

Pectineus.—This muscle arises from the symphysis pubis near the point of articulation with the marsupial bone. It is single and pointed at its origin, but towards its insertion it tends to divide into two parts, which are inserted into the posterior aspect of the femur below the level of the insertion of the obturator externus, and extending for some distance down the shaft of the bone. In Trichosurus the muscle is clearly divided into two parts right from the origin to insertion, and the division, partial or complete, is quite common amongst marsupials.

The *Adductor femoris mass.*—This group of muscles may be divided for convenience of description into a superficial stratum, which is very well developed and apparently corresponds to the adductor longus, and a deep stratum, smaller, much more feebly developed, less constant in its arrangement, and apparently corresponding to the adductor brevis and the adductor magnus.

The former stratum is well seen after removal of the gracilis, when four muscles are exposed, running parallel to each other, namely, the vastus internus, the superficial segment of the adductor mass (adductor longus), semimembranosus, and the semitendinosus, in this order from without inwards. The adductor longus arises from the subpubic arch, and is inserted into the front part of the patella at its inner margin. We were somewhat surprised to find such an unusual insertion, and we have not so far discovered any record of a similar insertion in any other marsupial. In Notoryctes the thigh bone is short, whereas the patella and the upper end of the tibial crest are relatively greatly developed, apparently to provide the necessary leverage for the quadriceps extensor mass. Not only is the patella very large, but it is irregular in form, being compressed laterally, and presenting a sharp margin in front and below. Associated with the insertion of the quadriceps extensor mass into the patella is the insertion of the adductor longus, and it is significant that the area of its attachment on the inner side of the anterior margin of the bone, together with that of the vastus internus, should be approximately coextensive with that of the vastus externus on the opposite side of the bone, suggesting, indeed, that the influence of these two lateral forces is exerted in maintaining the patella in the line of the axis of the limb—a very necessary provision when one considers the great size of the patella in proportion to the lower end of the femur.

The deep stratum of the adductor mass is seen on reflecting semitendinosus, semimembranosus, and adductor longus. Apart from the presemimembranosus, which has already been described, it consists of two portions, intimately associated together, which may represent the adductor brevis and the adductor magnus. They arise from the outer surface of the ischium near the tuberosity, and are inserted into the upper end of the inner surface of the tibia and the adjacent part of the lower end of the femur. On reflecting these two muscles, the presemimembranosus and the caudo-femoralis come into view.

ANTERIOR TIBIO-FIBULAR REGION.

Tibialis anticus.—A fusiform muscle which arises from the outer surface of the upper extremity of the tibia from the upper third of the shaft and slightly from the fascia covering it. It soon ends in a long slender tendon which passes under the broad annular ligament in a special compartment lying in the deep groove between the internal malleolus and the astragalus. It is inserted into the internal cuneiform bone, and gives an expansion to the base of the first metatarsal bone.

In Trichosurus and in the Koala (19) the slip to the first metatarsal is wanting, nor does Maccormick (9) mention any in Dasyurus viverrinus.

Extensor proprius hallucis.—Before dissection, this muscle is completely hidden by the tibialis anticus on the inner side and the extensor longus digitorum on the outer side. On separating them, however, a delicate muscular slip is seen which arises from the upper part of the shaft of the fibula. It passes down the leg, and soon ends in a long thread-like tendon which can be traced along the dorsum of the foot to the terminal phalanx of the hallux. Near its insertion it expands and gives off a few fibres which are inserted into the base of the first metatarsal. The relation of the tendon to the anterior annular ligament is very definite. It passes with the tendon of the tibialis anticus under the broad band of the annular ligament, and is enclosed in a little tough ligamentous ring attached deeply to the tibia and fibula a little above the level of the ankle joint. A short distance from its termination, the tendon crosses the insertion of the tibialis anticus. Maccormick (9) describes this ring of fascia in Dasyurus, and states that it acts as a pulley for the tendon, and he believes that the muscle acts as an abductor of the hallux, as well as an extensor. In the Koala (19) there is a separate extensor hallucis from the fibula to the great toe, though it was absent in the Thylacinus dissected by Cunningham (3).

Extensor longus digitorum.—This muscle is divisible into three parts, two of which lie in a superficial plane and the third in a deeper plane. The division between the two parts of the superficial layer is evident as high as the head of the fibula. The origin is from the head of the fibula, from the shaft of the fibula for the upper half of its extent, and from the deep fascia of the leg. Just below the middle of the leg it gives place to four fine tendons which pass beneath the anterior annular ligament, in special compartments. That tendon which goes through the outermost compartment goes to the fifth toe, those going through the next compartment go to the fourth and third toes. The deep stratum of the muscle separates high up, and after a very short course ends in a fine long hair-like tendon, the fourth of the series, which runs down in front of the extensor proprius hallucis under the anterior annular ligament being bound down to the interval between the tibia and fibula. It then runs along the dorsum of the foot to the second toe, crossing beneath the tendon going to the third toe, close to the ankle joint. All four tendons expand as they pass on to the dorsal aspect of the toes, and they are inserted in the usual manner.

Young (19), in describing this muscle in Koala, says that "the mass is easily separable into two parts, and in this respect Koala appears to differ from such marsupials as have been examined." We have also to record a division of the extensor longus digitorum in Trichosurus, and Mivart's description of the muscle in Echidna (10) shows that in monotremes it tends to be separable into two or perhaps three more or less distinct portions.

Extensor brevis digitorum.—Although careful search was made for this muscle in Notoryctes, no trace of it was found. In this respect the animal differs from the other marsupials which have been described. In Trichosurus the muscle is extremely small, arising from the upper surface of the greater process of the os calcis. Only two tendons were prolonged from it, and these passed to the second and third toes. A corresponding disposition is described by Young (19) in the Koala. This representative of the extensor brevis digitorum corresponds to the second component of the muscle found in Didelphys (13), in which animal three parts can be recognised:—(1) the peroneus quinti digiti, fibular in origin; (2) extensor brevis digitorum proper, also fibular in origin, going to the second, third, and fourth toes; and (3) extensor brevis hallucis, which is pedal in origin. In Thylacinus (3) the whole of the extensor brevis digitorum arises from the fibula.

PERONEAL MUSCLES.

The peronei are two in number—the peroneus longus and the peroneus brevis.

The *Peroneus brevis*, the anterior of the two muscles, rises from the outer side of the shaft of the fibula and from the upper extremity of the bone, in front of and below the foramen capitis. A few fibres also spring from the hook-like process which projects backwards from the head of the bone. The muscle passes downwards, and near the lower end of the fibula ends in a tendon which runs in a deep groove flanked by two tubercles on the outer aspect of the bone. Towards its insertion, which takes place into the anterior inferior angle of the outer aspect of the fifth metatarsal bone, it crosses the tendon of the peroneus longus on the outer border of the foot. We did not find any representative of the peroneus quinti digiti going to the fifth toe. In Trichosurus the tendon of the peroneus brevis is perforated near its insertion by the peroneus quinti digiti.

The *Peroneus longus* arises from the outer aspect of the fibula behind the former, and from the backwardly directed process at the upper end of the bone. In the lower part of the leg it ends in a rounded tendon which runs behind the external malleolus, and then turns round the outer border of the foot above the metatarsal bone of the fifth toe. The tendon passes next beneath the cuboid, and is finally inserted into the outer side of the base of the first metatarsal.

These two muscles seem quite constant in the marsupialia, but the insertion of the peroneus longus varies slightly. Leche (2) describes the muscle in Myrmecobius as being inserted into the internal cuneiform bone.

THE SUPERFICIAL MUSCLES OF THE CALF.

The *Gastrocnemius* is a two-bellied muscular mass, the outer head of which arises from the back of the head and the upper part of the shaft of the fibula. It seems probable that this head of origin represents not only gastrocnemius, but probably the soleus also, since the latter cannot be differentiated as a separate factor. The inner head of the gastrocnemius is divided into two parts, both of which arise from the femur. The superficial and larger part of this head arises from the posterior surface of the shaft of the femur in the middle third of its extent, whilst the deeper part arises immediately above the internal condyle. Both heads are prolonged into the tendo Achillis, which is inserted into the calcaneal spur.

The tendo Achillis appears to be more directly continuous with the inner head, the fibres from the outer head being inserted obliquely into its lateral margin and its deep surface. The more superficial fibres of the tendo Achillis, *i.e.*, those continuous with the inner head, pass to the outer side of the tendo Achillis at its insertion; whilst the deeper fibres, continuous with the outer head of the muscle, can be followed into the inner margin, the arrangement being somewhat similar to that described by Parsons (11) in Castor canadensis and other mammals.

The relationship of the tendo Achillis to the sheath prolonged from the tenuissimus has already been referred to.

The *Plantaris* is in contact with the deep surface of the outer head of the gastrocnemius and arises in common with it. It is very slender, and soon ends in a long, delicate tendon which crosses beneath the tendo Achillis and gains its inner side previous to entering the sole. It passes into the foot through a narrow passage or tunnel formed by the tibial sesamoid on the one hand and the fifth metatarsal on the other. It then expands and divides into three slender prolongations which have a distinct fibrous rather than a tendinous appearance. These processes pass to the intervals between the first and second, second and third, and third and fourth toes, where they end subcutaneously, each dividing into two parts at its termination.

In one of the two specimens of Notoryctes which we dissected, the arrangement just described was well marked, but in the other specimen the plantaris could not be traced beyond the entrance of the tunnel into the sole, at which point it fused with the fascia over the tibial sesamoid, and with the fascia joining the sesamoid to the calcaneal spur.

It will be convenient to refer here to a well-defined ligamentous band which lies in the sole between the plantaris stratum and the flexor tendons, and which was present in both the specimens we examined. It is attached behind to the plantar surface of the tibial sesamoid, and ends in front on the base of the first phalanx of the middle toe. It is difficult to say what is the significance of the band in question. It is so strong that we feel sure it has some important, though not obvious, function to perform. As described further on, the sesamoid bone from which it arises receives the insertion of the tibial flexor of the toes, and it may be that the ligamentous band represents the degenerate plantar portion of the tendon of the muscle, the course of which has been interrupted by the large sesamoid bone on the inner side of the foot.

In Trichosurus the plantaris passes over the tuberosity of the calcaneum, and in the sole terminates in two expansions, one becoming inserted into the base of the fifth metatarsal, the other into a sesamoid bone at the base of the first digit. In Thylacine (3) and in Dasyurus (9), the tendon ends, as in Notoryctes, in three processes, going towards the second, third, and fourth toes. In Cuscus (3) it is inserted into a plantar cartilage, whereas in Phascolomys (8) the muscle is absent.

In Dasypus, Parsons and Windle (18) describe the plantaris as continued into the sole of the foot, where it flattens out and sends slips to three or four of the digits, which slips are perforated by the tendons of the flexor longus digitorum. In Chlamydophorus (18), too, the tendon passes into the sole of the foot, where it divides into four slips.

THE DEEP MUSCLES OF THE BACK OF THE LEG.

There are three deep muscles on the back of the leg, the innermost of which represents the flexor digitorum tibialis; the intermediate one, the tibialis posticus; and the outermost one, the flexor digitorum fibularis.

Flexor digitorum tibialis arises by two heads: an inner, smaller, which is attached to the posterior surface of the tibia for the upper third of its extent; and an outer, larger head, which springs from the posterior aspect of the upper extremity of the fibula. The two bellies join together, and end in a long, slender tendon which passes down behind the internal malleolus, crossing superficial to the tendon of the tibialis posticus, both tendons lying in the same groove and occupying the same compartment of the well-marked internal annular ligament. After a course of about half an inch, the tendon is inserted into the upper extremity of the prominent tibial sesamoid bone, which lies in relation to the shaft of the metatarsal bone of the hallux. The part of the bone which receives the tendon is elevated to form a prominent tubercle.

In Dasyurus (9) the tendon ends in two parts, one going to the base of the fifth metatarsal, the other to the base of the first metatarsal and the internal cuneiform. In Phalangista (3) and Phascolarctos (2) the insertion is into the internal cuneiform bone; in Macropus (2) the muscle is rudimentary; it is absent in Hypsiprymnus (2); and in the Koala (19) it is inseparably united with the fibular flexor.

Flexor digitorum fibularis is the most powerful of this group of muscles. On its deep surface it is hollowed out for the reception of the fibula and on its inner aspect for the tibialis posticus. The fibres take origin from the head and posterior surface of the shaft of the fibula, from the fascia covering the pronator tibiæ, and from the intermuscular septum between it and the peroneus longus. The muscular fibres can be traced downwards on the tendon of insertion as far as the ankle-joint, beyond which the tendon passes into the sole along a special groove between the lower ends of the tibia and fibula, then traverses a second groove between the astragalus and the fibula, and is finally attached to the posterior end of the well-marked triangular-shaped sesamoid bone, situated in the middle of the sole, corresponding to the sesamoid bone in the hand which receives the various segments of the flexor longus digitorum. From the distal extremity of the plantar sesamoid bone, which is slightly bifid, four slender tendons pass forwards to the four inner toes, being enclosed in strong fibrous sheaths as far as their terminations. In one limb we dissected, the tendon to the fourth toe gave off a tendon to the fifth toe; but as this was not found in any other of our dissections, it would not seem to be the usual arrangement. All the tendons are inserted into the terminal phalanges in the usual manner. There are no lumbricals.

In connection with the plantar sesamoid bone, which as far as we know has not been recorded in any other marsupial, it is interesting to find that in some edentates there is a very similar arrangement. Windle and Parsons (18) state that in "the Dasypodidæ the tibial and fibular flexors unite in the lower part of the leg, and are inserted into a very large sesamoid bone in the sole of the foot, which is held in place by a fibrous band from the calcaneum, the equivalent of the accessorius. From the front of the sesamoid bone five tendons pass to the terminal phalanges of the five digits. In Chlamydophorus the sesamoid bone was replaced by a cartilaginous nodule." In Tolypeutes, also, according to Leche (2), the tendon of the flexor fibularis contains a sesamoid bone.

It will be noted that in Notoryctes there is only one set of long flexor tendons in the sole; whereas in the Koala (19), Trichosurus, Cuscus (3), and many other marsupials, there is an arrangement of perforating and perforated tendons such as is found in other mammals.

Tibialis posticus.—This muscle is usually feebly developed in marsupials, but in Notoryctes it is almost as large as the tibial flexor. It lies in a hollow situated in the upper part of the leg parallel with the upper part of the fibular flexor. It arises by two heads, internally from the fascia over the pronator tibiæ and externally from the shaft of the fibula for the upper third or fourth of its extent. It soon terminates in a long, narrow tendon which passes down behind the internal malleolus, crossing obliquely beneath the tibial flexor, and is inserted into a small elevation on the scaphoid bone. As it passes behind the inner ankle it lies in the same compartment of the internal annular ligament as the tendon of the flexor tibialis.

The tibialis posticus is double, according to Young (19), in the Koala, both parts having a fibular origin. One is inserted into the scaphoid, the other into the entocuneiform and the sesamoid at the base of the hallux. In Cuscus, also, Cunningham (3) describes two parts, both inserted into the scaphoid. In Phalangista vulpina (19) the muscle is single, but terminates in two tendons. It is single, as in Notoryctes, in Trichosurus, Didelphys (19), Dasyurus (19), and Thylacinus (3). In Hypsiprymnus (2) it is absent.

According to Windle and Parsons (18), the muscle is double in a large number of the edentates, the more external being inserted into the navicular or entocuneiform bone, whilst the other is often larger and passes to the tibial ossicle on the inner side of the foot.

Popliteus and pronator tibiæ.—The popliteus has hitherto been regarded by most writers as a derivative from a sheet of muscle which lies between the tibia and fibula, and which is known as the pronator tibiæ or peroneo-tibialis.

Recently, however, Messrs Bonney and Taylor (1) have shown, in a paper submitted by them as a thesis and now ready for publication, that the popliteus belongs to the same stratum as the flexor tibialis and flexor fibularis, and that it is a differentiated part of the muscle sheet from which these two flexors are derived. The pronator tibiæ is a separate and distinct interosseous muscle which constitutes the third or deepest muscular stratum of the leg. In their opinion both the popliteus and the pronator tibiæ are present as distinct muscles in the generalised form, and in a large number of mammals which they dissected this generalised arrangement was met with.

In many mammals, however, either one or other of these muscles is absent. The popliteus is absent in Notoryctes, Cynonycteris collaris (1), and, according to Fürst (6), in Pteropus and Vespertilio. According to Windle and Parsons (18), the edentata are characterised as an order by the large size of the popliteus, whilst the pronator tibiæ is absent. In the insectivora (2) the usual form of popliteus is present, but no pronator tibiæ.

Moreover, it is amongst the lizards, monotremes, and the less specialised members of the marsupialia that both the muscles in question exhibit the primitive arrangement; and Bonney and Taylor find that the rotatory movements between the two bones of the leg, so clearly seen in Lizards, are retained in these animals also. Further, the modification in the disposition of the muscles, which is evident in other mammalian orders, is correlated with absence of rotatory movements between the two bones of the leg.

In Notoryctes the pronator tibiæ alone is present, and stretches as a thin sheet of muscle between the tibia and the fibula. It reaches downwards as far as the lower ends of the bones, and upwards as far as the head of the fibula, where a small interval occurs through which the anterior and posterior compartments of the leg communicate. The fibres arise from the lower two-thirds of the outer surface of the tibia, the higher fibres being more posterior in position, whilst the lowest fibres approach the anterior border of the bone. From this origin the fibres are directed upwards and outwards to be inserted into the antero-internal aspect of the fibula, reaching upwards as high as the head. In Notoryctes no rotatory movements between the tibia and fibula are permissible.

Intrinsic Muscles of the Foot.

In Notoryctes there is an extraordinary reduction in the number of muscles of the region under consideration. Professor Wilson (17), in his description of the muscles of the hand, says: "I know of no other instance among marsupials where modification by suppression of the intrinsic musculature of the hand has gone on to such an extent as in Notoryctes. . . . There can be little doubt that the extreme degree of structural modifications here exhibited is simply the result of a very marked specialisation from functional requirements." We may add that these remarks apply with equal force to the intrinsic musculature of the foot.

Professor Cunningham (3) has already pointed out how highly unsatisfactory the result is, if we contrast the disposition of the intrinsic musculature of the feet of burrowing animals like Echidna, Bathyergus, and the Badger. Instead of there being one common type, as might be expected, the arrangement of the muscles varies considerably in the three species.

In Echidna the only layer well represented is the layer of contrahentes. In Bathyergus the flexores breves alone are developed, whilst in the Badger all three layers are well represented.

The results are just as unsatisfactory if we compare those of Notoryctes with either of the three animals mentioned, for suppression has gone on further in the Mole than in any one of them.

In the insectivorous moles, however, there is, according to Dobson (4), a remarkable conformity of structure as regards the intrinsic muscles of the foot. In all there is a marked diminution in number, so that a comparison of the intrinsic pedal muscles in Notoryctes with those in the true moles shows that there is a very considerable resemblance between them. In both groups the dominant feature is suppression. There are no adductors, and the other layers are but feebly represented. Indeed, in the *manus* of Condyluna, Scalops, Scapanus, and Talpa, all of which are true moles, suppression of the intrinsic muscles is complete. "There were no intrinsic palmar muscles," Dobson records, "in any of the species examined." There can be little doubt that the resemblance between the intrinsic pedal muscles in the marsupial and the insectivorous Moles is the result of similar adaptive requirements.

Four muscles only are present in the pes of Notoryctes. These are—(1) the abductor hallucis, (2) the flexor brevis hallucis, (3) the abductor minimi digiti, and (4) the flexor brevis minimi digiti.

(1) *Abductor hallucis.*—This muscle, though very small, was present in both specimens. It arises from the outer surface and posterior margin of the tibial sesamoid bone, and is inserted into the outer side of the base of the first phalanx.

(2) *Flexor brevis hallucis.*—This muscle lies to the inner side of the preceding, and in one specimen it looked like two parts fused together. It is very rudimentary, and arises deeply in the foot from the tibial sesamoid bone. The fibres are inserted into the inner side of the base of the first phalanx of

the great toe, and a few appear to join with the abductor hallucis, and to be inserted along with it.

(3) *Abductor minimi digiti* was well seen only in one of the limbs we dissected. It arises from the posterior end of the fifth metatarsal bone and from the ligament uniting this with the tibial sesamoid. It runs along the inner side of the metatarsal bone, and is inserted into a tubercle on the first phalanx, apparently dividing into two parts near its termination.

(4) *Flexor brevis minimi digiti.*—The muscle which we believe represents the short flexor of the fifth toe has somewhat anomalous attachments. It arises from the base of the plantar sesamoid bone, and, as it passes to its insertion, it crosses superficially the long tendon of the fourth toe. The muscular belly is somewhat fusiform in appearance, and is attached to the base of the terminal phalanx of the fifth toe.

Therefore, if our interpretation of the muscles in the foot be correct, the usual trilaminar arrangement found in marsupials has been deviated from very markedly. The modifications are, apparently, entirely in the way of suppression, since those which are left fall readily into one or other of the three layers which Professor Cunningham has described. The plantar layer of "contrahentes" is entirely suppressed. The two representatives of the dorsal layer of "abductores" are those of the first and fifth toes, whilst the intermediate layer of "flexores breves" is represented by the short flexors of the same toes.

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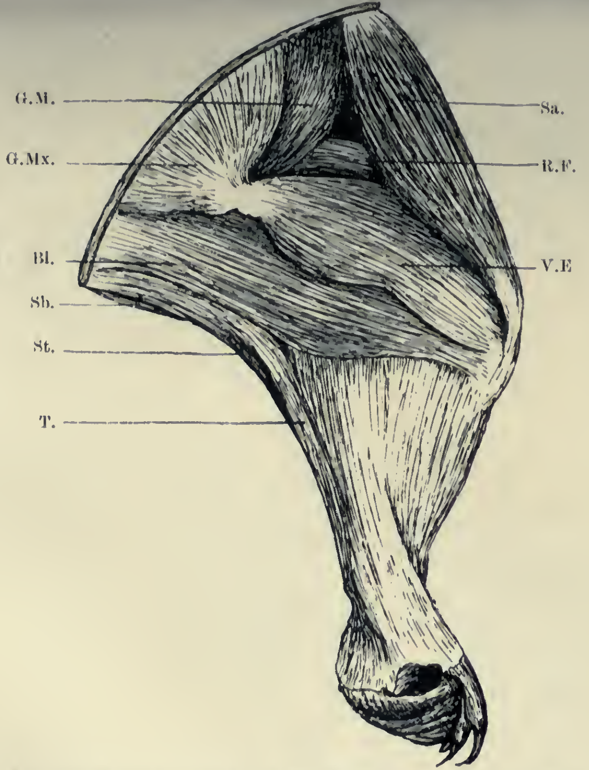

FIG. 1.—Superficial muscles of the gluteal region and the outer aspect of the thigh (×2). Sa., sartorius; R.F., rectus femoris; V.E., vastus externus; T., tenuissimus; St., semitendinosus; Sb., semimembranosus; Bl., biceps; G.Mx., gluteus maximus; G.M., gluteus medius.

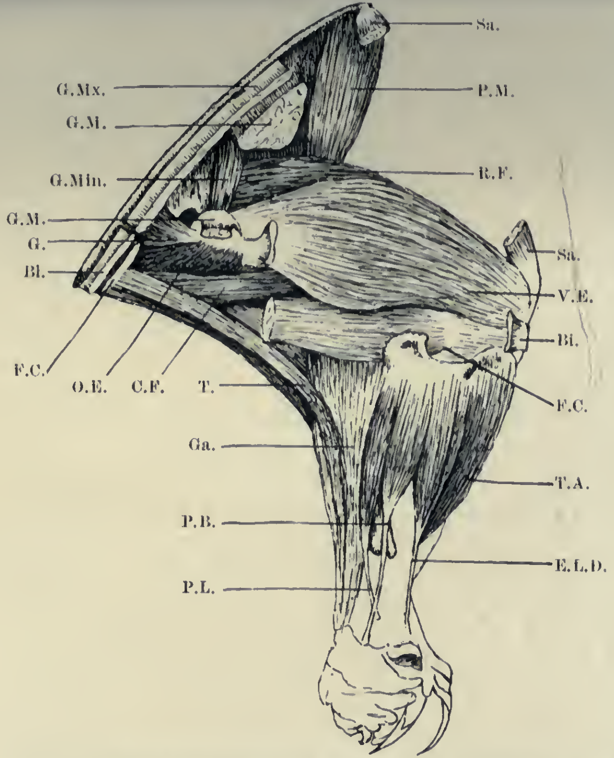

FIG. 2.—Deep muscles of the gluteal region and the outer aspect of the thigh (×2). Some of the superficial muscles of the leg are also shown. Sa., sartorius; P.M., psoas magnus; R.F., rectus femoris; V.E., vastus externus; Bi., biceps; F.C., femoro-coccygeus; T.A., tibialis anticus; E.L.D., extensor longus digitorum; P.L., peroneus longus; P.B., peroneus brevis; Ga., gastrocnemius; T., tenuissimus; C.F., caudo-femoralis; O.E., obturator externus; G., gemelli; G.M., gluteus medius; G.Mx., gluteus maximus; G.Min., gluteus minimus.

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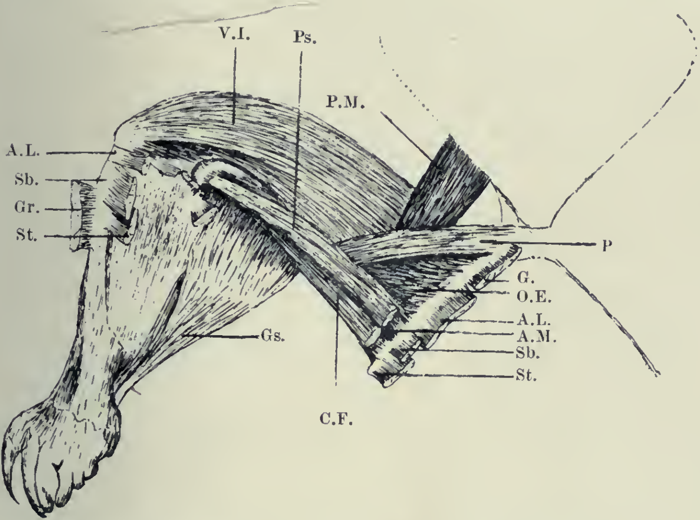
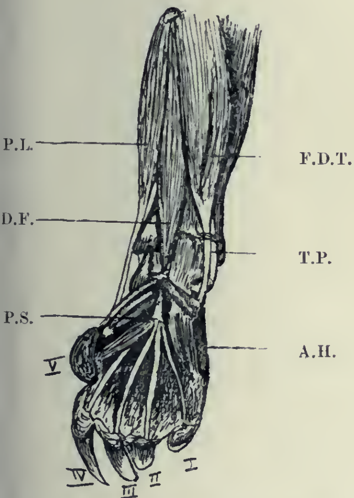


FIG. 3.—Muscles on the front of the thigh (×2). C.F., caudo-femoralis; Sb., semimembranosus; St., semitendinosus; A.M., two parts comprising the deep stratum of the adductor mass; A.L., adductor mass (superficial stratum); O.E., obturator externus; G. gracilis; P., pectineus; P.M., psoas magnus; Ps., presemimembranosus; V.I., vastus internus.



IG. 4.—Muscles of the posterior tibial region and sole of foot (×2). F.D.T., flexor digitorum tibialis; T.P., tibialis posticus; A.H., abductor hallucis; P.S., plantar sesamoid, with four tendons arising from its distal extremity; F.D.F., flexor digitorum fibularis; P.L., peroneus longus.

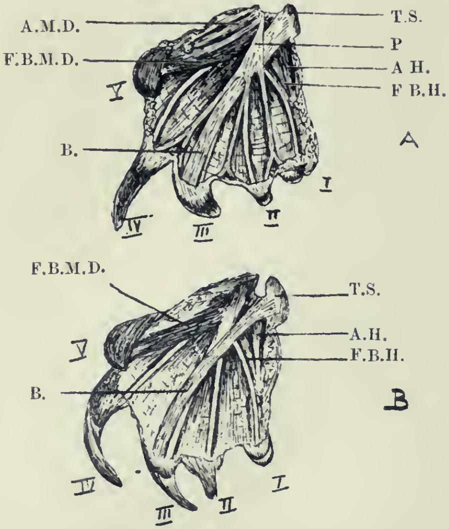


FIG. 5.—Muscles of the sole of the foot in two specimens, A and B, both left side (×2). T.S., tibial sesamoid; P., plantaris; A.H., abductor hallucis; F.B.H., flexor brevis hallucis; B., ligamentous band running from tibial sesamoid to third toe; F.B.M.D., flexor brevis minimi digiti; A.M.D., abductor minimi digiti.

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THE DEVELOPMENT OF THE RETINA IN AMPHIBIA: AN EMBRYOLOGICAL AND CYTOLOGICAL STUDY.

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(Plates XL.–XLII.)

Part II.

CONTENTS.

7. Formation of the Ganglionic Layer.

The layer of ganglionic nuclei is mapped out very early in development by the internal molecular layer, and, as already stated, the neuroblasts which constitute it are those which are first formed by division of the germinal nuclei. It may be again noted that these neuroblast-nuclei are, on the whole, larger than those which lie nearer to the external limiting membrane.

The ganglionic nuclei are at first arranged quite irregularly, usually in two layers (fig. 14), and their axis-cylinders, which become the fibres of the optic nerve, are found to develop very early, and are, indeed, the first processes to be given off by these nuclei. In the central point of the retinal cup the nuclei of this layer become more regularly arranged, so as to form a single layer in this region, by a migration towards the margin of the cup, where the irregular arrangement still holds good. Whenever the ganglionic nuclei become thus arranged in their permanent positions (Pl. XL., fig. 16) they give off their external processes, which enter and arborise within the internal molecular layer. These external processes of the ganglionic nuclei anchor them in position, and it is therefore obvious that their rearrangement so as to form a single layer can only occur previous to the growth of their external processes.

8. Formation of the Internal Nuclear Layer.

This layer when first mapped out consists usually of from three to four layers of closely arranged nuclei. Those which lie next to the internal molecular layer tend to be larger, as a rule, than those lying more externally, and are probably homologous with the amacrine nuclei of the chick's retina. They are the first of the nuclei in this layer to give off processes which enter the internal molecular layer (Pl. XL., fig. 14) and arborise there, and their processes usually extend somewhat more deeply into this layer than those of the more externally placed nuclei. The general rule appears to be, that the further a nucleus of this layer is placed from the internal molecular layer, the later does its process into that layer develop. A large number of the nuclei lying in the outer part of the internal nuclear layer appear, however, to remain for a long time quite free, without possessing by means of processes any attachment to the external or internal molecular layers. On account of this fact, one is often disappointed to find in sections a separation of the internal nuclear layer into an inner portion, consisting of nuclei which are attached by processes to the internal molecular layer, and an outer portion, consisting of these loosely attached nuclei—and that even after great care has been exercised in the preparation of the sections.

Bernard (4) has drawn attention to the fact that many of these externally placed nuclei show evidences of migration through the external molecular layer towards the external nuclear layer. Some of these nuclei may frequently be found imbedded to varying extents in the external molecular layer, an appearance which in many cases suggests the existence of this process of transmigration.

Bernard (4) also describes a migration of nuclei in the internal nuclear layer from the undifferentiated retinal rim towards the more central parts of the cup—noticeable in the early stages of retinal development. According to him, these nuclei have attached to them 'cytoplasmic trailings' which constitute their processes, and successive layers of these become deposited to form the internal and external molecular layers as the nuclei migrate towards the centre of the retinal cup. He considers, then, that the processes of these nuclei are cytoplasmic in nature, which differs from my view that they emerge from the nuclei themselves. This migration of these nuclei would imply a steady progressive increase in the thickness of the internal nuclear layer, concurrently with a corresponding growth of the internal molecular layer, as development proceeds.

My observations on this point go to show that both in the frog and toad, from the 21st day to the commencement of the metamorphosis (figs. 14 to 20), there is a marked increase in the thickness of the internal molecular layer, while during the same period the inner nuclear layer exhibits, if anything, a slight diminution in thickness. This latter result is certainly not due to an extensive migration of these nuclei into the external nuclear layer, for the number of rod- and cone-nuclei remains practically unaltered throughout the tadpole stage (compare figs. 15 and 18). There is thus a slight tendency in the early stages to a migration of the outer nuclei of the internal nuclear layer *towards* the undifferentiated margin of the retinal cup before they extrude their processes, just as has been already shown in the case of the ganglionic nuclei.

On comparing fig. 18 with figs. 19 and 20 it will be at once evident that, during the metamorphosis, and especially in its later stages, there is an enormous increase in the number of nuclei of all the retinal layers, but this increase will be found most marked in the internal nuclear layer. In addition to this there also occurs during the same period a great enlargement of the surface area of the retina, so that the diameter of the eye is much increased. This is difficult to explain as being entirely due to a migration of nuclei from the marginal portion of the cup, for it would imply a previous accumulation of these on a vast scale in that region. The marginal portion of the retinal wall is certainly somewhat thicker than the more central portion, but this is obviously insufficient to account for the enormous increase, both in the surface area and thickness of the retinal wall, which occurs within quite a short period (note the great increase in thickness of the inner retinal wall in figs. 19 and 20—70th and 85th days).

I was, however, much interested at having observed nuclei (especially in the internal nuclear layer), during the stage of metamorphosis, possessing a constriction in the middle so as to appear dumbbell-shaped. These nuclei are well seen by means of a one-twelfth oil immersion lens. The three nuclei represented in fig. 23 are taken from the same microscopic field (internal nuclear layer of 56th-day toad-tadpole), and they are represented in their relative positions to one another. One of these has a nucleolus in each segment, and the whole appearance suggests a process of direct division of this nucleus. The one to the right does not possess nucleoli, but it shows a completion of the process of direct division. The one to the left shows a constriction at one margin, and this, no doubt, is the beginning of the process of amitosis. I have also noticed nuclei in the ganglionic layer, and also those nuclei of the external nuclear layer nearest to the external molecular layer, which showed this appearance—an observation which proves that direct division occurs in the case of the nuclei of these layers as well. I have, however, been unable to detect it in the rod- and cone-nuclei of the external nuclear layer. It is significant to note that these evidences of amitotic division have been observed only at the end of the tadpole-stage and throughout the metamorphosis—the periods during which this great increase in the number of the nuclei of these layers occurs.

This observation is strengthened by noting the size of the nuclei of these layers throughout the whole period of development. Two distinct phases in the process of diminution can be seen to occur. Firstly, in the tadpole-condition there is a rapid rate of diminution in the size of the nuclei during the early stages (figs. 14 to 16), and a much slower rate of diminution during the later stages (figs. 16 to 18). The second phase takes place during the stage of metamorphosis. This is especially evident in the internal nuclear layer, and it is here that the process of amitotic division is most active (compare fig. 18 with fig. 20). The first phase in the diminution of the nuclei is entirely due to the giving off of processes, the number of the former remaining unaltered; while the second phase is due in great measure to amitotic division, their number being therefore increased.

Bernard[1] states that he has observed evidences of 'fragmentation' of these nuclei, and he also refers to figures in a paper by Borysiekiewitz[2] in which that observer represents 'twin ganglion-cells.' I regret, however, that I have been unable to consult this latter memoir.

This observation regarding direct division appears to me to have a twofold interest. In the first place, it controverts the opinion which is generally held that mitotic or karyokinetic division is practically universal throughout the animal kingdom.[3] It is, in the second place, important to note that in the early stages of retinal development all the nuclei are formed by karyokinetic division of the germinal nuclei. During the tadpole stage karyokinetic division ceases to occur in those portions of the retina the nuclei of which have become actively functioning, and it would appear as if it were impossible for such nuclei to again undergo karyokinetic division, and hence they multiply in number by direct division. It would thus seem that this alteration in the method of division exhibited by these nuclei is probably a result of the process of transition from their embryonic to their more mature condition.

In the latter part of the tadpole stage three varieties of nuclei may be recognised in the internal nuclear layer :—

(1) The largest nuclei are found directly in contact with the internal molecular layer, and, as already stated, are probably homologous with the amacrine nuclei of the chick's retina (fig. 18).

(2) Next to the external molecular layer may be seen here and there nuclei having a flattened appearance, with their long axis parallel to the limiting membrane (fig. 18). These are probably homologous with the horizontal nuclei of the chick's retina, for, like the latter, they are closely attached to the external molecular layer.

(3) Between these nuclei the rest of the layer is filled up with the bipolar nuclei, which give off external processes into the external molecular layer and internal processes into the internal molecular layer.

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[1] *Quart. Jour. Micr. Sci.*, vol. xlvi. pt. i. p. 30.

[2] *Untersuch. über den feineren Bau der Netzhaut*, 1887.

[3] Quain's *Anatomy*, vol. i. pt. ii. p. 183.

9. The External Nuclear Layer.

The nuclei of the external nuclear layer are those which are last formed by the division of the germinal nuclei, and are on this account to be looked upon as the youngest in the retina, just as the ganglionic nuclei are the oldest.

When this layer becomes marked off by the external molecular layer it consists of two rows of nuclei, but by far the largest number of the latter are to be found next to the external limiting membrane; and as the rod- and cone-nuclei become differentiated, it will be observed that the rod-nuclei become protruded, to varying extents beyond the external limiting membrane, into the bases of the rods. The rod-nuclei therefore lie further out than the cone-nuclei as a rule (fig. 17), and Bernard[1] also points out this fact in one of his papers.

During the metamorphosis the nuclei of this layer become more numerous (figs. 19 and 20), due to direct division of those nuclei next to the external molecular layer. It is also possible that a migration of nuclei from the internal nuclear into the external nuclear layer takes place as already referred to.

Those portions of the retina which lie towards the margin of the cup do not at first become differentiated into molecular and nuclear layers, but retain the primitive condition, and therefore show myelospongium with spongioblasts, and germinal nuclei lying underneath the external limiting membrane. Growth of the retina thus occurs in this position even after the rods and cones are well advanced in development. The margins of the two molecular layers project into this as yet undifferentiated portion of the retina, and, as its growth advances, their free margins also progress in development, and thus encroach always more and more upon it.

10. Development of the Rods and Cones.

The first evidences of the rods and cones are in the form of minute rounded vesicles, consisting of a clear transparent non-staining substance (fig. 11). These appear immediately underneath the external limiting membrane in the central part of

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[1] *Quart. Jour. Micr. Sci.*, vol. xlvi. pt. i. p. 38.

the convexity of the retinal cup. Each vesicle will, on careful examination, be observed to be interposed between a nucleus of the external nuclear layer and the external limiting membrane, but it soon becomes protruded so as to form a prominent projection beyond the latter structure (fig. 12). These vesicles will be found to be directly attached to the nuclei of the external nuclear layer—an appearance which suggests their origin as protrusions from these nuclei. If this be so, what is the nature of these non-staining globules? A clue to their identity is at once furnished by a study of the yolk-granules with which the inner retinal wall is crowded in the early stages of development, for it will be found that these rapidly become more and more achromatic in their behaviour towards staining agents (more especially iron-alum-hæmatoxylin). This change in their physical properties must also denote a corresponding alteration in their chemical constitution; and after a prolonged study of these structures I have come to the conclusion that this transformation is effected through the agency of an achromatic substance which is secreted from the retinal nuclei. This latter material would thus seem to have a sort of digestive action on the yolk-granules, the resultant globules being composed of a clear fluid substance, which consists of the yolk in solution in the achromatic ferment substance. The appearance illustrated in fig. 21, which represents a nucleus of the external nuclear layer of a 19th-day frog-tadpole, is of great significance in reference to this digestive action, for it shows the presence of three small globules, within two of which the remains of the yolk-granule may still be observed in the form of a small fragment which has not yet undergone the digestive process, and is on that account still freely acted upon by staining agents. It is intended to give in a future communication a more detailed description of this process of transformation of the yolk-granules into these clear homogeneous globules; but in the meanwhile it may be noted that similar globules may be observed in relation to the external poles of most of the nuclei in the inner retinal wall of young frog-tadpoles (*e.g.* at the 15th day). The further behaviour of the retinal nuclei towards these yolk-globules is no less striking, for it is found that the latter become actually ingested by these nuclei at, in the majority of cases, their external poles, which may on this account be termed their 'assimilative poles.' Evidences of this absorptive action are shown, firstly, by an accumulation of deeply-staining chromatic substance within the nuclei near their external poles, with an accompanying diminution in the size of the globules; and secondly, by an increase in the size of the nuclei during the period that this ingestive process is going on, *i.e.* from the 12th to the 21st day. In fig. 22 is represented a nucleus from the inner retinal wall of a 12th-day toad-tadpole, which shows the actual transformation of the achromatic yolk-globule into nuclear chromatic material at its assimilative pole. We are thus supplied with evidence which seems to prove that ingested material is immediately elaborated and stored up within the nucleus as chromatin. This fresh addition of chromatin elements produces a most characteristic appearance of the inner retinal wall at the 15th day, for at this date most of the nuclei show an accumulation of deeply-staining substance towards their external poles. Those globules, however, in relation to the nuclei of the external nuclear layer, do not appear to become ingested, and thus remain under the external limiting membrane as the rudiments of the rod- and cone-elements. As would naturally be expected, these nuclei do not therefore show this aggregation of chromatin towards their external poles.

Whenever these vesicles become protruded beyond the external limiting membrane they grow with such rapidity that in about four days (fig. 15) the volume of their contents is about the same as, or even greater than, the volume of the nuclei from which they arise. The corresponding nuclei also diminish in volume during the same period, but this is not sufficient to account for the great increase in the size of the visual elements. The latter now also begin to stain very deeply with iron-alum-hæmatoxylin, and this is in strong contrast to their previous achromatic nature. The achromatic material can, however, still be seen in the form of a clear globule imbedded in the midst of the deeply-stained substance (fig. 13). The vesicle has, moreover, become much diminished in size, obviously because part of it has blended with the staining material (fig. 13). This new staining reaction must of necessity indicate a great change in the nature of the constituent contents of the visual elements.

Its explanation is found when we examine the pigment-cells, for it will be noticed that their processes develop simultaneously with the rod- and cone-elements; and there must therefore be a sort of attraction, or *positive chemotaxis*,[1] as I would term it, between the two sets of structures (compare figs. 12 and 13). I am of the opinion that this mutual attractive property which is manifested in such a characteristic manner by these two sets of structures is not due to the action of light, for I find that the latter does not begin to assert its influence on the pigment-cell processes until about the 24th or 25th day, owing to the fact that it is apparently rigidly excluded from these by a thick layer of dense pigment with which the whole epidermis of the embryo is loaded; while, on the other hand, the first suggestions of the above-described phenomenon are observable at about the 15th day. What appears to occur is, that the vesicles, after their protrusion beyond the external limiting membrane, become imbedded in the developing processes of the retinal pigment-cells and ingest the pigment, transforming it into the above-mentioned deeply-staining material. This conclusion gains support from the fact that pigment-granules may be observed adhering to the developing rod- and cone-elements. In this relationship it is also important to note that the deeply-staining material of the newly-formed visual elements forms first on the outer side of the vesicle, that is to say, next to the pigment processes (fig. 13, *c*); later on, the staining matter tends to surround the vesicle (fig. 13, *a*); and, still later, part of the vesicle blends with the staining material, leaving only the small globule (fig. 13, *b*). In all probability it is the digesting portion of the vesicle which blends with the visual element, while the non-digesting portion remains to form the globule. It is possible that some of the nuclear chromatin as well may be extruded into the visual element, but this is obviously difficult to demonstrate.

This phenomenon illustrates a very interesting point, for it shows that the achromatic nuclear matrix of the vesicles contains a substance which, in its *nascent* condition at least, has the power of absorbing and digesting the retinal pigment. I say 'nascent condition,' because it is probable that this inherent digestive property is possessed in the most marked degree by this

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[1] 'Chemotaxis' now seems to be preferred in place of the older term 'chemiotaxis.'

nuclear achromatin immediately after it is excreted. We are thus provided with a double proof of the digestive power of this substance, for its action on the yolk-granules has just been alluded to, and we now possess distinct evidences of a similar property with reference to the pigment of the retinal pigment-cells. This nascent nuclear achromatin is thus to be regarded as an *unformed ferment or enzyme*.[1]

Miss Huie (16), at the close of her paper, expresses doubt as to which of the nuclear elements has the digestive action, so that these above observations appear to furnish an answer, and thus tend to throw further light upon the functions of the cell nucleus. In the case of the retina this digestive function must be of a peculiarly selective and potent character, for the pigment which is acted upon is known to resist the influence of ordinary digestive ferments.

11. The First Variety of Visual Element.

About the 23rd or 24th day (fig. 15) two kinds of visual elements become differentiated. The first consists of markedly cone-shaped structures, their basal part being attached to the nucleus, while their apical portion tapers off to a very fine point (fig. 15). Strangely enough, these are the rudiments of the rods, and in their bases the first protruded vesicle still persists as a clear spherical globule, which stands out in marked contrast to the surrounding deeply-stained material.

At this stage of development there also appears in these rod rudiments another structure, of the shape of a biconvex lens, which develops on the distal side of the globule, and contains an achromatic substance; it is on this account sharply marked off from the neighbouring chromatic material. This second structure becomes a very striking object in rods which have been stained with iron-alum-hæmatoxylin, for it is not in the least affected by this stain; while the segments of the rods on its outer and inner aspects stain very deeply, and thus bring it into prominence (fig. 15). Its nature would seem to be the same as that of the spheroidal body from which it is at least

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[1] The question regarding the presence of this enzyme-substance in embryonic tissues will be described at greater length in a future communication.

partly derived, for it appears when the globular body is beginning to disappear. Although, as already stated, it is usually shaped like a section of a biconvex lens, its outer margin may be plane instead of convex. A day or two later a very deeply-stained body appears by its side and abuts against its inner surface (fig. 16). This new body is concavo-convex, the concave surface being in contact with the inner convex surface of the structure previously described. These two objects together constitute the rod-ellipsoid, and they resemble the structures which Schultze[1] has described in the rods of the newt. The iron-alum-hæmatoxylin stain is, to my mind, the most perfect for demonstrating the rod-ellipsoid at this early stage, for by it this is shown to consist of two parts—a non-staining outer part and a deeply-staining inner part. When I first noticed the outer non-staining portion I thought that it might be due to a plane of cleavage at this spot, but on further study it was found to be so remarkably constant in position and in shape throughout the whole period of development that its presence was evidently not due to any mere mechanical effect of cleavage. Planes of cleavage can, however, be seen in those portions of the rods distal to the ellipsoid, but these are irregular, both in position and shape (fig. 17). Although this outer part of the rod-ellipsoid is not due to mechanical cleavage, still the outer segment is apt to separate from the inner segment at this point, which therefore denotes a weakness here.

The remains of the first protruded vesicles are to be seen in the inner segments of the rods until about the 30th day, and instead of being central in position in that segment, are found irregularly placed (fig. 15). The last remnant is frequently visible in the inner deeply-staining portion of the rod-ellipsoid, so that it probably terminates its existence by blending with the outer achromatic portion, or it may pass beyond this and enter the outer rod-segment.

The inner rod-segment at the end of the metamorphosis stains much less deeply, as also does the inner portion of the ellipsoid (fig. 20). This is easily accounted for by the fact that the rod-nucleus still continues to extrude some of its achromatic matrix

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[1] *Archiv für Mikros. Anat.*, Bd. v., 1869.

into the rod; this is especially evident in the toad, where this material is in the form of globular masses in the inner rod-segment, which blend later with the material of the rod (fig. 18). It is important to note here that the diminution in size of the rod- and cone-nuclei occurs not only in the early tadpole stage, but during the whole period of development also. Fig. 17 illustrates this point beautifully, for the nuclei in the central part of the retinal cup are much smaller than those near the cup-margin, which are just beginning to give off their processes. Probably some of this freshly-protruded achromatic nuclear matrix passes also into the outer segment; but it is obviously impossible to demonstrate the passage of this substance through the outer non-staining portion of the ellipsoid. A proof is, however, furnished by the fact that the volume of the inner segment does not increase, for it will be found that the distance of the rod-ellipsoid from the external limiting membrane remains practically the same as it was at its first appearance, while the thickness of this segment of the rod actually tends to diminish somewhat towards the end of the metamorphosis (fig. 20).

In the early stages the rod is, as already stated, distinctly cone-shaped, but after the development of the ellipsoid the outer limb increases markedly in length, while the point becomes very fine in the case of the frog, so that the whole element becomes rather needle-shaped and strikingly elegant in appearance (fig. 17). In the toad-tadpole the rod tends to be thicker and possesses a rather blunted extremity, and altogether looks a much clumsier and coarser structure. This needle-shaped character persists throughout the greater part of the tadpole stage, but at the beginning of the metamorphosis the apex tends to become more blunt and rounded, and the margins more or less parallel to one another. The diameter of the inner limb next to the nucleus also diminishes, so that its margins become parallel, and the characteristic rod-shape is thus produced. The rods have now a striking resemblance to an organ-pipe—the mouth being represented by the clear biconvex portion of the ellipsoid (fig. 19). During the later stages the outer segment is therefore the only part which shows an increase in size, and this is due most certainly to the ingestion of more pigment from the pigment-cells, for it stains as intensely as ever with iron-alum-hæmatoxylin.

The nuclei of the rods tend to become protruded to varying degrees beyond the external limiting membrane (fig. 17), and this is perhaps explained by the close interaction which exists between the rods and their nuclei. The latter are occasionally giving off more and more of their achromatic substance into the rods, and this is probably the cause of the nuclei themselves being drawn into the basal portion of the rods. It is certainly difficult to explain this phenomenon on any other possible grounds.

In concluding this part of the paper it is interesting to note that the rhodopsin-producing function of the rods, which is so characteristic a feature of these elements throughout life, is manifested even in the very earliest stages of their formation; for the substance in the outer rod-segments which stains so deeply with iron-alum-hæmatoxylin is probably rhodopsin, or a body closely allied to it. Kühne,[1] by an elaborate series of experiments, has shown that the retinal pigment-layer in the adult frog is essential for the production of visual purple or rhodopsin; for he finds that if the rods be separated from the pigment-layer, and the rhodopsin be then bleached by exposure to light, it is not regenerated under these circumstances, but, on the other hand, it becomes re-formed if the visual elements be allowed to again come in contact with the pigment-cell layer. Kühne's observations on the relation of the retinal pigment-cells to the rhodopsin-function of the rods in the adult frog thus receive striking confirmation during the embryonic stages. It may be further noted that the developing rods actually owe their growth to the ingestion of this pigment—the rod-nucleus apparently only supplying the necessary material by which this process of ingestion is carried out. It has also been pointed out that these nuclei extrude fresh globules of nascent achromatin at intervals throughout the whole period of development, a fact which seems to indicate that the digestive properties of the first protruded globule tend to become impaired, or even exhausted, and hence the reason for the

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[1] *Untersuchungen aus dem physiolog. Institut der Universität Heidelberg*, 1878–1882.

necessary acquirement of frequent supplies of this substance in order to maintain and preserve the ingestive function of the rods. This characteristic behaviour of these embryonic visual elements is thus simply an index of what occurs during the whole lifetime of the individual, so that the rod and its nucleus in the adult no doubt still preserve the same relationship to one another which they possess in the very earliest stages of development, namely—the nucleus supplies the essential material by which the process of ingestion, and thus the rhodopsin-function, is carried out, while the pigment-cells continue to furnish the supply of pigment which is also necessary for the performance and maintenance of this function. It is of interest at this point to note how certain processes, such as the rhodopsin-function of the retinal rods, which in the adult seem so obscure and difficult of interpretation, become readily understood and appreciated when compared with the corresponding processes which are found to exist in the embryonic condition.

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EXPLANATION OF PLATES XL., XLI., and XLII.

List of Abbreviations.

assim. p.	assimilative pole.
c_1.	first type of cone.
c_2.	second type of cone.
c. n.	cone nucleus.
ex. l. m.	external limiting membrane.
ex. m. l.	external molecular layer.
ex. n. l.	external nuclear layer.

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[1] I was enabled to consult this memoir at Leipzig through the kindness of the late Professor His, and omitted to take a note of its exact title and date of publication at the time.

f. of M.	fibre of Müller.
ga. l.	ganglionic layer.
ga. n.	ganglionic nucleus.
g. n.	germinal nucleus.
i. l. m.	internal limiting membrane.
i. m. l.	internal molecular layer.
i. n. l.	internal nuclear layer.
lens.	crystalline lens.
myel.	myelospongium.
neur.	neuroblast.
r. p. c.	retinal pigment cells.
r.	rod.
r. n.	rod nucleus.
vis. el.	visual elements.

All the figures were drawn with the aid of the *camera lucida* apparatus of Zeiss. For figs. 11, 14, 15, 16, 17, 18, 19, and 20, Zeiss's D lens and No. 3 ocular were employed; and for figs. 12, 13, 21, 22, and 23, Leitz's $\frac{1}{12}$-inch oil immersion lens.

Fig. 11 is a vertical section of the retina of a 15th-day frog-tadpole. The primitive arrangement of myelospongium and neuroblasts is shown, as also the first evidences of the visual elements, which are in the form of small homogeneous globules lying underneath the external limiting membrane. As yet there are no traces of the retinal pigment-cell processes.

Figs. 12 and 13 are intended to illustrate the existence of positive chemotaxis between the developing visual elements and the retinal pigment-cells. In fig. 12, which is from the retina of a 15th-day frog-tadpole, the visual elements are beginning to project beyond the external limiting membrane, and are producing an irregularity in the outline of the pigmented margin of the retinal pigment-cells. In fig. 14, which is from a 21st-day frog-tadpole, the visual elements are projecting well beyond the external limiting membrane, and have caused the pigment-cell processes to become protruded, and are, further, actively engaged in ingesting the pigment. In the specimen lettered (*d*) the nucleus has probably given off a fresh supply of achromatin, seeing that the primary globule has almost disappeared.

Fig. 14 is a vertical section of the retina of a 21st-day frog-tadpole, and shows very well the simultaneous formation of the visual elements and pigment-cell processes. The various retinal layers will be observed to be clearly differentiated at this stage.

Fig. 15 shows a further stage in the development of the visual elements, and a commencing differentiation of these into rods and cones. Some of the rods exhibit evidences of the presence of the rod-ellipsoid. The nuclei of the various layers are now actively engaged in giving off their delicate achromatic processes into the molecular layers. Frog-tadpole at the 25th day.

Fig. 16 is a vertical section of the retina of a 35th-day frog-tadpole. Note in this, firstly, the progressive diminution in the size of the nuclei of the various layers when compared with those in figs. 14

and 15, as described in Part I. of this paper. The visual elements show great strides in growth. The differentiation of these into rods and cones is proceeding apace, and two varieties of the latter may now be recognised (c_1 and c_2).

Fig. 17 is a vertical section of the whole retina of a 35th-day frog-tadpole, drawn to show more especially the external nuclear layer, the visual elements, and the pigment-cell processes. Note how the formation of the latter two sets of structures begins in the central point of the retinal cup and spreads in all directions towards the cup margin, at which place the primitive arrangement of germinal nuclei, myelospongium, etc. exists. Note particularly the progressive diminution in the size of the nuclei of the external nuclear layer as one proceeds from the marginal region towards the centre of the cup. The differentiation of the rods and cones is well marked at the cup-centre, while towards the marginal zone they simply show the primary globular protrusions. The retina from which this figure was drawn was fixed after the animal had been kept in the dark for three hours, and thus shows very clearly the concomitant growth of the visual elements and the pigment-cell processes. Note specially that these two sets of structures cease to exist at exactly the same point.

Fig. 18 represents a vertical section of the retina of a 53rd-day frog-tadpole, and shows a great increase in the size of the rods, which are now beginning to assume the adult appearance. The cones, on the other hand, are practically stationary in growth. Note the striking increase in the thickness of the internal molecular layer.

Fig. 19 is from a 70th-day frog-tadpole (at about the middle of the metamorphosis). Note the growth of the rods. The two types of cone are well seen.

Fig. 20 is from an 85th-day frog-tadpole (at the end of the metamorphosis). Note the increase in the thickness of the nuclear layers and the progressive diminution in the size of their nuclei, which is continued throughout the metamorphosis.

Fig. 21 is a nucleus of the external nuclear layer of a 19th-day frog-tadpole, with the primary visual element in the form of three globules, within two of which the remains of the yolk-granules are seen as minute staining particles. This serves to show the digestive action of the achromatic ferment substance, secreted from these nuclei, on the yolk-granules.

Fig. 22 is a neuroblast from the inner retinal wall of a 12th-day toad-tadpole, and shows the actual transformation of the globule of digested yolk into chromatin elements within the nucleus, this process of ingestion occurring at what I have termed the assimilative pole.

Fig. 23 represents three nuclei from the inner nuclear layer of the retina of a 56th-day toad-tadpole, which show distinct traces of direct division. It would appear that the increase in the number of the nuclei of the various layers which occurs during the metamorphosis, as shown in figs. 19 and 20, is due to this mode of multiplication of these.

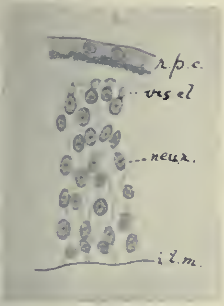

FIG. 11.

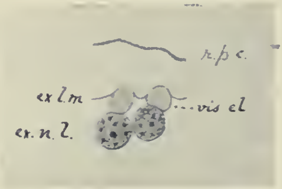

FIG. 12.

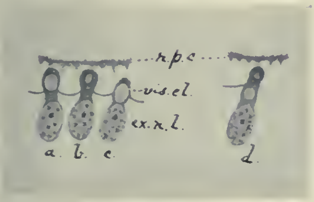

FIG. 13

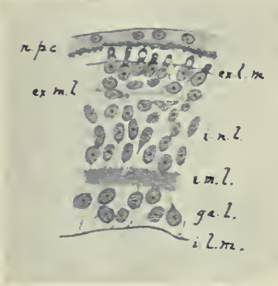

FIG. 14.

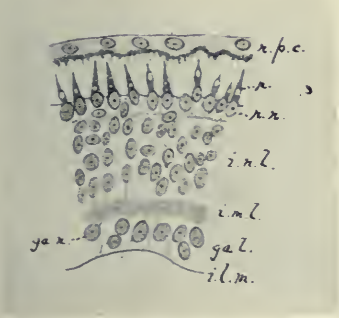

FIG. 15.

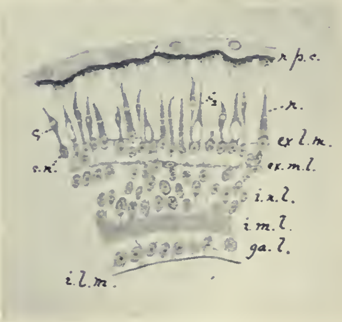

FIG. 16.

Dr JOHN CAMERON on the Development of the Retina in Amphibia.

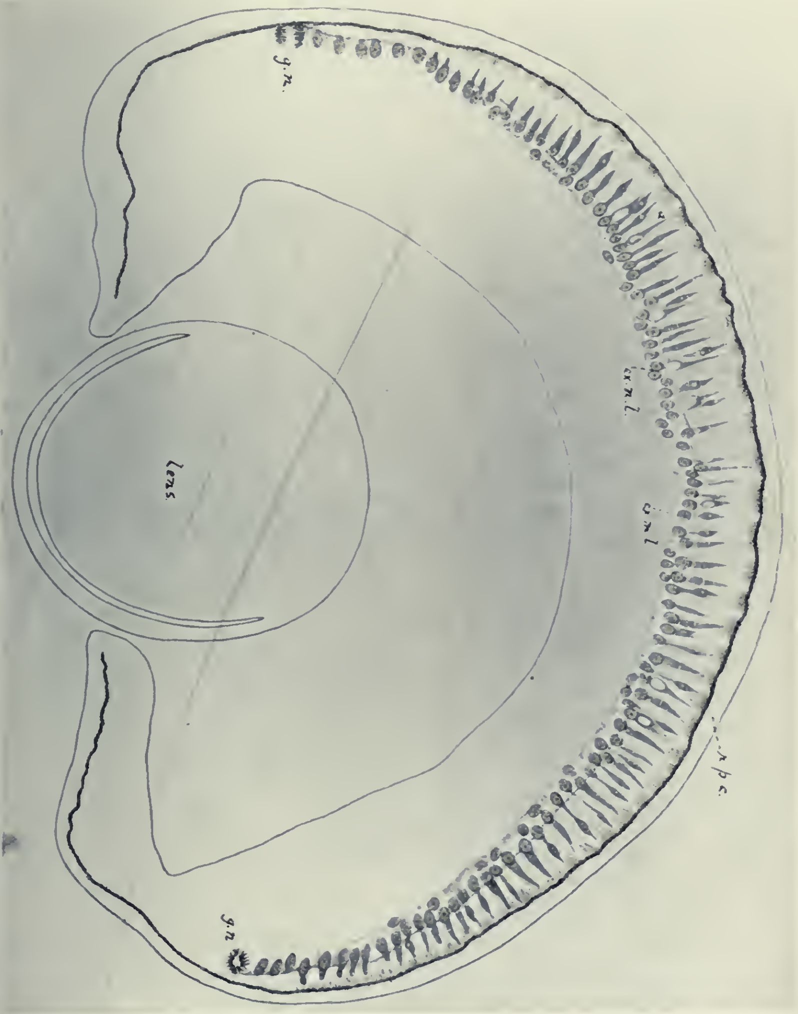

FIG. 17.

Dr JOHN CAMERON on the Development of the Retina in Amphibia.

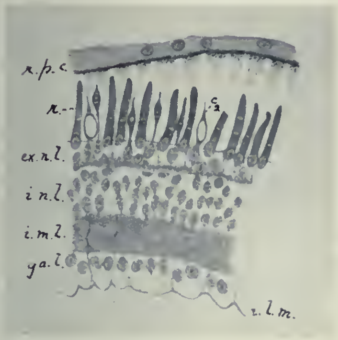

FIG. 18.

FIG. 19.

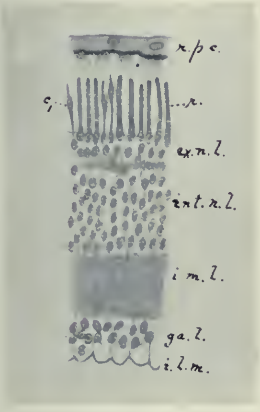

FIG. 20

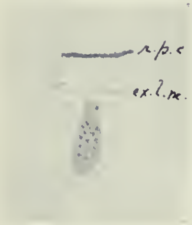

FIG. 21

FIG. 22.

FIG. 23.

Dr JOHN CAMERON on the Development of the Retina in Amphibia.

ANATOMICAL NOTES UPON THE MEMBRANOUS LABYRINTH OF MAN AND OF THE SEAL.

By ALBERT A. GRAY, M.D., F.R.S.E., *Aural Surgeon to the Victoria Infirmary, Glasgow; Pathologist, Glasgow Cancer Hospital.* (PLATES XLIII., XLIV.)

THE mystery which surrounded the internal ear, whether regarded from the point of view of the anatomist or of the physiologist, has in recent years been cleared up to a considerable extent. This is more particularly true of the anatomical aspect of the question, as indeed may be easily understood. There remain, however, some anatomical features which have only recently been described, and to which reference will be made in the following pages.

Perhaps the unsatisfactory character of the anatomical investigations of the inner ear is due to the fact that they have been made either by means of corrosion casts, by fine macroscopic sections, or by fragments obtained by dissection or by microscopic sections. Now, it is quite clear that none of these methods can be entirely satisfactory. Corrosion preparations show the bony cavity, not the membranous structures; fragments obtained by dissection lose their relative position; and microscopic sections, while revealing the finer details, destroy the picture of the whole organ. It is only in fishes in which the labyrinth lies free in the cranial cavity that investigation can be made by the ordinary anatomical methods. The same is partially true of amphibia and reptiles, in which, though the ear is surrounded by bone, yet the latter is for the most part cancellous in nature and easily dissected away mechanically.

In mammals very careful work has been done recently by Denker[1] and Alexander,[2] by means of corrosion preparations, and so far as these animals are concerned there is little more to be done by this method. With the membranous labyrinth the

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[1] *Vergleich. anat. Untersuch. u. d. Gehörorgan, etc.*, Veit and Co., 1899.

[2] *Arbeit. aus d. Anatom. Inst.*, Bd. xix. S. 571.

case is different, for there remains a large field still open. The following notes may be considered to be the beginning of an investigation in that subject. The classical work of Retzius[1] naturally forms the ground-plan upon which all subsequent researches have been built, though the work of earlier anatomists, such as Hyrtl, Hasse, and others, is apt to be forgotten in that of Retzius.

My own investigations naturally began with the human ear, since a knowledge of our own anatomy is to us of more importance than that of any other animal. Furthermore, the specimens were more easily obtained than those of other animals, and my first experiments on modes of preparation were carried out on the temporal bone of human subjects. No attempt will be made to recapitulate the known anatomy of the membranous labyrinth. That subject is quite sufficiently treated in the larger anatomical text-books.

Variations in Dimensions.

As may be understood, the human labyrinth is not of uniform size in different individuals. This is commonly suspected, but hitherto no definite attempt has been made to ascertain the nature and extent of these variations. The subject is not, perhaps, very interesting from the anatomist's point of view; but it must be remembered that, for the purposes of comparison with pathological conditions, it is of great importance that ordinary anatomical variations be known.

With this object in view I examined four specimens taken from individuals of presumably normal hearing power, and not suffering from any affection which could be associated with the labyrinth. The ages varied from thirty to sixty-five, and the individuals were of both sexes.

The accompanying table shows the measurements taken at various parts, and there is no need to recapitulate them. The more important features may, however, be referred to.

It will be seen that variations occur in all parts of the inner ear. In other words, none of the structures have a constant size. Least proportionate variation occurs in the length of the

[1] *Das Gehörorgan d. Wirbelthiere.*

TABLE I.

					Mean.
	mm.	mm.	mm.	mm.	mm.
Extreme length of the labyrinth from the vertex of the posterior canal to the innermost part of the cochlea	17	18	17	17	17·25
Diameter of the lowest whorl of the cochlea at the beginning of the first turn	9·0	8·0	7·5	8·5	8·25
Diameter of the second whorl of the cochlea	4·0	5·0	4·5	5·0	4·625
Diameter of the tube of the cochlea just in front of the round window	2·0	2·0	2·0	2·25	2·06
Diameter of the vestibule just above the oval window	3·25	3·5	3·75	3·5	3·5
Transverse diameter of the superior semicircular canal from limb to limb. Internal	4·0	4·25	4·0	5·0	4·3
Transverse diameter of the superior semicircular canal from limb to limb. External	8·5	8·25	7·5	7·75	8·0
Height of the superior semicircular canal from the vestibule	4·5	4·5	3·75	4·5	4·3
Diameter of the superior semicircular canal itself at the vertex	1·25	1·75	1·0	1·0	1·25
Transverse diameter of the posterior semicircular canal from limb to limb. Internal	4·75	3·75	4·5	3·5	4·02
Transverse diameter of the posterior semicircular canal from limb to limb. External	8·25	7·0	8·5	7·0	7·68
Height of the posterior semicircular canal from the vestibule	4·0	3·5	4·0	4·0	3·87
Diameter of the posterior semicircular itself at the vertex	1·8	2·0	1·5	1·5	1·7
Transverse diameter of the external semicircular canal from limb to limb. Internal	2·5	2·0	2·75	3·0	2·56
Transverse diameter of the external semicircular canal from limb to limb. External	7·0	7·0	6·5	7·0	6·87
Height of external semicircular canal from the vestibule	2·25	2·25	3·0	3·5	2·75
Diameter of the external semicircular canal itself at the vertex	1·55	1·5	1·5	1·25	1·44

whole organ from its outermost point on the vertex of the posterior canal to its innermost point on the lowest whorl of the cochlea. This variation is 1 mm. out of a total of 17·25 mm. The diameter of the cochlear canal is also of very constant size, the variation being within 0·25 mm. Greatest proportionate variation occurs in the internal diameter of the external canal—that is, the space between the limbs measured from concavity to concavity. Here the maximum is 3 mm. and the minimum 2 mm.

It is rather surprising to find that the transverse diameter, measured from limb to limb, is greater in the superior than in the posterior canal. The latter is undoubtedly the longer in most normal subjects, if not all. A careful examination of my specimens, however, showed that the discrepancy was only apparent. The superior canal is in the form of a wide, shallow arch, while the posterior is narrow and long. Owing to the extreme delicacy of the preparations, it was impossible to measure the length of the canals, as may be done on metal-corrosion of the cavity.

Variations in size may occur in one part of the labyrinth alone. Thus a large cochlea may be accompanied by small canals. Even more remarkable is the fact that a large lower whorl may be associated with a small second whorl.

Structural Features.

While my preparations show in general the same disposition of the structures of the labyrinth as that described by previous investigators, there are certain features which have not yet been noted.

The most interesting of these is the existence of an ampulla at the posterior end of the horizontal canal. This structure is shown clearly in Pl. XLIII., fig. 1. The presence of an ampulla in this position has never yet been suspected, owing, of course, to difficulties of preparation, but of the reality of its existence there is obviously no doubt. On first seeing this structure I was inclined to attribute its presence to changes during the preparation of the bone; but further investigation has proved that this explanation is incorrect. In the first place, the ampulla is not present in all cases, even when the method of preparation has been the same. Thus it was only present in four cases out of six which I examined. Its appearance also does not give the impression of an artifact produced by contraction during preparation; it is too rounded and symmetrical.

We are therefore compelled to look upon this accessory ampulla, as I propose to term it, as a real anatomical fact, and to bring it into relationship with what we already know of the labyrinth.

In the first place, we must consider whether the accessory ampulla is to be looked upon as a normal stucture or as an anomaly. Out of six labyrinths examined, it was found in four, that is, in more than 66 per cent. Should further investigations over a larger number of cases give the same percentage, then we will be forced to the conclusion that this accessory ampulla is a normal anatomical structure, and that its absence is to be considered as an anomaly.

A consideration of the comparative anatomy of the labyrinth throws some light on the occurrence of this accessory ampulla. We find that, though there has not yet been described any such structure in any of the mammals, there has been discovered in some of them a fusion of the posterior end of the horizontal canal with the ampullary end of the posterior canal. The animals referred to are the leopard, the horse, the polar bear, the whales and other cetacea. The accessory ampulla may therefore be a vestigial remainder of the condition found normally in these animals. This question also will probably be elucidated by further investigation into the anatomy of the membranous labyrinth of the lower animals.

The function of this ampulla is obscure. It can hardly be supposed to have any direct relation to sensation of any kind, unless possessed of a nerve-supply, and in none of the specimens examined by me was there any trace of such structure. It may therefore be concluded that in man at any rate its function is not sensory. On the other hand, it is quite clear from its shape that this ampulla must have some effect upon the flow or pressure of the endolymph in the canal, and this in its turn must affect to a certain degree the stimulation of the nerve-terminations in the other ampulla. To what extent this may be physiologically perceptible to the individual cannot, of course, be determined.

Calcareous Deposits.—A feature of interest revealed by these preparations is the presence of comparatively large, white, crystalline deposits in various parts of the labyrinth. These also have escaped previous observation, on account of defective methods of preparation. The paraffin used in my method prevents the access of the acid employed in decalcification, and the calcareous deposits finally appear *in situ* after the paraffin is removed.

I have referred to these crystals as calcareous, but one is not really justified in assuming that they are necessarily of that nature. In appearance they certainly do give the impression of being calcareous, and the similarity which they bear to the otoliths of the seal, which will be referred to later, would lead one to the same conclusion. Furthermore, their presence in the internal ear, where carbonate of calcium is undoubtedly found in the shape of the otoliths, is further evidence in the same direction. It would be impossible to ascertain their chemical composition with certainty without destroying the specimens, and this I was unwilling to do.

These presumably calcareous masses vary considerably in size and shape. The largest I have found was at the vertex of the superior semicircular canal: it measured more than one millimetre in length, and completely occluded the lumen of the canal, including the perilymphatic space as well as that of the endolymph. In another specimen two large flat masses lay in the ampulla of the horizontal canal. From such size they may vary downwards until they become invisible. They may be looked upon as otoliths, but appear to be irregular in their distribution; in this respect being unlike those found on the neuro-epithelium of the saccule, the utricle, and occasionally on the cristæ acusticæ of the semicircular canals. I have never found any present in the cochlea, their distribution in this respect being similar to that of the otoliths. They are shown in Pl. XLIII., fig. 2. The ordinary otoliths of the human subject are always very small, and cannot be distinguished by the naked eye. When seen lying in their natural position in the vestibule they give the impression of a very delicate nebula (fig. 1).

These crystalline deposits may be of pathological origin. I have found them in all the cases which I have examined hitherto, that is, in six cases; but it must be remembered that all the specimens were obtained from individuals past the age of thirty, and in most of the cases past the age of forty-five. In fact, they were obtained from patients who had died of malignant disease in some form. Again, the irregular distribution of the crystals in the vestibule and canals suggests a pathological origin, their absence in the cochlea being the only constant feature in their distribution. On the other hand, they do not appear to have had any deleterious effect on the patients' hearing power or faculties of locomotion, nor was there complaint of giddiness, and nystagmus during life was not recorded, though it may not have been looked for.

The important fact to remember, at least from the aurist's point of view, is that these crystalline deposits, whether they be pathological or not, do not necessarily produce disturbances of hearing or equilibrium, at any rate to such an extent as to make their presence felt by the patient.

Before leaving the consideration of the human labyrinth, there is one little point to which I would like to draw attention. The course of the nerve to the ampulla of the posterior canal is usually represented as diverging from the main stem of the auditory nerve at a very obtuse angle. In reality this is not the case, as will be seen from a glance at fig. 1. The nerve turns off almost at right angles to the main stem, and runs for a distance of two millimetres before reaching the ampulla.

The Labyrinth of the Common Seal (*Phoca vitulina*).

Owing to the kindness of my friend Dr D. O. M'Gregor, of the Victoria Infirmary, Glasgow, I had the opportunity of examining and preparing the ear of a seal. The animal had been shot by him at the request of the fishermen whose nets it had been destroying, and he forwarded the bones to me.

In regard to the ear the seal is one of the most interesting of all the mammals, and before going on to describe the labyrinth a reference may be made to the peculiar nature of the mucous membrane lining the bulla of the middle ear. In the year 1899 Denker[1] noted the large size of the bulla of the Greenland seal and the walrus. In a subsequent work[2] he refers to the same feature as occurring in the cetacea, and describes further the remarkable appearance of the mucous lining of the cavity. It is very thick and tough, and is possessed of a very rich supply of veins. Denker looks upon the whole mucous lining as being composed of cavernous tissue into which the blood can be poured to such an extent as to fill up the bulla almost entirely and drive out the air, or act in the reverse order, according to the requirements of the animal. This would enable the creature to rise to the surface with the head uppermost. Bonninghaus,[3] who also investigated the ear of the whale, does not agree with this view, and holds that the large venous spaces

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[1] *Op. cit.*

[2] *Arbeit. aus d. Anat. Instit.*, Bd. xix.

[3] *Arch. f. Ohrnh.*, Bd. lxi. S. 272.

of the bulla are only part of a venous system which is very largely developed throughout the whole animal, in order to accommodate the large amount of blood which is requisite for animals which remain so long under water at a time. I was not aware of this structure at the time when I received the temporal of the seal, and did not therefore make a careful examination of the middle ear, my attention being directed to the labyrinth; but I did notice the thick, tough, parchment-like mucous membrane, and can confirm the observations of Denker and Bonninghaus.

The internal ear of the seal is larger than that of any mammal that has hitherto been examined with the single exception of the walrus, and even here the difference in size is insignificant. The cetacea have a large cochlea, but the extremely small vestibule and canals in these animals give the whole labyrinth smaller dimensions than that of the seal and walrus.

The measurements of the various parts of the labyrinth are given in Table II., and in the adjacent columns are to be found the measurements of that of man and some of those of the porpoise. These will give the reader some idea of the differences in size of the various parts of the organ. The measurements of the porpoise's ear are taken from Denker's work on corrosion preparations. The extremely small size of the vestibule and semicircular canals in the porpoise—and, I may add, the cetacea generally—is in marked contrast to the large development of these parts in the seal. Both these animals live for the most part in the water, and one would expect that they would possess approximately similar organs of equilibration. Instead of this we find that, so far as size is concerned, they are further removed from each other than any other two mammals.

I have no intention of entering into physiological considerations in this paper, and will therefore only remark that, although both animals live in the water, yet the seal makes frequent and sometimes prolonged sojourns on land. This the cetacea never do. Furthermore, the seal breeds on land, while the cetacea breed in the water. This subject will be taken up in a later paper.

The internal auditory meatus, properly speaking, does not exist in the seal. The auditory nerve runs to the posterior

TABLE II.

	Man. mm.	Seal. mm.	Porpoise. mm.
Extreme length of the labyrinth from the vertex of the posterior semicircular canal to the innermost part of the cochlea	17·25	21·0	..
Diameter of the lowest whorl of the cochlea at the beginning of the first turn	8·25	10·0	9·0
Diameter of the second whorl of the cochlea	4·625	6·0	..
Diameter of the tube of the cochlea just in front of the round window	2·06	3·5	2·7
Diameter of the vestibule just above the oval window	3·5	5·5	..
Transverse diameter of the superior semicircular canal from limb to limb. Internal	4·3	7·0	..
Transverse diameter of the superior semicircular canal from limb to limb. External	8·0	10·5	1·3
Height of the superior semicircular canal from the vestibule	4·3	6·0	1·1
Diameter of the superior semicircular canal itself at the vertex	1·25	2·0	..
Transverse diameter of the posterior semicircular canal from limb to limb. Internal	4·02	4·0	..
Transverse diameter of the posterior semicircular canal from limb to limb. External	7·68	9·0	1·4
Height of the posterior semicircular canal from the vestibule	3·87	4·0	1·5
Diameter of the posterior semicircular canal itself at the vertex	1·7	1·75	..
Transverse diameter of the external semicircular canal from limb to limb. Internal	2·56	5·0	..
Transverse diameter of the external semicircular canal from limb to limb. External	6·87	10·0	..
Height of the external semicircular canal from the vestibule	2·75	4·0	..
Diameter of the external semicircular canal itself at the vertex	1·44	2·0	..
Diameter of the aqueduct of the vestibule	..	0·75	..

surface of the petrous bone, and then breaks up into its several branches, which pursue their course through bony channels of their own. But there is no bony canal containing the auditory nerve as a whole. In this respect also I can confirm the statement of Denker. Now, although there is no internal auditory meatus in the seal, there is a dehiscence of the bone on the internal surface of the vestibule, which corresponds in position to the cribiform plate found in other mammals. In other words, the internal surface of the vestibule is not completely invested with bone, but is only separated from the cranial cavity by a membranous diaphragm composed of the dura mater and the lining of the membranous labyrinth. The area of this diaphragm is about a quarter of a square centimetre. The seal is the only animal in which this peculiarity has been described, and it may not be common to all the different species of seal. Denker does not describe it in the ear of the Greenland seal, of which he has given an extremely accurate account. These two animals, the Greenland seal (*Phoca grœenlandica*) and the common seal (*Phoca vitulina*), differ in another respect in the anatomy of the internal ear, which will be referred to later.

In another feature my investigations confirm those of Denker—that is, in the great development of the fossa subarcuata. This cavity does not exist in man at all. It is found in some of the lower animals, but in none is it so largely developed as in the seal. Its opening is formed by the concave margin of the superior semicircular canal, from which region the cavity enlarges outwards in a spherical manner.

Turning to the membranous labyrinth itself, the first feature which strikes the observer, as noted above, is the remarkable size of the organ in all its parts. The accompanying table shows this better than any description, and there is no need to enlarge further upon the subject.

The Cochlea.—The cochlea has two and a half turns, being in this respect similar to that of man. The spiral ascent, however, is greater in the seal, and for this reason the organ has the appearance of a rounder cone than in man. The whorls also are more rounded in section, so that, viewed from the side, they do not stand out so sharply defined from one another as in the human subject. The ligamentum spirale is well developed in the seal, especially in the lower whorl (Pl. XLIV. fig. 3). The aqueduct of the cochlea is quite unlike that of man, being a wide canal with a diameter of 2·5 mm.; this is in agreement with the description by Denker of the same structure in the Greenland seal and the cetacea. It is not seen in fig. 3, as it bulked so largely as to obstruct the view of other parts, and was therefore removed.

The Vestibule.—The large vestibule is roughly quadrilateral in shape, and has eight openings, as in most though not all mammals—five from the semicircular canals, one from the cochlea, and two from the aqueduct of the vestibule. The aqueduct of the vestibule is much wider than in man and most animals, but not nearly so large as the aqueduct of the cochlea. It measures 0·75 mm. in diameter, and is 13 mm. in length from the vestibule to its expansion into the saccus endolymphaticus. The angle at which the aqueduct of the vestibule bifurcates is much less acute than in man; indeed, it is not much less than a right angle. After the union of the two branches the aqueduct passes only slightly upwards for a short distance, and then turns almost directly backwards, the downward curvature as seen in man being hardly noticeable. The oval window is not so elliptical as in man; it is rather nearer in shape to a segment of a circle, or even to a semicircle, the curved portion being the upper margin, while the diameter forms the lower margin.

The Otoliths.—Apart from its size, the most interesting feature about the vestibule is the presence of otoliths of remarkable magnitude. These are shown in Pl. XLIV. fig. 4. They are quite unlike the otoliths of any mammal hitherto recorded, and it is probable that they have some very special physiological significance. They have not been described by any investigators, this being the first notification of their existence. In the one specimen of the seal's ear which I possess there are two of these objects, one immediately behind the opening of the ampullæ of the superior and horizontal canals into the vestibule. This otolith measures about a millimetre in length, and is about half that in breadth. It is slightly concave, the concavity being directed upwards. It is, in fact, very similar in appearance to the otolith of some fishes, but of course much smaller. Its colour is milky white. The second otolith lies two millimetres behind and external to the first, and about one millimetre in front of the opening of the ampulla of the posterior canal into the vestibule. It is half the size of the first, and is quadrilateral in shape. Its colour is not white, as might be expected, but is pale brown.

From this description it will be apparent that in these structures we are reminded of the great development of the otoliths of the fish, and may reasonably assume that their physiological significance is similar. Both animals live in the water, and to that extent the function of equilibration will be required in similar degrees. In regard to these suggestions, however, it should be remembered that in the whale and other cetacea the vestibule is of peculiarly small dimensions (Denker). Whether otoliths are present in these animals or not is not known, as the methods of preparation have hitherto been faulty. When this question has been answered we will be in a better position to discuss the whole problem of the function of the vestibule and semicircular canals in a more confident way than at present. In the meantime I will only venture to prophesy that these structures will be found to possess a function of far deeper significance in animal life than is at present suspected.

The Semicircular Canals.—In keeping with the other portions of the labyrinth, the semicircular canals are of large size. This will be seen from a glance at the table. It will be seen, however, that the various canals do not bear the same proportion to each other as in man and most mammals. Thus, in man the posterior is the longest, while in the seal it is the shortest. The superior canal is very distinctly the longest in the seal.

The shape of the canals also is much more irregular in the seal than in any animal that I have examined. The horizontal canal is in the form of an irregular pentagon, its broadest side being the upper wall of the vestibule (fig. 4). The superior canal is not semicircular, but is represented more accurately by a quadrant of a circle. The posterior most nearly approaches a semicircle, but even it is far from being so regular as we find it in other animals.

In the specimen examined by me the posterior limb of the horizontal canal does not enter the vestibule midway between the two limbs of the posterior canal, but immediately above the ampulla of that canal. Thus the horizontal canal is on the whole on a lower plane than in man and other animals. In this connection reference must be made to the work of Denker on the Greenland seal. In his corrosion preparations this investigator finds that the posterior limb of the horizontal canal is even lower than that just described in the common seal. According to him, the plane of the horizontal canal lies entirely below the lower limb of the posterior canal, and from the plate which he gives it is clear that his description is correct. It is very remarkable, therefore, that two animals so closely related as the Greenland seal and the common seal should thus differ. Indeed, to judge from the plate which shows the labyrinth of the walrus, this animal possesses an internal ear which is more similar to that of the Greenland seal than the latter is to that

FIG. 1.

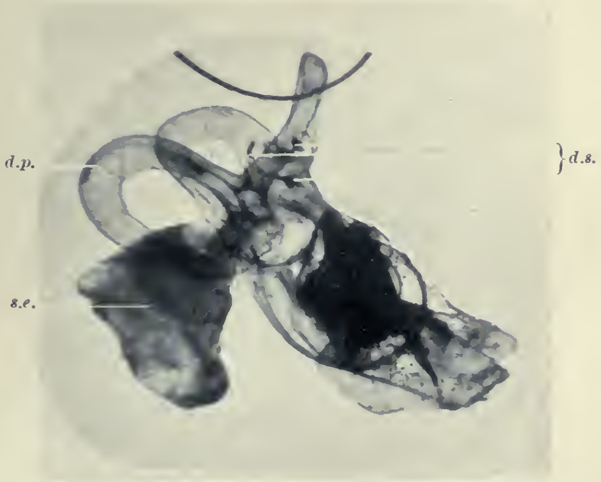

FIG. 2.

DR ALBERT A. GRAY.

FIG. 3.

FIG. 4.

DR ALBERT A. GRAY.

of the common seal. The difference just described should be taken in conjunction with the difference previously referred to as occurring in the vestibule.

DESCRIPTION OF PLATES.

Fig. 1.—Human Membranous Labyrinth.

c.	cochlea.
l.	ligamentum spirale.
n.c	cochlear nerve.
d.	dura mater lining internal meatus.
n.p.	nerve to the ampulla of posterior canal.
n.a.s.	nerve to the ampullæ of superior and horizontal canals.
h.c.	horizontal canal.
s.c.	superior canal.
a.a.h.	accessory ampulla of horizontal canal.
p.	posterior canal.
p.a.	ampulla of posterior canal.
a.v.	aqueduct of the vestibule.

Fig. 2.—Human Membranous Labyrinth.

d.s.	calcareous deposits in ampulla of superior and horizontal canals.
d.p.	calcareous deposit at vertex of posterior canal.
s.e.	saccus endolymphaticus.

Fig. 3.—Membranous Labyrinth of the Seal.

c.	cochlea.
l.	ligamentum spirale.
s.c.	superior canal.
h.c.	horizontal canal.
e.s.	saccus endolymphaticus.
n.s.'	nerve to superior and horizontal canals, cut near bifurcation.
f.o.	oval window.

Fig. 4.—Membranous Labyrinth of the Seal.

o.o.	otoliths.

Obituary Notices.

PROFESSOR AMBROSE BIRMINGHAM.

THE death of Professor Ambrose Birmingham at the early age of forty-one has given rise to feelings of the deepest regret and sorrow amongst his numerous friends. On this side of the Irish Channel the news came unexpectedly; only those who had the privilege of being on terms of close intimacy with him were prepared for the sad termination of so useful and honourable a life.

Birmingham was born in the village of Ballinrobe, Co. Mayo, on the shores of Lough Mask, one of the many picturesque sheets of water of which Ireland can boast. Educated in the first instance by the Christian Brothers, and later at Castleknock College, he early gave evidence of being possessed of abilities of no ordinary kind. Having chosen medicine as his profession, he entered the Catholic University School in Dublin, and after a student career of unusual brilliance, he graduated with first-class honours in the Royal University of Ireland in 1887.

Up to 1879 all the Chairs of Anatomy in Dublin were held by men who were likewise engaged in practice either as surgeons or as physicians. In that year Professor Macalister became Professor of Anatomy in Trinity College on the understanding that he was to devote his whole energies to the duties of his post. In 1883 the Royal College of Surgeons made a similar change in connection with its Chair of Anatomy, and in 1887 the Catholic University School of Medicine followed suit by the appointment of Professor Birmingham. Up to this time Sir Christopher Nixon had been the Professor of Anatomy, and it was he who noted that in Birmingham they had a man of the character and ability required for this position. Prior to taking up his duties as a teacher, Birmingham recognised that it was not only desirable but necessary that he should extend his experience by studying the subject he had been selected to teach in another school. For reasons which will be sufficiently obvious, it was considered undesirable that this should be done in Ireland, and consequently he came to Edinburgh and was specially trained for his new duties by Sir William Turner.

At the time that Birmingham joined the staff of the Catholic University the fortunes of its Medical School were at a very low ebb. It was soon seen, however, that in the new Professor of Anatomy they had secured a man of quite exceptional powers as an organiser and as a teacher. What he did for that school only those who were closely associated with him can fully realise. Not only did he carry on the duties of his own department with consummate success and efficiency, but soon he had in his hands the greater part of the administrative work of the school, and his restless and untiring energy in both of these spheres was not long in making itself felt. He reaped the reward of his labours in living to see a steady increase in the popularity and influence of the school as a centre of medical education in Ireland. In his death the Catholic University has suffered an irreparable loss.

Birmingham possessed in a high degree those qualities which go to make a good teacher. He had an attractive manner, fluency of speech, clearness of thought, and a forcible delivery. Leading such a busy life as an administrator, teacher, and examiner, it was hardly to be expected that he could devote much time to original research, and yet he is the author of a number of excellent papers on various anatomical subjects. A list of the more important of these is added to this sketch, and from this it will be seen that his inclinations lay more towards the topographical than the morphological side of Anatomy. Probably the article which he wrote upon "*The Organs of Digestion*" for the Text-book of Anatomy edited by Professor D. J. Cunningham is his best piece of work. It is questionable if there is any article on the same subject of a corresponding length which can compare with it for clear and accurate description, and in the judgment displayed in the arrangement and selection of the material. The conscientious way which he entered upon this work was characteristic of the man. From first to last it was a piece of research: every fact had to be verified before it was accepted and given a place in his text.

It is now two years since his health broke down. From the first it was known to his intimate friends and also to himself that there was no hope of recovery. To be thus cut asunder from work in which one has placed his whole heart; to have all ambitions suddenly and ruthlessly crushed out, was enough to try the fortitude of the bravest of men. Birmingham met his inevitable fate with remarkable courage and reserve; not a complaint came from his lips. He still did what work he could; he came to the weekly breakfasts of the Zoological Council as bright and cheerful as before. He died in Dublin on the 23rd of January, and those of us who knew him best feel that we have lost not only a true colleague but also a most faithful friend. D. J. C.

List of Published Papers.

In the *Journal of Anatomy and Physiology*.

"Homology and Innervation of Achselbogen and Pectoralis Quartus and the Nature of the Lateral Cutaneous Nerve,"—vol. xxiii.

"Variability in the Level of Attachment of the Lower Limb to the Vertebral Axis,"—vol. xxv.

"Anomaly of the Heart and Great Vessels,"—vol. xxvii.

"The Nerve of Wrisberg,"—vol. xxx.
"Topographical Anatomy of the Spleen, Pancreas, Duodenum, and Kidneys,"—vol. xxxi.
"Shape and Position of the Bladder in the Child,"—vol. xxxii.
"Arrangement of the Muscular Fibres at the Upper End of the Œsophagus,"—vol. xxxiii.
"Arrangement of the Muscular Fibres of the Stomach,"—vol. xxxiii.

In the *Trans. Roy. Acad. of Med., Ireland.*

"Notes on some Nerve Anomalies,"—vol. vi. 1888.
"Nerve Supply of the Sternalis,"—vol. vii. 1889.
"Mastoid Region, with special reference to Operations on the Part,"—vol. viii. 1890.
"Simple Unilateral (sigmoid) Kidney,"—vol. viii. 1890.
"Reports of Collective Investigation in the Anatomical Departments of Trinity College and the Catholic University,"—vol. ix. 1891.
"Spontaneous Enterectomy,"—vol. ix. 1891.
"Anatomy of the Mastoid Region, with Guides for Operating,"—vol. ix. 1891.
"Ossified Transverse Ligament of the Atlas,"—vol. x. 1892.
"Absence of the Ileo-cæcal Valve,"—vol. ix. 1893.
"Muscles of the External Ear,"—vol. xii. 1894.
"Horseshoe Kidney,"—vol. xii. 1894.
"Peculiar Lateral Sinuses,"—vol. xii. 1894.
"Asymmetry of the Sternum,"—vol. xiv. 1896.
"Some Points in the Anatomy of the Digestive System,"—vol. xviii. 1900.
"Peritoneum of the Pelvis" (with Professor Dixon),—vol. xix. 1901.

GEORGE BOND HOWES, born 7th September 1853, died 4th February 1905.

Not among the least sad of the things which fall to the lot of him who loses a dear friend, is often the duty of attempting the vain task of writing some adequate account of the departed one. The eye lends no aid to the faltering hand, and withal a flood of recollections overwhelms the writer. Before me lie two heaps of papers, the one Howes' published memoirs, the other a large pile of his letters, going back twenty years. It is of some of the latter and of the man, now no more, who wrote them, rather than about his original scientific works, that I would in this place put down a few words.

George Bond Howes, the eldest son of the late Thomas Howes, and grandson of the late Captain George A. Bond, H.E.I.C.S., was born in London on 7th September 1853. He was of Huguenot extraction. At the moment there are no particulars available of his earlier years beyond the vague statement that he was "privately educated." His whole scientific career of but thirty years was bound up with the history of the Royal School of Mines, later the Royal College of Science, South Kensington, S.W. Joining the zoological staff in 1874 as private assistant to the Professor, from 1880 to 1885 he was Huxley's chief assistant. In that year, on Huxley's retirement, he succeeded to his zoological duties, becoming full Professor of Zoology on Huxley's death in 1895, barely ten years ago.

He held the honorary degrees of D.Sc. (Vict.) and LL.D. (St Andrews), and he was a Fellow of the Royal Society, London, of the Zoological and Linnæan Societies, and honorary member of many learned societies.

His published papers are not numerous, hardly more than thirty in all, but Howes was not the man to write unless he had something worth recording, and they are of sterling value. Some seven of them appeared in the pages of this *Journal*, most of the others in the *Proceedings of the Zoological Society*, and one, the last and largest, in its *Transactions*.[1] In addition, there are three Presidential Addresses—two, in 1896 and 1897, to the Malacological Society, and one to Section D of the British Association for the Advancement of Science, at Belfast, in 1902. His writings are known to all morphologists and embryologists. In his scientific researches their author was, with a strong leavening of embryology, a representative of the old school of comparative morphologists, to which in this country Huxley, Flower, W. K. Parker, and others belonged. To the science of Embryology he only contributed papers on the Vertebrate Skeleton, the most difficult part of embryology; but, as of other sciences such as Palæontology, he possessed a remarkably minute acquaintance with the researches extant, and he knew well how to employ them in his teachings and in his writings. The pages of *Nature* during the past twenty years contain numerous signed and unsigned articles from his pen.

It is difficult to write about Howes as a scientific investigator and thinker. The reason of this is in part to be sought in the vast gulf between his mental and his bodily organisation. His mental powers were quite remarkable. His brain dominated the rest of his body, which was never that of a man of robust constitution. A few instances of his mental capacity may be given. His two addresses to the Malacological Society were so full of the closest knowledge of all the researches on recent and fossil Mollusca that they astonished some of his friends, who, like myself, had no idea that he possessed any particular interest in this group. A comment upon it elicited the modest remark that he had always had a liking for the Mollusca, yet he never published any work upon them. One of his greatest efforts was his Belfast address in 1902, his last published piece of work. In March of that year he wrote regarding it, "I think there

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[1] Howes, G. B. and Swinnerton, H. H., "On the Development of the Skeleton of the Tuatara, *Sphenodon punctatus*, with Remarks on the Egg, on the Hatching, and on the Hatched Young." *Trans. Zool Soc. Lond.*, vol. xvi. pp. 1–86, with 6 plates and 18 text illustrations.

must be a genius or some mystic force operating between us, for the title you suggest for my address is almost exactly that on which I have decided. I intend to go in for a defence of the comparative morphological method, and to show what it has achieved during recent years. *Limulus* will come in as a means of showing what errors can be possible by failure of appreciation of what is involved in the method." The address was first published without the references to literature, and it is a well-known fact that very few anatomists or zoologists were able, either at Belfast or afterwards, to recall anything like the whole of the researches mentioned. The names and titles were afterwards added, probably largely from his memory, and for those nineteen pages of print they reach the total of 186, all mentioned in the actual address. He used no notes in his lectures, began to speak "as soon as he got inside the door and on his way to the table, and lectured for eighty minutes, or even longer."[1] It was a frequent habit of his in conversation or correspondence to recall some particular piece of research, its author's name, place, volume, and year of publication, and even the page at which a certain passage would be found.

As a friend and companion there was a peculiar charm about him. He was not merely a zoologist, or a man of science, or a professor; his interests and sympathies were wide, embracing many fields of human activity. There is no saying what he might not have done for British science, and for zoology in particular, had he been endowed with greater bodily strength, and had he given less, much less, of his time and energies to various scientific matters other than teaching and research. With Sir George Humphry and Mr B. S. Lockwood, F.R.C.S., he helped to found the British Anatomical Society, and he was the first honorary treasurer, an office which he held for many years. He won the affection and esteem of British anatomists, among other reasons, because they knew that he appreciated the scientific work they were doing far more than any other zoologist or embryologist. Though he never studied medicine, he had dissected the human body, and he could have taught human anatomy as easily as physiology, palæontology or zoology, and comparative morphology. During the past ten years he was examiner in some six or seven universities. At the time of the second and fatal illness he was a Vice-President of the Zoological Society and Secretary of the Linnæan, and for many years he worked very hard for these two societies. Long before Huxley's death they had planned a new and re-written edition of the *Anatomy of Vertebrated Animals*. On the death of his master, the publishers still wished Howes to undertake the book, but this he refused to do, adding, characteristically, that Huxley's book must remain the classic it had become. In August 1895 he wrote, regarding a new edition of Huxley's *Vertebrates*, "I am most emphatically of opinion that it should not be. Years ago Huxley gave me the offer of a joint authorship of it, subject to his health and disposition to work it out. That never came; and

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[1] From statements by one of his pupils.

with his, as with all epoch-marking books, I consider it sinful to touch them. Such works should remain the monuments they are." None the less, he fully intended to write a new *Comparative Anatomy of Vertebrates*, a task for which his vast learning well fitted him. It would, indeed, have been a formidable book!

As he wrote in one of his last letters, not three years ago, latterly he had "a hundred and one scientific matters in hand," and he was ever getting more and more involved in work, demanding more of his time, and adding to his mental worries. Little wonder, then, that the delicate mechanism of his marvellous brain finally could no longer withstand the strain. The first real breakdown happened in July 1896. He was away on holiday in Dorset, and one morning, walking with a friend, he suddenly fell, remaining unconscious for five hours. Attempts were made to persuade him to take leave of absence and visit his zoological friends in Australia and New Zealand. These were in vain; and though thoroughly unfit for work, as he admitted in his letters, he commenced his teaching and other duties in October as usual. He was wont to speak of this attack as "a slight sunstroke," but others took a more serious view. In 1898, and later in June 1900, the date of my last visit to him, he appeared to be anything but well, and, like others, I tried to warn him that he was attempting far too much. His last letter is dated 24th January 1903, and a few days later the second blow fell. He took leave of absence for a year, resigned some of his offices, and went to Italy, and later on to the New Forest and to Torquay, to recruit. For a time he was reported to be gaining strength, and he returned to duty for a brief period from Easter 1904. But the rest had been taken several years too late. He lingered on in a very weak condition of body, but with mind unimpaired, at his residence in Chiswick, so well known to zoologists and anatomists from all parts of the world, and finally, quite unexpectedly, passed away in sleep at 9.30 p.m. on Saturday 4th February 1905, as his sorrowing wife writes, "quite clear, though weak to the last." He leaves a widow and one daughter to mourn his death.

His many friends know too well and feel but too keenly what they have lost in Howes. It is difficult to exaggerate the loss his death means to British science. As another of his friends writes, "I feel with you that we have lost the one man we would dearly have liked to have kept with us. He commanded the respect and love of all who knew him." It was not to be. We who still tarry may cherish the memory and profit by the work and example of one of the best and noblest men who have lived—and died—for science. I cannot more fitly close this feeble sketch of my friend and teacher than by quoting the closing words of his Belfast address, which are so characteristic of him, and which form one of the finest passages, and almost the last, he ever wrote:—

"We live by ideas, we advance by a knowledge of facts, content to discover the meaning of phenomena, since the nature of things will be for ever beyond our grasp."

J. BEARD.

Notices of Books, etc.

Biologische Untersuchungen. Von Professor Dr Gustaf Retzius. Neue Folge xi. mit xxxiii. Tafeln. Gustav Fischer, Jena, 1904.

This is the latest of the series of sumptuous volumes which we owe to Professor Gustaf Retzius of Stockholm. To say that it fully maintains the standard of the volumes which have preceded it, is the highest praise which can be accorded to it. Of the seven articles which it contains, that upon the body-form of the fœtus at different stages of its development is likely to attract the most attention. The illustrations in connection with this article are of singular beauty and most suggestive. Professor Retzius has already given descriptions and photographs of the brains of certain people who have attained celebrity during life. In this volume the brain of a statesman is carefully described and delineated. D. J. C.

The Human Sternum. By Andrew Melville Paterson, M.D., Derby Professor of Anatomy in the University of Liverpool. Williams and Norgate, 1904.

In this handsome monograph are published the three lectures which Professor Paterson delivered at the Royal College of Surgeons of England in November 1903. These contain the fruits of a long and laborious research into a highly complex and difficult problem—the morphology of the sternum. As might be expected from the independent character and originality of the author, the conclusions arrived at are widely different from the generally accepted views on this subject. Professor Paterson denies the costal origin and segmental character of the sternum. He styles the latter view a "nebulous transcendental notion." His contention is that the sternum is to be regarded as a part of the shoulder-girdle apparatus.

D. J. C.

The Edinburgh Stereoscopic Atlas of Anatomy. Edited by David Waterston, M.D., Lecturer and Senior Demonstrator in the Department of Anatomy, University of Edinburgh. T. C. & E. C. Jack, Edinburgh, 1905.

By a prospectus which was very widely circulated last summer, anatomists were prepared for the appearance of this atlas; now the first section of the work has been fairly launched in the form of fifty stereoscopic photographs which give views of the topographical anatomy of the thorax and brain. In looking over these illustrations, what strikes one first is the high quality of the photographs and the excellent way in which they have been reproduced. The dissections chosen for illustration have been selected with much judgment, and the small amount of text which accompanies each photograph is terse and to the point. We have no hesitation in saying that this atlas will prove of service to the student, and will be found of use in Anatomical Departments as an aid to the teacher. It is likely, also, that it will become highly popular amongst those who are engaged in the daily routine of medical and surgical practice. It affords a ready means of refreshing the memory in a graphic and realistic way upon many anatomical points of practical importance which most medical men find it difficult to retain. D. J. C.

Études Biologiques sur les Géants. Par Professor P. E. Launois et Dr Pierre Roy. Masson et Cie., Paris, 1904.

Those who are interested in Giantism and Acromegaly will find in this volume much valuable information on these apparently allied subjects. D. J. C.

Morphology and Anthropology. By W. L. H. Duckworth, M.A. London: C. J. Clay & Sons, 1904.

Before reading a book, it is often well to realise the public to which the author is appealing, and to bear this in mind in estimating its value. In the preface to this work Mr Duckworth suggests that it has been compiled for the students preparing for the Physical Anthropology and Human Anatomy Examination in the Cambridge Natural Science Tripos; and if this is the chief end in view, there is little doubt that the book is too voluminous and too studded with facts, many of which, though they ought to be recorded, lead the student nowhere. But although, from the student's point of view, the 564 pages might be compressed to 250, and more stress laid on general principles, to the exclusion of the patient record of facts which, as far as we can at present see, are of negative value, there can be no doubt that the book as it at present stands will be a most welcome addition to the libraries of all those who, having passed their examination days, are working at mammalian morphology. It is a most able and painstaking record of the work which has hitherto been done in estimating Man's place in Nature, and no reader can fail to be struck with the deep knowledge of recent research which the author displays, or the sympathetic and broad-minded way in which he lays out that work to its best advantage.

The introduction is devoted to a sketch of the past history of Anthropology and the various lines of research; this is followed by a chapter on the application of the methods of Morphology to the classification of the Mammalia, and another on the classification of the Primates. In this chapter (p. 49) the author gives a table showing a series of comparisons between Man, a generalised Primate, and *Galeopithecus volans*; but, from a study of this table, I am left with the impression that Galeopithecus is nearer the generalised Primate type than Man is, for the former differs from the type in seven points, while Man differs in eight. Mr Duckworth says that, "upon such evidence as is provided in the foregoing table, systematists have decided that Man is to be included within the Order Primates, while Galeopithecus is excluded from that order and relegated to the Order Insectivora." Perhaps this is a little hard upon the systematists, but it may be deserved.

The next three chapters are taken up with the general anatomy of the Primates, the brain, skull, and teeth being specially dwelt upon, after which the evidences of Human Embryology are considered, chiefly in relation to simian characteristics. In the next 120 pages the author revels in indices and craniometric and osteometric details which it is most valuable to have recorded and arranged for reference, especially as their advantages and disadvantages are pointed out by so able a critic, but which, I think, might safely be condensed in a student's text-book, especially as the practical result of them is so disappointing.

The chapter on the soft tissues is much more interesting; and in that on the human central nervous system which follows, Mr Duckworth shows the advantage he has derived from being so closely associated with Professor Elliot Smith. The morphological variations of the Hominidæ and the records of Palæontology form the concluding sections of an important and, for the most part, highly interesting book. There are 333 illustrations, most of them of a semidiagrammatic type. The presumption is that the author has deliberately sacrificed artistic quality to quantity, and has inserted a home-made drawing wherever it would help the text. Doubtless it would have been better to have had an equal number of woodcuts prepared by an artist; but if it was a choice between two alternatives, I certainly think that Mr Duckworth chose the right one. F. G. Parsons.

Studies from the Anthropological Laboratory, The Anatomy School, Cambridge. By W. L. H. Duckworth, M.A. London: C. J. Clay & Sons, 1904.

This book contains a series of thirty-six studies or original papers by Mr Duckworth on material in the Cambridge Anatomical Museum. Many of these are reprints of papers which have appeared elsewhere and are well known, but seven are quite new, and contain interesting and useful details. As might be expected, this work contains much of the original material which has been elaborated in the author's *Morphology and Anthropology*.

We are told in the preface that it is hoped that the present volume may be the first of a series dealing with the extremely rich collections contained in the Anatomical Museum at Cambridge This hope will be re-echoed by all anthropologists, and the Cambridge Museum may then boast of a most perfect and exhaustive catalogue. The remarks made on the illustrations of the author's other work apply to this.

F. G. Parsons.

Journal of Anatomy and Physiology.

ON THE ORIGIN OF VERTEBRATES DEDUCED FROM THE STUDY OF AMMOCŒTES.

By Walter H. Gaskell, M.D., LL.D., F.R.S., *University Lecturer on Physiology; Fellow of Trinity Hall, Cambridge.*

Part XII.—The Principles of Embryology.

In a series of papers I have given evidence for the belief that vertebrates arose from primitive arthropod forms, and have shown how it is possible to find in the vertebrate, in the right position without any reversal of surfaces, the homologues of all the invertebrate organs and structures. Bit by bit I have built up the whole story of the origin of vertebrates by the method of comparative anatomy, and have pointed out how absolutely the palæontological evidence is in accordance with my theory; at the very time when vertebrates first made their appearance, the sea was peopled by a dominant arthropod race resembling in a remarkable degree the earliest fish-like forms. The striking resemblance between such forms exists only as long as the dorsal surface of the one is compared to the dorsal surface of the other, and ventral surface to ventral surface; with the reversal of surfaces—such as is postulated in Patten's views—all such comparison disappears. All Patten's recent work[1] on Tremataspis, etc., is in favour of my theory, and dead against his view that vertebrates arose from arthropods which swam on their back, and so the alimentary canal became in position ventral to instead of dorsal to the nervous system.

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[1] "On the Structure and Classification of the Tremataspidæ," *Mem. d. l. Acad. Imp. d. sciences de St Petersburgh*, vol. xiii., 1903; "On the Structure of the Pteraspidæ and Cephalaspidæ," *The American Naturalist*, vol. xxxvii., 1903; "On the Appendages of Tremataspis," *The American Naturalist*, vol. xxxvii., 1903.

The keynote of my theory is the paramount importance of the central nervous system in all evolution; this is the organ which must steadily progress as we rise from lower to higher forms; this is the one organ in the body from which all our comparisons must start. This firm conviction of mine has led in the most natural and simple manner to the discovery of all the striking resemblances between the various vertebrate and arthropod organs as given in this series of papers. It only remains now to offer some suggestion as to the origin of those organs which are not represented in the arthropod but are newly formed in the vertebrate; in other words, to attempt an explanation of the notochord and the vertebrate alimentary canal.

It is impossible with our present palæontological material to discuss the origin of the notochord with the same feeling of security as in the case of those various organs and structures already discussed, where we were enabled to compare them in the two groups both anatomically and histologically. Until we know more of the ventral surface of the Protostracan ancestor, we must leave the sure ground of comparative anatomy and are obliged to fall back on embryology with its fragmentary attempts to recapitulate the phylogenetic history.

In order, then, to attempt to frame any hypothesis upon the origin of the notochord and the vertebrate alimentary canal, it is necessary, as a preliminary, to consider what are the principles of embryology upon which any such hypothesis must be based. It is especially necessary to do this, for I imagine that the main reason why my views and the evidence for them which I have continuously put forward for the last sixteen years, ever since my first publication in 1888,[1] have been passed over in silence, or received at most a curt and contemptuous dismissal as unworthy of serious consideration from many of those who represent morphology and embryology, is because in their minds no amount of striking coincidences in the topography of organs and in the structure of the elements composing those organs can have the slightest weight, if such comparison leads to conclusions contrary to the laws of embryology.

[1] *This Journal*, vol. xxiii. ; *Journ. of Physiology*, vol. x., p. 190.

The determination of kinship by the careful study of comparative anatomy has been in their minds entirely superseded by the study of the embryo.

What, then, are the laws of embryology upon which such weight is laid?

The current laws are based on the homology of the germinal layers in all Metazoa, and state that in all cases after segmentation is finished a blastula is formed, from which there arises a gastrula, formed of an internal layer, the hypoblast, and an external layer, the epiblast; subsequently between these arises a third layer, the mesoblast. These layers are strictly morphological conceptions, and are stated to be absolutely homologous in all cases, so that the hypoblast of one animal must be homologous to the hypoblast of another; in order, therefore, to compare two adult animals for the purpose of finding kinship between them, it is necessary to find whether parts such as the gut, which in both cases have the same function, arise from the same germinal layer in the embryo. We can, in fact, have no certainty of kinship, even although the two animals are built up as far as the adult state is concerned on a remarkably similar plan, unless we can study their respective embryos and find out what parts arise from the hypoblast and what from the epiblast. The homology of the germinal layers constitutes in all cases of disputed relationship the court of final appeal.

Such is the conception, a conception which, to be valid, must be based upon an absolutely clear morphological definition of the formation of the germinal layers, a definition not based on their subsequent history and function, but determined solely by the uniformity of the manner of their origin.

What, then, is a germinal layer? How can we tell it when it first arises? What is the morphological criterion by which hypoblast can be distinguished from epiblast, or mesoblast from either?

This is the question put by Braem,[1] in an admirable series of articles in the *Biologische Centralblatt*, and is one that must be answered by every worker who bases his views of the process of evolution upon embryological investigation. As

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[1] Braem, "Was ist ein Keimblatt," *Biol. Centralblatt*, vol. xv., 1895, pp. 427, 466, and 491.

Braem points out, the germinal layers are definable either from a morphological or physiological standpoint. In the one case they must arise throughout on the same plan, and whatever be their fate in the adult, they must form at an early stage structures strictly homologous in all animals. In the other case the criterion is based on function, and the hypoblast, for instance, is that layer which is found afterwards to form the definitive alimentary canal ; there is no longer any morphological homology; such layers are analogous; they may be, but are not necessarily, homologous. Braem gives a sketch of the history of the views held on the germinal layers, and shows how originally they were a purely physiological conception, and how gradually such conception changed into a morphological one, with the result that what had up to that time been looked upon as analogous structures became strictly homologous, and of fundamental importance in deciding the position of any animal in the whole animal series.

This change of opinion was especially due to the lively imagination of Haeckel, who taught that the germinal layers of all Metazoa must be strictly homologous, because they were all derived from a common ancestral stock represented by a hypothetical animal to which he gave the name Gastræa; an animal which was formed by the simple invagination of a part of the blastula, thus giving rise to the original hypoblast and epiblast, and he taught that throughout the animal kingdom the germinal layers were formed by such an invagination of a part of the blastula to form a simple gastrula.

If further investigation had borne out Haeckel's idea, if therefore the hypoblast was in all cases formed as the invagination of a part of a single-layered blastula, then indeed the dogma of the homology of the germinal layers would be on so firm a foundation that no speculation which ran counter to it could be expected to receive acceptance; but that is just what has not taken place. The formation of the gastrula by simple invagination of the single-layered blastula is the exception, not the rule, and, as pointed out by Braem, is significantly absent in the earliest Metazoa, in those very places where on the Gastræa theory it ought to be most conspicuous.

Braem discusses the question most ably, and shows again and again that in every case the true criterion upon which it is decided whether certain cells are hypoblastic or not is not a morphological one but a physiological one. The decision does not rest upon the answer to the question—Are these cells in reality the invaginated cells of a single-celled blastula? but, Do these cells ultimately form the definitive alimentary canal? The decision is always based on the function of the cells, not on their morphological position. Not only in Braem's paper, but elsewhere, we see that in recent years the physiological criterion is becoming more and more accepted by morphologists. Thus Graham Kerr,[1] in his paper on the development of Lepidosiren, says:

> "It seems to me quite impossible to define a layer as hypoblastic except by asking one or other of the two questions: (1) Does it form the lining of an archenteric cavity? and (2) Does it become a certain part of the definitive epithelial lining of the gut?"

The appearance of Braem's paper was followed by a criticism from the pen of Samassa,[2] who agrees largely with Braem, but thinks that he presses the physiological argument too far. He considers that morphological laws must exist for the individual development as well as for the phylogenetic, and finishes his article with the following sentence, a sentence in which it appears to me he expresses what is fast becoming the prevailing view:—

> "Mit dem Satz, den man mitunter lesen kann: 'es muss doch auch für die Ontogenie allgemeine Gesetze geben' kann leicht Missbrauch getrieben werden; diese allgemeinen Gesetze giebt es wohl, aber sie liegen nicht auf flacher Hand und bis zu ihrer Erkenntnis hat es noch gute Wege; das eine kann man aber wohl heute schon sagen, die Keimblätterlehre gehört zu diesen allgemeinen Gesetzen nicht."

I conclude, then, that we ought to go back before the time of Haeckel and ask ourselves seriously the question:—when we lay stress on the germinal layers and speak of this or that organ arising from this or that germinal layer—are we thereby adding anything to the knowledge that we already possess from

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[1] *Q. J. Micro. Science*, vol. xlv., p. 29.

[2] "Bemerkungen über die methode der Vergleichenden Entwicklungschichte, *Biol. Centralbl.*, vol. xviii., 1898, pp. 642 and 657.

the study of the anatomy and physiology of the adult body? If by hypoblast we only mean the internal surface or alimentary canal and its glands, etc., and by epiblast we mean the external surface or skin and its glands, etc., while mesoblast indicates the middle structures between the other two, then I fail to see what advantages we obtain by using Greek terms to express in the embryo what we express in English in the adult.

In my original paper,[1] written in 1888, I said with respect to my views of the origin of vertebrates—

> "So also I have not touched upon the embryological difficulties which apparently stand in the way of the acceptance of this view of mine; for I consider that their discussion ought to come, and will come best, after some conclusion upon the ancestor of the vertebrate has been arrived at upon anatomical, physiological, and phylogenetic grounds, and by that time, if we may judge from the change of opinion which is now going on, the embryological standpoint will have changed so much that perchance many of the present difficulties will be found to have vanished."

The time of which I then spoke has now come, and my prophecy does not seem to have been far wrong. If, as Samassa says, we can say with certainty to-day that the germ layer theory does not represent one of the universal laws of morphology, then we must seek for something else, for something which is universally applicable. What that something else may ultimately prove to be is impossible to predict; here I would like to state in a few words how the problem to be solved strikes one who has been accustomed to look on the evolution of the animal kingdom from the point of view of Anatomy and Physiology rather than from that of Embryology.

The study of the development of any animal can be treated in two ways: either we can trace back from the adult to the very beginning in the ovum, or we can trace forward from the fertilised egg to the adult. Both methods ought to lead to the same result; the difference is, that in the first case we are passing from the more known to the less known, and are expressing the unknown in terms of the known. In the second case we are passing from the less known to the more known, and are expressing the known in speculative terms, invented to

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[1] *Journal of Physiol.*, vol. vii., p. 205.

explain the unknown. What has just been said with respect to the germinal layers means that, however much we may study the embryo, and try to express the adult in terms of it, we finally come back to the first way of looking at the question, and, starting with the adult, trace the continuity of function down to the first formation of cells having a separate function.

Let us, then, apply this throughout, and see what are the logical results of tracing back the various organs and tissues from the adult to the embryo.

The adult body is built up of different kinds of tissues, which fall naturally from the standpoint of physiology into groups. Such groups are, in the first place:

1. All those tissues which are connected with the central nervous system, including in that group the nervous system itself.
2. All those tissues which have no connection with the nervous system.

In the second group the physiologist places all germinal cells, all blood and lymph corpuscles, all plasma cells and connective tissue and its derivatives—in fact, all free living cells, whether in a free state or in a quiescent, so to speak encysted, condition, such as is found in connective tissue.

In the first group the physiologist recognises that the central nervous system is connected with all muscular tissues, whether striped or unstriped, somatic or splanchnic, and that such connection is of an intimate character. Further, all epithelial cells, either of the outer or inner surfaces, whether forming special sense organs and glands, such as the digestive and sweat glands, or not, are connected with the nervous system.

Besides these structures, there is another set of organs about which we cannot speak definitely at present, which must be considered separately—all the cells, together with their derived organs, which line the body spaces. Whatever may be the ultimate decision as to this group of cells, it must fall into one or other of the two main groups.

The members of these two groups are so interwoven with one another that either, if taken alone, would still give the form of the body, so that, in a certain sense, we can speak of the body as formed of two syncytia, separate from each other, but interlaced, of which the one forms a continuous whole by means of cells connected together by a fluid medium or by solid threads formed in such fluid medium, while the other does not form a syncytium in the sense that any cell of one kind may be connected with any cell of another kind, but a syncytium of which all the different elements are connected together only through the medium of the nervous system.

If we choose to speak of the body as made up of two syncytia in this way, we must at the same time recognise the fundamental difference in character between them. In the one case the elements are connected together only by what may be called non-living material; there is no direct metabolic activity caused by the action of one cell over a more distant cell in consequence of such connection, it is not a true syncytium; in the second case there is a living connection, the metabolism of one part is directly influenced by the activity of another, the whole utility of the system depends upon such functional connection.

The tissues composing this second syncytium may be spoken of as the master tissues of the body, and we may express this conception of the building up of the body of the higher Metazoa by saying that it is composed of a syncytial host formed of the master tissues, which contains within its meshes a system of free living cells, none of which have any connection with the nervous system. This syncytial host is in the adult composed of a number of double elements, a nerve cell element and an epithelial element, such as muscle cell, gland cell, etc., connected together by nerves; and if such connection is always present as we pass from the adult to the embryo, if there is no time when, for example, the neural element exists alone free from the muscle cell, no time when the two can be seen to come together and join, then it follows that when the single-layered blastula stage is reached, muscle cell and nerve cell must have fused together to form a neuro-muscular cell. Similarly with all the other neuro-epithelial organs; however far apart their two components may be in the adult, they must come together and fuse in the embryo to form a neuro-epithelial element.

The close connection between muscle and nerve which has always been recognised by physiologists, together with the origin of muscle from a myo-epithelial cell in Hydra and other Cœlenterates, led the older physiologists to accept thoroughly Hensen's views of the neuro-epithelial origin of all tissues connected with the central nervous system. Of late years this conception has been largely given up owing to the statement of His that the nervous system arises from a number of neuroblasts, which are entirely separate cells, and have at first no connection with muscle cells or any peripheral epithelial cells, but subsequently, by the outgrowing of an axial fibre, find their way to the muscle, etc., and connect with it. I do not think that His' statement by itself would have induced any physiologist to give up the conception of the intimate connection of muscle and nerve, if the work of Golgi, Ramon y Cahal and others had not brought into prominence the neurone theory, *i.e.* that each element of the central nervous system is an independent element, without real connection with any other element, capable of influencing other cells by contact only. These two statements, emanating as they did from embryological and anatomical studies respectively, have done much to put into the background Hensen's conceptions of the syncytial nature of the motor, neural and sensory elements, which make up the master tissues of the body, and have led to the view that all the elements of the body are alike, in so far as they are formed of separate cells each leading an independent existence, without any real intimate connection with each other.

The further progress of investigation is, it seems to me, bringing us back to the older conception, for not only has the neuroblast theory proved very difficult for physiologists to accept, but also Graham Kerr,[1] in his latest papers on the development of Lepidosiren, has shown that there is continuity between the nerve cell and the muscle cell from the very first separation of the two sets of elements; in fact, Hensen is right and His wrong in their respective interpretation of the earliest stages of the connection between muscle and nerve. So also, it seems to me, the intimate connection

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[1] "On Some Points in the Early Development of Motor Nerve Trunks and Myotomes in Lepidosiren Paradoxa," *Trans. Roy. Soc. Edin.*, vol. xli., p. 119, 1904.

between the metabolism of the gland cell, as seen in the submaxillary gland, and the integrity of its nervous connection implies that the connection between nerve cell and gland cell is of the same order as that between nerve cell and muscle cell. Graham Kerr also states in his paper that from the very commencement there is, he believes, continuity between nerve cell and epithelial cell, but so far he has not obtained sufficiently clear evidence on this point.

Further, according to the researches of Anderson,[1] the cells of the superior cervical ganglion in a new-born animal will continue to grow healthily as long as they remain connected with the periphery, even though entirely separated from the central nervous system by section of the cervical sympathetic nerve, and conversely, when separated from the periphery, will atrophy, even though still connected with the central nervous system.

So also on the sensory side Anderson has shown that the ganglion cells of the posterior root ganglion will grow and remain healthy after separation of the posterior roots in a new-born animal, but will atrophy if the peripheral nerve is cut, even though they are still in connection with the central nervous system.

Further, although section of a posterior root in the new-born animal does not affect the development of the nerve cells in the spinal ganglion, and of the nerve fibres connecting the posterior root ganglion with the periphery, it does hinder the development of that part of the posterior root connected with the spinal ganglion.

These experiments of Anderson are of enormous importance, and force us, it seems to me, to the same conclusion as that to which he has already arrived. His words are (p. 511):

> "I suggest, therefore, that the section of peripheral nerves checked the development of motor and sensory neurones, not because it blocked the passage of efferent impulses in the first case and the reception of stimuli from the periphery in the second, but for the same reason in both cases, viz., that the lesion disturbed the chemico-physical equilibrium of an anatomically continuous (neuro-muscular or neuro-epithelial) chain of cells, by separating the non-nervous from

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[1] "The Nature of the Lesions which hinder the Development of Nerve Cells and their Processes," *Journ. of Physiol.*, 1902, vol. xxviii., p. 499.

> the nervous, and that the changes occurring in denervated muscle, which I shall describe later (and possibly those in denervated skin), are in part due to the reciprocal chemico-physical disturbance effected in these tissues by their separation from the nervous tissues; also that the section of the posterior roots checked the development of those portions of them still attached to the spinal ganglia, because the chemico-physical equilibrium in those processes is maintained not only by the spinal ganglion cells, but also by intra-spinal cells with which these processes are anatomically continuous."

What is seen so strikingly in the new-born animal can be seen also in the adult, and in Anderson's paper references are given to the papers of Lugaro and others which lead to the same conclusion.

These experiments seem to me distinctly to prove that the connection between the elements of the peripheral organ and the proximate neurone is more than one of contact.

We can, however, go further than this, for, apart from the observations of Apathy, there is direct physiological evidence that the vitality of other neurones besides the terminal neurones is dependent upon their connection with the peripheral organ, even though their only connection with the periphery is by way of the terminal neurone. Thus, as is seen from Anderson's experiments,[1] section of the cervical sympathetic nerve in a very young animal causes atrophy of many of the cells in the corresponding intermedio-lateral tract, cells which I supposed gave origin to all the vaso-constrictor, pilomotor, and sweat gland nerves. A still more striking experiment given by Anderson is the effect of the removal of the periphery upon the medullation of those efferent fibres which arise from these same spinal cells, for, as he has shown, section of the nerves from the superior cervical ganglion to the periphery in a very young animal delays the medullation in the fibres of the cervical sympathetic—that is, in præganglionic fibres which are not directly connected with the periphery but with the terminal neurones in the superior cervical ganglion. So also on the afferent side a sufficiently extensive removal of sensory field will cause atrophy of the cells of Clark's column, so that, just as in the case of the primary neurones, the secondary neurones

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[1] *Op. cit.*, p. 506.

show by their degenerative changes the importance of their connection with the peripheral organs.

In this way I can conceive the formation of a series of both efferent and afferent relays in the nervous system by proliferation of the original neural moiety of the neuro-epithelial elements, every one of which is dependent upon its connection with the peripheral epithelial elements for its due vitality, the whole system being a scheme for co-ordination of a larger and larger number of peripheral elements. Thus the cells of the vasomotor centre are in connection with the whole system of segmental vaso-constrictor centres in the lateral horns of the thoracic region of the cord, so that to cause atrophy of these cells a very extensive removal of the vascular system would be required. Each of the segmental centres in the cord supplies a number of sympathetic segments, the connection with all of which would have to be cut in order to ensure complete removal of the connection of each of its cells with the periphery, and finally each of the cells in the sympathetic ganglia supplies a number of peripheral elements, all of which must be removed to ensure complete severance.

Thus, if we take any arbitrary number such as 4 to represent the number of peripheral organ elements with which each terminal neurone is connected, and suppose that each neurone has proliferated into sets of 4, then a cell of the third order such as the vasomotor centre would require the removal of 64 peripheral elements to cause its complete separation from the periphery, one of the second order thoracic lateral horn cell 16 elements, one of the first order sympathetic ganglion 4 elements.

Such intimate inter-relationship between the neurones, both afferent and efferent, and their corresponding peripheral organs does not imply that all nerve cells are necessarily as closely dependent upon some connection with the periphery, for just as the proliferation of epithelial or muscle cells forms an epithelial or muscular sheet, the elements of which are so loosely, if at all, connected together that their metabolism is in no way dependent upon such connection, so also a similar proliferation of the neural elements may form connections between nerve cell and nerve cell of the same loose connection.

It is this kind of proliferation which, to my mind, would bind together the separate relays of efferent and afferent neurones, and so give origin to reflex actions at different levels. Such neurones would not be in the direct chain of either the afferent or efferent neurones, and so not directly connected with the periphery, and could therefore be removed without affecting the vitality of either the efferent or afferent chain of neurones. In other words, the vitality of the cells on the efferent side ought not to be dependent on the integrity of the reflex arc.

With regard to the development of the anterior roots, Anderson[1] has shown that such is the case, for section of all the posterior roots conveying afferent impulses from the lower limb in a new-born animal does not hinder the normal development of the anterior roots supplying that limb. Also Mott, who originally[2] thought that section of all the posterior roots to a limb caused atrophy of the corresponding anterior roots, has now come to the same conclusion as other observers, and can find no degeneration on the efferent side due to removal of afferent impulses.

Again, the process of regeneration after section of a nerve is not in favour of the neuroblast theory. There is no evidence that the cut end of a nerve can grow down and attach itself to a muscular or epithelial element without the assistance of a nerve tube down which to grow. When the cut nerves connected with the periphery degenerate, that applies only to the axis cylinder and the medullary sheath, not to the neurilemma; the connective tissue elements remain alive and form a tube into which the growing axon finds its way, and so is conducted to the end plate or end organ of the peripheral structure.

Possibly, as suggested by Mott and Halliburton,[3] the products of degeneration of the axis cylinder and medullary sheath stimulate these connective tissue sheath cells into active proliferation, and so bring about the great multiplication of cells arranged as cell chains, which are so often erroneously spoken of as forming the young nerves. These sheath cells are then

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[1] *Op. cit.*, p. 504.

[2] Croonian Lectures, 1900.

[3] "On the Chemistry of Nerve Degeneration," *Phil. Trans. Roy. Soc. B.*, vol. cxciv., 1901, p. 437.

supposed to re-form and secrete a pabulum which is important for the process of regeneration of the growing down axis cylinder and medullary sheath. Without such pabulum regeneration does not take place, as is seen in the central nervous system, where the sheath of Schwann is absent.

Again, it is becoming more and more doubtful whether the peripheral terminations of nerves are ever really free.

As far as efferent nerves are concerned the nervous element may entirely predominate over the muscular or glandular, as in the formation of the electric organs of the Torpedo and Malapterurus, but still the final effect is produced by the transformation of the muscle or gland cell. On the afferent side especially free nerve terminations are largely recognised, or, as in Barker's book, nerves are spoken of as arising in connective tissue. Thus the numerous kinds of special sense organs, such as Pacinian bodies, tendon organs, genital corpuscles, etc., are all referred to by Barker[1] under the heading of "sensory nerve beginnings in mesoblastic tissues."

Yet the type of these organs has been known for a long time in the shape of Grandry's corpuscles or the tactile corpuscles in the duck's bill, where it has been proved that the nerve terminates in special large tactile cells derived from the surface epithelium.

So also with all the others, further investigation tends to put them all in the same category, all special sensory organs originating from a localised patch of surface epithelium. Thus Anderson has shown me in his specimens how the young Pacinian body is composed of rows of epithelial cells, into each of which a twig from the nerve passes; so also the tendon organ is built up on a similar plan; and here, as Sherrington points out, the nerve always passes to the surface and then bends back to supply the tendon organ, thus indicating how the nest of epithelial cells has wandered inwards from the surface to form the tendon organ.

Again, Meissner's corpuscles and Herbst's corpuscles are evidently referable to the same class as Grandry's and the Pacinian.

Finally, in the fishes we find the special sense organs of the

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[1] *The Nervous System*, p. 383.

lateral line and other accessory sensory organs, all of which are indisputably formed from modified surface epithelial cells.

The whole of this evidence seems to me directly against Barker's classification of sensory nerve beginnings in mesoblastic tissues; in none of these cases are we really dealing with free nervous tissue alone, the starting point is always a neuro-epithelial couple.

We may then, I would suggest, look upon the adult as formed of a neural syncytium, which we may call the host, which carries with it in its meshes a number of free cells not connected with the nervous system. If, then, we confine our attention to the host and trace back this neural syncytium to its beginnings in the embryo, we see that, from the very nature of the neuro-epithelial couple, each epithelial moiety must approach nearer and nearer to its neural moiety, until at last it merges with it, the original neuro-epithelial cell results, and we must obtain as far as the host is concerned a single-layered blastula as the origin of all Metazoa.

It follows, further, that there must always be continuity of growth in the formation of the host, *i.e.* in the formation of the neuro-epithelial syncytium, that therefore cells which have been previously free cannot settle down and take part in its formation, as, for instance, the formation of any part of the gut epithelium or of muscle cells from free living cells.

Further, since the neural moiety is the one common element to all the different factors which constitute the host, it follows that the convergence of each epithelial moiety to the neural moiety as we pass from the adult to the embryo is a convergence of all outlying parts to the neural moiety, *i.e.* to the central nervous system, if there is a concentrated nervous system; conversely in the commencing embryo the place from which the spreading out of cells takes place, *i.e.* from which growth proceeds, must be the position of the central nervous system if the nervous system is concentrated. If the nervous system is diffuse, and forms a general sub-epithelial layer, then the growth of the embryo would take place over the whole surface of the blastula.

Turning now to the consideration of the second group of tissues, those that are not connected with the central nervous system, we find that they include among them such special cells as the germinal cells, free cells of markedly phagocytic nature, and cells which were originally free and phagocytic, but have settled down to form a supporting framework of connective tissue, and are known as plasma cells. In the embryo we find also in many cases free cells in the yolk, forming more or less of a layer, which function as phagocytes and prepare the pabulum for the fixed cells of the growing embryo; these cells are known by the name of vitellophags, and in meroblastic vertebrate eggs form somewhat of a layer known by the name of periblast. Such cells must be included in group 2, and, indeed, have been said again and again to give origin to the free living blood corpuscles of the adult. In other cases they are said to disintegrate after their work is done.

In the adult the free living lymphocytes and hæmocytes reproduce themselves from already existing free living cells, but as we pass to the embryo there comes a time comparatively late in the history of the embryo when such free living cells are not found in the fluids of the body, and they are said to arise from the proliferation and setting free of cells which form a lining epithelium. Such formation of leucocytes has been especially described in connection with the lining epithelium of the cœlomic cavities, as stated in my last paper, so that anatomists largely look upon the origin of these free cells to be from the cœlomic epithelium, or mesothelium, as Minot calls it.

Then, again, the free cells which form the germinal cells can be traced back to a germinal epithelium, which also is part of the cœlom. Thus the suggestion arises that in the embryo there is formed a cellular lining to a cœlomic cavity (mesothelium) composed of cells which have no communication with the nervous system, and are capable of a separate existence as free individuals, either in the form of germinal cells or of lymphocytes, hæmocytes, and plasma cells, so that these latter free cells may be considered as living an independent existence in the body, and ministering to it in the same sense as the germ cells live an independent existence in the body. Again, the function of this mesothelium apart from the germ cells is essentially excretory and phagocytic. It is the cells of the excretory organs as well as the lymphocytes which pick up carmine grains when injected. It is the cells of the modified excretory organs, as mentioned in my last paper, which, according to Kowalewsky and others, give origin to the free leucocytes.

We see, then, that the conception of a syncytial neuro-epithelial host holding in its meshes a number of free cells leads directly to the question: What is the cœlom? to which category does its lining membrane belong? and further, also: What is the origin of these free cells?

The Metazoa have been divided into two great groups, those which possess a cœlom (the Cœlomata; Lankester's Cœlomocœla) and those which do not (Cœlenterata, Lankester's enterocœla).

As an example of the latter we may take Hydra, because it is a very primitive form and because its development has been carefully worked out recently by Brauer.[1]

In Hydra we find a dermal layer of cells and an inner layer of cells separated by a gelatinous mass known as mesoglœa; in this mass between the dermal and inner layers are found scattered cells, the interstitial cells. Now, according to Brauer the position of the germ in Hydra is the interstitial cell layer. One cell of the ovarium becomes the egg-cell, the others have their substance changed into yolk grains, forming the so-called pseudo-cells, and as such afford pabulum to the growing egg-cell. Thus we see that in between the dermal and gastral layer of cells a third layer of cells is found, composed of free living germ cells, some of which, by the formation of yolk granules, become degraded into pabulum for their more favoured kinsfolk.

These interstitial cells are said to arise from the dermal layer, or ectoderm, but clearly, as in other cases, germ cells constitute a class by themselves and cannot be spoken of as originating from ectoderm cells or from hypoderm cells.

So also in Porifera, Minchin[2] states (p. 29):

> "In addition to the collared cells of the gastral layer, and the various cell elements of the dermal layer, the body wall contains numerous wandering cells or amœbocytes, which occur everywhere among the cells and tissues. Though lodged principally in the

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[1] "Ueber die Entwicklung von Hydra," *Zeitsch. f. Wiss. Zool.*, Bd. 52, p. 169.

[2] *A Treatise on Zoology*, edited by Ray Lankester. Part II. "The Porifera and Cœlenterata." 1900.

dermal layer, they are not to be regarded as belonging to it, but as constituting a distinct class of cells by themselves. They are concerned probably with the functions of nutrition and excretion, and from them arise the genital products."

Further (p. 31):

"At certain seasons some of these cells become germ cells; hence the wandering cells and the reproductive cells may be included together under the general term archæocytes."

Also (p. 51):

"The mesoglœa is the first portion to appear as a structureless layer between the dermal and gastral epithelia, and is probably a secretion of the former."

He also points out that in these, the very lowest of the Metazoa, the separate origin of these archæocytes can be traced back to a very early period of embryonic life. Thus in *Clathrina blanca*[1] the ovum undergoes a regular and total cleavage, resulting in the formation of a hollow ciliated blastula of oval form. At one point the future posterior pole of the larva are a pair of very large granular cells with vesicular nuclei, which represent undifferentiated blastomeres and are destined to give rise to the archæocytes, and, therefore, also to the sexual cells of the adult. Thus, as he says, from the very earliest period a distinction is made between the "tissue-forming" cells (my syncytial host) and the archæocytes.

We see, then, that the origin of all these free living cells can be traced back to the very earliest of the Metazoa. Here between the dermal and gastral layers there is secreted by these layers a gelatinous material, the mesoglœa. This material is non-living, non-cellular. In it live free cells which may either be germ cells, amœbocytes, or collencytes (connective tissue cells). If this mesoglœa was a fluid secretion, then we should have a tissue of the nature of blood or lymph; if it was solid, then we should have the foundation of connective tissue, cartilage, and bone.

From this primitive tissue it is easy to see how the special elements of the vascular, lymphatic, and skeletal tissues gradually arose, the matrix being provided by the cells of the syncytial host and the cellular elements by the archæocytes.

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[1] *Op. cit.*, p. 68.

In fact we have no right to speak of these lowest members of the Metazoa as not being triploblastic, as possessing nothing corresponding to mesoblast, for in these free cells in the mesoglœa we have the origin of the mesenchyme of the higher groups. Thus Lankester, talking of mesenchyme, says[1]:

> "I think we are bound to bring into consideration here the existence in many Cœlentera of a tissue resembling the mesenchyme of Cœlomocœla. In Scyphomedusœ, in Ctenophora, and in Anthozoa, branched fixed and wandering cells are found in the mesoglœa which seem to be the same thing as a good deal of what is distinguished as mesenchyme in Cœlomocœla. These appear to be derived from both the primitive layers; some produce spicules, others fibrous substance, others again seem to be amœbocytes with various functions. It appears to be probable that, though it may be necessary to distinguish other elements in it, the mesenchyme of Cœlomocœla is largely constituted by cells, which are the mother cells of the skeletotrophic group of tissues, and are destined to form connective tissue, blood-vessels, and blood."

Thus we see that the earliest Metazoa were composed of a dermal and gastral epithelium, with a sub-epithelial nervous system connecting the parts together, which formed, as it were, a host, carrying around free living cells of varying function, all of which may be looked on as derived from archæocytes, *i.e.* germ cells.

From these the cœlomatous animals arose, and here also we find, according to present-day opinion, that the cœlom arose in the first place in the very closest connection with the germ cells or gonads. Thus Lankester,[2] in his review of the history of the cœlom, states:

> "The numerous embryological and anatomical researches of the past twenty years seem to me to definitely establish the conclusion that the cœlom is primarily the cavity, from the walls of which the gonad cells (ova or spermata) develop, or which forms around those cells. We may suppose the first cœlom to have originated by a closing or shutting off of that portion of the general archenteron of Enterocœla (Cœlentera), in which the gonads developed as in Aurelia or as in Ctenophora. Or we may suppose that groups of gonad mother cells, having proliferated from the endoderm, took up a position between it and the ectoderm, and there acquired a vesicular arrangement, the cells surrounding the cavity in which liquid accumulated.

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[1] *A Treatise on Zoology*, edited by Ray Lankester. Part II. "The Enterocœla and the Cœlomocœla," p. 30.

[2] *Op. cit.*, p. 9.

"The cœlom is thus essentially and primarily (as first clearly formulated by Hatschek) the perigonadial cavity or gonocœl, and the lining cells of gonadial chambers are cœlomic epithelium. In some few groups of Cœlomocœla the cœloms have remained small and limited to the character of simple gonocœls. This seems to be the case in the Nemertina, the Planarians, and other Platyhelmia. In some Planarians they are limited in number, and of individually large size; in others they are numerous."

When Lankester says that the lining cells of gonadial chambers are cœlomic epithelium, that is equivalent to saying that the lining cells of the cœlom form an epithelium which was originally gonadial, provided that, as seems to me most probable, his second suggestion, of the cœlom being formed from gonadial mother cells which have taken up an intermediate position between endoderm and ectoderm and there acquired a vesicular arrangement, is the true one.

It does not seem to me possible to conceive of the gonads arising from cells of the epiblast or of the hypoblast, in the sense that such cells are differentiated cells belonging to a layer with a definite meaning.

When we consider that the gonad gives origin to the whole of a new individual, that in the Protozoan ancestors of the Metazoa their ultimate aim and object was the formation of gonads, it seems a wrong conception to speak of the gonads as formed from cells belonging either to the gut wall or to the external epithelium. The gonads must stand in a category by themselves; they represent a whole, while the other cells represent only a part; they cannot therefore be derived from the latter. They may, and indeed do, give rise to cells of a subordinate character, but they cannot rightly be spoken of as derived from such cells.

The very fact mentioned by Lankester, that in the lowest cœlomatous Metazoa, the Platyhelminthes, the cœloms are limited to the character of simple gonocœls, strongly points to the conclusion that all the cœlomic cells were originally of the nature of gonadial cells, and therefore free living and independent of the rest of the cells of the body.

Whether the germ cells appear, as in Hydra, to be derived from the ectoblast, or, as is usually stated, from the endoblast, in neither case ought they to be classed with the internal or external epithelium; they are germ cells, and the epithelium which they form is neither epiblastic nor hypoblastic, but germinal, forming originally a simple gonocœle, afterwards, in the higher forms, the cœlom with its cells of various function. Thus, to quote again from Lankester[1]:

> "The cœlomic fluid and the cœlomic epithelium, as well as the floating corpuscles derived from that epithelium, acquire special properties and importance over and above the original functions subservient to the maturation of the gonadial cells . . . . the most important developments of the cœlom are in connection with the establishment of an exit for the generative products through the body wall to the outer world, and further in the specialisation of parts of its lining epithelium for renal excretory functions."

Such exits led very early to the formation of cœlomoducts, which are true outgrowths of the cœlom itself (p. 14):

> "The cœlomoducts, and the gonocœls of which they are a part, frequently acquire a renal excretory function, and may retain both the function of genital conduits and of renal organs, or may, where several pairs are present (metamerised or segmented animals), subserve the one function in some segments of the body, and the other function in other segments."

The origin of the cœlom and its derivatives from a germinal membrane, as suggested by Lankester, appears to me most likely, and, if true, it carries with it conclusions of far-reaching importance, for it necessitates that all the cells which line true cœlomic cavities and their derivatives belong to the category of free living cells, and are not connected with the nervous system.

The cells in question are essentially those which line serous cavities and those which form excretory glands like the kidneys. In this latter organ we ought especially to be able to obtain a clear answer to this question, for is it not a gland which secretes into a duct, and might therefore be expected to be innervated in the same way as other secretory glands?

Although there is a strong *prima facie* presumption in favour of the existence of renal secretory nerves, yet according to the universal opinion of physiologists no evidence in favour of such nerves has hitherto been found; all the phenomena of excretion of urine consequent on nerve stimulation are explainable by

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[1] *Op. cit.*, p. 13.

the action of nerves on the renal vessels, not on the renal cells.

Not only is the physiological evidence negative up to the present time, but also, I think, the histological; on the one hand, Retzius has failed to find nerve connections with kidney cells; on the other, Berkley has obtained such evidence with the Golgi method, but failed entirely with methylene blue. I do not think myself that the evidence of the Golgi method alone is sufficient without corroboration by other methods, and, in any case, Berkley's evidence does not show the nerve fibres terminating in the kidney cells, as can be shown by modern methods in the case of epithelial cells of the surface, etc. Quite recently another paper on this subject has appeared by Smirnow, who appears to have obtained better results than those given by Berkley.

Apart from these physiological and histological considerations, this question is also dependent upon the nature of the development of the excretory organs, for, according to Lankester, all excretory organs may be divided into the two classes of nephridial organs and cœlomostomes, of which the former are largely derived from epiblast. We should therefore expect to find secretory nerves to nephridial organs, though possibly not to cœlomostomes. The kidneys of the Mammalia are supposed to be true cœlomostomes, although, according to Goodrich's researches, the excretory organs in Amphioxus are solenocytes, *i.e.* true nephridia.

As to the lining epithelium of the peritoneal, pleural, and pericardial cavities—*i.e.* the mesothelium—there is no definite evidence that these cells are provided with nerves. Such surfaces are remarkably insensitive in the healthy condition, and the pain in such cavities is essentially a pressure phenomenon and referable to special sense organs, such as Pacinian bodies, etc., rather than to the mesothelium itself.

These sense organs are identical in structure with those in the skin, and, as Anderson has shown,[1] the nerves of these organs medullate at the same time as those in the skin, and both obtain their medullary sheaths earlier than any other nerves, whether afferent or efferent. However difficult it

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[1] Brit. Assoc. Reports, 1898, p. 718.

may be to explain, only one conclusion seems to me possible—these Pacinian bodies, like the skin Pacinians, originate from a nest of surface epithelial cells, a conclusion which is likely enough on my theory of the origin of vertebrates, but not, as far as I can see, on any other.

At the present moment the weight of evidence is to my mind in favour of the lining endothelium of the cœlomic cavities being composed of free cells, unconnected with the nervous system rather than the reverse, but I must confess that the question is undecided. If it be true that the cœlomic lining is partly enterocœlic and partly gonocœlic, as Lankester teaches, then it would be natural that its cells should be in connection with the nervous system, to some extent at all events. This view is, however, based on very slender foundations.

If the mesothelium is composed of cells capable of becoming free, it cannot give rise to the skeletal muscles, and it cannot therefore be right to speak of the skeletal muscles as derived from the lining cells of a part of the primary cœlom.

The phylogenetic history of the musculature of the different animals points strongly to its intimate connection with and derivation from surface epithelial cells rather than from cœlomic mesothelial cells. Thus in the cœlenterates, as seen in Hydra, the muscular layer arises directly from a modification of the surface epithelial cells; and right up to the Annelids, even to the highest form in the Polychœta, we still see it stated that the musculature, both circular and longitudinal, arises from the ectoderm. In the Oligochœtes and Hirudinea, according to Bergh,[1] there are five rows of teloblasts on each side, of which four are ectodermic and give rise to the nerve ganglia and the circular muscles, while one is mesoblastic and forms the nephridial organs and the longitudinal muscles. (The latter statement is, according to Bergh, well known, and is not particularly shown by him. These longitudinal muscle bands are always close against the nervous system at their first formation, and may well have been derived in connection with it.)

It is apparently only in the Vertebrata that the lining cells of the cœlomic cavity are definitely stated to give origin to the

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[1] "Neue Beiträge z. Embryol. d. Anneliden," *Zeitsch. f. Wiss. Zool.*, vol. l., p. 469.

body musculature, and taking into account on the one hand the evidence of Graham Kerr[1] as to the intimate connection between nerve cell and muscle cell from the very beginning, and on the other the manner in which all the skeletal muscles of the adult are lined with a lymphatic endothelium, I am strongly inclined to believe that at the closing up of the myocœle, when the myomer separates from the mesomer, the lining cells remain scattered in among the forming muscle cells and form the ultimate lymphatic tissue of the muscles.

If this is really so, then the evidence in favour of the mesothelium being composed of free cells not connected with the nervous system would be much strengthened, for, on the one hand, an intimate relation exists between the connective tissue cells and the endothelium of the roots of the lymphatic vessels, a relation which, according to Virchow, has rendered it impossible to draw any sharp line of distinction between the two; and, on the other, the lymphatic endothelium merges into the lining cells of the great serous cavities of the body.

It is impossible to conceive of an animal possessing a nervous system which is not in connection with sensory and muscular tissues; an isolated nerve cell is a meaningless possession; but it is equally natural to conceive of a germ cell being isolated, capable of living an independent existence. Such a difference between the two kinds of tissues must have existed from the very commencement of the Metazoa, so that we must, it seems to me, imagine that in the formation of the Metazoan from the Protozoan the whole of the body of the latter did not break up into a mass of separate gonads, each capable of becoming a free living Protozoan similar to its parent, but that a portion proliferated into a multinucleated syncytium while the remainder formed the free-living gonads. This multinucleated syncytium, or host, as it might be called, would still continue to exist for the purpose of carrying further afield the immortal gonads, which need be no longer all shed at one time. In such an animal as *Volvox Globator* we have an indication of the very kind of animal postulated as connecting the single-celled Protozoa and the multicellular Metazoa, for it consists of a

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[1] *Loc. cit.*

many-celled case which forms a hollow sphere, each of the cells being provided with flagella for the purpose of locomotion of the sphere, except a certain number which are not flagellated; these latter leave the case to swim freely in the fluid contained within the sphere, and forming spermaries and ovaries, conjugate, maturate, and then are set free by the rupture of the encircling locomotor host.

This conception of the predecessors of the Metazoa being composed of a mortal host, holding within itself the immortal sexual products, leads in my mind naturally to the idea of the separate development of the host from that of the germ cells *ab initio*, so that the study of the development of the Metazoa means the study of two separate constituents of the Metazoan individual—on the one hand, the elaboration of the elements forming the syncytial host; on the other, of those derived from the free living independent germ cells. The elaboration of the host means the differentiation of the protoplasm into epithelial, muscular, and nervous elements, by means of which the gonads were carried further afield and their nourishment as well as that of the host ensured.

From the very earliest time I imagine the rôle of the nervous system as the middleman between internal and external muscular and epithelial surfaces was initiated.

The further evolution of the host consisted in a greater and greater differentiation and elaboration of this neuro-epithelial syncytium, with the result of a steadily increasing concentration and departmental centralisation of the main factor of the syncytium; in other words, led to the origin and elaboration of a central nervous system.

In the interstices of this syncytium the gonads were placed, and at first, doubtless, the life of the host ended when all the germ cells had been set free. Reproduce and die was, I imagine, the law of the Metazoa at its earliest origin, and throughout the ages, during all the changes of evolution, the reminiscence of such law still manifests itself even up to the highest forms as yet reached. With the differentiation of the syncytial host there came also differentiation of the free living gonads, so that only some of them attained to the perfection of independent existence, capable of continuing the species, while others became subordinate to the first and provided them with pabulum, manufacturing within themselves yolk spherules, and thus in the shape of yolk cells ministered to the developing egg-cell. Thus arose a germinal epithelium of which only a few of the elements passed out of the host as perfect individuals, the remainder being utilised for the nutrition of these few. Such yolk cells of the germinal epithelium would still, however, retain their character as free cells, totally independent of the syncytial host, and situated as they were between the internal and external epithelium, capable of amœboid movement, would naturally have their phagocytic action utilised either as yolk cells for the providing of pabulum to the egg-cell, or as excretory cells for the removal and rendering harmless of deleterious products of all kinds. Thus the free cells of the body would become differentiated into the three classes of germ cells, yolk cells, and excretory cells.

Further, the mass of gonads, which originally occupied so large a space within the interior of the host, necessarily, as the tissues of the host differentiated more and more, took up less and less space in proportion to the whole bulk of the host, and formed a germinal mass of cells between the outer and inner epithelial layers. This germinal mass formed an epithelium, some of the members of which acted as scavengers for the inner and outer layers of the host, with the result that fluid accumulated between the two parts of the germinal epithelium in connection respectively with the external and internal epithelial surfaces of the host, and thus led to the formation of a gonocœle, which, by obtaining an external opening, a cœlomostome, gave origin to the cœlom.

Again, with the longer life of the host, the setting free of the gonads no longer necessitating the destruction of the host, and also the gonads themselves requiring a longer and longer time to be fed up to maturity, the bulk and complexity of the whole organism increased and special supporting structures became a necessity. The host itself could and did provide these to a certain extent by secretions from its epithelial elements, but the intermediate supports were provided by the system of phagocytic cells utilising the fluids of the body, at first in the shape of plasma cells able to move from place to place, then settling down to form a connective tissue framework, and, later on, cartilage and bone.

So also were gradually evolved the whole of the endothelial structures, all the lymph cells, blood cells, etc., all having their origin from the free cells of the body, which themselves originated in the extension of a germinal epithelium. Just as in a hive the egg-cells may form the fully developed sexual animal, whether drone or queen bee, or the asexual host of workers, so in the body of the Metazoa the free cells may form either male or female germ cells, spermatozoa or ova, or a host of workers, scavengers, repairers, food providers, all useful to the community, all showing their common origin by their absolute independence of the nervous system.

Two points of great importance follow from this method of looking at the problem. First, the evolution of the animal kingdom means essentially the evolution of the host, for that is what forms the individual; secondly, as the host is composed of a syncytium, the common factor of whose elements is the neural moiety, it follows that the tissue of central importance for the evolution of the host must be, as indeed it is, the nervous system.

Further, seeing that the growth of the individual means the orderly spreading out of the epithelial moiety away from the neural moiety, it follows that the germ band or germ area from which growth starts must be in the position of the nervous system.

If, then, the nervous system in the animal is a concentrated one, then the growth will emanate from the position of such nervous system. If, on the other hand, the nervous system is diffused, then the growth will also be diffused.

In these papers I have throughout argued that the ancestors of vertebrates belonged to a great group of animals which gave origin also to Limulus and scorpion-like animals; it is therefore instructive to see what is the nature of the development of such animals. For this purpose I will take the development of the scorpion, as given by Brauer,[1] for he has worked out such development with great thoroughness and care. His

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[1] "Beiträge zur Kenntniss d. Entwicklungsgeschichte d. Skorpions," *Zeitsch. f. Wiss. Zool.*, vols. lvii. and lix., parts 1 and 2.

papers show that the segmentation is discoidal, and results in an oval blastodermic area lying on a large mass of yolk. Very early there separates out in this area genital cells and yolk cells, which latter move freely into the yolk and prepare it into a fluid pabulum for the nutrition of the cells of the embryonic shield or germ band. These free yolk cells do not take part in the formation of the germinal layers, nor does the endoderm when formed give origin to free yolk cells.

The cells of the germ band form a small compact area, in which by continual mitosis the cells become more than one-layered, and soon it is found that those cells which are against the fluid pabulum form a continuous layer and absorb the nutritious material for themselves and the rest of the embryo. While this area is thus increasing in thickness by continuous development, the group of genital cells remains always apart, increasing in number, but always in a state of isolation from the cells of the rest of the growing area. Thus from the very first Brauer's observations on the development of the scorpion point to the formation of a syncytial host containing separate genital cells. The continuous layer of cells against the fluid pabulum, which is already functioning as a gut and may therefore be called hypoblast, spreads continuously over the yolk, as also does the surface epithelial layer, or epiblast. Such spreading is always a continuous one for both surfaces, so that the yolk is gradually enclosed by a continuous orderly growth from the germ band, and not by the settling down of free cells in the yolk here and there to form the gut lining. This steady orderly development proceeds owing to the nourishment afforded by the activity of the free cells or vitellophags and the absorbing power of the hypoblast, a steady growth round the yolk which results in the formation of the gut tube, the outer covering and all the muscular and excretory organs. Where, then, is this starting point? this germ band from which the whole embryo grows? It forms the mid ventral area of the adult animal, it corresponds exactly to the position of the central nervous system. The whole phenomenon of embryonic growth in the scorpion is exactly what must take place on the argument deduced from the study of the adult that the animal arises as a neuro-epithelial syncytium, and we see that that layer of cells forms the alimentary tube which is situated next to the food material. It is not a question whether such layer is ventral or dorsal to the neural cells, but whether it is contiguous to or removed from the food material.

Take, again, a meroblastic vertebrate egg. Again we find free cells passing into the yolk to act as vitellophags, the so-called periblast cells; again we see that the embryo starts from a germ band or embryonic shield, and spreads from there continuously and steadily; again we see that that layer of cells which is against the yolk absorbs the fluid pabulum for the growing cells; again we see that the area from which the whole process of growth starts is that of the central nervous system, and again we see that those cells which are contiguous to the food form the commencing gut, and are therefore called hypoblast, though in this case they are ventral not dorsal to the neural layer.

The comparison of these two processes shows that there is one common factor, one thing comparable in the two, one thing that is homologous and is the essential in the formation of that part of the animal which I have called the host, and that is the central nervous system; whether the epithelial layer which lies ventral to it or the one that is dorsal forms the gut depends upon the position of the food mass. Where the food is, there will be the absorbing layer. Where the food is not, there will be no gut formation, whatever may have been the previous history of that layer. If, then, we suppose, as I do, that the vertebrate arose from a scorpion-like animal without any reversal of dorsal and ventral surfaces, and that the central nervous system remained the same in the two animals, then the comparison of the development of the two embryos shows that the one would be derived from the other if the yolk mass shifted from the dorsal to the ventral side of the nervous system. This would leave the dorsal epithelial layer of the original syncytium free from pabulum, it would no longer be an absorbing layer, it would no longer form the definitive gut, *but it would still tend to form itself in the same manner as before, would still grow from a ventrally situated germ band dorsalwards to form a tube, would recapitulate its past history, and show how the alimentary canal of the arthropod be-*

came the neural canal of the vertebrate. Although it is formed in the same way as before, it is no longer recognised as homologous of the scorpion alimentary canal, but because it no longer absorbs pabulum, and does not therefore form the definitive gut, it is called an epiblastic tube, and, in the words of Ray Lankester, has no developmental importance.

All the arthropods are built up on the same type, and in all the development may in its broad outlines be referred to the type just mentioned. So also with the vertebrate group; in both cases the position of the central nervous system determines the starting area of embryonic growth. In both cases the absorbing layer shows the position of the definitive gut. A concentrated nervous system of this type is common to all the segmented animals from the annelids to the vertebrates, and in all cases the germ band which indicates the first formation of the embryo is in the position of this nervous system.

As far as the embryo is concerned, there is no great difficulty in the conception that the yolk mass may have shifted from one side to the other in passing from the arthropod to the vertebrate, for in the arthropod the embryo at first is surrounded by yolk and then passes to the periphery of the egg. If it is permissible to speak of a dorsal and ventral surface to an egg, and we imagine the egg held with such dorsal surface uppermost, then the yolk would be situated ventrally to the embryo, as in the vertebrate, if the protoplasmic cells of the embryo rose from their central position to the surface through the yolk, while if they sank through the yolk, the yolk would be dorsally situated to the embryo, as in the arthropod.

In cases where there is no yolk, or very little, as in Lucifer and Amphioxus respectively, the embryo is compelled to feed itself at a very early age; such embryos form a free swimming pelagic ciliated blastula, the invagination of which, for the purpose of collecting food material out of the open sea, is the simplest method of obtaining nutriment. Here, as in other cases, it is the physiological necessity which determines the method of formation of the gut, and such similarity of appearance as exists between the gastrula of Lucifer and that of Amphioxus by no means implies that the gut of the adult Lucifer is homologous with the gut of Amphioxus.

I have compared two meroblastic eggs of the two classes respectively, because the scorpion's egg is meroblastic. I imagine that no real difficulty arises with respect to holoblastic eggs, for the experiments[1] of O. Hertwig and Samassa show that by centrifugalising, stimulation, and breaking down of large spheres the holoblastic amphibian egg may be converted into a meroblastic one, and then development will proceed regularly, *i.e.* in this case also the growth proceeds from the animal pole, the large cells of the vegetal pole, like the yolk cells of the meroblastic egg, manufacture pabulum for the growing syncytial host.

I have ventured in this short sketch to put before the world the way in which the search for principles in Embryology presents itself to my mind. I am well aware there are many problems I have not discussed which arise immediately in the mind in connection with this view of mine, such, for instance, as those concerning malignant growths, skin grafting, and many others. Much more consideration and discussion must be given to current views on Embryology before the principles I have put forward can be expected to take the place of the present germinal layer theory. I have treated the subject in this short and perfunctory manner because I desire to finish up the series of papers on the Origin of Vertebrates in this Journal without allowing any side issues, however fascinating, to draw me away until that task is completed. It was, however, necessary to say something in order to explain how, in my opinion, the conversion of the alimentary canal of the Arthropod into the neural canal of the Vertebrate was not only not contrary to the principles of Embryology, but that the formation of the Vertebrate neural canal embryologically takes place exactly as it ought to do on the Recapitulation Theory.

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[1] Quoted in Ziegler's *Lehrbuch der vergleichenden Entwicklungsgeschichte der niederen Wirbelthiere*, 1902, pp. 256–258.

CAMBRIDGE, *December* 1904.

ON PRESSURE EPIPHYSES. By F. G. PARSONS, F.R.C.S.,

St Thomas's Hospital, London.

In a previous paper I have tried to show that the epiphyses into which tendons are inserted have something of the nature of sesamoid bones, and may be conveniently placed in a group by themselves under the name of 'traction epiphyses.' In this I wish to make some observations on those epiphyses which occur at the articular ends of long bones, by which the pressure is transmitted from bone to bone, and which may therefore be called 'pressure,' or 'articular' epiphyses.

I am very far from thinking that I have solved the question of these epiphyses, but I hope that I can bring forward some new evidence about them which may bring their final solution nearer.

In considering the subject, I want to follow three distinct lines of thought and investigation:—1. How these epiphyses come. 2. What use they are. 3. Why they come. These three lines will at times become more or less entangled, but I shall do my best to keep them as clear as I can.[1]

1. *How Epiphyses come.*—The first indication of any preparation for articular epiphyses is found in the lower or more generalised Amphibia, the Urodela and Discoglossidæ. In these creatures the ossification of the shaft of the long bones stops before it reaches the articular ends, and leaves a mass of cartilage which remains throughout life without either calcifying or ossifying. There is no epiphysis here, but the place for it is provided. It is worth noticing that most of these animals are aquatic. In the more specialised Anura—the higher frogs and toads—superficial calcification occurs in the cartilaginous ends of the bones when the animal is nearly or quite full-grown, and the calcified epiphysis fits over the diaphysis in the same way

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[1] It may prevent misconception if it is stated that by an articular epiphysis is meant an ossification or calcification in the cartilage at the articular end of a long bone.

that the cover fits on to a pill-box. In a half-grown frog which I killed last March, and which was apparently one year old, no calcification at all had occurred in the articular ends, even of the femur. In such of the Reptilia as have limbs articular epiphyses are fairly constant, and many of the Lacertilia are better off in this respect than are the Mammalia, since they have epiphyses at both ends of their metacarpal and metatarsal bones, as well as a definite articular epiphysis in the upper end of the ulna. Sometimes these epiphyses are calcifications, as in Varanus (see fig. 9); but at others, as in Iguana, they become ossified.[1] The so-called epiphyses of the Sauropterygia will be referred to later.

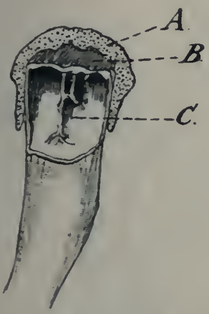

FIG. 1.—Upper end of femur of full-grown frog. *A*, calcified epiphysis; *B*, cartilage; *C*, cavity of diaphysis.

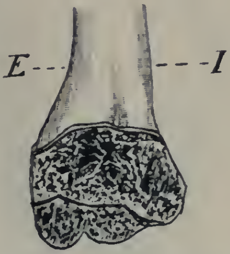

FIG. 2.—Lower end of humerus of Iguana lizard showing bony epiphysis.

Birds are striking instances of the ease with which a bone can grow without any epiphyses. As far as I know, there is only one instance of a true epiphysis in their long bones, and that is at the upper end of the tibiotarsus of the Gallinaceæ and Ratitæ; it is a good test of the youth of a pullet, since it joins up soon after the full size is reached. I think that this is a traction epiphysis, since it does not occupy the whole articular surface of the bone, and since the ligamentum patellæ is attached to it. I have recently examined the long bones in a series of pigeons ranging from four days to six weeks old. At four days there are two cones of gradually ossifying cartilage,

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[1] In Holden's *Osteology* (1887), the Sauropsida are stated not to have true epiphyses.

the apices of which are close together in the middle of the bone, at the point where the primary centre of ossification occurred, while the bases, quite unossified, form the articular ends. These two cones are ensheathed by a layer of periosteal bone, which of course is thickest opposite the apices of the cones, and thins off as the two extremities are approached. As life goes on, the ossification extends towards the bases of the cones, but for a short time it is checked at some little distance from the articular end: this, of course, is the equivalent of the epiphysial line of other vertebrates, but it is comparatively transitory, and ossification creeps on until the articular end is reached, except for a narrow strip of articular cartilage. At six weeks the bone has almost attained its adult dimensions. The apices of the cones meanwhile are gradually absorbed and replaced by marrow, which in the case of the humerus and femur will, in its turn, be replaced by the air-sacs. I would here point out, in parenthesis, that these cones probably represent the so-called epiphyses of the Plesiosaurus, which I am indebted to the kindness of Mr Smith Woodward for showing me. I have not been able to find that this reptile possessed anything corresponding to true epiphyses.

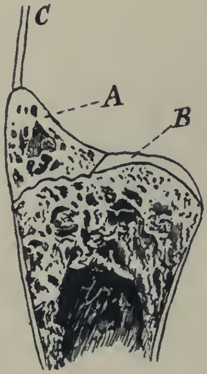

FIG. 3.—Upper end of tibio-tarsus of common fowl. *A*, epiphysis; *B*, articular cartilage; *C*, ligamentum patellæ.

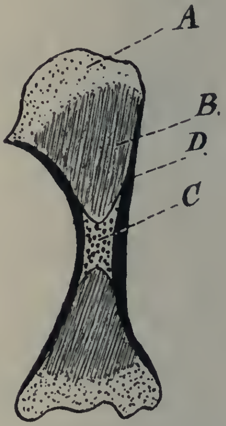

FIG. 4.—Humerus of pigeon four days old. *A*, cartilage; *B*, cone of calcifying cartilage; *C*, medulla; *D*, periosteal bone.

In terrestrial vertebrates other than birds the epiphysial line or place where the bases of the cones cease to ossify is much less transitory than in birds, and it retains its relative position to the articular ends. The cartilage beyond it may remain cartilaginous, as in the Urodele amphibians and Discoglossidæ; it may calcify, as in most of the Anura and in many of the reptiles, *e.g.* chameleon and monitor lizard; or it may form the seat of a true epiphysis or osseous deposit, as in so many of the mammalia and in some reptiles, though there is reason for believing that even in the mammals the true ossification is preceded by evanescent calcification. The question of where the bone which forms the mammalian epiphysis comes from is an interesting one, and one of which, so far, I have not found any description. If we accept the present view, that bone is never formed *de novo* in cartilage, but is always perichondrial in its origin, and invades previously calcified cartilage from the surface, we are forced to the conclusion that the osseous epiphyses come originally either from the perichondrium surrounding the articular cartilaginous cap or from the bone of the shaft on the other side of the epiphysial line.

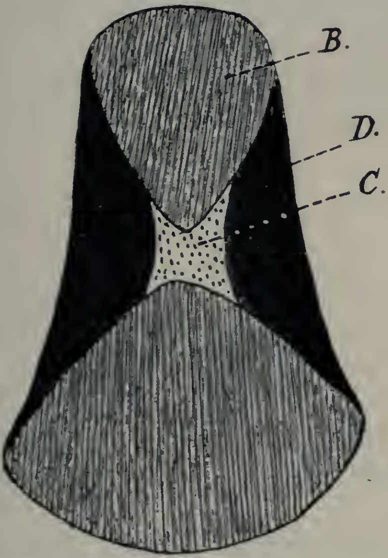

FIG. 5.—Diagram of humerus of Plesiosaurus. *B*, cone; *C*, medulla; *D*, periosteal bone. (Compare with fig. 4.)

From a careful examination of sections of newly appearing epiphyses, I feel confident that the latter is the case, and that vessels, doubtless bearing osteoblasts with them, shoot out from the zone of advancing ossification at the end of the diaphysis into the very centre of the cartilaginous cap, that is, to the part which is least subject to the effects of pressure, and which hitherto has presumably been the part least well-nourished (see fig. 8). Whether calcification has preceded this irruption of ossification I have not as yet been able to get specimens at the right stage to show, but there is no reason to believe that ossification here follows other than the normal course; and as calcification is a normal precursor of ossification, we may, I think, safely assume that it occurs. There is one other point in connection with how epiphyses come which is well known, but I should like to state it here, because it will be of use in a subsequent line of thought: it is, that the larger the cartilaginous mass at the end of a long bone, the earlier will an epiphysis appear in it; for instance, the lower end of the femur, the head of the tibia, and the head of the humerus are in man the largest cartilaginous masses, and it is in these that ossification first occurs. In the puppy and kitten the cartilage at the upper end of the humerus is larger than that at the lower end of the femur, and in these animals the epiphysis in the head of the humerus appears on the first or second day after birth, while that in the lower end of the femur does not come till the ninth or tenth day. The same rule holds good to a certain extent with the ossification of

FIG. 6.—Humerus and femur of kitten three days old, showing that the upper cartilage (with its epiphysis) of the humerus is larger than the lower cartilage of the femur (without an epiphysis).

the carpal and tarsal elements—the bigger they are the earlier does ossification begin; the os magnum of man starts in the first year, while the pisiform finishes about the eleventh. In the foot, too, the calcaneum and astragalus begin to ossify before birth, though I confess there is some interference with the due sequence in the case of the navicular. Another interesting likeness in the ossification of these hand and foot bones to that of the articular epiphyses of the long bones is, that the first ossific deposit occurs in the very centre of the cartilage, and nowhere near the perichondrium.

The next question I wish to discuss is the use of these epiphyses, and I think we may at once feel confident that, however useful they may be, they are not essential; for birds get on quite well without them, and in some cases in mammals they appear so late in life that much or all of the growth of the bone has been effected without them: this is the case in the human ulna, which grows perfectly comfortably until the sixth year without any epiphyses at all, while the human clavicle reaches the eighteenth year before the epiphyses comes, and I have considerable reason to suspect that in some cases it never appears at all. At any rate the bone has practically attained its full size without any epiphysis.

Of course, the fact of showing that a thing is not essential does not prove that it is not useful, and one must consider the possible uses of these epiphyses. In the first place, they may conceivably assist in the growth of the bone, but this must be a very slight advantage, since the growth is almost entirely on the diaphysial side of the epiphysial line, and the ulna, which has no articular epiphysis in its upper end and a late appearing one below, keeps pace quite easily with the radius which has epiphyses at both ends.

Then it has been suggested that the deposit of bone beyond the epiphysial line acts as a protection to the line of growth, but from a common-sense point of view it would seem that the elastic pad of cartilage must be a better protection against pressure than when it is calcified or ossified; and if any animal requires a protection against shock to the growing line of the femur it must be the frog, yet in it we find that until growth is nearly complete no calcification occurs. Another suggestion is, that by having a deposit of bone in the articular end, this end is able to adapt itself to the change of shape which is constantly occurring during growth. This seems to me quite unnecessary, since everywhere bone is constantly being absorbed and relaid by the osteoclasts and osteoblasts, and if any bone has a complicated articular extremity it is the mammalian ulna where it enters into the elbow-joint, but this is the chief point where no articular epiphysis is found. I must confess that I have heard no satisfactory explanation of the good which these epiphyses do, but I am bound to draw attention to a point which I think has not been hitherto noticed, and that is, that in the Ungulates (ox, sheep, and chevrotain, and presumably others) the epiphyses appear long before birth, and a lamb of two days old shows them as well developed as in a human being of twelve or thirteen years. When one remembers that these animals are able to run after their mothers almost as soon as they are born, it certainly looks as if there were a provision of Nature for a condition of things which would happen later on, but still it does not show what use the epiphyses are to the young animal. This question of whether Nature can provide for some mechanical need which has not yet arisen, is one which leads us from a physical to a metaphysical inquiry; and I can only express a belief that some mechanical cause will be found for the early appearance of these Ungulate epiphyses when the subject comes to be further inquired into. It is quite certain that other animals can run about quite well while

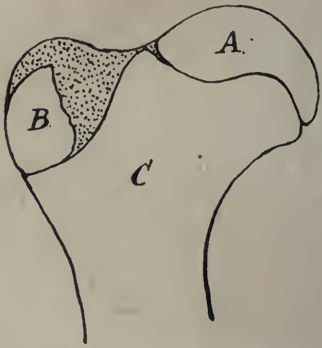

FIG. 7.—Upper end of femur of lamb two days old.

many of their bones still have their ends almost entirely cartilaginous.

Why Epiphyses come.—Even if it were possible to point out some perfectly satisfactory use for epiphyses, it would still be necessary to consider the mechanical stimulus which causes the ossification to start, and to seek for an explanation of the fact that some epiphyses appear early, others late, while in some articular ends no epiphyses at all are developed. Of course, this inquiry opens up the larger one of why, at a certain stage in the development of the embryo and in the history of the vertebrate Phylum, deposit of bone or lime salts occurs at all. To say that the cartilage is stiffened thereby is simply stating the effect, not the cause. Probably the answer to the riddle is a chemical one, but we may fairly consider whether the rough methods of the anatomist may not give some suggestions for further research as far as the epiphyses are concerned. The first suggestion that occurred to me was that intermittent pressure might account for an increased vascularity in the articular end of the bones, and so lead to deposit of lime salts, and this was favoured by the fact that most epiphyses appear after birth; but clearly this would not account for the lower end of the femur and head of

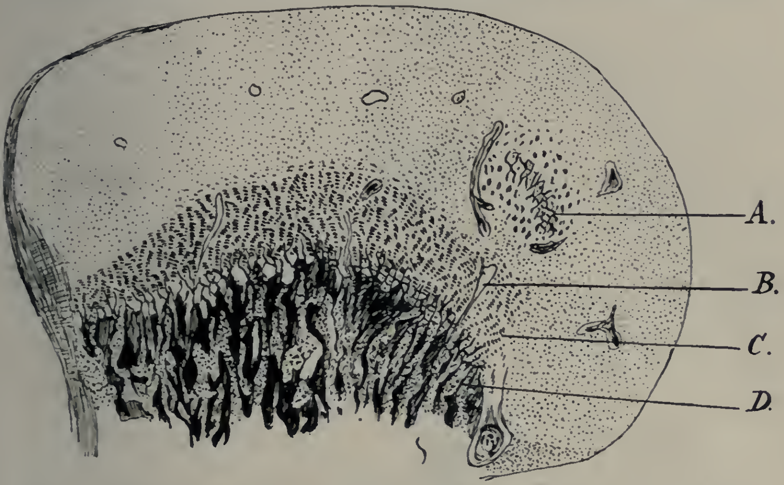

FIG. 8.—Upper end of humerus of deerlet (Tragulus) before birth, seen with a 2-inch objective. *A*, epiphysis; *B*, vessel; *C*, zone of calcifying cartilage; *D*, bone of diaphysis.

the tibia, which show bony deposits at the time of birth, and it is altogether inconsistent with the fact that many Ungulates have all their epiphyses before they are born. It is also negatived by the appearance of the epiphyses in the very centre of the cartilaginous end, where pressure must be least. It is true to a certain extent that they begin to appear in the terrestrial vertebrates, but in the aquatic mammals, like the whales, sea cows, and seals, they are just as well developed as in the terrestrial mammals. There is one fact, however, which makes me think that the effects of pressure should not be entirely set on one side, and that is the behaviour of the upper end of the ulna: in the mammals there is no articular epiphysis here, only the traction one, which below man seldom encroaches on the articular surface of the joint. Professor Fawcett lately demonstrated a second one, which is also clearly of a traction or non-articular character. In the reptiles an articular epiphysis as well as a traction one is found, and it will be noticed that in these animals the ulna receives its share of the weight of the body, while in the mammals it hardly does anything in this way, as the broad head of the radius usually lies right in front of it and takes all the pressure. Another explanation was suggested to me by a

FIG. 9.—Ulna of monitor lizard (Varanus). *A*, upper calcified articular epiphysis; *B*, lower calcified articular epiphysis; *C*, separate olecranon.

conversation with Mr S. G. Shattock, who pointed out to me that in certain tumours containing cartilage, calcifications often occurred, always in the deepest part of the cartilage, and that when once this deposit of lime salts had taken place vessels rapidly grew in from the surrounding fibrous and vascular parts, and ossification succeeded the calcification. This would mean that epiphyses begin as a degenerative process in the least vascular part of the cartilaginous end of the bone, that is to say, the centre of it, and one would expect that the larger the mass of cartilage the less well-nourished would the centre of it be, and so the more liable to the early deposit of lime salts. This theory, then, is in harmony with the two main laws which we have seen govern epiphyses—(1) that they appear in the centre of their cartilage, and (2) the larger the cartilage the earlier will the epiphysis appear. This, however, is entirely a speculative suggestion.

If some light has been thrown on the appearance of the epiphyses, we are still quite in the dark as to why the ossification of the diaphysis should be checked at the future epiphysial line. An explanation which has probably occurred to many people is, that the perichondrium is reflected off near the articular ends to form the capsule of the joint, and so the extremity is less well-nourished, but in bones like the humerus and femur the reflection of the capsule does not correspond with the epiphysial line, and in the spines of the vertebræ, where there is no reflection off of the perichondrium, ossification only extends to a certain distance from the extremity, leaving the cartilaginous end to be ossified by a separate centre.

Possibly the direction of the nutrient artery may have something to do with the fact that at one end the diaphysial bone extends farther than at the other. It is perhaps the best known law of epiphyses that the one towards which the artery runs is the last to appear and the first to join. The reason it is the last to appear is, I have no doubt, because the cartilage at that end is smaller, owing to the diaphysial bone having encroached farther, so that the appearance of the epiphysis is only secondarily dependent on the direction of the artery, even if it be so at all. A very good example of this is the lower end of the human fibula: the artery is directed, as usual, away from the knee, but the lower cartilaginous end of the bone, towards which it runs, is, contrary to the general rule, larger than the upper, and the epiphysis appears in the lower end first, thus showing that the size of the cartilaginous end has a more important relation to the appearance of an epiphysis than the direction of the artery has. I have paid a good deal of attention to the direction of nutrient foramina in the mammalia, and have found that, while no doubt the general rule that they run towards the elbow and away from the knee holds good, there are numerous exceptions, especially in the humerus, radius, and femur. For instance, the artery runs away from the elbow in the humerus of the zebra and tapir, and in the radius of the deerlet, the dog, the antelope, and the horse; while it runs towards the knee in the femur of the rabbit, hare, sloth, dog, red deer, gnu, pig, and rock kangaroo, and for this reason I am not inclined to lay very much stress upon any deductions drawn from its constant direction in man.

ON IMBRICATION OF THE PAPILLARY RIDGES IN MAN.

By WALTER KIDD.

THE papillary ridges on the palmar and plantar surfaces in man are arranged like the ridges of a ploughed field which have been flattened down by such an agency as that of a light roller passed over them. Thus a relatively broad surface in which the orifices of the sudoriparous glands are seen is presented, and the two sides of each ridge pass into the adjoining furrows at the same angle. This arrangement is the normal one in man and other primates. It is figured in certain classical text-books,[1, 2] in drawings of sections of the skin, in a manner which seems too diagrammatic, for the tops of the ridges are there represented as bluntly-pointed instead of being level. This shape of the ridges can be easily ascertained in the living subject with a lens if care be taken to examine the surface in profile in a strong light.

But closer examination of various regions of the palmar surface has shown that there are exceptions to the above rule as to the contour of the ridges. On the terminal phalanges of all the digits, and in a diminishing degree on the 2nd and 1st phalanges, there is a departure from the normal arrangement. On these regions the papillary ridges are imbricated, and the distal edge of each ridge projects slightly above the level of the proximal edge. The effect of this is that the papillæ, covered by their epidermis, are more closely in contact with any surface if the digits are passed in a distal or forward direction than if they are passed over the surface in a proximal direction. In the exercise of a special discrimination of a more or less rough surface, the action of passing the pulps of the digits away from the body is followed instinctively, and the arrangement here described and figured supplies the anatomical reason for this fact. It is obvious that the elevated position of the tactile bodies here given subserves the higher development of the

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[1] Quain's *Anatomy* (1893), vol. i. pt. ii. p. 413, fig. 471.

[2] Gray's *Anatomy* (1901) [65].

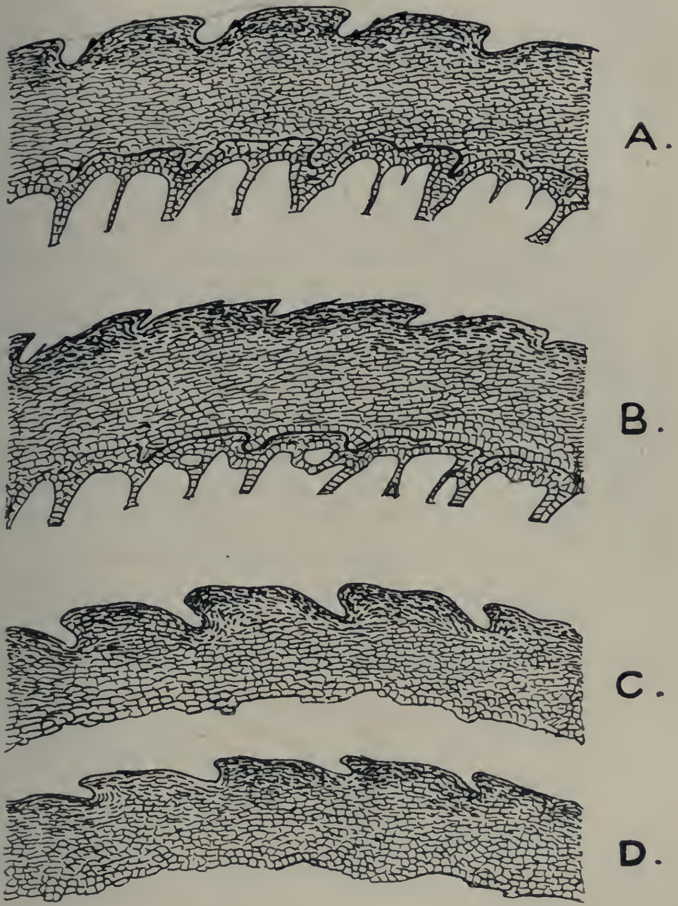
sense of touch, and this small character of the ridges must be looked upon as a special adaptation of some value to man. On those regions where no imbrication of the ridges is found sensation is less acute.

On the terminal phalanges the varied patterns classified by Dr Francis Galton as arches, loops, and whorls have the effect of so arranging the ridges that in different digits of the same hand, and in different individuals, a somewhat varied degree of imbrication of the ridges comes into play.

On the tips of the digits the ridges lie in wide curves concentric with the free edges of the nails, and over the rest of the terminal phalanges are arranged either in wide ellipses inclosing an arch or a loop, or in oval or circular patterns inclosing a whorl. Thus at each border of the terminal phalanges the imbrication of the ridges is more or less obliquely arranged towards any surface over which the digits are passed, and this small detail has some confirmation in the tendency which one naturally feels, in examining critically any surface, to pass the digits obliquely across it rather than straight forward. On the tip of the 1st digit (pollex) the ridges are somewhat differently placed, and instead of being curved and concentric with the nail, they are oblique, so that they are mainly at a right angle to any opposing surface on which the hand may be placed in examining it as to its quality or degree of roughness. The position of this digit in the normal action of the hand is slightly pronated, and the peculiar arrangement of the ridges on its tip is doubtless correlated with that position.

On the 1st phalanx of the 1st digit and the 1st and 2nd phalanges of the other four digits the imbrication becomes less marked, though it is usually present, and here the ridges lie chiefly in a transverse direction, though in certain individuals they are oblique, in varying degrees. But in whatever way they are disposed on these phalanges the imbrication comes into play, and is of some value according to its degree of development.

In regard to imbrication of the ridges, the foot in many cases shows a remarkable difference from the hand. In figures C and D are shown sections from the skin over the hallux and 1st metatarso-phalangeal joint in the case of a man with a large, well-formed foot, in which the imbrication of the ridges in both



DESCRIPTION OF FIGURES.

A. Manus, human, 5th digit terminal phalanx, thin section at right angles to papillary ridges, imbrication distal.

B. Manus, human, 5th digit terminal phalanx, thick section at right angles to papillary ridges, imbrication distal.

C. Pes, human, hallux terminal phalanx, thick section at right angles to papillary ridges, imbrication proximal.

D. Pes, human, plantar surface, over metatarso-phalangeal joint, thick section at right angles to papillary ridges, imbrication proximal.

regions is in a proximal direction. In the foot a proximal imbrication of the papillary ridges has evidently the effect of presenting them more efficiently to the underlying surface during flexion of the fore part of the foot in normal walking. I am at present engaged in examining as many feet as possible, with a view to ascertaining if this proximal imbrication is constant.

The palmar and plantar surfaces of certain monkeys, *Cebus fatuellus*, *Macacus silenus*, *Macacus cynomologus*, *a Mangabey*, *Cynocephalus porcarius*, *Papio hamadryas*, and *Lemur catta*, have been examined with a strong lens, and by this method no imbrication has been found. But certain exceptions to this have appeared when sections of the skin have been examined microscopically as follows:—*Cynopithecus niger*, manus, 16 sections showed two regions with imbrication of ridges; pes, 16 sections showed six regions with imbrication of ridges. *Lemur rufifrons*, manus, 4 sections showed one region with imbrication. *Cercopithecus cynosurus*, manus, 3 sections, no imbrication.

No anthropoid ape has been examined, as no dead specimen can be obtained, and this close examination in a very bright light cannot be carried out with these timid creatures.

SKULLS FROM THE ROUND BARROWS OF EAST YORKSHIRE. By WM. WRIGHT, M.B., D.Sc., F.R.C.S., *Demonstrator of Anatomy, University of Birmingham.* (PLATES XLV.–L.)

(*Continued.*)[1]

SKULL 17 is that of an adult female. The right side of the cranium posteriorly is wanting—rendering the accurate determination of the index of breadth impossible. The skull is, however, undoubtedly dolichocephalic. The molar teeth are not markedly flattened, nor are the sutures of the vault closed.

The coronoid and condyloid processes of the mandible are unusually low, and the ramus unusually wide. The genial tubercles are represented by a sharp spine 4 mm. in length. The skull is orthocephalic and orthognathic. The temporal portions of the frontal bone are flattened, giving it an ill-filled appearance. The teeth are marked by brown vertical fissures.

Norma Verticalis.—It is a typical example of the class named Pentagonoides subtilis.

Norma Lateralis.—It closely resembles the skull described and figured by Sergi, and by him termed Ellipsoides africus sphyroides.

Norma Facialis.—It is of the pentagonal type.

Norma Occipitalis.—It is pentagonal, with a slight and shallow concavity just above the mastoid processes, indicating a somewhat ill-filled condition of the skull in this region.

This skull has a further interest, in that it has the closest resemblance possible, if viewed from the norma facialis, to the skull figured by Topinard from the Reihengräber. From the norma lateralis the resemblance is not quite so close.

SKULL 18. This skull was found in the same barrow as the one last described. It is that of a male upwards of forty years of age.

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[1] First part published in vol. xxxviii. of this Journal, p. 119.

It is very markedly dolichocephalic, having so low a breadth index as 65·53. The face, with the exception of the lower jaw, was entirely wanting. There was distinct overlapping of the right lower central incisor by the left, due to overcrowding. The coronal suture was closed, the sagittal and lambdoidal sutures only partially so. One would have perhaps *a priori* expected the sutures to close in a reverse order, considering the great length of the skull. The mental protuberance was bifid, and the angle of the jaw was square and dependent.

Norma Verticalis.—It is an excellent example of the class called Ellipsoides pelasgicus longissimus.

Norma Lateralis.—The above classification is confirmed if the skull be regarded from this aspect.

Norma Occipitalis.—It is pentagonal, the upper lateral boundaries being straight, giving it an ill-filled appearance.

SKULL 19. This is the skull of a child nine years old, judging from the fact that the lateral incisors and canine teeth were still not erupted. The skull is brachycephalic, hypsicephalic, orthognathous, chamæoprosopic, and mesorhine. The sutures of the calvarium are all open; the bregma is occupied by a large Wormian bone the long axis of which is sagittal, and which measures 30 by 15 mm. The pterion was in H on both sides, the left spheno-parietal suture measuring 13 mm., the right 11 mm.

Norma Verticalis.—It belongs to the ovoid group of skulls.

Norma Lateralis.—From this aspect it has a box-shaped appearance belonging to the cuboid group of skulls.

Norma Facialis.—It is somewhat intermediate between the ovoid and triangular types.

Norma Occipitalis.—It is a broad pentagon with a slight sagittal elevation above.

With the body were found a knife of black flint and a food vase.

SKULL 20 is that of a male upwards of forty years of age. It is mesaticephalic and leptoprosopic. It has very marked supraciliary eminences. The glabella is prominent, and the nasion is sunken. The whole length of the upper border of the orbit is thickened, as is also the external angular process. All the osseous asperities are exaggerated. The chin and angle of mandible are well formed; the latter is tuberculated. The molars are flattened. The coronal and sagittal sutures are closed; the lambdoidal is in process of closing.

Norma Verticalis.—It belongs to the sphenoid group, being slightly longer than the most typical examples, however.

Norma Lateralis.—It resembles the skull figured by Sergi, which he terms Sphenoides tetragonus.

Norma Facialis.—It is a long example of the parallelepipedoidal type.

Norma Occipitalis.—It is a high pentagon.

With this body was found a flint dagger, a flint knife, and a stud or button of jet.

Skull 21 is that of an adult male of middle age. It is mesaticephalic, chamæocephalic, orthognathous, and chamæoprosopic. The supraciliary eminences were very marked; I estimated their thickness to be 20 mm. The glabella is prominent, and the nasion is sunken. The metopic suture was persistent. The sagittal suture was closed at the obelion; the coronal suture was open. There were two large Wormian bones in the lambdoidal suture, one on either side close to the lambda. There was a very deep canine fossa. All the muscular asperities were well marked.

Norma Verticalis.—From this aspect it appears to be a long example of the ovoid type.

Norma Lateralis.—It resembles the type Ellipsoides Isocampylos in having an even curve of medium height merely broken by the supraciliary eminences, and by the asperities for muscular attachment.

Norma Facialis.—It is an example of the parallelepipedoidal type.

Norma Occipitalis.—A pentagon of medium height.

With this body were found the leg bone of an ox and some peat mould.

Skull 22 is merely a male calvarium with a small portion of the base of the cranium and the lower jaw. The coronal and sagittal sutures are closed, the lambdoidal is in process of closing. The sagittal suture lies at the bottom of a longitudinal groove. The glabella and supraciliary eminences are prominent, the nasion and ophryon are sunken. The anterior and middle clinoid processes are well developed and united. The chin is bifid.

Norma Verticalis.—It is a very good example of the type Ellipsoides pelasgicus longissimus.

Skulls 21 and 22 were found in the same barrow, the former being in the primary interment, and the latter in a secondary one.

With the body to which Skull 22 belonged were found a bronze dagger, a handle of bone with two rivets, some curved pieces of bronze, and a bow or handle of a small bucket of wood, containing probably food. This body, indubitably, therefore, was interred in the Bronze Age, and yet the skull of it is extremely long, being an example of the longest type of skull known. The interesting fact, therefore, is disclosed that in the Bronze Age in Yorkshire there were long-headed individuals worthy of an elaborate interment. We are further reminded that we should not associate too much the Bronze Age and round barrows with a round-headed race.

Skull 23 is that of an adult female. It is mesaticephalic, orthocephalic, orthognathic, chamæoprosopic, and mesorhine. The coronal, sagittal, and lambdoidal sutures are all open.

The metopic suture is persistent. There is an epipteric bone on the left side; the pterion is incomplete on the right side.

There are distinct signs of the suture between the squamous portion of the mastoid and the mastoid proper. The chin is well developed, and the angle of the jaw is slightly tuberculated.

Norma Verticalis.—It belongs to the ovoid group.

Norma Lateralis.—It resembles the skull called Ellipsoides cuneatus, but has a straighter forehead, and is considerably higher. From this norma it shows a well-marked post-coronal depression.

Norma Facialis.—It is ovoid.

Norma Occipitalis.—It is a rounded pentagon a little above medium height.

With this skull were found a necklace of jet, discs, a pricker of bronze, and a food vase.

SKULL 24 is that of an adult male. It is mesaticephalic, hypsicephalic, orthognathous, chamæoprosopic, and leptorhine.

The coronal suture is closed near the bregma and the pterion.

The sagittal suture is closed only at the obelion. The lambdoidal suture is open. The supraciliary eminences are marked. The supraorbital rim is swollen and the external angular process thickened. All the asperities for the attachment of muscles and ligaments are exaggerated, such as the temporal ridge, inion, external occipital crest, torus occipitalis transversus.

There is a deep canine fossa.

Norma Verticalis.—The skull is somewhat intermediate between a typical ovoid and a typical beloid type.

Norma Lateralis.—From this aspect the skull appears to be intermediate between Isobathys Siculus and Beloides Adriaticus.

The otherwise even curve described by the cranial vault as seen from this aspect is broken in a very distinct manner at the lambda, due to a flattening of the post-parietal region whereby the superior occipital squame is made to occupy a plane much posterior to that occupied by the posterior part of the parietal bone.

Norma Facialis.—It is parallelepipedoidal.

Norma Occipitalis.—A high, rounded pentagon.

With this body were found the burnt bones of a youth, the head of a dog, and some decayed bones.

SKULL 25 is that of an adult female. It is mesaticephalic, chamæocephalic, chamæoprosopic, and leptorhine. The sutures of the cranial vault are all open. The pteria are in H; the spheno-parietal suture on the left side measures 12 mm.

There is a supraorbital foramen on either side, also grooves on the frontal bone for the divisions of the supraorbital nerves.

Norma Verticalis.—It is intermediate between the ovoid and the pentagonal types.

Norma Lateralis.—The vault describes a beautiful, almost uniform curve, and the skull resembles the type called Isobathys Siculus.

Norma Facialis.—It is ovoid.

Norma Occipitalis.—A low, rounded pentagon.

With this body were found a food vase, the point of a bronze pricker, spear head, root end of a stag's horn, burnt human bones, and chippings of flint.

The Skulls 23, 24, 25 were obtained from the same barrow.

SKULL 26 is an adult male skull. It is very brachycephalic, orthocephalic, orthognathous. The sagittal suture is almost entirely closed; the coronal and lambdoidal are open, the latter having on each side a Wormian bone in it. Here again *a priori* we would have expected in a very brachycephalic skull that the sagittal suture would have been later than the other sutures in closing, whereas we find that it is earlier. There was only one parietal foramen, but it was a large one. The supraciliary eminences and external angular processes were greatly thickened.

There were deep canine fossæ. There was an extremely narrow auditory meatus on one side; the condition seems to have been congenital. The molar teeth were flattened. The squamous portions of the temporal bones had sprung somewhat from the side of the cranium, due either to gravitation changes during life, or to posthumous distortion.

Norma Verticalis, Norma Lateralis.—It is a typical example of the type called Sphenoides latus.

Norma Facialis.—It is parallelepipedoidal.

Norma Occipitalis.—A broad, somewhat rounded pentagon.

With this skeleton were found some flint flakes and pieces of animal bones.

SKULL 27 is that of a female. It is mesaticephalic, hypsicephalic, orthognathous, leptoprosopic, and leptorhine. There are four large Wormian bones near the lambda, three other smaller ones in each lambdoidal suture. The suprameatal spines and the torus occipitalis transversus are well marked. The frontal and parietal eminences are distinct. There is a supraorbital foramen on the left side. The molar teeth are not flattened.

Norma Verticalis.—It is distorted, but probably belonged to the Ellipsoid group.

Norma Lateralis.—It is an example of the type called Ellipsoides Isocampylos.

Norma Facialis.—Ellipsoid.

Norma Occipitalis.—A pentagon of medium height.

With this skeleton were found flint tools, animal and human bones.

SKULL 28 is that of an adult male. It is dolichocephalic.

The coronal and lambdoidal sutures are open; the sagittal is closed, there being a slight sagittal ridge. The supraciliary eminences are marked without being exaggerated; the external angular process is thickened; the inion is very pronounced, projecting from the surface of the cranium some 6 mm. The malar eminences are marked, and the tubercle on the posterior border of the malar bone is large.

Norma Verticalis, Norma Lateralis.—It is an excellent example of the type Ellipsoides pelasgicus longissimus.

Norma Facialis.—Parallelepipedoidal.

Norma Occipitalis.—A high pentagon, having an ill-filled appearance and a trace of a sagittal ridge.

Skulls 27 and 28 were obtained from the same barrow.

In the grave in which Skull 28 was found there were also the skeleton of a child, a flint knife, and a deerhorn pick.

SKULL 29 is that of an adult male. It is dolichocephalic.

The supraciliary eminences are very exceptionally prominent, and overhang the orbits. The glabella is prominent, and the nasion and ophryon are depressed.

The sagittal suture is closed; the coronal suture is normal; the left lambdoidal suture has a Wormian bone in it.

The external angular process is much thickened. There is a supraorbital foramen on the left side.

Norma Verticalis.—It belongs to the class called Ellipsoides pelasgicus longissimus.

Norma Lateralis.—It resembles the Neanderthal skull, particularly in the lowness of the forehead and the exaggeration of the supraciliary eminences. It differs from it in having an almost vertical decline in the occipital region.

Norma Facialis.—Parallelepipedoidal.

Norma Occipitalis.—A high, rounded pentagon.

With this skull were found a bone pick, human and animal bones.

Skull 30 is that of a male. It is dolichocephalic, and has some resemblance to the skull last described. The supraciliary eminences jut forwards, the external angular process is thickened. There are well-marked temporal ridges and inion.

The pterion is in H, the spheno-parietal suture measuring 7 mm. There is a Wormian bone at the lambda, and two others in the lambdoidal suture.

Norma Verticalis.—Ellipsoides pelasgicus longissimus.

Norma Lateralis.—The forehead is not so low as in the case of Skull 29. The superior occipital squame bulges backwards somewhat, otherwise it is a good example from this aspect of Ellipsoides pelasgicus longissimus.

Norma Facialis.—The face is too fragmentary to allow of classification from this aspect.

Norma Occipitalis.—A pentagon, somewhat ill-filled, with a trace of a sagittal elevation.

With this body were found a food vase, flints, and burnt human bones.

Skull 31 is that of an adult female. It is brachycephalic, hypsicephalic, orthognathous, chamæoprosopic, and mesorhine.

The supraciliary eminences are only faintly discernible.

The frontal and parietal eminences are apparent. The sutures of the vault are open and normal.

The pteria are in H. The left spheno-parietal suture measures slightly more than does the right one, namely, 22 mm. to 21·5 mm. There is a distinct paramastoid process on the left side. The temporal portions of the skull are convex.

Norma Verticalis.—It belongs to the sphenoid group of skulls, being a short and broad example.

Norma Lateralis.—It is a good example of Sphenoides tetragonus.

Norma Facialis.—It is a typical ovoid.

Norma Occipitalis.—A pentagon, somewhat flattened above.

With this body was found the body of a child.

Skulls 30 and 31 were obtained from the same barrow.

In the grave with Skull 31 and the corresponding skeleton were many other human bones.

SKULL 32 is that of a male. It is mesaticephalic, chamæoprosopic, and mesorhine. The supraciliary eminences are marked, the external angular processes are thickened. The sagittal suture is closed; the lambdoidal is closed at the lambda; the metopic suture is only closed above; the coronal suture is not closed.

There is a Wormian bone at the left asterion. The temporal ridges, malar eminence, and inion are all well marked.

The molar teeth are flattened; the angle of the mandible is tuberculated.

Norma Verticalis.—A typical example of the Ellipsoid group.

Norma Lateralis.—The inferior occipital squame is unusually low, being lower than the tip of the mastoid process. It resembles the type called Ellipsoides embolicus.

Norma Facialis.—Parallelepipedoidal.

Norma Occipitalis.—A rounded pentagon of slightly more than medium height. With this body were a flint disc, human and animal bones.

SKULL 33 is that of a female. It is brachycephalic, hypsicephalic, chamæoprosopic, orthognathous, and mesorhine. The frontal and parietal eminences are discernible.

Sutures of the vault in large measure closed, also those forming the pterion. There are signs of the metopic suture persistent at its upper and lower extremities. The angle of the mandible is tuberculated, and the masseteric fossa is ridged.

The molar teeth are flattened.

Norma Verticalis.—It is Ellipsoid.

Norma Lateralis.—It has a somewhat rectangular appearance, due to the forehead being somewhat vertical, and to the inferior occipital squame, as in the last skull, being situated below the mastoid process. It resembles from this aspect the type named by Sergi, parallelepipedoidal.

Norma Facialis.—Ellipsoid.

Norma Occipitalis.—A rounded pentagon.

With this body was found an ornamental food vase.

Skull 34 is that of a male. It is mesaticephalic, orthognathous, leptoprosopic, and leptorhine. The asperities for muscles and ligaments are all very well developed. The supraciliary eminences, the upper border of the orbit, and the external angular processes, are thickened. There are deep canine fossæ. There are supra-orbital foramina.

There is also a bony arch over the great occipital nerve as it crosses the superior curved line of the occipital bone.

There is an exostosis on the mandible, developed apparently in the fibres of the depressor anguli oris.

A shallow groove passes transversely over the vertex behind the coronal suture. The lambdoidal and sagittal sutures are closed; the coronal is in process of doing so.

Norma Verticalis.—It belongs to the Ellipsoid group.

Norma Lateralis.—The skull is ellipsoid, although, as with the last skull, it shows a tendency to become rectangular.

Norma Facialis.—Parallelepipedoidal.

Norma Occipitalis.—A high pentagon.

With this body were found the bones of a pig.

This skull and Skull 33 were obtained from the same barrow, and if we discount the sexual characters, such as the sloping forehead and marked supraciliary eminences of the male and the flat, vertical forehead of the female, they possess a marked resemblance to each other. With Skull 34 were human and animal bones.

Skull 35 is that of a male. It is brachycephalic. The supraciliary eminences, upper border of orbit, and external angular processes, are thickened. The asperities for muscles and ligaments are well developed. The sagittal suture is closed above and below; the lambdoidal is open. There is a partly ossified falx cerebri.

Norma Verticalis.—It is of the sphenoid group.

Norma Lateralis.—It resembles very closely the type called Sphenoides latus.

Norma Facialis.—It is quadrate.

Norma Occipitalis.—It is a broad pentagon. With this skeleton were found chips of flint and a perforated hammer head.

Skull 36 is that of a male. It is mesaticephalic, orthocephalic, orthognathous, and leptorhine. The supraciliary eminences, upper border of the orbit, and external angular processes are thickened. The inion and torus are very well marked. The coronal suture is closed near the bregma and pterion. The sagittal suture is only closed at the obelion.

The lambdoidal suture is not closed.

Norma Verticalis.—Ellipsoid.

Norma Lateralis.—Ellipsoid Isocampylos.

Norma Facialis.—Parallelepipedoidal.

Norma Occipitalis.—A high pentagon, somewhat ill-filled. A flint knife and some human bones were found with this skeleton.

Skull 37 is that of a male. It is mesaticephalic, leptoprosopic, and mesorhine. Supraciliary eminences, upper rim of orbit, and external angular processes are all thickened. The coronal suture is open, the sagittal suture is closed posteriorly; the lambdoidal is partly closed, there being in it a very large Wormian bone on the right side, measuring 51 mm. by 40 mm.

All asperities well developed. An abscess cavity exists in connection with the second left lower bicuspid.

Norma Verticalis.—Ellipsoid, with also a slight pentagonal appearance, due to the backward bulge of the superior occipital squame.

Norma Lateralis.—It is Ellipsoides Isocampylos, with the exception of the forementioned bulge of the occipital squame.

Norma Facialis.—Parallelepipedoidal.

Norma Occipitalis.—Rounded pentagon of medium height.

With this were interred a flint knife and the teeth and bones of an ox.

Skull 38 is that of a female. It is mesaticephalic, chamæoprosopic, orthognathous, and mesorhine. The frontal and parietal eminences are discernible. There is a supraorbital foramen on the right side. There is an abscess cavity in connection with the first right upper bicuspid. It is an old skull, most of the alveolar portion of the jaws having been absorbed. All the sutures are closed.

Norma Verticalis.—It is a long pentagonal skull.

Norma Lateralis.—It is an excellent example of what Sergi calls the Parallelepipedoides Sardiniensis type.

Norma Facialis.—Ovoid.

Norma Occipitalis.—It is pentagonal, the lower lateral margins sloping downwards and inwards.

With this body were found a child, some cremated remains, the antler of a red deer, and some flint.

Skull 39 is a male skull in a fragmentary condition. It is brachycephalic. The supraciliary eminences only fairly marked. The temporal portions of the frontal are convex.

The sutures are open. There is a distinct keel along the former site of the metopic suture. The chin is bifid and square; the angle of the mandible is somewhat rounded.

Norma Verticalis.—Ovoid.

Norma Lateralis.—The Isobathys Siculus division of the ovoid type.

Norma Facialis.—Ovoid.

Norma Occipitalis.—A broad pentagon.

With this skull were found worked flints and animal bones.

Skull 40 is also a male skull in a fragmentary state. It is mesaticephalic. The supraciliary eminences and asperities are well developed.

Norma Verticalis.—Ellipsoid.

Norma Lateralis.—Ellipsoides Isocampylos, although the upward slope of the vertex from the frontal eminence to the obelion gives it also something of the appearance of Trapezoides africus.

Skull 41 is that of a male. It is mesaticephalic, orthocephalic, orthognathous, leptoprosopic, and leptorhine. The supraciliary eminences and the various asperities are well developed.

The rim of the orbit is not thickened, but on the contrary is thin and sharp. The sutures of the vault are normal.

Norma Verticalis.—It is ellipsoid, with a slight pentagonoid appearance.

Norma Lateralis.—The isocampylos nature of the forepart of the cranium is interrupted posteriorly by a flattening from the obelion to the lambda; another flattening from the lambda to the inion; and yet another from the inion to the opisthion.

Norma Facialis.—Parallelepipedoidal.

Norma Occipitalis.—High pentagon.

The Skulls 38, 39, 40, and 41 were all obtained from the same barrow.

SKULL 42 is that of a female. It is mesaticephalic, hypsicephalic, orthognathous, and leptorhine. All the sutures of the vault are open; there are two Wormian bones in the left lambdoidal suture. The left spheno-parietal suture measures 17 mm.

Norma Verticalis.—Ellipsoid.

Norma Lateralis.—Ellipsoid.

Norma Facialis.—Quadrate.

Norma Occipitalis.—A rounded, high pentagon.

With this skull was found a flint knife.

SKULL 43 is that of a male. It is mesaticephalic and leptorhine. The supraciliary eminences and asperities are all marked.

The sagittal suture is closed except near the bregma; the lambda and adjoining portions of the lambdoidal sutures are closed; the coronal suture is open.

Norma Verticalis.—A long example of the pentagonoid type.

Norma Lateralis.—Ellipsoides Isocampylos, with the exception that the even curve is interrupted by a slight flattening of the vertex in the posterior part of the parietal region.

Norma Facialis.—Parallelepipedoidal.

Norma Occipitalis.—A high pentagon.

With this skull was found the antler of a roebuck.

Skull 44 is that of a male. It is dolichocephalic, chamæocephalic, orthognathous, leptoprosopic, and leptorhine.

The supraciliary and malar eminences are not well marked.

The asperities for muscles and ligaments, however, are well marked. The ramus of the mandible is very wide. The angle of the jaw is square, and marked by tubercles. The masseteric fossa is ridged for the insertion of the tendinous portion of the masseter muscle. The coronal suture is closed near the pterion. The sagittal suture is closed posteriorly. There are two large Wormian bones in the left lambdoidal suture.

The molar teeth are flattened.

Norma Verticalis, Norma Lateralis.—Ellipsoides pelasgicus longissimus.

Norma Facialis.—Parallelepipedoidal.

Norma Occipitalis.—A rather low pentagon, with a trace of a sagittal elevation.

Skull 45 is a male skull. It is brachycephalic, hypsicephalic, orthognathous, and leptorhine. The supraciliary eminences, upper rim of the orbit, and external angular processes are thickened. The asperities are well developed. The coronal and sagittal sutures are normal and open. There are two Wormian bones in the left lambdoidal suture. There is an epipteric bone on the left side, measuring 17 mm. by 2 mm. There are three small mental foramina on the left side.

Norma Verticalis, Norma Lateralis.—Sphenoides latus.

Norma Facialis.—Quadrate.

Norma Occipitalis.—A rounded pentagon.

Skull 46 is a male skull. It is mesaticephalic, orthocephalic, mesognathous, leptoprosopic, and mesorhine. The glabella is prominent, and the nasion is sunken. The supraciliary eminences and asperities are well developed. There is a supraorbital foramen on the right side. The coronal suture is open, the sagittal is closed only at the obelion; the lambda and adjacent portion of the lambdoidal suture are closed.

Norma Verticalis.—Ellipsoides largo.

Norma Lateralis.—On the whole it resembles most the type Ellipsoides Isocampylos, but the forehead bulges forwards more, and there is a flattening in the posterior parietal region which is not found in the most typical examples of this class.

Norma Facialis.—Parallelepipedoidal.

Norma Occipitalis.—A rounded pentagon of medium height. With this skull were found a flint dagger, two flint knifes, a jet ring, and amber stud.

Skull 47 is that of a female. It is brachycephalic, hypsicephalic, orthognathous, leptoprosopic, and mesorhine. The sutures are all normal. The left spheno-parietal suture measures 11·5 mm., the right suture measures 13 mm.; this is the first time I have found the length of the right suture exceed that of the left in this series of skulls.

Norma Verticalis.—Sphenoides.

Norma Lateralis.—Sphenoides tetragonus.

Norma Facialis.—Ovoid.

Norma Occipitalis.—A pentagon, with the parietal eminences well marked, and yet the skull appears well filled.

With this body were found the bronze point of a small bodkin and some splinters of flint.

Skull 48 is that of a female. It is brachycephalic, leptoprosopic, and leptorhine. Although the supraciliary eminences are well marked, the other osseous asperities are not. There are two supraorbital foramina on the right side for the two divisions of the supraorbital nerve. The sagittal suture is closed at the obelion; the coronal and lambdoidal are open. The pteria are in H. The spheno-parietal suture measures 13 mm. The frontal and parietal eminences are marked.

Norma Verticalis.—Sphenoid.

Norma Lateralis.—Sphenoides tetragonus.

Norma Facialis.—Ovoid.

Norma Occipitalis.—A high pentagon.

With this skeleton were interred some flints and potsherds.

Skull 49 is that of a female. It is very brachycephalic, hypsicephalic, orthognathous. The supraciliary eminences and their asperities are not well marked. The frontal and parietal eminences are marked.

The sutures are normal, except for a Wormian bone on the left side in the lambdoidal suture. The left pterion is in H, the spheno-parietal suture measuring 20 mm. on the left side, 18 mm. on the right. There are two supraorbital foramina on the left side.

Norma Verticalis, Norma Lateralis.—Sphenoides latus.

Norma Facialis.—Too incomplete for classification.

Norma Occipitalis.—Medium broad pentagon.

Skull 50 is that of a female. It is brachycephalic, orthocephalic, and orthognathous. The supraciliary eminences are discernible, the other osseous asperities are not. The frontal and parietal eminences are well developed. The sagittal suture is closed; the coronal and lambdoidal are partially so.

A shallow longitudinal groove runs along the site of the sagittal suture. There is a supraorbital foramen on the left side.

Norma Verticalis.—Ovoid.

Norma Lateralis.—It is a good example of the type called Trapezoides africus, but since the skull has been largely built up from fragments, one cannot emphasise the presence of the type.

Norma Facialis.—Ovoid.

Norma Occipitalis.—A rounded pentagon of medium height.

Skull 51 is that of a female. It is brachycephalic, chamæoprosopic, and mesorhine. The frontal and parietal eminences are well developed. The sutures are normal, except for Wormian bones at the lambda and at the left asterion.

The pteria are in H. The left spheno-parietal suture measures 18 mm. Although judging from the sutures the skull is not that of an old woman, the alveolar portion of the lower jaw is largely devoid of teeth and absorbed, due apparently to a diffuse suppurative process.

Norma Verticalis.—Ellipsoid, and also slightly pentagonal.

Norma Lateralis.—Ellipsoid. The otherwise uniform curve of the cranium is pronouncedly broken at the lambda by the backward position of the superior occipital squame.

Norma Facialis.—Ellipsoid.

Norma Occipitalis.—A pentagon of medium height.

SKULL 52 is that of a male. It is dolichocephalic and leptoprosopic. The supraciliary eminences and other asperities are well developed. The nasion and ophryon are sunken.

There is a well-marked prominence at the posterior end of the posterior root of the zygoma. The sutures are normal.

There is an abscess cavity in connection with the second upper bicuspid tooth. The temporal portions of the frontal bone are flattened.

Norma Verticalis.—Pentagonoides subtilis.

Norma Lateralis.—Ellipsoides palasgicus longissimus. The pentagonal appearance from the vertex is probably due to some flattening of the posterior parietal region as seen from this aspect.

Norma Facialis.—Ellipsoid.

Norma Occipitalis.—A pentagon of medium height.

SKULL 53 is that of a child of about six years of age. The upper central incisors are not erupted. The skull is mesaticephalic.

Norma Verticalis.—Ovoid.

Norma Lateralis.—It is somewhat box-shaped, resembling the type Cuboides procerus, due to the high forehead and the sharp occipital decline. The conceptaculæ cerebelli are almost horizontally disposed.

Norma Facialis.—Ovoid.

Norma Occipitalis.—A pentagon of considerable height.

With this body was found a wood vase, with another smaller one inverted over it. There were also a few articles made of bone.

SKULL 54 is that of a male. It is brachycephalic.

The sutures are normal. The left lower wisdom tooth is small, the right seems never to have been present.

Norma Verticalis.—Ovoid.

Norma Laterallis.—Isobathys Siculus.

Norma Facialis.—The facial portion of the skull was absent.

Norma Occipitalis.—Rounded pentagon, somewhat flattened above.

Skull 55 is that of a male. It is brachycephalic.

The sutures are open. The supraciliary eminences and other asperities are discernible. The temporal portions of the frontal bone are convex. The nasal bones are thin.

Norma Verticalis.—Ovoid.

Norma Lateralis.—The forehead is high and the occipital decline is steep, the skull being thus cuboid in shape.

With this body, in front of the face, was found a knife of black flint.

Skulls 52, 53, 54, and 55 were all obtained from the same barrow. The last three were in a fragmentary state.

Skull 56 is that of a male. It is dolichocephalic, orthocephalic, orthognathous, leptoprosopic, and leptorhine. The supraciliary eminences and other asperities are only faintly marked. The forehead is very narrow. The sutures are normal.

The left spheno-parietal suture measures 9 mm., the right measuring 11 mm. The temporal portions of the frontal bone are very flat.

Norma Verticalis.—Ellipsoides.

Norma Lateralis.—Ellipsoides pelasgicus longissimus.

Norma Facialis. — Ellipsoid, slightly pentagonal, due to flattening of the upper sides of the skull.

Norma Occipitalis.—A high pentagon, with a trace of a sagittal ridge.

Skull 57 is that of a male. It is dolichocephalic, leptoprosopic, and leptorhine. The supraciliary eminences and other asperities are well developed. All the sutures of the vault are closed. The molar teeth are worn down posteriorly and palatally above, anteriorly and labially below, due to what appears to have been some osteoarthritic change in the temporo-maxillary joint followed by subluxation of the mandible, causing the labial edge of a lower molar tooth to rub against the palatal edge of the opposing molar. The glenoid cavity, eminentia articularis, and the condylar processes of each side are flattened.

Norma Verticalis, Norma Lateralis.—Ellipsoides pelasgicus longissimus.

Norma Facialis.—Ellipsoid.

Norma Occipitalis.—A rounded pentagon.

With this skeleton were found some animal bones and a jet link.

Skull 58 is that of a female. It is dolichocephalic, orthocephalic, orthognathous, and mesorhine. The coronal and sagittal sutures are closed, the lambdoidal is open. The symphysis menti is shallow, the alveolar portion being largely absorbed.

Norma Verticalis, Norma Lateralis.—Ellipsoides pelasgicus longissimus.

Norma Facialis.—Ellipsoid.

Norma Occipitalis.—A pentagon of medium height.

With this skeleton were found some food vases.

Skull 59 is that of a male. It is mesaticephalic, hypsicephalic, orthognathous, leptoprosopic, leptorhine.

The sutures of the vault are open. The right pterion is indistinct; the left spheno-parietal suture measures 16 mm.

The supraciliary eminences and other asperities are well developed. The nasion is depressed. There is a small paramastoid process on the left side. The occipital condyles are unusually massive and dependent. The nasal bones are short, stunted, thickened, and jut almost horizontally forwards.

Norma Verticalis.—Beloid.

Norma Lateralis.—It resembles the type called Beloides Adriaticus.

Norma Facialis.—Ellipsoides.

Norma Occipitalis.—A high pentagon.

Skull 60 is that of a female. It is mesaticephalic, hypsicephalic, orthognathous, chamæoprosopic, and mesorhine.

The supraciliary eminences and other asperities are not well developed. The sutures are normal. There is a supraorbital foramen on the right side, and a groove for the nerve on the frontal bone.

Norma Verticalis.—Ellipsoid.

Norma Lateralis.—Ellipsoid Isocampylos.

Norma Facialis.—Ellipsoid.

Norma Occipitalis.—A pentagon of medium height.

Skull 61 is that of a female. It is mesaticephalic and in a fragmentary state. All the sutures are open. No asperities noticeable.

Norma Verticalis.—A broad pentagon.

Norma Lateralis.—Ellipsoides depressus.

Norma Facialis.—Ellipsoid.

Norma Occipitalis.—A low pentagon.

Skulls 59, 60 and 61 were found in one barrow; along with them were some burnt human bones.

Skull 62 is that of a male. It is mesaticephalic.

The supraciliary eminences and the other asperities are well developed. The sagittal suture is closed; the coronal and lambdoidal sutures are partly closed.

Norma Verticalis.—Ellipsoid.

Norma Lateralis.—Ellipsoides Isocampylos.

Norma Facialis.—The skull is too fragmentary to allow of classification from this aspect.

Norma Occipitalis.—A rounded pentagon.

With this body was found a black flint knife and a stud or button.

The skulls here described, and of which the various measurements have been given, were on the whole in surprisingly good condition considering the length of time they had been buried. The mode of interment is shown in the accompanying photograph of a female skeleton *in situ* (Pl. XLV.).

It will be noticed that the lower limbs are not so markedly flexed as is usually said to be the case. Behind the head is a bone hair-pin made from a tibia; in front of the face and by the left foot are seen flint knives. The skull has the typical long ellipsoid shape so frequently characteristic of the skulls from these burials; the teeth, again, are typical in their regularity and good preservation.

The skulls were, with few exceptions, those of adults of middle life. In the majority of them the sutures were entirely, or in part, open, and the teeth not markedly flattened. Almost invariably the first suture of the vault to close was the sagittal suture, the coronal and lambdoidal closing together at a later date. The sagittal began to close at the obelion, the coronal at the bregma and pterion, the lambdoidal at the lambda.

The maintenance or closure of the sutures of the vault had little apparent effect on the shape of a skull.

In Skull 18, for instance, we have a very long skull in which the coronal suture, where growth-producing length might particularly be expected to take place, has closed before an antero-posterior suture like the sagittal.

In Skull 26, again, which is very brachycephalic, the sagittal suture is closed, whilst the coronal and lambdoidal are still open.

The pteria were invariably in H. The spheno-parietal suture ranged from 7 to 22 mm. In every case but two in which the suture could be measured the left one was greater than the right. Epipteric bones were present in two skulls; in both cases they were on the left side. Wormian bones were found in fourteen other skulls, twice at the asterion, once at the bregma, three times at the lambda, and twelve times in the lambdoidal suture.

The metopic suture was open in six skulls, four of which were obtained from the same barrow.

In sixteen skulls there were supraorbital foramina, in three of them the foramina were bilateral, in two there were two present on one side, evidently for the two divisions of the nerve.

In several skulls the frontal bone was marked by sharp longitudinal grooves for the supraorbital nerve and its main branches.

Broad shallow grooves were occasionally found crossing the vertex behind the coronal suture and passing backwards along the sagittal suture or line of the superior longitudinal sinus.

In contradistinction to this last condition, as a consequence of some flattening on either side of the vault, the suture was occasionally found on a slight sagittal elevation. These sagittal grooves and elevations were no doubt respectively due to a well and ill-filled state of the cranium.

Another marked feature of these skulls was the irregularity of the cranial curve in the neighbourhood of the lambda.

As will be seen from the illustrations, not infrequently the superior occipital squame bulged backwards, giving rise to the condition known as capsulares 'hinterhaupt.'

Several of the skulls had exaggerated asperities. In some cases the supraciliary eminences were almost an inch thick. In such cases the glabella was prominent, whilst the ophryon and nasion were sunken. Such irregularities were usually associated with others for muscular and ligamentous attachments, such as prominent inion, external occipital crest, temporal ridges and oblique ridges in the masseteric fossa of the mandible.

The canine tooth produced in several skulls a prominent canine eminence with deep fossæ on either side. Other skulls, despite their belonging to the male sex, had a relatively smooth surface.

The teeth, with few exceptions, were in an excellent state; the exceptions, however, were noteworthy. In three cases there were signs of a past alveolar abscess in connection with the bicuspid teeth. The alveoli of the lower jaw were largely absorbed in two skulls, in one of which the lambdoidal suture was still open. Several skulls had carious teeth. There was distinct overlapping of the lower incisors in a few skulls, due to overcrowding. The upper wisdom tooth in one skull was of the size of a bicuspid tooth. The upper lateral incisor of the right side in one skull had never been present, and the one on the left side was unusually small.

Turning to the measurements, I found that in most cases most of those of the cranium could be taken and relied upon.

Unfortunately the same could not be said of those of the face; this is all the more unfortunate, as I am of opinion that it is from the norma facialis that most of the racial features of a skull can be observed. The measurements, however, were only taken when their reliability could be trusted. This explains their frequent paucity.

Thirty-two skulls were those of males, twenty-six those of females, and of four the sex was doubtful.

The cephalic index of breadth ranged from 65 to 92.

Twenty of the skulls were dolichocephalic, eighteen were brachycephalic, and twenty-four mesaticephalic.

The cranial capacity as taken by means of millet seed ranged from 1345 to 1620 c. cm. in the female, and from 1460 to 1515 c. cm. in the male, the average being, in the case of the former, 1404 c. cm., and 1487 c.cm. in that of the latter. No case of prognathism was observed amongst the skulls, they being either mesognathous or much more frequently orthognathous. The anterior nares were found to be either mesorhine or leptorhine.

The skulls were not possessed of an unusual height: with only two exceptions they were ortho- or hypsicephalic. The palatal index averaged 114; that of ten English skulls examined by Flower was 117. The nose projected well from the forehead. The naso-malar index, estimated according to the method of Oldfield Thomas, was 109—sixteen Caucasian skulls examined by him having one of 111. The zygomata were well within the contour of the crania from the norma verticalis, the stephano-zygomatic index being 97. The teeth were microdont; the molar index averaged 41·3, the exact index arrived at by Flower for British races. Concerning the indices suggested of late by Professor Arthur Thomson, I found as he found, and as we should *a priori* expect, that the mandibular index was greater with the dolichocephalic than with the brachycephalic skulls; in other words, the longer the skull, the greater the gonio-symphysial length of the mandible compared to the bicondyloid width. The mandibular index of nine dolichocephalic skulls averaged 87, of nineteen mesaticephalic 86, and of eight brachycephalic 83. The coronoid index averaged 39 in the case of the dolichocephalic, 37 in that of the mesaticephalic, and 35 in that of the brachycephalic; in other words, the greater the length of the jaw the farther from the fulcrum would the power exerted through the temporal muscle be applied. Turning, however, to a consideration of the co-relation between these indices of the mandible and the cephalic index, I was unable to discover any evidence of such. I found, on the contrary, that with seven skulls the cephalic index of which happened to be the same, viz., 78, the mandibular index varied from 72 to 89, and the coronoid from

32 to 41. Although it may be that the length of the jaw and the position at which the power is applied have some bearing upon skull shape as judged by the cephalic index, their influence, so far from being overpowering, is scarcely if at all appreciable: that, at least, is the conclusion at which I have arrived after an examination of these skulls.

Classifying the skulls according to the method advocated by Sergi, I found that forty-two belonged to the Ellipsoid class, ten to the Sphenoid, seven to the Ovoid and Beloid, and three to the Cuboid. The most common varieties of the ellipsoid class were the Ellipsoides pelasgicus longissimus and Ellipsoides Isocampylos. The former is a very long skull with flattened sides, as seen from the norma verticalis. The latter is a slightly shorter skull, possessing an even curve from ophryon to opisthion. Other less common varieties of this class were Ellipsoides depresssus, characterised by the possession of a low compressed curve, Ellipsoides embolicus and cuneatus, characterised by being somewhat wedge-shaped in the occipital region, and distinguished by the former being higher than the latter. Ellipsoides africus rotundus and Ellipsoides parallelepipedoides were also represented. In each case the skull is long and of a low height; in the latter the sides are flattened.

In the sphenoid group of skulls I found examples of Sphenoides latus, Sphenoides tetragonus, and Sphenoides trapezoides, illustrations of which accompany the description of the skulls.

The skulls of the cuboid group are characterised by possessing a somewhat rectangular shape.

The Ovoid and Beloid groups are not always readily distinguished from each other, and I have grouped them together.

Several of the skulls grouped as Ellipsoid were also from the norma verticalis slightly pentagonoid in shape, due in most cases to the backward bulge of the occipital squame.

From the norma facialis the long quadrangular face of the parallelepipedoides type was very common amongst the skulls of the male sex.

From the indices, and perhaps still more from the classification according to shape, and from the accompanying illustrations, we see that we have here a very mixed series of skulls.

Most of Sergi's more definite types are clearly recognisable, but I found no examples of his sphæroides and platycephalus types, or of such varieties as Ovoides byrsoides or Ovoides lophocephalus.

My results agree with those obtained by Professor Rolleston (description of and remarks on thirteen pre-historic skulls in Canon Greenwell's *British Barrows*), in that we both find that the two most common types are the long ellipsoid and the sphenoid. I cannot, however, agree with him that the intermediate types are relatively rare.

Drs Thurnam and Davies in their account, in *Crania Britannica*. of skulls taken from barrows in Yorkshire, only describe and figure skulls of an ellipsoid type; they make no reference to any of a sphenoid type.

Some of the skulls, and I would particularly instance Skull 17, had a very close resemblance to the skull which Topinard figures from the 'Reihengräber.' One is on this account inclined to believe that some of those here buried were racially connected with the old Franks buried on the banks of the Rhine.

To return, we have a mixed series of skulls representing the men inhabiting East Yorkshire in the Bronze Age. They are divisible broadly into two classes, a dolichocephalic and a brachycephalic. Whilst the extreme types represented by Ellipsoides pelasgicus longissimus and Sphenoides latus are very different, we still find many varieties of intermediate types.

We may explain this by supposing that we have here one race, and that the different types are to be regarded as mere individual variations. I have already said that in my opinion it is from the norma facialis we are most likely to observe the racial features of a skull. Unfortunately, but few of these skulls have the facial portion complete, yet from those which could be measured and examined, the shape and proportions of the orbit and the nose, the prominence of the cheek bones, the projection of the face, and the relations of the jaws to each other, presented little with which one could contend against such an explanation. I have also referred to some skulls marked by certain asperities for muscular and ligamentous attachments, but here again they were found alike on long skull and round skull. The same remark applies to such eminences as the supraciliary and malar.

The other hypothesis is that we have a mixture of two races, one dolichocephalic, the other brachycephalic; this supposition derives support from the frequency with which such extreme types as Ellipsoides pelasgicus longissimus and Sphenoides latus are met.

It is usually stated that Europe in Early Neolithic times was inhabited by a long-headed race; that in Late Neolithic times—the so-called Æneolithic Age—a round-headed race passed across from East to West. Representatives of these two races are frequently found buried together in the barrows of Continental Europe of the late Neolithic Age. I find similar representatives of a mixed race in the round barrows of East Yorkshire. The conclusion to which one is therefore driven is that at the dawn of the Bronze Age, colonists from this mixed race passed over from the Continent to England, occupying, amongst other places, the East Riding of Yorkshire. This differs from the conclusion which I believe is usually accepted, viz., that in the Bronze Age a pure brachycephalic race passed into England, and that the mixture of types found in the round barrows here is due to the peaceful intermixture of the new arrivals with those who were already in possession. To grant this conclusion one must believe that a pure round-headed race could have made its tardy progress across Europe unmixed—an assumption which to my mind is unwarranted and incredible. Another fact which supports one in believing that the intermixture had taken place at an early epoch is that the presence of bronze articles and the practice of incineration cannot be associated more with the round-headed individuals than with the long-headed. I would finally reiterate, the round barrows of East Yorkshire must not be associated with a round-headed race.

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[Tables.

Skulls from Round Barrows in East Yorkshire—continued.

	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
	♀	♂	?♂	♂	♂	♂	♀	♂	♀	♂	♀	♂	♂	♂	♀
Cranial Measurements :															
Glabello-occipital length	187	206	173	185	194	193	178	185	180	180	174	194	180	194	178
Ophryo-occipital length	186	...	173·5	182	191	...	176	185	178	180	172	193	175	190	177
Maximum breadth	131	135	140	140	154	...	138	145	142	157	138	139	130	140	151
Basio-bregmatic height	133	...	134	..	135	...	132	139	120	135	139	...	...	...	136
Stephanic breadth	103	...	125	121·5	...	...	122	125	117	123	116	119	...	...	138
Minimum frontal breadth	94	100	96	104	108	..	95	103	96	102	97	95	...	101	107
Frontal longitudinal arc	129	121	125	131	133	128	122	121	124	128	120	125	128	134	132
Parietal longitudinal arc	135	121	136	126	132	138	121	132	116	134	122	252	132	131	129
Occipital longitudinal arc	120	126	108	118	131	...	115	113	123	115	107		...	125	113
Fronto-occipital arc	384	368	369	375	396	...	358	366	363	377	349	377	...	390	374
Foramen magnum length	36	...	37	...	...	...	36	35	38	...	39	..	...	...	40
Basio-nasial length	95	...	91	...	103	...	103	114	...	101	109	...	...	...	98
Auriculo-nasial radius	91	...	90	104	102	...	93	103	91	94	99·5	114	95	...	96
Auriculo-bregmatic radius	120	..	118	127	126	...	115	124	119	122	117·5	112	124	...	126
Auriculo-bregmatic arc	294	322	305	315	330	...	304	322	295	320	295	318	316	...	329
Bi-auricular width	...	122	123	121	130	...	120	128	116	141	126	126	...	...	128
Transverse circumference	..	444	428	436	460	...	424	450	411	461	421	444	...	..	457
Horizontal circumference	512	553	503	522	556	...	504	534	510	540	501	535	500	536	527
Sagittal circumference	515	...	497	...	...	...	497	515	...	...	497	..	...	...	512
Cranial capacity	...	...	...	...	...	...	...	...	1345	...	...	...	...	...	1620
Facial Measurements :															
Basio-alveolar length	90	..	82·5	..	99	...	98	108	...	95	102	...	...	...	93
Auriculo-alveolar radius	98	...	90	108	106		96	103	92	96	108	112	96	...	98
Auriculo-mental radius	111	...	98·5	136	123	...	116	124	112	118	125	130	118	...	111
Nasio-alveolar length	66	...	59	68	67	65	61	68	56	64	72	75	...	68	68
Nasio-mental length	110	...	98	125	110	114	105	116	99	112	116	115	...	112	118·5
Bi-zygomatic breadth	...	...	122	133	135	...	130	136	118	...	123	...	..	...	133
Maximum bimaxillary breadth	93·5	...	91·5	94	100	...	92	93	82	98	...	...	...	...	95
Bidacryal breadth	18	...	18·5	23	24·5	...	21	22	18	23	19	...	...	23	23
Bimalar breadth	...	...	92·5	103	106	...	102	104	90	104	101	...	...	...	107
Naso-malar line	...	...	99	112	115	...	109	116	99	110	111	...	...	...	117
Nasal height	...	...	48·5	48	...	...	48	49	43	50	54	...	...	...	50
Nasal breadth	...	...	25·5	26	...	...	25	23	20·5	28	23	...	...	..	25
Orbital breadth	39	...	R 39 L. 38·5	R. 42 L. 42	43	...	43	45	R. 40 L. 38	R. 43·5 L. 43·5	45	42	...	42·5	44
Orbital height	34	...	R. 33 L. 34	R. 33 L. 34	33	...	33	32	R. 30 L. 30	35	34·5	35	...	34	35
Palato-maxillary length	53·5	..	46	59	56	...	52	55	52	55	54·5	59	60	...	57

	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
	♂	♀	♂	♂	♂	♂	♀	♂	♂	♂	♀	♂	♂	♂	♂
Cranial Measurements :															
Glabello-occipital length	193	177	185	182	191	199	182·5	181	185	191	176	185	197	171	195
Ophryo-occipital length	192	178	181	178	192	196	184	...	...	187·5	176	182	193	169·5	195
Maximum breadth	151	143	146	155	147	157	145	147	145	147·5	138	140	141	139	156
Basio-bregmatic height	...	134	...	...	142	...	130	...	...	139	135	...	137	138	138·5
Stephanic breadth	131	121	124	126	130	136	114	123	125	127	119	140	118	120	136
Minimum frontal breadth	103	93·5	98·5	99	101	110	88	100	103	103	96	82·5	100	100	111
Frontal longitudinal arc	140	145	132	133	143	142	267	133	130	148	130	133	126	122	139
Parietal longitudinal arc	215	125	248	127	130	132		129	142	126	131	130	143	126	262
Occipital longitudinal arc		109		...	129	123	114	...	102	113	102	...	116	115	
Fronto-occipital arc	385	379	380	...	399	40	381	...	374	387	363	...	385	363	401
Foramen magnum length	...	38	33	...	41	...	34	...	...	42	41	...	39	...	41
Basio-nasial length	...	95·5	114	...	104	...	96	...	...	100	97	...	106	94	102
Auriculo-nasial radius	107	92·5	...	...	98·5	106	88·5	...	...	101	93·5	...	98	...	...
Auriculo-bregmatic radius	131	121·5	...	...	127	128	115	...	...	130	121	...	122	...	...
Auriculo-bregmatic arc	336	306	...	320	323	337	298	322	326	328	303	310	308	308	328
Biauricular width	134	123	125	...	129	138	108	130	126	115	123	...	118	...	...
Transverse circumference	470	429	...	...	452	475	406	452	452	443	426	...	426	...	...
Horizontal circumference	554	509	523	550	538	577	513	520	528	536	506	520	539	498	556
Sagittal circumference	...	512·5	527	...	548	...	511	...	...	529	501	...	530	...	546
Cranial capacity	...	1430	...	...	...	...	1415	...	...	1515	1320	...	...	..	...
Facial Measurements :															
Basio-alveolar length	...	92	92	...	98	...	88·5	...	...	93	88	. .	96	89	100
Auriculo-alveolar radius	101	97	...	...	103	106	87·5	...	...	103	94	...	98	...	...
Auriculo-mental radius	122	113	...	...	129	126	105	...	...	127	115	...	123	...	...
Nasio-alveolar length	70	62	78	..	75	73	57	62	...	78·5	63	69	76	65	68
Nasio-mental length	120	107	130	...	125	130	...	123	...	132	102	123	128	112·5	121
Bizygomatic breadth	144·5	124	140	...	...	143	116	130	...	126	...	...	128	...	132
Maximum bimaxillary breadth	96	87·5	...	..	103	88	84	98	...	89	91	...	90	...	...
Bidacryal breadth	24	20	18	19	19	24	17	...	...	20	20·5	...	20	19	20
Bimalar breadth	109	96	105	...	104·5	110	92	...	...	103	100	...	102	...	...
Naso-malar line	119	103	116	...	116	121	98	...	...	116	111	...	116	...	...
Nasal height	52	51	57	52	53	55	47	...	...	55	48	...	57	51	52
Nasal breadth	27	25	24	...	25	28	23	...	...	26·5	23·5	...	23	24	26
Orbital breadth	46	40	47	42	45	...	42	...	...	45	43	44	...	43	..
Orbital height	36	32	39	34	36	...	32	...	...	39	33	34	...	34	...
Palato maxillary length	54	53	57	...	54·5	...	47	...	...	55	50	52	56	54	60
Palato-maxillary breadth	60	60	61	...	68·5	...	...	...	...	60	61·5	05	59·5	62	..
Molar length	42	40	...	40	42	...	...	....	...		R. 41 L. 39	42·5	41	42	...

Skulls from Round Barrows in East Yorkshire—continued.

	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62
	♀	♀	♀	♀	♀	♂	?♂	♂	♂	♂	♂	♂	♂	♀	♀	♂
Cranial Measurements:																
Glabello-occipital length	169	177	168	179	176	188	177	173	168	195	194·5	177	190	169	186	187
Ophryo-occipital length	169	176	168	180	177	185	...	...	...	195·5	190	176	188	167	..	..
Maximum breadth	138	142	149	144	143	142	141	152	146	139	134	131	149	134	147	141
Basio-bregmatic height	136	...	130	132	...	...	...	...	...	144	...	126	153	138	125	...
Stephanic breadth	119	126	129	128	122	118	...	...	...	116	115	109	118·5	111	...	114
Minimum frontal breadth	94	97	96	103	92	93	...	...	...	99	101	85	102	87	101	87
Frontal longitudinal arc	132·5	124	130	119	130	128	130	121	...	139	133	118	138	120	120	130
Parietal longitudinal arc	118·5	114	110	125	123	134	125	123	..	139	134	117	129	114	130	110
Occipital longitudinal arc	107	123	108	120	120	111	110	109	...	132	121	115	120	109	113	130
Fronto-occipital arc	358	361	348	364	373	373	365	353	...	410	388	350	387	343	363	370
Foramen magnum length	36	...	37	36	...	...	35	35	...	33	...	39	35	38	...	...
Basio-nasial length	93·5	...	98·5	100	...	...	109	101	...	102	...	104	116	101	...	...
Auriculo-nasial radius	89	101	92	95	...	106	...	...	...	99	99	93	106	92	..	...
Auriculo-bregmatic radius	121	123	116	116	...	129	...	...	...	126	124	115	131	115	...	...
Auriculo-bregmatic arc	314	315	314	303	310	325	330	315	...	300	302	288	321	296	322	315
Biauricular width	120	123	126	129	...	120	109	129	...	127	120	110	138	126	117	123
Transverse circumference	434	438	440	432	...	445	439	444	...	427	422	398	459	422	439	438
Horizontal circumference	496	503	505	518	514	525	502	517	...	531	528	492	535	486	526	515
Sagittal circumference	487·5	..	483·5	500	...	...	509	489	...	545	...	493	538	482	...	...
Cranial capacity	...	...	1345	...	..	...	...		...	1460	...	...	...	...	...	...
Facial Measurements:																
Basio-alveolar length	88	...	92	98	...	...	...	...	...	99	...	102	99	99	...	...
Auriculo-alveolar radius	95·5	103	95	203	...	103	...	...	...	107	106·5	97	101	102	...	...
Auriculo-mental radius	118	119	...	126	...	125	...	..	...	125	122·5	114	123	118	...	...
Nasio-alveolar length	68	76	64	63	67	67	...	...	...	68	71	63	71	105	...	...
Nasio-mental length	110·5	126	...	109	109	118	...	...	..	113	123	97	122	61	...	...
Bizygomatic breadth	119	125	...	...	...	131	...	.	...	123	133	103	135	120	...	...
Maximum bimaxillary breadth	93	90	...	92	...	95	...	..	...	98	94		97	90	...	..
Bidacryal breadth	17	18	...	26	20	17	...	...	...	22	19	16·5	19	...	..	...
Bimalar breadth	96	98	...	103	...	...	...	..	...	97	103	90	101	...	...	...
Naso-malar line	101	109	...	110	...	..	...	..	...	108	114	97	114	...	...	...
Nasal height	50	55	50	...	51	...	...	..	...	51	52	49	49	49	...	...
Nasal breadth	26	26	...	...	27	...	...	.	...	24	26	24	23	25	..	..
Orbital breadth	41·5	42	42	...	41	...	...	..	...	41	43·5	38	..	41	...	...
Orbital height	34	33	31·5	..	33	...	...	..	...	32	35	32	...	33	...	...
Palato-maxillary length	50	55	...	52	...	...	..	...	..	58	54	...	54	50	...	...
Palato-maxillary breadth	61	61		58						62	58		61	57·5		

Skulls from Round Barrows in East Yorkshire—continued.

	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
	♀	♂	?♂	♂	♂	♂	♀	♂	♀	♂	♀	♂	♂	♂	♀
Measurements of Mandible:															
Symphysial height,	32	32	26	34	30	..	30	35	27	27	32	29	31	29	33·5
Coronoid height,	56	68	47·5	67·5	64	...	59	70	49	61·5	53·5	64	...	65	56
Condyloid height,	47	72	44	64	58	...	55	63	50	66	53·5	62	...	60	50
Gonio-symphysial length,	85	82	72·5	96	91	...	81	..	80	81	89	93	...	92	80
Bicondyloid width,	...	129	112	124	110	...	116	128	111	126	112	128	...	...	126·5
Bigonial width,	...	93	90	93·5	98	...	83	101	83	...	100	103	...	...	95
Width of ramus,	36	39	28·5	38·5	30	...	31	36	26	36	35·5	31	...	30	28
Condylo-symphysial length,	96	98	91	106	108	...	100	...	96	...	...	103	...	..	99
Condylo-coronoid width,	37	38	32	38	38	...	37	...	32·5	...	...	37	...	...	36
Indices:															
Cephalic breadth index,	70	65·5	80·9	75·5	79·4	...	77·5	78·4	78·9	87	79·3	71·6	72	72	84·8
Cephalic height index,	71·1	...	77·5	...	69·6	...	74	75	...	75	79·9	...	...	...	76·4
Facial index (Kollmann),	...	...	80·3	94	81·5	...	80·7	85	90·9	...	94·3	...	...	...	88·7
Upper facial index (Kollmann),	..	...	48·4	51	50	...	47	50	48	...	58	...	...	...	51
Stephano-zygomatic index,	..	...	102	84	...	...	94	92	99	...	94	...	...	...	104
Gnathic index,	94·7	...	90·5	...	96	...	95	94·7	...	94	93·5	...	...	...	95
Auriculo-gnathic index,	103	...	100	104	104	...	103	100	101	102	108	98	101	...	102
Naso-malar index,	...	...	107	109	108	...	107	111	110	106	110	...	...	...	109
Nasal index,	...	...	52	...	...	...	52	47	47	...	42·6	...	...	...	50
Orbital index,	R. 90 L. 87	...	R. 85 L. 88	81	80	...	...	71	R. 75 L. 79	80	76	83	..	80	80
Palatal index (Flower),	114	...	132	110	115	..	113	111	108	118	114	109	113	...	109
Molar index (Flower),	...	...	...	...	49	...	41	36	...	41·5	39	...	...	...	43
Mandibular index (Thomson),	...	76	81	85	98	...	86	...	86·5	...	...	80·5	...	..	78
Coronoid index (Thomson),	39	38	35	36	35	...	37	..	33·8	...	..	36	...	...	36

Skulls from Round Barrows in East Yorkshire—continued.

	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
	♂	♀	♂	♂	♂	♂	♀	♂	♂	♂	♀	♂	♂	♂	♂
Measurements of Mandibles :															
Symphysial height,	33	28	34	36	34	33	28	...	33	33	27·5	33	35	30	31
Coronoid height,	57	53·5	68	71	68	66	53	...	61	73	54	64	71	58	71
Condyloid height,	59	49	74	65	66	65	52	...	62	67	54	56	71	58	70
Gonio-symphysial length,	96	78	88	95	88	91	79	...	88	88	83	91	87	87	91
Bicondyloid width,	138·5	121	130	...	127	133	106	121	123	122	114·5	126	117	122	126
Bigonial width,	105	92	104	...	93	107	79	...	103	101	89	104	87	...	101
Width of ramus,	37	28	36	31	31	33	30	...	33	33	26	34·5	41·5	31	36·5
Condylo-symphysial length,	103	105	111	...	105	...	...	113	104	109	102	109	...	...	...
Condylo-coronoid width,	40	37	45	...	41	...	..	35	38	37	33	39	...	...	...
Indices :															
Cephalic breadth index,	78	80·7	79	85	75·8	78·9	79·5	81·2	78·4	77	78·5	75·7	71·5	81·3	80
Cephalic height index,	...	75·7	...	...	73	...	71·5	...	...	72·7	76·7	...	69·5	80·7	71
Facial index (Kollmann),	83	86·3	93	...	..	90·9	...	94·5	...	95·5	...	...	100	...	91·7
Upper facial index (Kollmann),	49	50	56	...	...	51	49	50	...	62	...	...	60	...	50
Stephano-zygomatic index,	90·5	97·5	88·5	...	...	95	98	94·5	...	117	...	...	92	...	103
Gnathic index,	...	96·8	81	...	94	...	90·6	...	...	93	90·7	...	90·5	94·7	98
Auriculo-gnathic index,	94	105	...	...	104	100	100	...	...	102	100	...	100	...	...
Naso-malar index,	109	107	110·5	...	111	110	106·5	...	...	112	111	...	113	...	...
Nasal index,	52	49	42	...	47	51	49	...	...	48	47·5	...	...	47	...
Orbital index,	80	80	83	81	80	...	76	...	...	86	77	77	...	80	...
Palatal index (Flower),	111	113	107	...	126	...	...	...	...	109	123	125	106	115	...
Molar index (Flower),	...	42	..	...	40	...	...	...	...	...	R. 42 L. 40	...	38·5	45	...
Mandibular index (Thomson),	74·5	87	84·5	..	83	...	...	93·4	85	89	89	86·5	...	...	...
Coronoid index (Thomson),	39	35	40·5	...	39	...	...	31	36·5	34	32	36	...	...	...

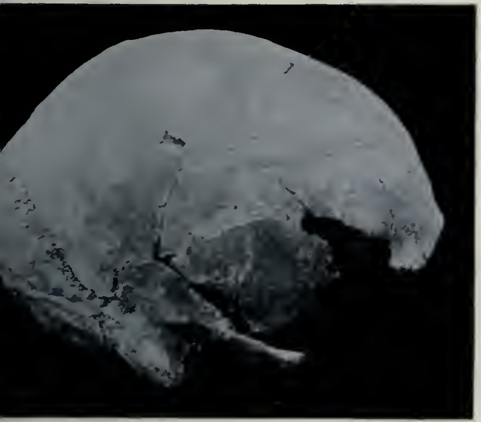
Dr Wm. Wright.

Skull 17.

Skull 17.

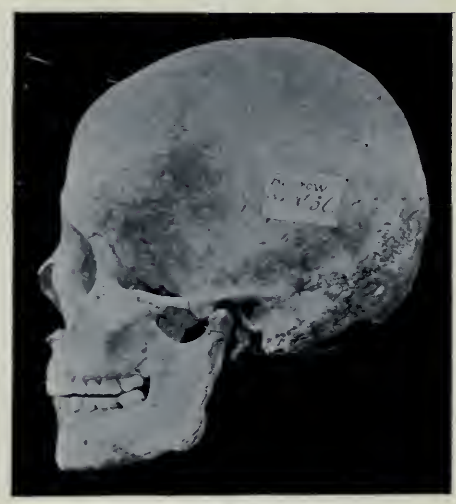
Skull 18.

DR WM. WRIGHT.

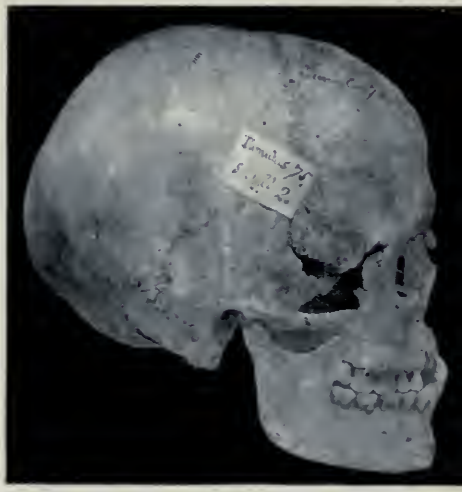

Skull 18.


Skull 18.


Skull 14.

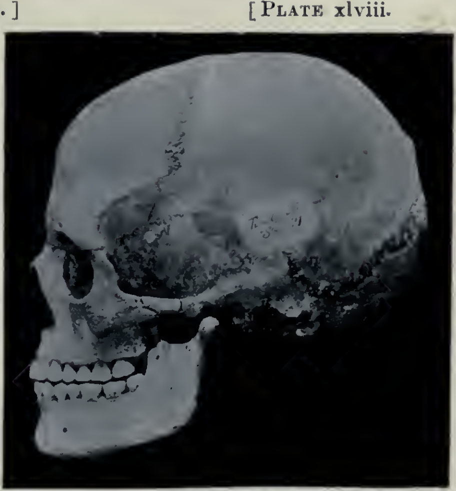

Skull 15.


Skull 23.


Skull 23.

Dr WM. WRIGHT.

Skull 24.



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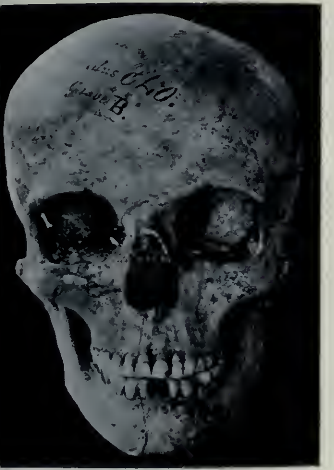


Skull 26.

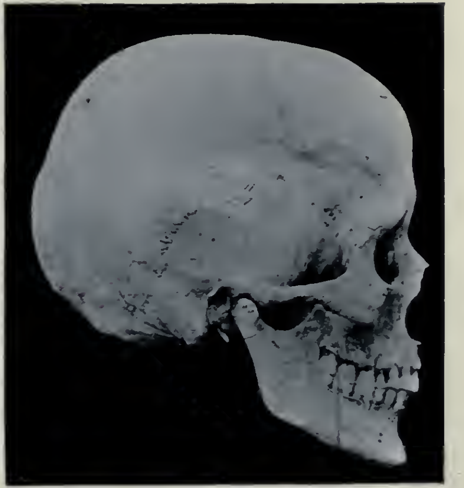
Skull 29.

Skull 29.

Skull 31.

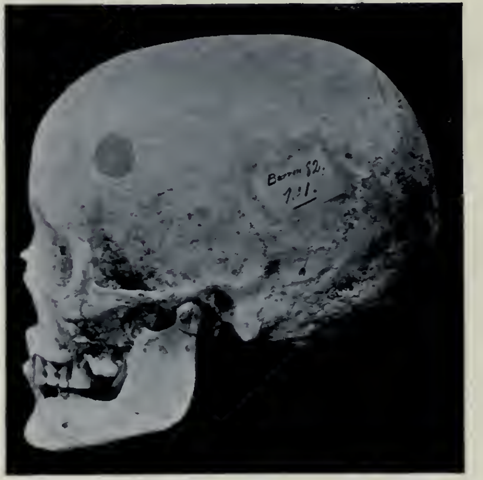
DR WM. WRIGHT.

Skull 32.



Skull 33.

Skull 34.



Skull 38.

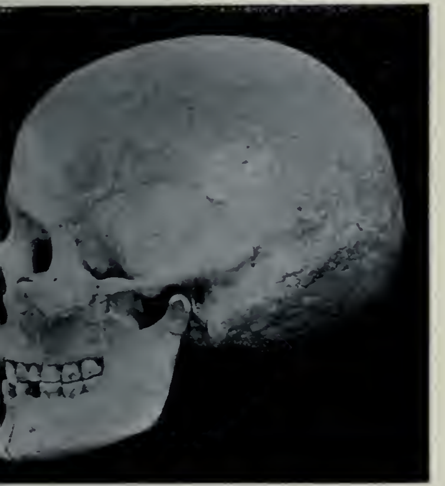
Skull 41.

. Skull 41.

DR WM. WRIGHT.


Skull 49.


Skull 51.


Skull 56.


Skull 56.


Skull 59.


Skull 59.

DR WM. WRIGHT.

Skulls from Round Barrows in East Yorkshire—continued.

	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62
	♀	♀	♀	♀	♀	♂	?♂	♂	♂	♂	♂	♀	♂	♀	♀	♂
Measurements of Mandible :																
Symphysial height,	28	34	...	30	31	28	28	31	...	30	35	21	35	24	31	28
Coronoid height,	60	59	...	63	67	72	47	58	...	72	63	56	63	51	57	67
Condyloid height,	61	58	...	60	54	59	43	52	...	59	53	55	65	51	51	67
Gonio-symphysial length,	83	83	...	85	85	94	68	83	...	87	92	76	91	84	82	90
Bicondyloid width,	121·5	119	...	123	...	126	102	113	...	118	125	109	119	118	...	107
Bigonial width,	92	85	...	90	...	91	82	90	...	86	98	84	92	96	...	87
Width of ramus,	31	31	...	35	32	37	30	34	...	35	38	28	35	31·5	...	40
Condylo-symphysial length,	95	...	...	...	...	110	81	102	...	109	...	95	102	102	...	105
Condylo-coronoid width,	35	...	...	...	...	41	28	39	...	40	...	39	40	41	...	40
Indices :																
Cephalic breadth index,	81·6	80	88·7	80·5	81·3	75·5	79·6	88	87	71·3	69	74	78·4	79	79	76
Cephalic height index,	80·5	...	77	73·7	...	...	...	...	...	73·8	...	71	80·5	81·7	...	...
Facial index (Kollmann),	92·8	100	...	...	88·6	90	...	...	...	91·8	92·5	106	90·3	87·5	...	...
Upper facial index (Kollmann),	57	61	...	...	...	51	...	...	...	55	53·5	61	52·5	51	...	...
Stephano-zygomatic index,	100	100	...	...	...	108·5	...	...	...	90	100	106	88	92·5	...	...
Gnathic index,	93	...	93	98	...	...	...	...	...	97	...	98	85	98	...	...
Auriculo-gnathic index,	107	102	103	108	...	97	...	...	...	108	107·5	104	95	111	...	...
Naso-malar index,	105	111	...	107	109	...	...	...	...	111·5	110·5	108	113	...	...	...
Nasal index,	52	47	...	...	...	...	...	...	...	47	50	50	47	51	...	...
Orbital index,	82	78	75	...	80·5	...	...	...	...	78	81	84	...	80·5	...	...
Palatal index (Flower),	122	111	...	111	...	...	...	...	...	107	107·5	...	113	115	...	...
Molar index (Flower),	44	...	...	...	...	...	...	...	...	41	...	...	...	39	...	...
Mandibular index (Thomson),	78·5	...	...	...	...	80·5	79	90	...	92		87	85·5	86·5	...	98
Coronoid index (Thomson),	37	...	...	...	...	37	34·5	38	...	36·5	...	41	39	40	...	38

THE ANATOMY OF A SIRENOMELIAN MONSTER. By GILLMAN MOORHEAD, M.D., M.R.C.P.I., *Physician, Royal City of Dublin Hospital.*

WHILE the occurrence of double monsters, and of monsters with multiple arms and legs, is comparatively common, those forms in which fusion, more or less complete, of the limbs of a single fœtus constitutes the anomaly, are undoubtedly rare. Up to the period at which the work of Geoffrey Saint-Hilaire on monstrosities made its appearance in 1836, no adequate attempt had been made at a classification of monsters in general, and in particular those monsters in which the two lower limbs are united to form a single terminal and median appendage were only casually and generally referred to under such terms as Monopodia and Sympodia. To St-Hilaire belongs the credit, as has been recognised by all succeeding writers, of distinguishing the sub-varieties of this class, and of applying the name Symeles to the group. Both this name and also those which he applied to the sub-varieties have been universally adopted.[1]

Early references to the Sympodia are not at all common, and almost all those which are found scattered in the literature before 1800 deal more with mythical and legendary reports than with actual verified occurrences. The fact, however, that even legends exist points to the occasional appearance of nereid-like human fœtuses, and the structure of such is certainly sufficiently striking to afford a more than usually solid basis for much folklore. Perhaps the earliest systematic attempt to explain the origin of human and other monstrosities is that of Aristotle in chapter iii. of the fourth book of his work *On the Generation of Animals.* In it he discusses in a truly scientific manner the various theories then current; and, after advancing one of his own, enumerates the various forms of monstrosities with which he was acquainted. In his fairly extensive list no reference to the Symelian type is to be found, and since Aristotle

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[1] Since writing the above I find that Ballantyne, in the second volume of his *Antenatal Pathology*, just published, prefers the term Sympodia.

was the exponent of all scientific knowledge at that time, we must conclude that no authentic case was then known. Pliny, on the other hand, in addition to his numerous references to the true sea nereids and tritons of the ancients, states in chapter ii. of the seventh book of his Natural History, on the authority of Ctesias, that there existed near the country of the Troglodytes a race of men called Monocoli, who, although possessed of only one median lower limb, were able to walk and jump with much agility. These Monocoli were also, he states, called Sciapodæ, because they were accustomed to recline on their backs during the heat of the sun, and to protect themselves from its rays by their overspreading foot. This legend, I think, may fairly be regarded as being inspired by the occasional occurrence of Symelian fœtuses, especially in view of the tendency of writers in those days to look upon monstrosities as the chance occurrence, among men, of beings belonging to another race or type. As such it may be looked upon as the earliest reference to Sympodia; and it appears to have impressed subsequent writers, for it is referred to and even figured in the work of Lycosthenes in 1557 under the heading "Scipodes and Monomeri," and also in that of Aldrovandus, which appeared in 1642. Before either of these last-mentioned dates, however, a short but unequivocal account of a typical Sirenomelian fœtus appeared in the work entitled *Julii Obsequentis, Prodigiorum Liber*. In this book the specimen described is figured, and resembles in all respects the fœtus that I am about to describe, with the exception of the fact that, in addition to the lower limb deformity, it was devoid of arms. In 1836, as already stated, Saint-Hilaire adopted a definite name and classification, and, furthermore, collected most of the previous references in the literature, with the exception of those I have recorded above. The last important English paper upon the subject was that by Manners-Smith in the *Journ. of Anat. and Phys.*, 1896. It consists of a description of two Symelian monsters, and contains an almost complete bibliography. Since that date only very few cases have been described; and after a fairly complete search through the literature I have only been able to discover one or two additional papers, the most important of which consisted of an accurate description of a formalined

Sirenomelian monster, and appeared in Bd. clxxi. of *Virchow's Archiv* under the title "Ein Fall von Sirenbilding," by Abramov and Rjisanow. For a full bibliography, Ballantyne's work on *Antenatal Pathology* may be consulted.

The fœtus now described belongs to the Sirenomeles, or third variety of Saint-Hilaire, in which the lower limbs are united in a single median extremity, which tapers below to a point or rounded stump without a distinct foot. This variety is more common than either of the other two forms (Symeles and Uromeles), in which less perfect union of the lower extremities is present. The present specimen was born at full term in the Rotunda Hospital, Dublin, and had the appearance of being dead for some days. For permission to dissect and describe it I am indebted to the late Dr W. Neville, pathologist to the hospital.

Superficial Appearance.—In general appearance the fœtus was normal in every respect above the level of the umbilicus. Below that level it gradually tapered to a rather sharp point which presented somewhat the appearance of a toe, and which was marked at its extremity by a dorsal depression resembling the head of a nail. This median limb projected forwards, making an angle of about 150° with the trunk, and presented on each side in the neighbourhood of the knee joint a rounded swelling. On its anterior aspect there was situated in the middle line, just below the symphysis pubis, a puckered scar, which, as the sole representative of the external genitals, may be called the genital scar. Posteriorly no anus was present, but high up over the back of the coccyx there was placed an anal scar similar to that described in front.

Thoracic and Abdominal Viscera.—The thoracic viscera were normal in every respect, except that the thymus gland was of unusually large size. In microscopical structure this gland was, however, quite normal.

In the abdomen the stomach and small intestine were quite normal, and had normal peritoneal connections. The appendix also was normal. The cæcum lay above the right iliac fossa, and was distended with meconium, as was also the transverse colon. The descending colon was enormously distended, and terminated below in a pointed extremity which lay in the left iliac fossa. Almost the whole of the descending colon was free, being only attached by a loose mesenteric fold to the peritoneum over the hypogastric artery. The liver, gall-bladder, pancreas, and spleen were normal. No kidneys, ureters, or bladder were present. The suprarenal capsules were very large, and lay in the normal position on the posterior abdominal wall. In microscopical structure they were normal.

The aorta entered the abdomen in the normal manner, and immediately after it emerged from under cover of the pancreas gave off a large single branch which passed almost directly forwards towards the umbilicus. This branch was much larger than the continuation of the aorta within the abdomen ; shortly after its origin it divided into two branches, which ran side by side for a short distance, and again united into a single trunk before reaching the umbilicus, so that only a single artery entered the umbilical cord. The hypogastric artery in its intra-abdominal course was covered by a peritoneal fold which practically divided the lower part of the abdomen into two symmetrical lateral halves. In the right half were contained the small intestines, while in the left half lay the distended sigmoid flexure attached by its mesentery to the fold of peritoneum over the artery. The aortic trunk, below the origin of the hypogastric artery, continued downwards on the posterior abdominal wall, and divided on the 4th lumbar vertebra into the two common iliac vessels; these last-named, after giving off small internal iliac branches to the pelvis, were continued as the external iliac vessels, to become continuous with the femorals under Poupart's ligaments.

The cavity of the pelvis was only represented by a slight depression in the peritoneum on each side of the median peritoneal fold. In this depression there lay on each side the testes, which were normally developed, and which presented on their posterior aspect well-formed epididymes. From the epididymis, the vas deferens passed upwards on each side in the peritoneal fold over the hypogastric artery, and gradually narrowing, finally disappeared from view close to the neighbourhood of the pancreas. Microscopically the vas was traced a little further up as a small duct lined with columnar cells. The microscopical appearance of the testes and epididymes was normal.

Among the special points of interest in connection with the viscera the following may be noted:—

(1) No trace of kidneys or bladder could be met with, although searched for most carefully, and that in a fœtus preserved in formalin. This is in accord with what has generally been found in this class. Manners-Smith, however, described the presence of cystic kidneys and of a small bladder in one of his cases, and in Abranow's and Rjisanow's case cystic kidneys were also found, but neither bladder nor ureters. It is noticeable that in neither of these two cases were suprarenal capsules present. In the present case kidneys were absent, and the suprarenal capsules were of unusually large size.

(2) The condition of the lower end of the intestinal canal in Sirenomelians varies considerably. In the majority of cases no anus or rectum is present, and the sigmoid flexure terminates in the manner described. In one case, however, a narrow canal, closed both above and below, was present as the representative of the rectum, and in another the sigmoid flexure terminated in a narrow canal which opened at the surface just underneath a tail-like process.

(3) The presence of well-formed testes within the pelvis is rare. In most of the male cases described these organs have been found within the upper part of an imperfect inguinal canal. In the present case no trace of an inguinal canal could be detected.

Muscular System.—The muscles of the upper portion of the body, including the latissimus dorsi and the abdominal muscles, were normal, except that there was no inguinal canal present among the last-named.

In describing the muscles of the inferior extremity, considerable difficulty is experienced in determining the names to apply to them. On the whole, I think it would be better to avoid doing more than indicating the group to which any given muscle is supposed to belong; but in accordance with other writers I have placed the supposed name of each muscle in brackets after a description of its origin and insertion. Those found on the anterior aspect of the lower limb are as follows:—

(1) A muscle which arose from the anterior superior iliac

spine and the portion of the ilium below it, and which passed downwards and inwards to be inserted into the tibiæ below the knee-joint (M. sartorius). This muscle was supplied by the anterior crural nerve.

(2) A muscle which arose from the front and side of the body and horizontal ramus of the os pubis, and running down parallel to the first-named muscle, was inserted into the front of the tibiæ below the knee-joint (M. gracilis). This muscle was also supplied by the anterior crural nerve.

(3) A muscle which lay on a deeper plane than the two preceding, and which, arising from the front of the body and descending ramus of the os pubis, passed outwards to be inserted by a wide insertion along the outer border of the fused femora. This muscle probably represented fused adductors, as it was supplied by the obturator nerve.

(4) A muscle which arose from the front of the lower two-thirds of the fused femora, and from a strong fibrous cord which intervened between it and its fellow on the opposite side. The fibres of this muscle passed downwards and outwards, and ended in a strong tendon, which was inserted into the outer aspect of the fused tibiæ just below the knee-joint. The muscle was supplied by the obturator nerve, and must therefore be regarded as belonging to the adductor group, though resembling the short head of the biceps.

(5) The psoas muscle arose normally within the abdomen on each side, and was inserted into the posterior aspect of the horizontal ramus of the os pubis.

(6) The iliacus muscle arose normally within the pelvis, and after passing under Poupart's ligament, was inserted into the side of the fused femora just below the head of the bone, and deep to the superior adductor group.

(7) A small muscle, supplied by a twig of the anterior crural nerve, lay on each side on the front of the fused tibiæ. The pair blended below into a single tendon, which was inserted into the terminal cartilaginous nodules of the lower limb.

On the posterior aspect the following muscles were found:—

(1) A muscle corresponding to the gluteus maximus arose from the lower part of the dorsum ilii on each side. The muscles of each side blended with one another below the coccyx, and were

inserted into the deep fascia of the back of the thigh. Above the origin of these muscles a large mass of fat covered over the dorsum ilii.

(2) Deep to the gluteus maximus, a muscle (gluteus medius and minimus) arose from the dorsum ilii and tuber ischii, and was inserted into the summit of the great trochanter region of the femora. This muscle was fused with its fellow in the middle line. It had no intra-pelvic origin.

(3) The whole of the back of the femora was covered by a large muscular mass (extensor group) which arose from the back and sides of the fused bones, and was inserted below into two separate patellæ which covered over the back of the joint. Into this mass there passed backwards on each side a muscle which arose from the ilium immediately behind the origin of the so-called sartorius, and which probably corresponded to the rectus femoris muscle. It is not represented in the drawing, but lay parallel and behind the upper portion of the sartorius before blending below with the extensor group. The two extensor groups were united in the middle line by a strong fibrous septum, but separated somewhat as they approached the patellæ. Each patella was united by a distinct ligamentum patellæ to the tibiæ. This entire group of muscles was supplied by the anterior crural nerve.

(4) A small slender muscle arose from the back of the tibia on each side. The two united into a single tendon, which was prolonged along the posterior aspect of the end of the limb. No nerve was traced to this muscle.

Other muscles:—

(1) The quadratus lumborum muscle was present, and normal.

(2) Covering over the region of the thyroid foramina within the pelvis was an irregular muscular mass which passed directly backwards and was inserted into the fascia of the pelvis. No other intra-pelvic muscles were present.

Nervous System.—The *brain* was so soft when the fœtus was obtained that no systematic examination of it could be carried out. A superficial examination of the cortex, however, revealed nothing abnormal.

Spinal Cord.—This terminated at the lower end of the 4th lumbar vertebra. The lumbar swelling appeared unusually big, otherwise the cord was quite normal. Sections revealed nothing abnormal either in the nerve cells or parts of nerve fibres. So far as I am aware, only one other observation has been made in the spinal cord in Sirenomelians, and that by Odisio. In his case the cord presented in the lumbar region a longitudinal group of fibres lying between the central canal and the anterior fissure. This was carefully looked for in my case, but was not present. The large size of the lumbar swelling corresponds with the large size of the cervical enlargement found by Trennier in a case of Amelia.

Peripheral Nerves.—The cutaneous nerves of the abdominal wall and thorax were normal. The external cutaneous nerves rose normally on each side from the lumbar plexus, and were distributed on the outer side of the lower limb as far as the knee. No genito-crural nerve was present. The anterior crural nerve was very large; it arose normally on each side from the 2nd, 3rd, and 4th lumbar nerves, and left the pelvis on the surface of the iliacus muscle. The main trunk, after giving off twigs to supply the sartorius, gracilis, and rectus femoris muscles, and also a branch which accompanied the femoral artery and supplied the muscle on the front of the tibiæ and the skin over the upper region of the front of the leg, turned directly backwards, and ended in the mass of extensor muscles at the back. The obturator nerve arose from the 3rd and 4th lumbar nerves on each side. It supplied the upper and lower adductor group of muscles on the front of the thigh, after its emergence from the pelvis in the usual manner. The lumbo-sacral cord was normal: it turned downwards into the pelvis, and joined with the remaining sacral nerves to form a single nerve band which left the pelvis through a foramen immediately in front of the sacrum. This trunk terminated in the gluteal muscles at the back.

Vascular System.—The general direction of the outer and external iliac vessels has already been described. A small internal iliac vessel was present on each side, and emerged from the pelvis along with the great sciatic nerve, to end in the gluteal group of muscles. The femoral artery immediately below Poupart's ligament gave off a rather large muscular twig which accompanied the anterior crural nerve into the extensor group of muscles. The main trunk then continued down along the front of the thigh between the sartorius muscle and the adductor groups of muscles, and reaching the front of the tibia below the knee, was continued down as a very slender trunk on each side towards the extremity of the limb. A superficial saphenous vein was present on each side, and joined the main femoral vein below Poupart's ligament.

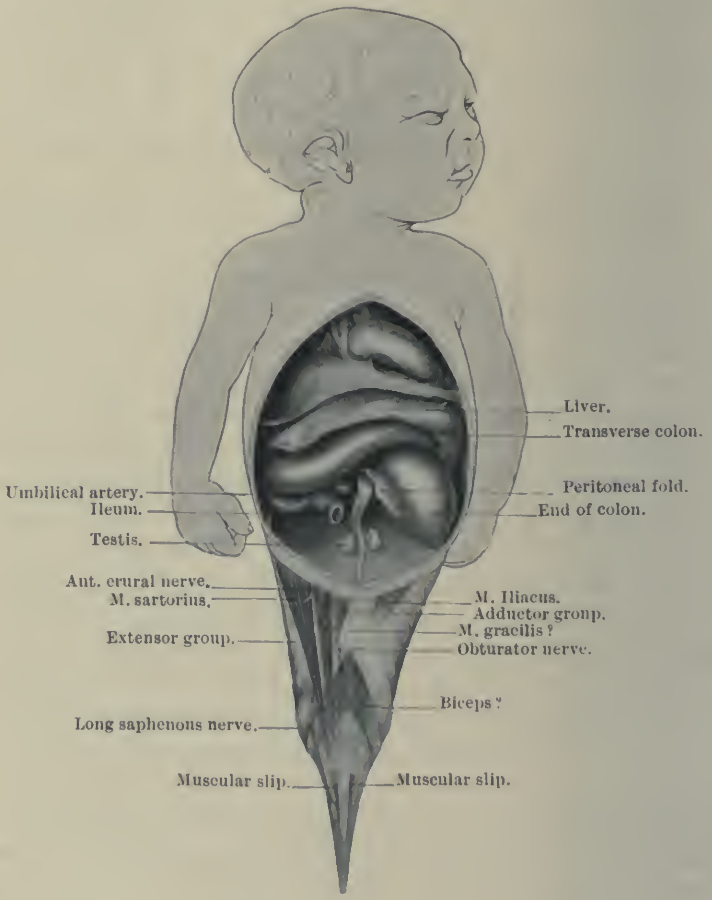

FIG. 1.

The anterior wall of the abdomen has been removed to show the contained viscera, and a partial dissection of the fused lower limb has been made.

Osseous System.—The bones of the head and arms were normal. There were thirteen ribs on each side, thirteen dorsal vertebræ, and five lumbar vertebræ. This abnormality in number of ribs and vertebræ is in accordance with what is usually found in these monsters, and is of importance, I think, in showing that the anomaly is more than a local one. The body of the last lumbar vertebra articulated on each side with the ala of the ilium. The sacrum and coccyx were represented by four incomplete bony vertebræ, and by four cartilaginous nodules, the whole structure being directed almost straight backwards between the iliac bones.

The appearance of the pelvis is well seen in the accompanying figure (fig. 2). The iliac fossæ were expanded and directed more forwards than inwards, and the iliac crests were very slightly curved. The bodies of the pubic bones were directed forwards in the shape of a beak projecting over the upper part of the femora. The true pelvis was very shallow, and had an almost complete osseous floor, owing to the union in the middle line of the tubera ischii and of the ischial spines. The union took place in such a way as to leave three outlets from before backwards. The first constituted the sub-pubic angle, and was filled in by fibrous tissue; the second intervened between the tubera ischii and the ischial spines, and the third between the ischial spines and the front of the sacrum. Through this last-named the gluteal nerves escaped from the pelvis.

The femora were completely fused (fig. 2), the only evidence of their bilateral origin being a slight groove along the middle line both in front and behind, and the presence of a small foramen in the lower third of the shaft. The cartilaginous heads projected outwards on each side from the upper end of the bone to articulate with the acetabular. Posterior to them an extensive shelf of bone was present immediately below the pelvis, representing the fused great trochanters. Each hip-joint was surrounded by a distinct capsule, and both the acetabular surfaces of the innominate bones and the heads of the femora were much flattened. The lower end of the femora presented three separate articular surfaces, separated from one another by septa of fibrous tissue which passed down to be attached to the intervals between corresponding articular surfaces upon the tibiæ. The two lateral articular surfaces were of the normal shape of the internal condylar surface of the femora, while the middle surface was triangular in shape and presented in the centre a slight ridge as indication of its bilateral character. As already stated, two separate patellæ were present on the back of the joint.

FIG. 2.

A. Pelvis and skeleton of the fused lower limbs as seen from the front.
B. Pelvis and skeleton of the fused lower limbs as seen from behind.

Both tibiæ were completely fused to form a single bone, large and expanded at its upper end, and gradually tapering below. No trace of the fibulæ was present (fig. 2). The lower end of the limb was composed of five small cartilaginous nodules, united to one another and to the lower end of the tibiæ by fibrous tissue. In the upper two of these nodules a bony centre was present.

It is not my intention to discuss here the various theories that have been advanced to account for the occurrence of Sirenomelian monsters, but before concluding, I would wish to express the opinion that no mechanical-compression theory can account for all the abnormalities found in this type, and that therefore it is necessary to refer the cause back to some defect of the early ovum. How compression by the amnion, or a fusion of lower limbs after original separate development, can account for the irregularities in number of the vertebræ and ribs, is, I think, impossible to conceive. The irregularity of the bones of the trunk is indeed, I think, the strongest evidence that exists in favour of primary as against secondary malformation, inasmuch as all the other peculiarities present can to some extent be explained by a theory of compression.

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CRANIO-CEREBRAL TOPOGRAPHY.

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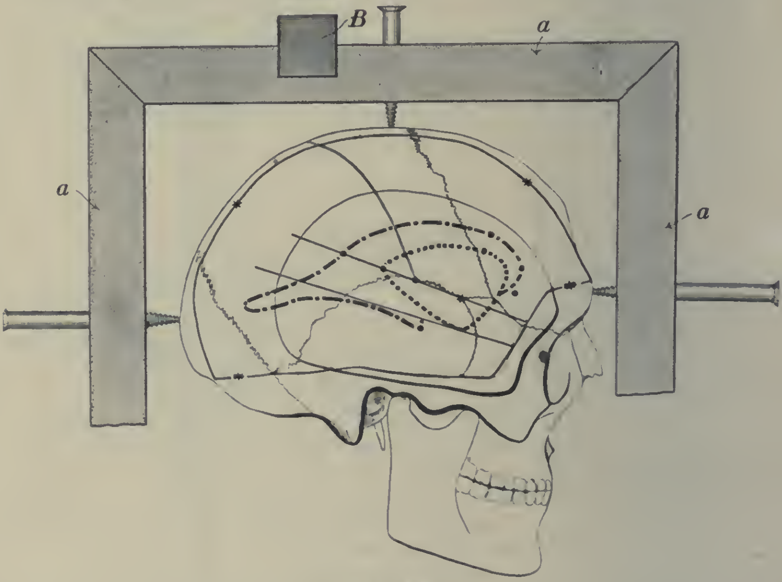
In this investigation of the topographical anatomy of the brain the photographic method was adopted. The precautions taken against errors likely to occur were somewhat novel, and may, therefore, be briefly described.



* Lines of saw-cut.

Fig. 1.—The surface markings of the fissures of Rolando and Sylvius of the island of Reil, and the lateral ventricle, as given by Thane and Godlee in *Quain's Anatomy*.

The brain was hardened *in situ* by injection of a 15 per cent. solution of formaldehyde into the internal carotid arteries, the other arteries to the brain having been tied. This was done as soon after death as possible, and the body left in the supine position.

The day following, the scalp was removed and the cranium sawn through along the lines indicated in fig. 1, the isolated portion of bone being held in place by its attachment to the dura mater.

The topographical markings given by Thane and Godlee,[1] Anderson and Makins,[2] and Chiene,[3] were drawn on the skull in black ink. These markings were selected as they are found in well-known text-books on anatomy, and are among the most commonly used by surgeons in this country.

Hare's[4] line for the fissure of Rolando, also very commonly in use by surgeons, was found to closely correspond to that of Thane and Godlee.

FIG. 2.—The surface markings of the island of Reil, the lateral ventricle, and corpus callosum, arrived at by taking the averages in the six heads examined.

The head was then mounted in an apparatus designed to enable me to place the cranium and camera in such relation that rays from the centre of the lateral aspect of the head to the lens would be at right angles to the sagittal plane.

One portion of the apparatus seen in fig. 1, rigidly and

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[1] *Quain's Anatomy.*

[2] *A Treatise on Anatomy*, by Morris.

[3] See article by Mr Harold Stiles in the *Text-book of Anatomy*, edited by Cunningham.

[4] *Journal of Anatomy and Physiology*, Jan. 1884.

accurately made, forms three sides of a square, and through each side is a stout screw—one applied to the glabella, another to mid-line on the vertex, and the third to the external occipital protuberance. A bar (fig. 1, B) is fixed rigidly to the part of the apparatus above described at right angles to the plane of the screw points, and therefore to the sagittal plane of the head.

The head, firmly fixed in the above apparatus, was then fastened to a rigid post-mortem room table by means of plaster-of-Paris, with the bar B in the horizontal plane and directed towards the camera.

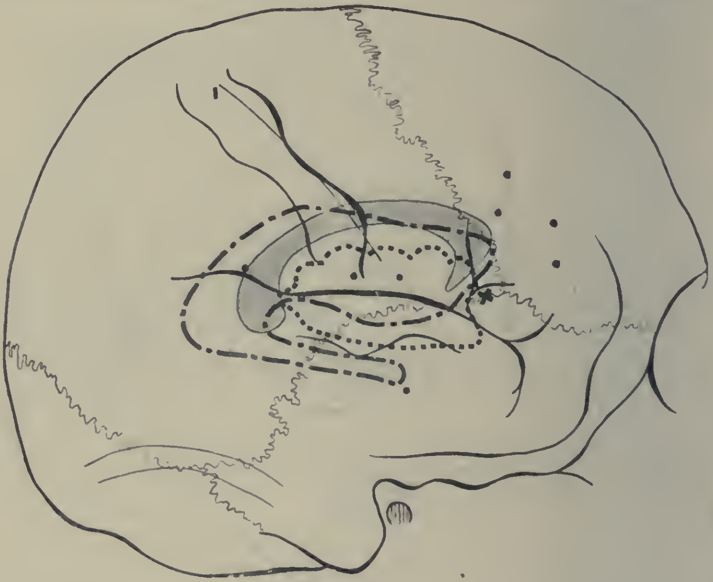
FIG. 3.

The camera was then manipulated into its proper position, which was ascertained by sighting along the bar B at a point in proper relation to the lens.

A centimetre measure was placed on one of the side bars of the apparatus, so that measurements could afterwards be made in the sagittal or parallel planes.

A 16-inch focus lens was used, and placed 15 feet away from the head.

The head was now carefully focussed, and successive photographs taken of the skull with the surface markings, of the convolutions, the island of Reil, the lateral ventricle, and the corpus callosum.

The camera was not moved, and as the head was rigidly fixed by plaster-of-Paris, it was not disturbed during the dissections necessary to expose the various parts.

The "positive" of the surface of the skull was "thrown on" white diagram papers by an enlarging apparatus, and the various parts of interest were traced.

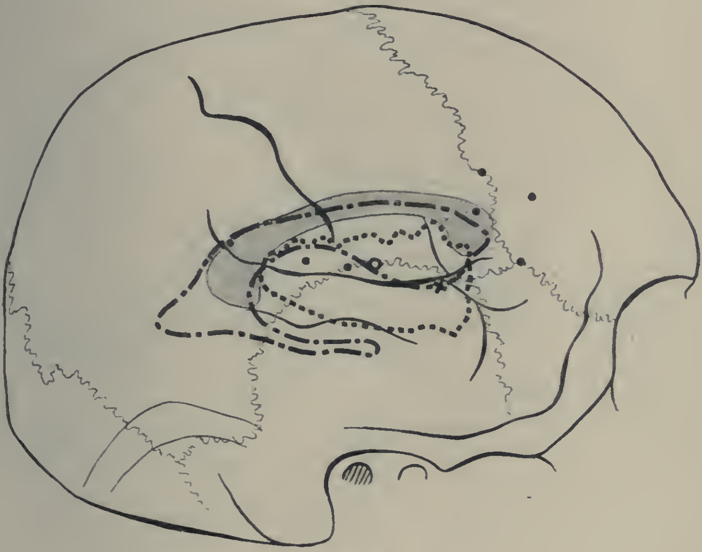

FIG. 4.

The other positives were similarly treated in succession, the paper being moved in each case until the outline of the skull marked on the paper from the first positive coincided with that of the positive under examination.

In this way the six illustrations were originally produced, showing the relations of the parts of the brain to the lateral surface of the skull, and of the parts to one another.

The left side of six heads of adults between the ages of 40 and 66 were so examined. Most investigators either do not state the number of heads examined, or have limited their observation to one or two specimens.

The results of the investigation are in great part in agreement with the descriptions of the cranio-cerebral topography given in text-books, but there are some interesting differences.

The surface-markings of the fissures described by Thane and Godlee and others are, on the whole, supported by the six specimens. The method advised by Professor Thane in *Quain's Anatomy* gives the most accurate results. In most of the cases the posterior horizontal limb of the fissure of Sylvius was a little lower than indicated by the above methods—as much as one centimetre in three cases.

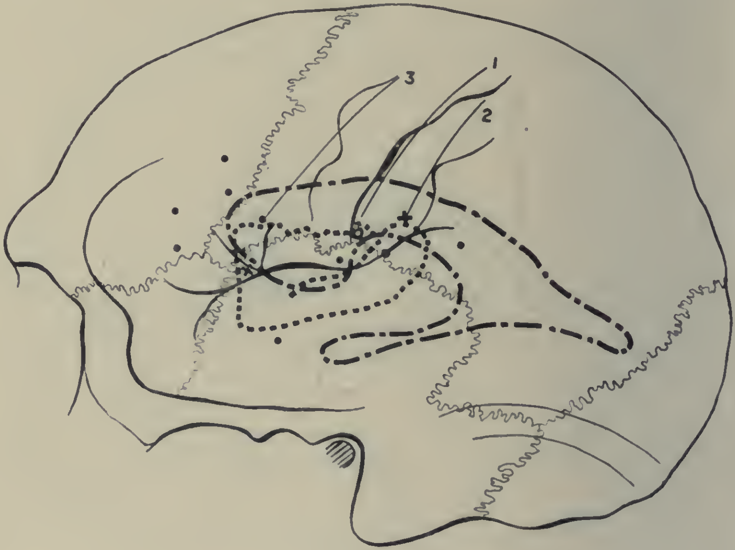

FIG. 5.

The island of Reil, in all cases but one, lay posterior to the coronal suture, and in the single exception the superior angle was only just under cover of the frontal bone. In the five cases the anterior limiting sulcus was found at its most anterior part to lie between the coronal suture and a point 1½ centimetres behind that suture.

This differs from the description in *Quain's Anatomy*, in which the island is placed in considerable part under cover of the frontal bone.

The posterior angle was found in all cases to be 1·5 to 2 centimetres behind the surface-marking given for it by Thane and Godlee.[1]

A line drawn upwards at right angles to Reid's base line from a point 2 centimetres behind the posterior margin of the external auditory meatus would cut the Sylvian line of Thane and Godlee at about the posterior extremity of the island of Reil.

The superior and inferior limiting sulci vary much in their relation to the squamo-parietal suture, and these variations have a distinct relation to the vertical measurement of cranium. However, a line drawn backwards, parallel with the upper border of the zygoma, from a point 1·5 to 2 centimetres above the Sylvian point of Thane and Godlee, would fairly accurately mark the superior limiting sulcus.

FIG. 6.

The inferior sulcus at its anterior part corresponds with the markings given in *Quain's Anatomy*.

The tracings show very well how much more the temporo-sphenoidal operculum overlaps the island than the superior opercula.

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[1] *Journal of Anatomy and Physiology*, 1903.

In the six heads examined the lateral ventricle was considerably posterior to the position given for it in *Quain's Anatomy*, and, on the whole, situated as Symington found it in the head he examined by another method, and as indicated in Fraser's plates.[1]

In the average of the six specimens the superior limit of the lateral ventricle was a little less than three inches above the upper margin of the zygoma.

The anterior limit of the anterior horn in four cases was at or just posterior to the coronal suture, and in the remaining two this suture was just perceptibly behind the anterior extremity of the ventricle. This is in agreement with the observations of Fraser and Symington, but considerably posterior to its position described in *Quain's Anatomy*.

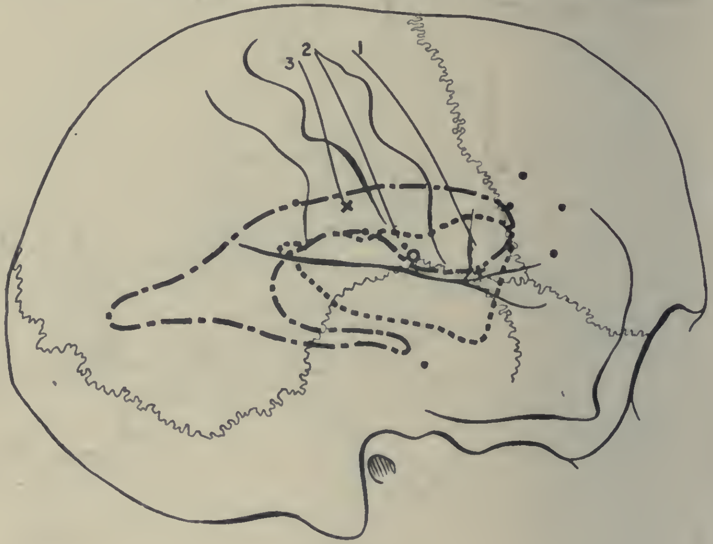

FIG. 7.

The ventricle at the junction of the body with the posterior and descending horns can be sufficiently accurately marked by a point five (5) centimetres above and three (3) centimetres behind the external auditory meatus, using Reid's base line as the horizontal. This, again, corresponds with Symington's observations.

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[1] *A Guide to Operations on the Brain*, by Alex. Fraser.

The tip of the descending horn was found in all cases in the position ascribed to it by Thane and Godlee—on the pre-auricular line one (1) centimetre below the parallel line.

The floor of the anterior horn in its lowest part in most cases almost coincided with the anterior part of the temporo-parietal suture.

The foramen of Monro lay very constantly on the pre-auricular line at and immediately above the fissure of Sylvius and temporo-parietal suture.

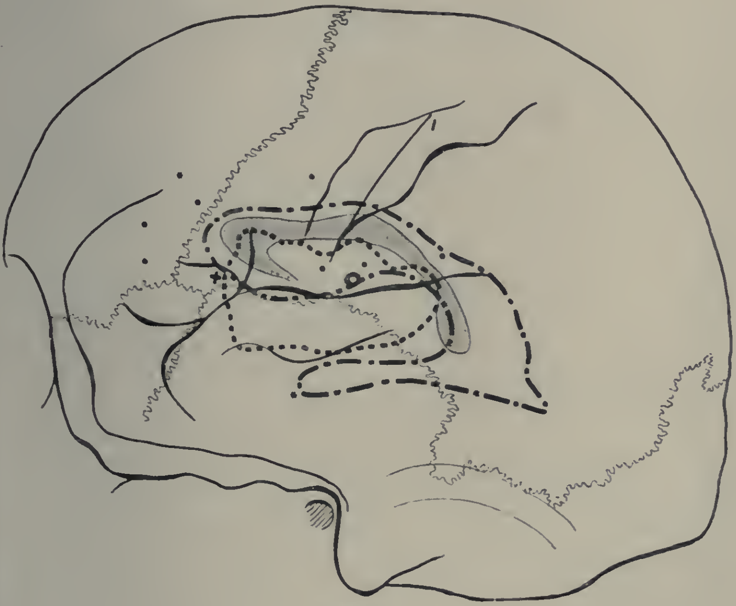

FIG. 8.

The corpus callosum was examined in three cases. The superior surface practically corresponded to the superior limit of the lateral ventricle.

The anterior extremity in one case reached the coronal suture, in another was ·75 cm. in front, and in the third ·5 cm. behind the suture.

The posterior limit of the splenium may be indicated by the point given for the junction of the body with the posterior and descending horn of the lateral ventricle.

There are indications that the coarser variations in the relations of the brain to the surface of the skull are dependent on the form of the cranium as has been suggested, and probably each type of skull has its own cranio-cerebral topography.

Before, however, any definite statement can be made on this point it would be necessary to examine at least two of each of the commoner types of head.

THE DEVELOPMENT OF THE RETINA IN AMPHIBIA: AN EMBRYOLOGICAL AND CYTOLOGICAL STUDY.

By JOHN CAMERON, M.D. (Edin.), D.Sc., *Carnegie Fellow, Research Fellow of St Andrews University; Demonstrator of Anatomy, United College, University of St Andrews.*

(PLATES LI.–LII.)

PART III.

CONTENTS.

12. THE SECOND VARIETY OF VISUAL ELEMENT.

THE differentiation of the primary visual elements into two distinct types or varieties takes place about the 23rd or 24th day, as already stated in Part II. of this paper. Those which belong to this second variety are readily distinguishable from the rods by the narrowness of the inner segment. This characteristic distinction will be at once recognised on studying the two visual elements (from a 23rd-day frog-tadpole), which are represented side by side in fig. 24 (Pl. LI.). The body of the cone thus tends to become markedly spindle-shaped as development advances, while it is attached to the corresponding nucleus by this attenuated inner segment, which is very variable in length, as shown in figs. 25 and 26, and forms a sort of delicate connecting stalk.

This second type of visual element, which has been rather infelicitously termed 'cone,' possesses, in the centre of the spindle, a small clear vesicle (figs. 24 to 26) which represents the remains of the original yolk-globule (this constitutes the so-called 'oil-globule' found in Amphibian cones, and about which more anon), while distal to this body there exists in most cases a clear achromatic area, which, like the outer part of the rod-ellipsoid, is usually somewhat biconvex in shape; and between the two is a narrow segment, which stains usually very markedly with iron-alum-hæmatoxylin, and probably corresponds to the deeply-staining portion of the rod-ellipsoid. These two structures must therefore form the 'cone-ellipsoid.' Distal to this body there are frequently to be seen clear clefts or spaces lying transversely in the outer segment of the cone; but these are irregular both in outline and distribution, and are apparently due to artificial cleavage at these points.

The cones, like the rods, thus owe their early growth to the ingestion of pigment from the retinal pigment-cells; in other words, they *actually perform a rhodopsin-function* (see Part II.). The importance of this observation will be better appreciated if the ultimate fate of these Amphibian cone-elements be carefully studied, for it is found that many of them become converted into rods during the later stages of development. The actual process of transformation will be fully described in section 13.

The cones do not tend to increase much in size during the tadpole stage. This deficiency of growth may be explained by the fact that no further supplies of achromatin material from the corresponding nucleus can be observed to pass along the finely attenuated stalk towards the body of the cone. The necessary addition of fresh ingesting material is thus cut off, and it would therefore appear that the ingestive power of the achromatic nuclear substance contained in the yolk-globule must become early exhausted, and prevent the occurrence of further growth. In the case of the rods, however, the necessary supply of fresh nuclear achromatin is kept up (as shown in Part II.), and accounts for the persistence of the rhodopsin-function, and thus the progressively rapid growth of these elements. There is not such a close interaction, therefore, between the cone-nucleus and cone as there is between the rod and its nucleus; and this probably explains why the cone-nuclei do not tend to become protruded into the inner segments of the cones, but instead remain in the external nuclear layer, near to the external molecular layer.

13. Ultimate Fate of the Cone-elements.

In the introduction to this paper I have referred to the statement of Bernard's (7), that the cones of the Amphibia are merely early stages in the formation of new rods. I am also decidedly of this opinion, for I have been able to trace the mode of formation of Schwalbe's rods (*i.e.* those with narrow inner segments) from these spindle-shaped structures. This renewal of growth on the part of the cones is seemingly due to the restoration of the rhodopsin-function, which appears to be effected by fresh supplies of nuclear achromatin being forced in small quantities along the narrow stalk of the cone. This passage of material from the nuclei in such minute successive emoluments is extremely difficult to prove from direct observation; but remarkable collateral evidence of the existence of such a process is found in those instances where the cone-nucleus suddenly gives off a large globule of its achromatic substance, which at once distends the stalk of the cone. This phenomenon, which is illustrated in figs. 29 (Pl. LI.) and 30 (Pl. LII.), will be described later in section 14.

The transformation of the cones into Schwalbe's rods appears to take place during the stage of metamorphosis in the larval condition, and consists in a lengthening and broadening of the outer part of the spindle, with a concomitant narrowing of the body of the structure, so that the walls of the outer segment become more or less parallel to one another, as shown in fig. 27. The yolk-globule blends with the clear part of the cone-ellipsoid (as has been already described in Part II. in the case of the rods) to form the ellipsoid of the newly completed rod. This outer segment remains attached to the corresponding nucleus by the still narrow stalk of the originally spindle-shaped structure, this arrangement serving as a clue to the origin of this peculiar type of rod (fig. 27). The term 'cone' is therefore quite a misnomer in the case of the Amphibia; for this structure owes its development and growth to the ingestion of pigment from the retinal pigment-cells, that is to say, it exercises a rhodopsin-function like the rods. It is also important to note that probably all the cones become transformed sooner or later into rods; and, further, the Amphibian rod, in the early stages at least, has more the shape of a cone than the spindle-shaped structure which receives this title (fig. 24).

It is thus evident that the cones of Amphibia do not possess the high degree of morphological significance which is usually assigned to the corresponding structures in the retina of man and other higher Vertebrates. It certainly appears to me that the exact relationship which the cones of the higher Vertebrata bear to the rods is not yet perfectly understood or appreciated, and would probably form a profitable and instructive field of research; for continued investigation will likely show that the cones in these higher Classes also, at some stage of their life-history at least, perform a rhodopsin-function as well as the rods.

14. THE SECOND TYPE OF CONE-ELEMENT.

In the early stages of retinal development the above-described rod- and cone-elements are the only ones to be found; but about the 35th day, or perhaps earlier, another type of element somewhat suddenly makes its appearance. This new structure consists of a basal portion, which is distended with a clear, homogeneous, and practically achromatic substance, together with a fine pointed extremity. The origin of this element from the cone is quite easy to demonstrate; for it is simply produced by the narrow stalk of the latter becoming distended, owing to the sudden discharge into it of a large amount of nascent achromatin from the corresponding nucleus. On this account I propose to term this structure 'the second type of cone'; but I ought to mention that I have observed instances where this structure seemed to have been produced by a similar discharge of nuclear achromatin into what appeared to have been previously the base of a rod. In fact, it is quite possible for such a phenomenon to occur in the case of the rods also, seeing that their nuclei are regularly engaged in giving off fresh supplies of nascent achromatin (see fig. 24).

This great loss of nuclear contents must of necessity denote a great drain on the nucleus; and, indeed, in those fortunate instances where the cone-nucleus has been fixed in the act of giving off its globule of achromatin, it will be found in a condition of marked collapse, as represented in figs. 29 and 30. It may be observed that in fig. 29 the newly-extruded nuclear substance has blended with the remains of the yolk-globule, and the fact that the contents of these two bodies are capable of being so readily miscible with one another seems to render untenable the idea that the remnant of the first protruded vesicle in the cone is really 'oily' in nature. In fig. 30, on the other hand, these two bodies have not yet fused together, so that they still form distinct and separate structures. We are thus afforded with another and perhaps still more striking proof of the extrusion by these retinal nuclei of this peculiar material, which in the nascent condition is so decidedly achromatic in its staining reactions. I hope to show in a later communication that this characteristic phenomenon, which I propose to term the *nuclear achromatin function*, is also exhibited by the nuclei of other embryonic tissue, such as muscle, etc.

If the basal globule of this second type of cone be examined by very high powers (*e.g.* a $\frac{1}{12}$-oil immersion lens), it will be observed to exhibit a course network or reticulum, which, however, appears to exist chiefly on its surface (figs. 28 to 30). This is probably due to the unequal expansion of the stalk of the cone, some parts becoming greatly thinned out, while at other points thickenings have been left, which were compelled to take an irregular zigzag direction on the bulging surface of the vesicle, and thus to present the appearance of a network. In addition to this, the contents of the vesicle itself begin to exhibit a faint staining reaction, due to what might be termed a maturing or '*ripening*' of the nuclear achromatin—a transformation which this substance seems to undergo almost universally throughout the retina; for I have already pointed out that the processes of the nuclei in the other layers, which are also at first extremely achromatic, soon undergo a similar process of ripening, in virtue of which they become more readily influenced by the action of staining agents than they were at their first appearance.

When two spindle-shaped cones happen to develop side by side, and the stalk of one becomes distended in this way, then the structure known as a 'double cone' is produced, as has been already shown by Bernard.[1] Such a structure is illustrated in fig. 31, where it will be observed that the fine attenuated stalk of one cone becomes moulded along the lateral aspect of the large basal vesicle, and, indeed, in many instances it lies in such close contact as to appear blended with it; and thus the two together seem to form a single cone-element with a double extremity. The so-called double cones of Amphibia are therefore due to different types of cone being situated side by side, each maintaining, however, its independent existence and distinctive character.

The second type of cone also becomes gradually transformed into a rod during the period of metamorphosis, but it is somewhat difficult to determine with accuracy the various steps or stages of the process by which this is brought about. The distal limb becomes elongated and filled with deeply-staining material, just as in the case of the rods; but the achromatic vesicle tends to linger for a considerable time in its basal portion. As a result of this detention, the active properties which it possesses in virtue of its nascent condition become in all probability rapidly impaired, a fact which perhaps explains the slow rate of growth of this type of visual element. The contents of the basal vesicle, sooner or later, pass into the outer segment, and there they blend with the deeply-stained material. The outer segment is thus enabled to resume its rhodopsin-function, though in rather a feeble fashion; and in this way it slowly increases in size, so that by degrees the whole structure becomes gradually transformed into a rod. Some of the contents of the basal vesicle persist as the clear part of the rod-ellipsoid.

15. THE NATURE OF THE 'OIL-GLOBULE' FOUND IN THE CONES OF AMPHIBIA.

Numerous observers have described in the cones of Amphibia the presence of a minute spherical globule, which is strongly refracting, and may be colourless, or tinted of various colours.

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[1] *Quart. Jour. Micr. Sci.*, vol. xliii. p. 33.

The term 'chromophane' has been applied to this body, which is usually spoken of as being fatty in nature. Thus Charles[1] describes it as consisting of coloured fat, while Halliburton[2] considers that it belongs to the group of pigments called lipochromes. Its exact constitution, however, does not appear to have been as yet determined with accuracy.

A valuable clue to its chemical nature is obtained on studying its developmental history; for I have previously indicated that it consists of the remains of the original yolk-globule. It has, further, been shown that it is found in both the rod- and cone-rudiments (see figs. 24 and 34). In the case of the rods it soon terminates its existence by blending with the clear part of the rod-ellipsoid, but in the cones it persists much longer as a distinct and separate structure, although, when these also become transformed into rods, the globule has a fate similar to that already indicated in the case of the rods. Since the origin of this body from the yolk-granules is so well defined in the Amphibian retina, it follows that lecithin, or some derivative thereof, must enter very extensively into its composition, so that there are decided reasons for considering that it is fatty in nature.

It was in the next place determined to study the refractivity of these globules when examined through the polariscope, and it was found that when the retinal tissue was fixed, stained, and mounted in balsam in the ordinary way, these structures appeared to be singly refracting. It was, of course, considered highly probable that the various stages of preparation might have the effect of altering their physical characters, so that it was deemed necessary to study this question of refractivity in teased fresh retinæ. Owing to the want of detail, from the absence of the effect of staining agents, it was somewhat difficult to locate the rod- and cone-layer, and thus to identify these globules; but there were structures which seemingly corresponded to these bodies, and which appeared bright in the dark field of the polarising microscope, and on this account were to be recognised as being doubly refracting in character.

It was, however, determined, in view of the difficulty of

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[1] *Physiological and Pathological Chemistry*, London, 1884, p. 345.

[2] *Text-book of Chemical Physiology and Pathology*, London, 1891, p. 464.

observing these globules in fresh retinæ, to obtain collateral evidence in regard to the refractive power of lecithin, granting, of course, that the oil-globule of the cones really consisted of this substance. Lecithin was therefore prepared from the yolk of egg by the method of Diaconow.[1] A little of the white substance thus obtained was mounted on a slide and examined by means of the polariscope, when it was found to be decidedly doubly refracting.

Remarkable evidence of the fact that these globules are derived from yolk-material is furnished by a comparative study of their presence in the Vertebrate series; for it is found that they are absent from the cones of man and the higher mammals, where the yolk of the ova is at a minimum, and are, on the other hand, a marked feature of the cones in the four lower Vertebrate classes, in which, as is well known, this yolk-substance is very plentiful; and, moreover, they are especially prominent in the cones of birds, in whose ova the yolk may be said to attain its maximum amount.

16. The Layer of Optic Nerve Fibres.

The fibres of the optic nerve take origin as axis-cylinder processes from the nuclei of the ganglionic layer. Like the protrusions from the nuclei of the other retinal layers, they are at first markedly achromatic in their behaviour towards both nuclear and cytoplasmic stains, a characteristic property which renders the demonstration of this retinal layer extremely difficult during the earlier stages of development. Very gradually, however, these axons undergo the process of ripening which has been already described in section 14, so that towards the end of the metamorphosis the individual fibres become much more readily influenced by staining agents, and thus form a well-defined layer in the Amphibian retina. A reference to fig. 32 will show the appearance of this layer at the 85th day, which practically represents the end of the metamorphosis. Note how the fibres are arranged in groups, a fact which renders their presence more readily recognisable.

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[1] Described fully on page 527 of Halliburton's *Text-book of Chemical Physiology and Pathology.*

In this paper I have undertaken to describe the embryology of the various retinal layers only, so that it is not intended here to trace the further development of the optic nerve, more especially as I propose to deal with the latter subject more fully in another communication.

17. Development of the Retinal Pigment-cells.

The layer of retinal pigment-cells is directly formed from the outer wall of the optic cup, and the presence of pigment in these becomes very early manifest, in fact almost immediately after the invagination of the optic vesicle. The pigment rapidly increases in amount, and is at first irregularly distributed throughout the layer, but very soon it becomes collected together so as to form a definite zone in those portions of the cells which are directed towards the developing visual elements. This condition is well shown in fig. 33, which represents the appearance both of the pigment-cells and of the visual elements at the 15th day. It will be observed that there are as yet no evidences of the pigmented processes. I have already very fully described (in Part II.) the attractive influence or positive chemotaxis which the developing visual elements exert on the pigment-cells, whereby these two sets of structures develop simultaneously. In fig. 33 the visual elements are still lying underneath the external limiting membrane; but signs of the existence of this positive chemotaxis are already indicated even at this stage, firstly, by the accumulation of pigment along the free borders of the cells, and secondly, by the irregular sinuous outline which that border exhibits, as if it were just on the point of protruding its processes. In fig. 34 both the visual elements and the pigment-cell processes will be observed to have made great strides in development. Fig. 17 (which illustrates Part II. of this paper) demonstrates very well the concomitant growth of these two sets of structures, for it shows a complete section of the retina of a 35th-day frog-tadpole. The animal from which this section was prepared remained in a totally dark chamber for about three hours before killing, so as to ensure the full retraction of the pigment processes, and thus the influence of light on these structures was completely eliminated. The rods and cones in the central portion of the retinal convexity are seen to be in the most advanced stage of development, as are also the pigment processes which are situated opposite them. Towards the margins of the retinal cup, however, it will be observed that the rods and cones, as also the pigment-cell processes, are less well developed. Still further forwards, where the visual elements are in the primary vesicular stage, the pigmented processes are also just beginning to show. Finally, where the rod- and cone-layer ceases to exist, there also the pigment-cells become devoid of processes.

About the 23rd or 24th day the pigment-cell processes begin to be influenced by light, for after that date it was found necessary to keep the tadpoles in the dark for three hours before killing them, so as to ensure the complete retraction of the former. This protrusion, however, of these processes, owing to the attractive influence exerted on them by the developing visual elements, before the action of light has begun to manifest itself, has led me to believe that in the ordinary adult condition light does not act directly upon the pigment-cells and cause the elongation of their processes, but that this really occurs indirectly through the medium of the visual elements. What probably happens is, that the light stimulates the rods and cones first of all, and this effect causes the latter to exert their attractive influence on the pigment-cells, and thereby cause the latter to protrude their processes, just as during the early developmental stages. This will, of course, require experimental proof, and I hope to undertake an investigation on these lines at a no distant date.

The writer (10) has shown that the rate of protrusion of the retinal pigment-cell processes under the influence of light is about the same as that of the pseudopodia of white blood corpuscles, and that their movements are to be regarded as being amœboid in character. In the same paper it is also pointed out that the pigment-granules do not move backwards and forwards within the processes, but are borne along with the movements of the protoplasm in which they lie. This latter substance is remarkably achromatic in character, and perhaps corresponds to the hyaloplasm of which the pseudopodia of amœboid cells appear to consist.[1] I am further of the opinion that it corresponds to the achromatic substance which is extruded from the other retinal nuclei, and is therefore probably formed in a similar manner from the nuclei of the retinal pigment-cells. This, unfortunately, is extremely difficult to prove by actual observation, seeing that the nuclei of these cells are surrounded by an extensive cytoplasmic envelope, which prevents a successful cytological study of them. Indirect evidence is, however, yielded by the presence of the "yellow fat-globules" which are found in the retinal pigment-cells of Amphibia (fig. 35). It is not a difficult matter to trace the origin of these from the yolk-granules, so that apparently the nuclei of these cells secrete their achromatin, which in the nascent condition attacks the yolk-granules and converts them into yolk-globules, *i.e.* the 'yellow fat-globules.' These bodies, like those of the cones, thus also probably consist for the most part of lecithin or a derivative thereof, and the yellow pigment contained in them is usually known as lipochrin,[2] which is one of the lipochromes.[3]

The pigment-cell processes may be observed to be arranged in groups corresponding to the individual pigment-cells, while those belonging to each cell are also frequently found forming smaller collections (fig. 35).

18. Summary and Main Conclusions.

1. It is first of all necessary to mention that the value of Bles' fluid as a fixative for the retina cannot be too highly praised, while the use of the iron-alum-hæmatoxylin stain, as applied by the method which is described in the Introduction of this paper, has given most excellent results (Part I.).

2. It is important to again emphasise the great value of recognising in the inner wall of the retinal cup four groups of structures, namely, germinal nuclei, neuroblast-nuclei, spongio-

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[1] See Quain's *Anatomy*, vol. i. pt. ii. p. 178.

[2] This is the name given by Kühne. See *Untersuch. aus dem physiol. Institut der Universität, Heidelberg*, 1878–1882.

[3] *Text-book of Chemical Physiology and Pathology* by Halliburton, p. 459.

blasts and myelo-spongium; for these all play a most important part in the differentiation of the various layers of the retina (Part I.).

3. One of the most important results which has been attained in this research is with regard to the origin of the processes of the 'cells' in the inner retinal wall. It has been shown that the processes of the cells in the ganglionic and internal nuclear layers emerge from the nuclei, and not from any surrounding cytoplasm, for the presence of the latter cannot be demonstrated in the embryonic retina. Moreover, the first rudiments of the rods and cones are partly in the form of protrusions from the nuclei of the external nuclear layer (Part I.).

4. These processes have been shown to consist for the most part of nuclear achromatin, which in the nascent condition stains very feebly with the materials which are usually employed for this purpose. Hence I propose to entitle this the '*achromatin function*' of these nuclei (Part I.).

5. This extrusion of these processes is evidenced by a progressive diminution of the corresponding nuclei, which takes place throughout development (Part I.).

6. This extruded nuclear achromatin gradually undergoes a process of ripening as development progresses, so that these extrusions which in the early stages are extremely difficult to demonstrate, become later quite a well-marked feature of the retina. In this connection note especially the layer of optic nerve fibres (Part III.).

7. The nuclei in the inner wall of the embryonic retina (except the nuclei of the fibres of Müller) do not possess any surrounding cytoplasm, and there is a persistence of this primitive embryonic condition even in the adult Amphibian retina (Part I.).

8. Mitotic division is usually believed to be almost universal in the case of animal cells, but in the developing retina there is abundant proof of the occurrence of amitotic or direct division of nuclei. In the early tadpole stage, before the retinal nuclei begin to function, growth takes place by mitotic division of the germinal nuclei which are set apart for that purpose. After the retinal nuclei have become actively functional they appear to lose the power of undergoing mitotic

division, and now multiply by amitosis. This peculiar sequence of mitotic and amitotic division in the early life-history of the same nuclei is of great cytological interest (Part II.).

9. The mode of development of the rods and cones is also of great interest. It was mentioned incidentally in Part I. that the first rudiments of these structures consist of nascent achromatin from the nuclei of the external nuclear layer. This substance attacks the yolk-granules, and, by a process of digestion, apparently transforms these into clear achromatic vesicles, which I have termed yolk-globules (Part II.).

10. These, by their protrusion beyond the external limiting membrane, exert a *positive chemotaxis* on the retinal pigment-cells, which causes the processes of the latter to develop simultaneously with them (Part II.).

11. Moreover, what is more important still, the rod- and cone-rudiments actually ingest this pigment, and metabolise it into a substance which stains very intensely with iron-alum-hæmatoxylin (Part II.).

12. This substance, which is *rhodopsin* or some allied body, appears to act as food-material to the rods and cones, for the latter grow with wonderful rapidity after becoming protruded beyond the external limiting membrane. The rod- and cone-nuclei are also found to give off fresh supplies of achromatin in order to maintain this ingestion of pigment (Part II.).

13. The latter is simply an index of what occurs during the lifetime of the individual. The rhodopsin-function of the rods would thus appear to be carried out by two factors—the pigment-cell processes supplying the pigment, while the nuclei of the rods and cones furnish the achromatic material, which is not only necessary but also essential for the maintenance of this function (Part II.).

14. The cones, like the rods, owe their early growth to the ingestion of pigment; in other words, they actually perform a rhodopsin-function. The significance of this observation is enhanced when it is noted that the cones of Amphibia are simply early stages in the formation of new rods, as has been already shown by Bernard (Part III.).

15. The temporary stoppage of growth of the cones is due to the supply of fresh achromatin from the nucleus being cut off

Hence the absence of this essential factor must prevent the continuance of the rhodopsin-function. This affords a ready explanation of the well-known fact that the cones of the adult frog are unable to exercise a rhodopsin-function (Part III.).

16. Two types of cone-element are readily recognisable in the developing Amphibian retina. Firstly, spindle-shaped structures which possess a fine stalk; and secondly, those which contain a large basal vesicle. The latter form is produced from the first type by a large amount of achromatin being suddenly forced into the base of the cone from the corresponding nucleus. This latter phenomenon demonstrates most clearly the existence of the 'achromatin function' (Part III.).

17. The so-called double cones of Amphibia are due to different types of cones becoming developed side by side, each, however, maintaining its independent existence and distinctive character (Part III.).

18. The so-called 'oil-globule' of the Amphibian cone, about which so much has been written, is simply the remains of the original yolk-globule. It is, moreover, found in both the rod- and cone-rudiments, and in each case appears to terminate its existence by blending with the clear part of the ellipsoid. Lecithin, or some derivative thereof, probably enters largely into its constitution, seeing that it is directly derived from the yolk (Part III.).

19. The optic nerve fibres arise as axis-cylinder processes of the ganglionic nuclei, and they appear very late as a distinctive retinal layer, owing to the fact that they are at first achromatic, like the processes of the other retinal nuclei. They undergo a process of 'ripening,' in virtue of which they become gradually more and more partial to staining agents, and thus admit of being more readily demonstrated (Part III.).

20. The concomitant growth of the pigment-cell processes and the visual elements, which I regard as due to positive chemotaxis, has been already alluded to. These processes I consider to be pseudopodia, while the clear achromatic substance in which the pigment-granules lie is probably derived from the nuclei of the retinal pigment-cells, and thus corresponds to the protrusions from the other retinal nuclei (Part III.).

21. The 'yellow fat-globules' which are found in the retinal

pigment-cells of Amphibia are, like the globules of the rods and cones, derived from the yolk-globules; and on that account probably consist chiefly of lecithin, or some derivative thereof (Part III.).

22. It is possible that in the ordinary adult condition light does not act directly upon the pigment-cells and cause the elongation of their processes, but that this really occurs indirectly through the medium of the visual elements. What probably happens is, that the light stimulates the rods and cones first of all, and this effect causes the latter to exert their attractive influence on the pigment-cells, and thereby cause the latter to protrude their processes, just as during the early developmental stages (Part III.).

23. These researches on the retina furnish us with suggestive information regarding the functions of the cell-nucleus, and will, it is hoped, impart to the latter a much wider morphological and physiological significance. A double proof of the fact that the nuclear achromatin, of embryonic nuclei at least, in the nascent condition possesses digestive properties, is furnished by its action on the yolk-granules and on the pigment-granules of the retinal pigment-cells. This observation appears to lead one to the conclusion that this nascent nuclear achromatin must contain an unformed ferment or enzyme—a statement which gathers interest in view of some recent researches (especially by Hartog) on the existence of enzymes in embryonic tissues. It has been further shown that many of the nuclei absorb the digested yolk-globule, and, after elaborating it, store it up as nuclear chromatin. It would thus appear that the achromatin is that part of the nuclear organ which exercises the digestive and ingestive action on food-material, while the chromatin is to be regarded as the primary product of nuclear metabolism. The nuclear chromatin, again, appears to be capable of retransformation into a substance which in the nascent condition is achromatic in character, and is in this form extruded from the nucleus (Part II.).

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EXPLANATION OF PLATES.

List of Abbreviations.

ax.	axis-cylinder.
b. ves.	basal vesicle of cone.
c_1.	first type of cone.
c_2.	second type of cone.
c. ell.	ellipsoid of cone.
c. g.	globule of cone.
c. n.	nucleus of cone.
ex. l. m.	external limiting membrane.
f. of M.	fibre of Müller.
i. l. m.	internal limiting membrane.
i. m. l.	internal molecular layer.
nuc. achr.	nuclear achromatin.
op. n. f.	optic nerve fibres.
oil gl.	oil-globule of pigment-cells.
r. ell.	ellipsoid of rod.
r. g.	globule of rod.
r. n.	nucleus of rod.
r. p. c.	retinal pigment-cells.
st.	stalk of cone.
vis. el.	visual elements.
y. g.	yolk-globule.

All the figures were drawn with the aid of the *camera lucida* apparatus of Zeiss. In all instances Leitz's $\frac{1}{12}$-inch oil immersion lens and No. 3 ocular were employed; and figs. 25 to 31 were further magnified by drawing out the tube of the microscope.

Fig. 24 shows a rod and a cone developing side by side, and illustrates very well the differentiation of these structures. The cone is recognised by the narrowness of its inner segment. Each element will be observed to contain the remains of the yolk-globule, and also an ellipsoid. The rod is receiving supplies of fresh nuclear achromatin in the form of three minute globules. Frog-tadpole at the 23rd day.

Fig. 25. The first type of cone at the 35th day. Note the con-

tinued lengthening and narrowing of the stalk, as also the spindle-shaped body.

Fig. 26. A cone with a greatly elongated and attenuated stalk.

Fig. 27. A Schwalbe's rod which is developed from the first type of cone. The globule has fused with the clear part of the ellipsoid. The outer segment has become greatly elongated and broadened, but the narrow stalk still persists. Frog-tadpole at the 67th day.

Fig. 28. The second type of cone, showing the enormous basal vesicle. The latter consists of a fresh supply of achromatin which has fused with the cone-globule. This type is directly derived from the first type of cone.

Fig. 29 shows the distension of the stalk of a cone by the sudden discharge into it of achromatin from the cone-nucleus—the latter thereby appearing in a collapsed condition. This fig. therefore shows the actual mode by which the second type of cone is derived from the first type. The freshly acquired achromatin has blended with the cone-globule. Frog-tadpole at 35th day.

Fig. 30 also shows the mode of derivation of the second type of cone. The newly extruded achromatin has not yet fused with the cone-globule. Note the slightly collapsed condition of the nucleus. Frog-tadpole at 35th day.

Fig. 31 shows a so-called double cone, which really consists of two distinct cone-elements, belonging always to different types. The stalk of the one often seems to be blended with the basal portion of the other, the two thereby appearing to form a unified structure.

Fig. 32 shows the appearance of the layer of optic nerve fibres at the 85th day (at the close of the metamorphosis). In the early stages it is difficult to demonstrate this layer, owing to the achromatic character of the individual fibres; but the latter gradually undergo a process of ripening, which enables them to be more readily influenced by staining agents.

Fig. 33. The condition of the retinal pigment-cells at the 15th day. As yet there are no processes, but the pigment has accumulated along the free margins of the cells, while the latter are showing an irregular outline. Note the position of the visual elements under the external limiting membrane.

Fig. 34. The condition of the retinal pigment-cells at the 21st day. The processes are now well formed, and have developed concomitantly with the visual elements, due probably to positive chemotaxis. At this stage the processes are not at all influenced by the action of light.

Fig. 35. The condition of the retinal pigment-cells at the 70th day. The processes show the full extent of retraction, owing to the animal having been kept in the dark for three hours previous to fixation of the retina. Note the collection of processes into groups corresponding to each cell, and also into still smaller aggregations. One of the so-called 'oil-globules' which are found in the retinal pigment-cells of Amphibia is also figured.

FIG. 24.

FIG. 25.

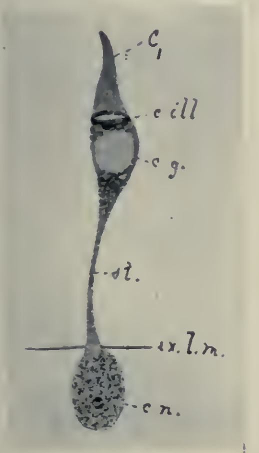

FIG. 26.

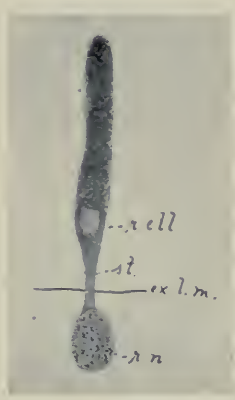

FIG. 27.

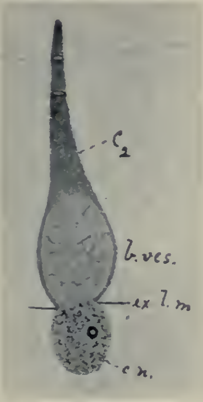

FIG. 28.

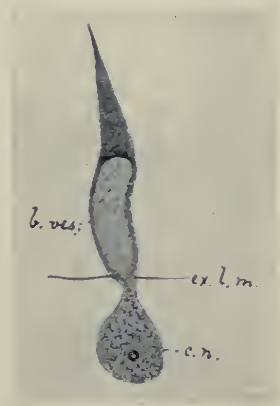

FIG. 29.

DR JOHN CAMERON on the Development of the Retina in Amphibia.

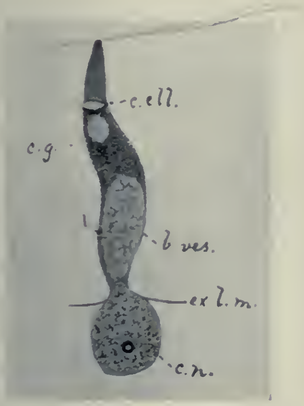

FIG. 30.

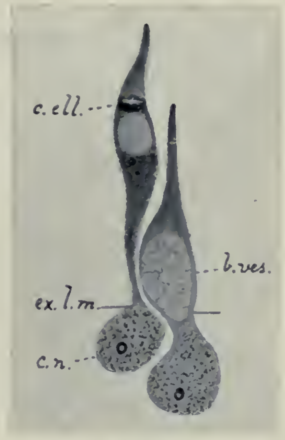

FIG. 31.

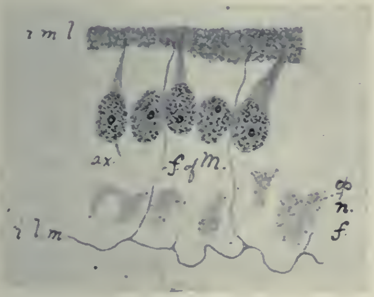

FIG. 32.

FIG. 33.

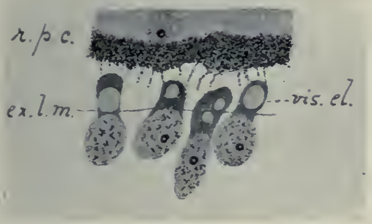

FIG. 34.

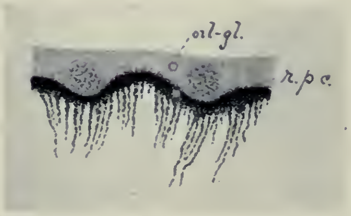

FIG. 35.

Dr JOHN CAMERON on the Development of the Retina in Amphibia.

A NOTE ON THE VARIATIONS OF THE TIBIA AND ASTRAGALUS.

By D. Macrae Aitken, F.R.C.S.E., *late Demonstrator of Anatomy, New School, School of Medicine of the Royal Colleges, Edinburgh.*

The present note, based on observations on loose bones kept for teaching purposes in the anatomical department of the New School, Edinburgh, is an attempt to show some co-relation between the commoner variations of the tibia and astragalus, the conditions of the same bones in the fœtus, and of the variations reported as occurring in congenital talipes equino-varus. The last apparently simulate the conditions described by Thomson [1] and Charles [2] in the bones of Oriental races.

It will be convenient to follow the latter author and to recognise two types of tibia and astragalus, viz. (1) the Oriental, (2) the European.

The characteristics of the Oriental type [3] are:—

In the tibia: (1) extra facets at the lower end; (2) backward displacement of the upper extremity; (3) convexity of the external condylar facet; (4) a marked degree of platycnemia.

In the astragalus: extra facets on the upper surface of the neck, and prolongation of the pyriform facet on to the inner side of the neck.

Of 55 specimens of the tibia examined in the present research, 32 per cent., and of 62 specimens of the astragalus, 45 per cent., were of the Oriental type. Further comparison showed that the Oriental type of tibia was shorter and much slighter in build than the European, and also that the impressions for the attachment of muscles and the groove for the tendon of the tibialis posticus were less distinct in bones of the former type.

The average angle of torsion, the Oriental type of tibia, was 15°, much less than that of the European type (22°).

In the astragalus the angle between the axes of the neck and of the body was greater in bones of the Oriental type, the average being 21°, as compared with 15° in the European type.

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[1] *Journ. of Anat.*, vol. xxiii.

[2] *Idem*, vol. xxviii.

[3] *Loc. cit.*

This angle produces inversion of the anterior part of the foot, and is opposed in direction to the torsion of the tibia.

In congenital talipes equino-varus, in addition to the well-known inversion of the neck of the astragalus, there is a failure of the external rotation at the lower end of the tibia, so that the internal malleolus often lies in a plane posterior to that of the external malleolus.[1]

With the exception of platycnemia and the small angle of torsion, all the characteristics of the Oriental type have been described as apparent in the fœtus and new-born infant. In Europeans these fœtal characteristics are said to disappear in the course of the second year of life.[2]

I have not been able to find any statement of the usual angle of torsion of the tibia of the infant. In the few cases I have examined, it has always been very small or even zero.

Platycnemia and backward displacement of the upper end of the tibia seem to occur together. They are both characteristic of bones of races who habitually adopt the squatting attitude, and so frequently throw an antero-posterior strain on the tibia. In the present series of bones, 29 out of 55 showed more or less backward displacement of the upper end, and their average platycnemic index was 67·1, nearly as low as that of the bones classed as Oriental (66·8), and much lower than the European type (72.5). Backward displacement of the upper end of the tibia must mean that the weight of the body is transmitted from the condyles of the femur obliquely forwards to the shaft of the tibia, and nature meets this strain by increased growth in the antero-posterior diameter.

The usual statement that platycnemia is associated with over-development of the tibialis posticus muscle, was not borne out by the appearance of the bones examined; those with the lowest platycnemic index were slender and smooth, and showed least evidence of attachments of powerful muscles, while the large, strongly marked bones of the European type had the highest index.

The following inferences seem therefore justifiable:—

1. The variations described as belonging to the Oriental

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[1] Robt. Jones and Ridlon, *Med. Ann.*, 1896.

[2] Waterston, *Edin. Thesis*, 1900.

type are due to the persistence of peculiarities impressed on the skeleton *in utero,* and are not uncommon in bones of Europeans.

2. Congenital talipes equino-varus is a persistence of the same features in an exaggerated degree.

3. An explanation of platycnemia may be found in altered lines of transmission of the body weight, and not in the traction of a hypothetically powerful tibialis posticus muscle.

ON THE LIMITS OF THE SENSIBILITY TO ODOURS AND OF THE METHODS OF DETECTING EMANATIONS.

By M. Berthelot.

(Contributed by Dr Walter Colquhoun, Physiological Laboratory, University of Glasgow.)

In the study of emanations, which has recently been so fruitful in results, the important question arises as to the order of magnitude of the quantities of matter involved. Is the order of magnitude comparable to that of the minute quantity of odoriferous substance in the air in contact with the olfactory mucous membrane which can be detected by odour? The writer published exact experiments on the limits of sensibility to odours in the *Annales de Chimie et de Physique*, 7^e series, tome xxii. p. 460, 1901. By the exact methods described in that paper it was found that the limits of sensibility of the olfactory organ of the experimenter to the odour of iodoform, was the hundredth of one-billionth of a gramme disseminated in 1 cubic centimetre of air.

Suppose, now, a gramme of iodoform to be placed in a vessel of small capacity communicating by a tube, provided with stopcock, with a receiving vessel of 100 c.c. capacity, into which the volatilised matter enters. A cubic centimetre of air can be withdrawn at intervals from the 100 c.c. receiver to be tested by the nose for presence of odour. Suppose also that an hour elapses before the odour can be detected in the 1 c.c. of air withdrawn, and at the end of that time the receiver is removed and replaced by a similar one, and so on. Under the conditions stated, a gramme of iodoform would lose one-billionth of a gramme in an hour, and if the operations were continued for a year, it would lose $365 \times 24 = 8760$ billionths of a gramme, or rather less than one-hundredth of a milligramme. It would thus take one hundred years for the gramme of iodoform to lose one milligramme. Had musk been used instead of iodoform for the experiment, the weight lost would have been 1000 times less, according to estimations which have been made under less accurate conditions than those of the writer.

Such considerations prove that chemists, when using a delicate means of investigation such as the spectroscope, which in its sensitiveness may be compared to the olfactory organ, should be cautious in their statements regarding decomposition of chemical elements. Thus, if, in investigating the properties of an apparently pure mass of a certain element, the properties of another element are indicated by the delicate means of detection employed, that is no proof of decomposition of the first element. It might be impossible to extract the second element from the first if its mass were only one-thousandth of that of the principal element. Yet, as has been pointed out, apparatus exists which can detect one-hundredth of one-billionth of a gramme of iodoform in 1 c.c. of air, and perhaps one-thousandth of that mass in the case of musk.

A CURIOUS ABNORMALITY OF THE RENAL ARTERIES.

By Charles R. Whittaker, L.R.C.S., L.R.C.P., etc.,
Demonstrator of Anatomy, Surgeons' Hall, Edinburgh.

As is well known, variations of the renal arteries are very frequently met with in the dissecting-rooms; I think, however, that the following abnormality is worthy of being put on record.

A branch 4 inches long, the calibre of which was equal to that of an ordinary quill toothpick, arose from the left renal, and, crossing the abdomen obliquely, passed under the left spermatic artery and over the aorta opposite the third lumbar intervertebral disc. It next became an anterior relation of the inferior vena cava, and, passing behind the right spermatic veins, it divided into two branches, an upper which entered the hilum of the right kidney and anastomosed with the right renal, and a lower which lay behind and below the commencement of the ureter and entered the kidney below the hilum.

The right kidney possessed two renal veins, a superior lying posterior to the renal artery, and an inferior which passed across the abnormal artery and received the right spermatic veins. Although the right kidney had such an excessive vascular supply, its dimensions were unaltered.

ABSTRACT OF PAPER ON OSSIFICATION OF THE LOWER JAW OF MAN. By Edward Fawcett, M.B. Edin., *Professor of Anatomy, University College, Bristol.*[1]

In completion of the preliminary communication on this subject to the Anatomical Society, at the Summer Meeting held at Oxford last year, the author has found that the first differentiated structure observable in the anlage of the lower jaw is the inferior dental nerve, and it is in the neighbourhood of this that the other parts of the jaw appear—thus, on the inner side, Meckel's cartilage, on the outer, the membrane bone, forming the jaw. The nerve divides anteriorly into mental and incisive branches; in front of the latter, and below it, membrane bone commences, say, about the sixth (18 mm. embryo) week of fœtal life. This bone extends outwards under the mental nerve, and from this 'membranous' centre the angle, coronoid process, alveolar borders, and so-called splenial are formed—not by independent ossification, but by extension of ossification into the fibrous blastema between the insertions of the mandibular masticatory muscles. This is especially the case with regard to the coronoid process. Ossification proceeds rapidly in these parts, and they soon thicken, appearing when the jaw is made translucent by Canada balsam as separate centres, which they are not. The inner alveolar border is formed by ingrowth of the membrane bone over Meckel's cartilage, and under the inferior dental nerve, this ingrowth commencing just behind the mental nerve, and extending backwards, to end finally at the lingula. Long before this the mylo-hyoid nerve has reached the mylo-hyoid muscle, so there is no need for a separate splenial. This backwardly growing alveolar border is succeeded by an inwardly and forwardly growing one, which, commencing internally to the mental foramen, extends inwards towards the middle line—seen best in sagittal sections.

The inferior dental and incisive canals are formed by spicules of bone growing from the outer to the inner alveolar wall. The first to form is one just behind the mental nerve, the second is that which closes in the incisive branch, and the third appears near the future inferior dental foramen, *i.e.* near the lingula (third month).

Meckel's cartilage, at first unossified, enlarges in front; behind, it bends suddenly outwards in direction of Eustachian tube between inferior dental and lingual nerves. Its distal end—from mental foramen to symphysis—becomes included within membrane bone, and undergoes ossification, ossification commencing about the tenth week. The proximal end at the fourth month can be seen lying in a groove on the inner side of the internal lateral ligament, which is attached to the lingula at this time.

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[1] Owing to want of space, the extended paper offered by Professor Fawcett could not be printed in this number of the *Journal*.—Ed.

During the third month a rod of cartilage appears in the condyle, neck of the jaw, and base of the coronoid process. This soon ossifies from one centre. It is unsheathed by membrane bone. It has no connection with Meckel's cartilage, nor has the interarticular fibro-cartilage.

Each half of jaw thus normally ossifies from three centres:—

1. The greater part being from membrane.
2. From Meckel's cartilage.
3. From cartilage in condyle, neck, base of coronoid process, independent of Meckel's cartilage.

Abnormalities.—Coronoid may in part ossify independently; os mentale may result from independent ossification internal to mental nerve and foramen.

FIFTEENTH REPORT ON RECENT TERATOLOGICAL LITERATURE.

By Bertram C. A. Windle, M.D., Sc.D., F.R.S., *President of Queen's College, Cork.*

[The author of this report will feel greatly obliged if writers on teratological subjects will supply him with reprints of their papers for use in the preparation of future reports.]

I. Experimental.

Schaper (i.), in a paper on the *influence of radium on development*, states that the emanations produce an arresting effect on cell-division, on embryonic differentiation and on embryonic growth, as well as on the processes of regeneration. These effects, however, first show themselves after a longer or shorter latent period.

II. General.

Rabaud (ii.), in the course of a disquisition on the subject of *atavism and its relation to teratological phenomena*, points out that there are quite a number of simple abnormalities, such as muscular variations, and of more grave conditions of a truly teratological nature which have no relationship whatever to atavism. Of those which appear to be atavistic there are two classes. In the one the character is totally new, and the modified species gains a morphological resemblance to some other form; this is the condition well known as the convergence of forms. In other cases we find ourselves in presence of a character which has never ceased to belong to the species in question, but which has been modified, under the influence of surrounding conditions, so as to resume, to all appearance, the value which it previously possessed In this case there is direct and continuous filiation; but it is not the filiation which explains the anomaly, it only renders it possible, when certain conditions are given. Rabaud (iii.), in a paper on *anatomical stigmata and mental degeneration*, criticises severely but justly the fashion of describing all sorts of abnormalities as stigmata of mental degeneration, with the concealed hypothesis that they are in some manner connected with the mental condition, and warns observers against the danger of assuming that because, for example, a malformed ear may be met with in cases of mental degeneration, the existence of such a form of ear must be a stigma of such mental defect.

Pearl (iv.) gives the following conclusions as the result of his examination into the question of deaths from malformations in relation to the *greater variability of men and women.* The forms of abnormality included under the head are those grouped under Title No. 150 of the International Classification of Causes of Death, a title which covers all the commoner forms of malformation. The mean age at death from fatal congenital malformations of these kinds is essentially the same in men and women. Hence it may safely be concluded that the mean intensity or degree of the malformations is not essentially greater in one sex than in the other. But the variation in the age at death from such malformations, as measured by the standard deviation and the coefficient of variation, is significantly greater in women than in men, and hence we may conclude that, in intensity or degree of the malformations, woman is more variable than man. These observations are based on an analysis of the Twelfth American Census Report.

DAVENPORT (v.), in a paper on *colour-inheritance in mice*, says that when the parents are of the same colour, especially if they are pure bred, there is a strong tendency for the offspring to be of the same colour as the parents. In the case of albinos this tendency is so strong that the offspring are probably always albinic; if both parents are black, the tendency to black offspring is also very strong; if chocolate, the result is more variable; if yellow, still more intermediate. The results indicate that there are various degrees in the strength of inheritance of different colours. When the parents are of dissimilar colour, the offspring show different kinds of inheritance in the different cases. When gray and white are crossed, the offspring are gray with a little white, and this white is the more reduced the purer bred the albinic parent; the gray is dominant. Likewise, in the cross of gray and black, black is quite shut out, and the same is true of gray and piebald rats. The wild gray colour is strongly prepotent. Melanism and albinism act quite similarly in crossing. Both are in the nature of 'sports.' Perhaps 'purity of the germ-cells' is the mechanism of isolation for which we have been so long looking, by which mutations are preserved from the 'swamping effect of intercrossing.' When gray and chocolate are crossed, the gray is incompletely dominant. When black and white are crossed, typical reversions appear; neither colour is dominant. When black is crossed with yellow, the result is highly variable. If white and yellow be mixed in various proportions for several generations, the progeny takes on various shades of yellow, and may acquire the wholly new colour of chocolate. Similarly, black may result from a mixed ancestry in which there is no black. In this paper, and in a second on *Wonder Horses*, the relations of the observations made to the Mendelian law are discussed, and the writer concludes that, while Mendelian principles seem applicable to some cases of crosses between sports and the normal species, there seem to be others where neither Mendel's nor Galton's law of inheritance holds.

NEUMANN (vi.), in a paper on the relation between the *nervous system and the production of certain abnormalities*, concludes that in a certain very early embryonic period the condition of dependence upon the normal state of the nerve-centre for possibility of development in the muscle comes to an end, and that at a later period of development the growth can go on without any obvious signs of degeneration, in spite of the injury to the nerve-centre. Hence between the very early period alluded to and the time of extra-uterine life—during which the centre again exercises a very obvious influence of a trophic nature upon its muscle—there is intercalated a time when no such connection is observable.

The 'STANDARD' (vii.) during the year published a very interesting account of an *albino colony* established near Cape Cod. These people are called the 'red-eyed Pittsleys,' and have for more than a century formed a colony at this place. As usual, the hair is white and the eyes are red. The first of the family known to have been an albino was one Robert Hoggsley—a name subsequently changed to Piggsley, and finally to Pittsley—who was born *c.* 1731 and died *c.* 1786. There has been a great deal of intermarrying amongst his descendants, because others objected to allying themselves with any of the Pittsleys. Not all the children were albinos, sometimes only three or four out of a dozen, for large families were the rule amongst this people. But the normal offspring invariably went off amongst strangers, leaving the albinos behind. The albinos went further into the forest. Now and then, members of the clan reverting to the ordinary type were married out of the cousinship. The result of this has been, in certain cases, to carry the albino taint into other families. The writer of the article in question learnt that there are not only white-headed Pittsleys now, but that a family of white-headed Reynoldses has grown up in recent years, and may very likely in time to come constitute a similar clan.

BRISSAUD and MEIGE (viii.) describe a case of *infantilism and acromegaly* in a man aged 30–31, whose height is 1·852 m. His parents were of ordinary stature. He has no hair on his face, and very little on pubes or axilla. The testes are the size of those of a child of 5 or 6. The pelvis and thighs approximate to the female type. The lower extremities are out of proportion long. The face is elongated at the expense of the inferior. maxilla. The feet are enormous, but the hands are not unduly large.

CAGNETTO (ix.) describes two cases of tumour of the hypophysis. The first of these was a telangiectatic sarcoma which crushed the anterior segment of the hypophysis. There was no sign of acromegaly. In the second case, where acromegaly was present, the tumour, an adeno-carcinoma, was of larger size, and there were metastatic growths in the spinal canal. The first case showed no acromegaly, though there must have been great interference with the functions of the hypophysis; the second, according to the writer, seems to indicate that the correct hypothesis is that acromegaly begins as a primary affection of metabolism, which excites a hyperplastic process in the bones of the skull and limbs, and sometimes also—in a selective manner—in the hypophysis coincidently.

PONCET and LERICHE (x.) describe the cases of a brother and sister, both *dwarfs*. Both possess large heads and short lower extremities, and both have fully developed secondary sexual characteristics. They are not chondro-dystrophic, for all the epiphyses are well-knit, but belong to the class of primordial dwarfs, the 'naines par excellence' of v. Hansemann. The authors, in this and a second paper (xi.), claim that dwarfs of this kind are atavistic in their nature, and represent the dwarf races which—they consider—formerly inhabited large portions of the globe.

Bayon (xii.) has a lengthy and interesting paper on *cretinism* and its differential diagnosis from other kinds of *dwarfishness*. He gives an account of several cases of cretinism, and notes especially the following points:—(1) The remarkably retarded condition of the ossification in the three skeletons which he examined. (2) Not only is early spheno-occipital synostosis (tribasilar synostosis) not present, but these elements remain separated from one another for an unusually long period. (3) The obvious presence of a thymus at an age (*e.g.* 19) when it has usually only left remnants. (4) The absence of a normal thyroid body in the four cases which he examined histologically. An account of other varieties of dwarfs and some historical notes on cretinism conclude the paper.

Weygandt (xiii., xiv.), in two papers, deals with the subject of *cretinism*, of which condition he gives a number of instances, with microscopic and other views of the bones. He points out that cases such as that of Virchow's 'congenital cretin,' with premature synostosis of the cranial bones (tribasilar synostosis) at birth, have nothing to do with cretinism, but belong much more properly to the class of chondrodystrophia.

Pernet (xv.) calls attention to the remarkable similarity between the cases of *achondroplasia* and the proportions of the Egyptian god Ptah, as evidence of the ancient character of this ailment.

Gilford (xvi., xvii.) deals with the condition of *dwarfishness*; ateleiosis, *i.e.* continuous youth, and progeria, *i.e.* premature old age. The latter condition, which he has been the first to describe, is one in which the degenerative processes of life proceed too rapidly. He describes three cases in which individuals died at an early or comparatively early age, and with all the evidences of senility, and all these were dwarfs. Nos. 1 and 2 were boys, both of whom died at the age of 17, and No. 3 was a woman, who died at the age of 43, presenting all the appearances of an octogenarian. A remarkable fact in connection with the clavicle in the first case is that it was only the size of that of a new-born child; it had no centre of ossification at the sternal end, but the cartilaginous cap was very large in comparison with the shaft. The pituitary body seemed to be normal, but was not microscopically examined.

Cases of *transposition of the viscera* have been recorded by Hartland (xviii.), Pritchard (xix.), and Liddon (xx.).

Batneff (xxi.) describes a case of *hermaphroditus spurius femininus*, in which there was not merely a large hypospadiac penis, with closed scrotum, but also a prostate. The vagina, distally very narrow, was connected with the urethra. The uterus was rather small, but the tubes and ovaries were in every way normal.

Moiser (xxii.) describes another *hermaphrodite*, aged 19, of rather masculine type, with ill-developed breasts and a much-hypertrophied clitoris, 1½ inches in length. The meatus urinarius was in the normal position for the female. As the result of a laparotomy—for persistent abdominal pain, which turned out to be due to appendicular concretions—it was discovered that the patient possessed neither uterus, ovaries, testicles, nor tubes. There was a short blind vagina. LIEBE (xxiii.) describes two cases of true bilateral *hermaphroditism* which occurred in pigs; and CAMERON (xxiv.) has a paper on the condition of *hermaphroditism* in general. HOUZE (xxv.) describes a *microcephalic child* born of a sub-microcephalic father, whose father, again, had a skull of unduly small size. All these three are exceedingly brachycephalic, and the first two are very hypsicephalic.

EMMS (xxvi.) describes a case of *multiple malformations*, including ectopia vesicæ, of a curious kind, atresia ani, and double talipes calcaneus in a new-born child. SCHWALBE (xxvii.) describes two new cases of *epignathus*, one of which existed in an anencephalic fœtus, a rare example. The writer considers that, the more complicated the structure of the epignathus, the earlier must have been the termination of the teratological process to which it owed its origin. PATTI (xxviii.), dealing with deformities which accompany *syringomyelia*, states that these are more frequently seen in the upper extremities; out of 138 cases of the condition, 115 were situated in this part of the body. RABAUD and ANTHONY (xxix.) contribute an anatomical study of an exencephalous fœtus, the protrusion occurring in the frontal region. There was also hare-lip and cleft-palate. The writer considers that the position of the aperture of exit of a cerebral hernia is not of much importance. If it occurs early, the point will correspond with that of greatest pressure or of least resistance; if later, it can only take place at a fontanelle.

STERNBERG and LATZKO (xxx.) give a most careful and detailed—too detailed for abstract—account of the microscopic examination of *the nervous system of an anencephalic fœtus*, with a second part dealing with its bearing on the physiology of the central nervous system. BARDEEN (xxxi.) has a statistical paper on the variations in the number of vertebræ, in which he points out that regional variation in the vertebral column is an inherited condition which makes itself evident early in embryonic development. In the skeletons of white females thus far specifically reported, variation in the number of presacral vertebræ is less frequent than in the male skeletons. Variation in the female negro spinal columns is slightly greater than in those of the male negroes. In the negroes of Baltimore, in most of whom there is probably an intermixture of white blood, variation in the number of presacral vertebræ seems to be greater than in the white races. There is an equal tendency towards reduction and towards increase in the number of presacral vertebræ.

EIGENMANN and KENNEDY (xxxii.) describe some *abnormalities in fish*. (1) A specimen of catfish (*Pygidium rivulatum*) on the left side had, instead of the normal maxillary barbel, one which was dichotomously branched near its base into a dorsal and a ventral branch. The dorsal branch was evidently the normal barbel, the ventral being the adventitious one. The ventral branch was but slightly shorter than the dorsal, which again was a little shorter than its fellow of the right side. (2) A specimen of *Xiphorhampus jenynsii* with adventitious left ventral fin. The right and left ventrals are normally developed and of equal size. The left ventral is possibly placed a little higher than the right. The adventitious ventral is placed between the two normal ventrals, and slightly in advance of them and near the left one. It is shorter than the normal left, and possesses one ray less, eight instead of nine, and its first ray was bent sickle-fashion.

All teratologists will congratulate BALLANTYNE (xxxiii.) on the completion of his encyclopædic work on *Antenatal Pathology and Hygiene*, a work which must form an essential part of any library in which books on the all-important subject of variation find a place. The references to the literature alone are of the utmost value, and the whole work is a monument of research and painstaking examination into the vast number of recorded cases of a teratological nature.

III. DUPLICITY.

A series of interesting cases of multiple births which have been recorded during the past year may first be set down as bearing upon the subject of the present section.

NIJHOFF (xxiv.) reports a case of *quintuplets* borne by a woman aged 34, whose family had been a very prolific one. Her mother had borne twins, the wives of two of her maternal uncles had each borne twins once, and one maternal aunt had been the mother of triplets. Of the children borne at this multiple birth. the first and second were females, and so were the fourth and fifth, the middle child being a male. The placenta was single, but divided into three unequal parts. In the discussion which followed the reading of the paper in question, OLSHAUSEN (xxxv.) remarked that the Dutch—to which race the woman in question belonged—were a very prolific race, and that he himself knew of a family where the woman had on three occasions borne triplets, and on no less than twenty-five times had given birth to twins. GOWDEY (xxxvi.) gives an instance of *quadruplets* borne by a woman aged 36; two of the children were males and two females. Two of the placentæ were quite separate, and two had coalescing margins with separate chorions to each. WATSON (xxxvii.) describes a case of *triplets* in a Hindu. All three were males—one was a fœtus papyraceus—and there was a single placenta. DIX (xxxviii.) attended a woman in two consecutive confinements, on both of which occasions she had *twins*. Her mother had twins twice, her sister once, and her aunt had twins at forty. The husband was a twin, and his first cousin had borne twins once and triplets once. WILDER (xxxix.) has a lengthy and most interesting paper on *Duplicate Twins and Double Monsters.* He believes that the main factor in the formation of a diplopage or a duplicate twin is the changed relationship of the cells, a cell or part of a cell developing differently when isolated than when in contact with another. A sea-urchin blastomere in the two-celled stage, when in its normal relation to its fellow, develops but one side of a bilateral larva; but when this contact is severed, it develops both. Similarly, if the relation is lost in part and retained in part, a double monster is the result, from the same cause. Separate duplicate twins have escaped two dangers—(1) that of an incomplete separation of the two blastomeres of the two-celled stage, and (2) that of a secondary fusion of the later blastomeres owing to close proximity: in the one case they would have become diplopagi; in the other, one would have been an autosite, the other a parasite. The writer has made a number of observations on the patterns of the palms of the hands and soles of the feet, and finds that the prints obtained show that the soles of the feet of duplicate twins and the palms of their hands exhibit a striking correspondence in main lines and in patterns, and also exhibit the same tendency to a bilateral symmetry when the two sides are compared. In fraternal twins there is either a striking contrast, or else the similarity, at best, is no greater than among other members of the same family. GEMMILL (xl.) gives a careful account, illustrated with elaborate figures, of the anatomy of *Double Monsters amongst Trout Embryos.* As is well known, these are, with very rare exceptions, either cases of anterior duplicity or of union by the yolk-sac. His explanation ot this fact is that, in all these cases, two centres of gastrulation form on the edge of the blastoderm at a greater or less distance from one another. The spreading of the blastoderm over the yolk-mass goes on freely all round, except at or near the primitive streak. There, changes take place which lead to increase in length of the embryonic axis, and which are interpreted by many as concrescence. If the two centres of gastrulation happen to be near one another, the whole of the blastoderm edge separating them eventually will be used up in the process of concrescence; the later-formed parts of the embryonic axis will be drawn closer and closer to one another, until in their turn the axes themselves coalesce. The degree of union will be in inverse proportion to the original distance from one another of the two centres of gastrulation. Should the two centres of gastrulation be so far apart that the middle portion of the intervening blastoderm edge is not involved in concrescence, but is left free to extend over the yolk-mass, the two embryonic axes will be independent along their whole length, and the only structures which connect them will be the blastoderm and the yolk-sac. According to this view, double monsters showing anterior duplicity are the result of what may be called primary fusion, that is, concrescence of their growing embryonic axes. In birds, typical concrescence can occur only during the earliest stage of formation of the primitive streak, *i.e.* so long as the groove of the sickle and knob is open Any subsequent concrescence can take place only by the incidental drawing in and utilisation of lateral blastema at the growing zone. This process cannot exercise the same compelling influence in approximating the growing embryonic axes as it may do in fishes. The question of the origin of the different kinds of double monstrosities in birds and mammals is complicated by other factors, and cannot be discussed fully here; but the considerations suggested above may throw some light on the fact that practically all double monstrosities among fish with united bodies show anterior duplicity, whilst in mammals and birds there are as many or more cases of posterior duplicity. SCHWALBE (xli.) has compiled a valuable *résumé* of the recent literature in connection with the subject of *double monstrosity*, which should be consulted by all working at this topic. KORSCHELT (xlii.) treats very fully of the subject of *duplicity amongst the Lumbricidæ*, with a full account of the microscopic examination of various specimens. WEINBERG (xliii.) describes an example of *diprosopus tetrotus hemicranius*, with complete spina bifida and absence of the spinal cord. The combination of any form of duplicity with anencephaly is a somewhat rare occurrence. BENNETT and PATTEN (xliv.) give a description of a pair of *xiphopagous twins*, with the particular object of deciding how far it might have been possible to have separated them by operation. There was much fusion of the livers, and the pericardial sacs were united, forming a single cavity. The union of the ventricles of the heart was only superficial, but the auricles freely communicated with one another. GALLIVAN (xlv.) describes a case of *pleuropagous twin* in which the difficulty of delivery was very great. Another very full account of the anatomy of a pair of *xiphopagous twins* has been given by BERRY (xlvi.).

IV. HEAD AND NECK.

HANKE (xlvii.) describes the brain in a case of *congenital, bilateral anophthalmus.* Nothing was to be seen of optic nerves, chiasma, or tract. The external geniculate ganglion is reduced in size, and consists almost entirely of neuroglia; the ganglion cells are very much reduced in size and number, and a few sparsely scattered fine fibres are to be seen at the periphery of the ganglion. The anterior corpus quadrigeminum is not altered in its shape. There is no stratum zonale. The tractus peduncularis transversus is completely absent. The most important observation is that the fourth layer of the calcarine cortex is wanting. GROSSMAN (xlviii.) records a case of *double congenital anophthalmus.* In the inner half of the right lower lid was a bluish subcutaneous cyst, about half an inch in diameter, a so-called coloboma cyst. ANTON (xlix.) describes a case of *absence of both cerebellar hemispheres.* The fourth ventricle was roofed in by a very vascular membrane, which ended towards the corpora quadrigemina as a thin gelatinous plate. The anterior and posterior cerebellar peduncles were absent. In the place of the transverse pontine fibres was a structureless gelatinous plate. The inferior olives appeared to be absent. BANCHI (l.) adds another to the list of brains showing *absence of the corpus callosum* A second case of the *same nature* is narrated by ARNDT and SKLAREK (li.). DWIGHT (lii.), in a paper on *anatomical anomalies causing malposition of the head and distortion of the face,* gives the following:—(1) Diminution in number of the non-rib-bearing vertebræ, causing shortness of the neck. (2) Fusion of cervical vertebræ, which may take place anywhere; but the second and third vertebræ are particularly likely to be fused. (3) The atlas may be fused with the occiput, either solely at the joint, in which case the atlas is well developed and placed nearly or quite symmetrically, or the fusion may also involve one half of the posterior arch, which is but slightly developed and incorporated with the border of the foramen magnum. In this form there is always a median deficiency at the posterior arch, the lateral mass of the atlas is more prominent on the free side, and the corresponding end of the transverse process is both higher and further advanced than the other, throwing the face to the opposite side. GALLAVARDIN and LAVY (liii.) describe a case of *congenital torticollis,* where the right sterno-mastoid had undergone complete tendinous change, the cleido-mastoid being muscular but atrophic. Sections of the upper cervical portion of the spinal cord showed well-marked atrophy of the right anterior horn, the cells of which were much reduced in size. The theory is that the commencement of the condition was an anterior polio-myelitis. MURRAY (liv.) has obtained replies to questions of his with regard to the comparative frequency of occurrence of *hare-lip and cleft palate* in different parts of the world, and as a result states that these conditions are common amongst the natives of India, China, and Java, but are never seen amongst the natives on the shores of Lake Nyassa or in Hawaii and the neighbouring islands. EDINGTON (lv.) has a paper on *cysts of the median line of the neck,* which he classifies as: (*a*) thyreo-glossal, (1) infrahyoid, (2) suprahyoid; (*b*) ranula; (*c*) dermoid; (*d*) sebaceous. CAMPBELL (lvi.), a case of *fleshy appendages* on the left cheek of a child affected on the same side with anophthalmus. TUCKER (lvii.) describes a case of *proptosis* associated with oxycephaly of very marked character in a Mahratta. SCHWALBE (lviii.) gives two fresh cases of horizontally divided parietal bones occurring in hydrocephalic fœtuses, and a full list of all the known cases of this rare condition.

V. THORAX.

LENORMANT (lix.) describes a *dermoid cyst* of the sternum in a boy aged 14. It was congenital, and situated in front of the manubrium. In the same paper a case of *sternal fistula* in a boy aged 7½ is also described. BIRD (lx.) describes another case of *dermoid cyst of the sternum* in a man aged 45. RITCHIE (lxi.) gives an account of a *dermoid cyst* and embryoma of the *anterior mediastinum* occurring in a man aged 24. The cyst contained sebaceous matter, and was lined with fine hairs. The solid growth situated near this, and the secondary tumours from the same found in the lungs, liver, and spleen, were histologically identical with chorion epitheliomata. The author thinks that two different views might be held as to the etiology of this tumour: (*a*) either it is really a teratoma formed from an ovum included in the thorax, or from an aberrant division of the cells of the ovum from which the individual in whose body it was found was formed; or (*b*), less probably, there was a dermoid caused by an inclusion of the epiblast of the third visceral cleft, in connection with which the thymus gland is developed, and along with this a sarcoma of a special kind happened to be formed. WHYTE (lxii.) records a case of congenital *absence of the right breast and pectoralis major* in a male. His father exhibits the same abnormality, but it has not appeared in any of the children. ROSANOW (lxiii.) describes two *abnormalities connected with the breast.* (1) Female aged 20. There are two exceedingly large breasts, which, in the recumbent posture, reach down to the navel. On each side there is also a supernumerary breast, median to the axillary line and between the third and fifth ribs. These are regularly formed and provided with strongly pigmented nipples. Both contained milk (the woman had just been confined). (2) The left breast has two nipples, situated vertically the one above the other. The lower is placed at the lower free edge of the breast. Milk could be drawn from either of them.

CRISPIN (lxiv.) describes a case of *gynæcomastia* which occurred in a Sudanese, and says that he believes this to be not at all an uncommon condition in that race. VILLEMIN (lxv.) and THOMAS (lxvi.) record cases of congenital *atresia of the œsophagus.* LEFAS (lxvii.) describes a *cardiac malformation.* There is only one auricle and one ventricle. From the aorta, which has the usual valves, spring two separate vessels, the right and left pulmonary arteries. There is no ductus arteriosus. LETULLE (lxviii.) describes a case where the heart had only a *single ventricle.* The patient lived to the age of 16. NAU (lxix.) records a further case of *cardiac malformation.* There was a patent septum between the two auricles, and also one between the two ventricles, and no pulmonary orifice. EBBINGHAUS (lxx.) gives another case of *heart defect* which occurred in a man aged 52. The inter-auricular septum was of membranous texture, with fifteen perforations. Two of these were nearly an inch in diameter—the heart was three times the normal size—and the posterior of these was partly closed by a perforated membrane. Again, there was in the right auricle an extensive fine network stretching from the upper margin of the Eustachian valve to the region between the two caval orifices, with a few fine fibres extending to the inter-auricular septum.

SINIBALDI (lxxi.) has a note on some rare forms of *aberrant chordæ tendineæ.* DU SÉJOUR (lxxii.) records a case of *supernumerary* (azygos) *lobe of the right lung.* LICKLEY (lxxiii.) has a statistical inquiry into the question of the connections of the *seventh and eighth ribs with the sternum*

VI. ABDOMEN.

BATE (lxxiv.) records a rare case of *malformation of the anus.* The middle line behind the scrotum was occupied by a thick fold of skin, about one and a half inches long, continuous in front with the median raphe of the scrotum, and attached posteriorly just behind the anal opening. The fold was laterally compressed by the buttocks, and fæces passed equally freely on either side of it. This fold of skin was like that of the scrotum, and had a slightly marked central raphe. The anus underneath was rather small. The writer says that this case emphasises the importance of the 'anal membrane' and the so-called 'bouchon cloacal' in the formation of the ano-rectal tube. Hewetson (lxxv.) describes another case of *cloacal defect*. There was a complete absence of urethral, vaginal, and anal orifices; a single perineal depression, which was not subdivided into uro-genital and anal portions. Labia majora were present, and united behind the perineal depression in a scrotum-like posterior commissure. There was an entire absence of labia minora, clitoris, and hymen. Bladder normal, except for fistula, and urethra rather narrow. A complete double uterus and vagina. The rectum ended as a conical blind tube just behind and adherent to the right vaginal wall. Ribbert (lxxvi.) found in a fœtus 27 cm. in length, which presented various malformations, a small complex *cyst* between the cartilaginous sacrum and the rectum. Petit (lxxvii.) describes a *testicular teratoma* removed from the abdominal cavity of a cryptorchid horse. The tumour contained bone, cysts with small hairs, cartilage, and striped muscular fibres. Shattock (lxxviii.) showed at the Pathological Society a very remarkable *dermoid of the ovary*. A teratoma of fat, covered with skin, projected into a smooth-walled daughter-cyst. It was furnished with two ill-formed lower limbs, between which was a vulva, and behind the latter a median perineal raphe; above the vulva grew a tuft of long pubic hair, whilst the rest of the teratoma was covered with lanugo only. At the base of the mass was a smooth cavity in which there lay a blind coil of intestine. In each of the lower limbs there was an elongated compound skeletal element, and in the trunk of the teratoma was a rudimentary spinal column terminated by a pelvic girdle. On one side was a rudimentary upper limb. The presence of medullated nerve-tissue was demonstrated in connection with the spine. The causation of dermoids of this class is fully discussed, and the author gives it as his opinion that the ovarian teratomatous cyst resulted from the fertilisation of the primordial ova in the embryo, so that the embryo furnished a second imperfect individual, the origin of which was not, therefore, synchronous with, but later than, itself. Bayer (lxxix.) describes an *abdominal teratoma* existing in a man between the spleen and the liver. It was of the size of a fœtal head, and contained bone, hair, sebaceous and sudoriparous glands. Knaggs (lxxx.) has a paper on *diaphragmatic hernia* of the stomach, and other cases of *diaphragmatic herniæ* have been contributed by Nau (lxxxi.) and Corrado (lxxxii.). Kantor (lxxxiii.) describes a case of *malformed liver* in which there was no left lobe, the right lobe was hypertrophied, and the falciform ligament was remarkably broadened. Several cases of *congenital intestinal atresia* have been recorded by Clogg (lxxxiv.), and a case of congenital *absence of continuity between the large and small intestine* by Souter (lxxxv.). Hedinger (lxxxvi.) found congenital *diverticula from the vermiform appendix* in a fœtus affected also with different malformations, such as polydactyly and deficiency in size of the penis. There were numerous small and large subserous knots, containing in many cases pouches of intestinal wall. Barlet (lxxxvii.) gives a case of *supernumerary kidney*, the individual in question possessing two on the left side and one on the right. The two on the left side were fused with one another, and had two separate ureters. A case of *single kidney* situated in the middle line is recorded by Butterworth (lxxxviii.), and three cases of *congenital absence of one kidney* have been described by Uhl (lxxxix.) Herbet (xc.) describes a finger-like *diverticulum from the right ureter* of a male subject, discovered in the dissecting-room. It was 32 mm., and situated 3 cm. from the opening of the ureter into the bladder. Mocquot (xci.) describes a case of congenitally *atrophic penis* in a man otherwise well developed. The testes were of the normal size and the pubic hair well grown. There were no signs of infantilism. Heinricius (xcii.) records two cases of *uterus duplex bicornis*. (1) A rudimentary vaginal septum: the uterus was double, and the last pregnancy had taken place in the right side. (2) Uterus divided into a right organ of normal size and a left which was smaller. Two cervices and a vaginal septum 4 cm. long. Mond (xciii.) narrates a case of *absence of vagina*. External examination failed to show any trace of uterus or ovaries.

VII. Extremities.

Gaitskell (xciv.) delivered a woman of a child which showed complete *deficiency of both upper extremities*. After its death he made an anatomical examination, which showed that all the muscles round the shoulder were inserted into a fibrous aponeurosis which capped over the acromio-clavicular joint, and arose from all the points from which the deltoid normally arises. The clavicle was normal, but the processes of the scapula were much altered. Keyser (xcv.), dealing with a case of *Sprengel's deformity* (congenital elevation of the scapula), divides the cases of this kind into four groups: (1) where there is a bridge of bone between the vertebral border of the scapula and the spine; (2) where there is complete absence of one or more muscles connected with the shoulder girdle; (3) where there is a long and everted supraspinous portion of the scapula; (4) where there is no osseous bridge and the scapula is normal or smaller than usual, with short or otherwise defective muscles. The great majority of cases fall into the last category. Two further cases of the same deformity have been recorded by Fairbank (xcvi.). Dwight (xcvii.) describes a peculiar unilateral *supracondyloid foramen* which he believes to be unique. Bertin and Oui (xcviii.), a case of *ectromelia* affecting all four extremities. R.Up. part of arm only rounded at the extremity, which presents two depressions; humerus alone present.

L.Up. hand had only four digits, and the index and medius were syndactylous. R.Lr. very short and conical. At the summit was a small swelling terminated by a toe. Femur only present. L.Lr. longer, but of same character; ends by a rudimentary foot. Contains femur and another bone articulating therewith, probably the tibia.

Prentiss (xcix.), in a lengthy and finely illustrated paper on *polydactyly, especially in the pig*, sums up the result of his observations thus:—Polydactylism is confined almost entirely to the manus, which is interesting, because it is the condition met with in fossil pigs. The supernumerary digits are always on the radial side of the second normal digit. In 19 of 36 cases a single extra digit is present; in 5 cases this had 2 phalanges, in 9 it had 3, and in 5 its metacarpal was fused to that of digit ii. Of the remaining 17 specimens, 13 were hexadactyle. In more than a third of the cases examined the skeletal, muscular, and nervous organs of the manus give some evidence that the extra digit is vestigial. The so-called trapezium may represent this carpal element plus the rudiment of digit i. The extra digits articulate with the trapezium in nearly every case; they therefore represent the development of a vestigial pollex, but may vary extremely from the normal pollex structure. There may be cases where the extra digit is formed by the duplication of digit ii., but there is strong evidence against this being the general rule. Two supernumerary digits may be formed by the duplication of the vestigial pollex; but there is no ground for believing that one of them is a "pre-pollex." On the general question of polydactyly the author concludes that: (1) the extra digits generally occur symmetrically in manus or pes, or both, and are more common in the manus. (2) The extra digits are formed most commonly in connection with the fifth and first digits in man; with the first digit in the fowl, Carnivora, and swine; with the second digit in ruminants and Equidæ. In general, polydactyly may be said to affect digits which are normally much reduced or modified. (3) Cases in which more than five digits occur cannot be attributed to reversion alone. (4) Palingenetic polydactylism is limited to those forms in which—the number of functional digits being normally reduced to fewer than five—the digital rudiments develop and reproduce, more or less completely, the structure of homologous digits typical of some ancestral form. The evidences of comparative anatomy, embryology, and palæontology show this to be the case in the horse, ruminants, and swine; possibly in the pes of Carnivora. (5) This eventual dominance of a digital character, which has been transmitted in a recessive condition through many generations, is in strict accordance with Mendel's law of heredity. (6) Neogenetic and palingenetic forms of polydactyly are, like other new characters, extremely variable; as they are hereditary, we may conclude that duplications of both functional and vestigial digits are due to variations in the gametes. (7) The polydactyle abnormalities of man and the domestic animals may be classified as follows:—(I.) *Teratological polydactylism* includes those cases of digital duplication and malformation which are produced by external influences; it occurs rarely in animals, often in correlation with other monstrosities. (II.) *Neogenetic polydactylism* includes those digital variations, or sports, which are the result of some internal cause, presumably germinal variation. *a.* Duplication of *unmodified* functional digits occurs occasionally in all animals, and is transmissible. *b.* Variation of *modified* but functional digits is the ordinary form of polydactylism in man, the cat, and the fowl (pes), and it is also transmissible. (III.) *Palingenetic polydactylism* includes those cases in which digital rudiments, or vestiges, develop into extra digits. *a.* The extra digits reproduce more or less completely the structure of the homologous functional digits of related fossil ancestors; this condition is found in the horse, ruminants, swine, and the pes of the dog. *b.* The extra digits arise as variations or duplications of rudiments, or vestiges; they are neogenetic in so far as they do not reproduce ancestral conditions. Examples are the hallux and pollex having three phalanges, and the various duplications of these digits found in the manus of swine and in the pes of Carnivora. Ballowitz (c.) has an account of the relation of the muscles and tendons in cases of *polydactyly*, in relation to the etiology of this malformation. After giving elaborate tables of muscular arrangements, he concludes that the anatomical relations of the tendons, like those of the bones, have shown that the atavistic explanation of the condition has failed, and that at present the teratological explanation –that of fission— holds the field. He also states that, as a result of an extensive examination of cases of polydactyly, he has never found one in which the so-called radial elements, *e.g.* pisiform and calcanean tuberosity, have shown any alteration in the direction of forming lateral elements of carpus or tarsus. Ballowitz (ci.) has a further paper in the *same subject*, in which he concludes that the malformation is due to disturbances of development caused by the amnion. Two useful trees of *polydactyle families*, which may be noted for the use of those dealing statistically with this matter, have been published by Hey (cii.) and Armstrong (ciii.). Hilbert (civ.) saw a child with syndactylous indices and medii, and with syndactylous fourth and middle toes, the union being in all cases only superficial. There was also a supernumerary hallux on each foot. The same conditions exactly were present in the father and in the grandfather of the child. According to the grandfather, the great-grandfather was similarly affected. Shaw (cv.) gives an account of a mother and daughter both affected with similar *digital malformations.* These consist in absence of function in interossei, lumbricales, thenar and hypothenar muscles, and seem to be due to some defect in the anterior horns of the gray matter in the eighth cervical and first dorsal spinal elements. Lehmann-Nitsche (cvi.) describes a case of *brachyphalangy* of the right hand, with partial syndactyly of the index and middle fingers, observed in an Indian of Tierra del Fuego. Klippel and Rabaud (cvii.) describe a case in which, on the left side, the *pollex was much reduced in size* and possessed no muscles. The ungual and second phalanges were very small, though normal. The abnormality was thus intercalary, not terminal, and it was partial. On the right side the hand was normal, but the thenar eminence was much smaller than usual. Mouchet (cviii.) describes a case of *ectromelia of the thumb* and absence of the first metacarpal, with persistence of the radius. Dwight (cix.) says that Pfitzner described the *os magnum* as consisting of (*a*) os capitatum proprium, the chief and proximal portion of the bone; and (*b*) o.c. secundarium, the ulnar distal portion of the dorsal aspect; and (*c*) subcapitatum, the distal extremity of the palmar aspect. Each of these portions forms a part of the distal articular surface. The capitatum secundarium had been seen as a separate bone by Gruber, but Pfitzner never saw an isolated subcapitatum. Dwight has now seen this in both hands of the same subject, and has thus been able to confirm Pfitzner's surmise. Munro (cx.) records a case of congenital *absence* of one *tibia*.

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(The compiler of this report desires to express his acknowledgments to some of the abstracts published in the *British Medical Journal.*)

Notice of New Book.

The Ancient Races of the Thebaid. By Arthur Thomson, M.A., M.B., Professor of Anatomy, Oxford, and D. Randall-Maciver, Laycock Student of Egyptology, Worcester College, Oxford. Clarendon Press, Oxford, 1905.

THIS work is a monument of prodigious labour, and is by far the most important contribution to Egyptian craniology that has hitherto appeared. Only those who have had practical experience can realise the amount of work involved in the preparation of these great tables of figures, and in the setting forth and classification of these numbers which is here done with care and accuracy. The authors have provided for their readers a short prefatory sketch of the history of the period represented by these remains, and have explained the methods by which the data have been obtained and worked up by them. The section on craniometric method is a useful and critical essay of practical value to all workers in this field of research. The measurements are treated in several ways, and the results shown both tabularly and graphically. A new feature is the comparison of these with the results of the physiognomical classification introduced by Sergi. It is a great pity that the photographs of crania are on so small a scale that they are of little aid to the reader.

Any one who examines in the field the material available for the study of the ancient races of Egypt cannot fail to have the conclusion forced on him that the population of the Thebaid in early historic time was as much mixed as it is now. Heads narrow and broad, features coarse and fine, hair woolly or lank and straight, lips full or thin, etc., can all be found in the same cemetery, and it is satisfactory to note that the authors, from the standpoint of craniometry alone, have recognised the existence of this mixture. Whether a larger experience will support their hypothesis of a progressive secular enlargement of skull due to progressive culture is problematical, for the study of Egyptian literature leaves on the mind of the student an impression of amazingly small progress during its successive centuries. Evolutional changes there are, both linguistic and technical, but these are seldom in the direction of advance, and there is singularly little evidence of increase in the intellectual or ethical vigour of the race.

Egypt was at all times, like other bureaucracies, a country of strong social contrasts. We have this forcibly depicted for us in such compositions as the "Instructions of Dauuf, son of Khert'u," and others of the class. It is therefore to be expected that, alongside of the carefully made tombs and carefully prepared mummies of the governing classes, there should be those of the outlying agricultural and industrial peoples. A large number of such exist in the so-called tombs of the new race, and for the most part the differences in custom and surroundings shown by these are nothing more than can be explained on the ground of their cultural position. The measurements of several hundred crania from these graves, and of several groups of equal numbers for dynastic graves at Assūan, at Qūrneh, and other places, have convinced the writer that, as far as these can be regarded as of anthropological value, we have to deal with the same mixture of racial factors in both groups. The assumption that the new race is a pure race is, if judged by this criterion, quite unfounded. It consists of the same factors as the dynastic, only, as one might expect in different proportions, probably bearing to it much the same relation that the occupants of the better class of graves in the Cambridge cemetery bear to the mixture of English, Irish and Scotch tramps, Scandinavian, Mediterranean, Lascar, and Negro sailors, who found their way thither by way of the Anatomical Laboratory of the University.

The study of a work like this (which is certainly one of the best monographs on the craniometry of one people), and of the material used in its compilation, raises in the mind of the anatomist the question, What is the real value of the present methods in craniometry? It is all very well for the outsider, who cannot appreciate the numerous factors, each of them independently variable, which go to make up such an apparently simple unit as cranial length, to regard this and other measurements as integers that may be manipulated according to any approved method of mathematical treatment; but with the most profound belief that the mathematical method is the only one which should be used in dealing with appropriate data, I confess to an equally profound disbelief in the value of the treatment of such numbers as cranial indexes, or, indeed, almost any of our available single measurements, as if they had any homogeneity or comparability, and those who strive to deduct race-characters therefrom are simply following a will o' the wisp.

The authors evidently have some such distrust as to the conclusive character of the deductions from these numbers, and they have given a section on Sergi's method of classification as applied to their material. The difficulty of constructing a system of clear definitions for his several divisions is the chief and probably insuperable obstacle in the way of the employment of this method which, while very useful in the museum with selected specimens, is very difficult of application in the field, when one is dealing with hundreds of mixed crania. Yet there is no doubt that there is a certain, although perhaps an indefinable, series of family likenesses among skulls, irrespective of detailed measurement, which helps the expert in the recognising of skulls of certain typical races. It is not likely that we shall ever attain to an ideally perfect system of anthropometry, but in the meantime it behoves all those who are interested in that work to seek for some improved method in which the numerical data will have some morphological meaning.

A. Macalister.

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PROCEEDINGS OF THE

ANATOMICAL SOCIETY OF GREAT BRITAIN AND IRELAND.

JULY 1904.

THE Summer Meeting of the Society was held in the Museum, Oxford, on Friday morning, 29th July 1904, from 10 A.M. to 1 P.M. The President, Professor J. SYMINGTON, F.R.S., was in the chair, and a large number of members and visitors were present.

The minutes of the last meeting were read and confirmed.

The following gentlemen, recommended for election by the Committee of Management, were unanimously elected members of the Society:—H. D. SHEPHERD, M.B., F.R.C.S. (Edin.), proposed by R. J. A. Berry, D. J. Cunningham, and Peter Thompson; GUSTAV MANN, M.D., B.Sc., proposed by A. Thomson, Peter Thompson, and W. Wright; W. E. BENNETT, M.B., F.R.C.S., proposed by B. C. A. Windle, W. Wright, and Peter Thompson.

The following papers were then brought before the Society:—

(1) Professor FAWCETT read a preliminary paper on *the Ossification of the Lower Jaw of Man.*

He stated that Meckel's cartilage underwent ossification from the region of the mental foramen to the middle line.

That it did not alone form that part of the jaw between the mental foramen and the symphysis, for it was covered in front by membranous ossification as far as the middle line, an ossification which is continuous with the so-called dentary centre.

Towards the end of the second month a cartilaginous mass has appeared in the condyle, and extends down the neck through the root of the coronoid process to reach the level of the lower end of the anterior border of that process.

He doubted if any separate splenial centre was ever developed. He was also doubtful if any 'angular' mass of cartilage appeared, and became secondarily ossified. The appearances of the specimens he had examined suggested that probably the whole membranous part of the jaw developed from one centre, but his specimens were not young enough to enable him to speak definitely on this point.

Dr Low said he had also been engaged for a number of years in the study of the development of the lower jaw in man and mammals. The results of his observations were that, first of all, ossification appeared in membrane on the outer aspect of Meckel's cartilage—*the dentary*—and this extended forward as a plate of bone right up to the middle line in front. From this dentary plate a shelf grew up and in for the support of the tooth germs, while Meckel's cartilage lay below this plate.

Ossification then commenced in Meckel's cartilage opposite the site of the mental foramen, and from this extended forward; and later, this part of Meckel's cartilage became surrounded by ossification from the dentary. Later, distinct cartilaginous masses appear in the condyle, the coronoid process, and the angle, and these, in turn, undergo ossification. In certain mammals these cartilaginous nuclei are much more definite than in man, and have no connection whatever with Meckel's cartilage.

Mr Keith asked whether Professor Fawcett considered that the cartilage of the condyle and coronoid processes were formed independently of Meckel's cartilage.

Professor Fawcett replied that the two were apparently independent: the cartilage in the condyle and coronoid process was developed long after Meckel's cartilage.

(2) *On the Significance of certain Epithelial Masses in connection with Developing Teeth.* By H. W. Marett Tims.

When the jaws of fœtal mammals of various stages are examined, certain spherical epithelial masses lying to the labial side of developing teeth, and connected with the neck of its enamel organ, may be observed. Such spherical masses have already been seen in connection with pm^4 of the dog and gymnura, and with the so-called molars of the guinea-pig. They are also to be seen to the labial side of $\iota^{\bar{1}}$, $\iota^{\bar{2}}$, and $\bar{c}$ in the human fœtus of three months.

In these examples the masses are composed of distinct epithelial cells, forming a spherical mass with a neck, at first widely open, and directly continuous with the cells of a dental groove. In a four and a half months fœtus these bodies are still to be seen lying close to the edge of the jaw, but the cells have become more elongated, concentrically arranged, and distinctly granular.

From the constancy of their position in relation to a developing tooth, from their temporary existence, and from their spherical shape, they have, I think, some morphological significance. The only suggestion which occurs to me is, that they represent vestiges of a previous dentition. If this be so, then the human fœtus shows better-marked vestiges of a pre-milk dentition that any other animal with which I am acquainted.

The argument advanced in favour of the usually accepted interpretation of the marsupial dentitions is, that the early condition in which the young are born would tend to favour the retention of the pre-milk dentition. If the epithelial masses bear the interpretation above suggested the argument has not the same force, since they are so well marked in any animal with a prolonged period of gestation.

(3) Dr Lickley read a paper on *the Morphology of the Intertransverse Muscles*. This paper will be published *in extenso* in the October number of the *Journal of Anatomy and Physiology*.

(4) *On the Varying Form of the Stomach in Man and Anthropoids.*

By D. J. Cunningham.

1. First part of the paper confirmed, and to some extent supplemented, the observations of Professor His, as detailed in his paper published last year in the *Archiv f. Anat.*

2. The second part of the paper dealt with certain physiological conditions of the stomach which are now frequently seen in formalin-hardened subjects. The condition specially dealt with is one in which the stomach presents a capacious cardiac part and a long narrow tube-like pyloric part. Dr Cunningham showed that this is not a gastric state, which can be explained by tight lacing, as is inferred by Professor His. He exhibited slides in which it was evident in two males, a female, and also in the stomach of a full-time fœtus, and he referred to Mr Cannon's observations on the movements of the stomach of the cat observed by means of X-rays.

3. In the third part of the paper the question of hour-glass stomach was discussed. Dr Cunningham supported the views of Mr Moynihan. He held that this form of stomach might be due to physiological and to pathological causes; but it had yet to be shown that it ever was a congenital condition. Dr Cunningham showed the slide of a stomach of a full-time fœtus divided by a physiological constriction into a cardiac expanded part and a tube-like pyloric part.

(5) Professor F. Keibel (Freiburg) showed models to illustrate *the Development of the Urogenital Apparatus, the Liver, the Pancreas, and the Spleen of Echidna.* A detailed description of his investigations has already been published, and some of the more important results of his work are enumerated below:—

1. In front of the mesonephros there are vestiges which are to be regarded as the pronephros. The position of the nephrostomes and the absence of glomeruli afford some evidence of their real nature.

2. In Echidna the mesonephros is very highly developed. It contains large numbers of nephrostomes, and it is probable that it

acts functionally with the kidneys for some time after the animal is hatched.

3. The rudiments of the cortex of the suprarenal bodies appear very early, and are developed from the cœlomic epithelium. The medullary portion is derived from the sympathetic nervous system, and unites with the cortex at a very late period in the development of the animal.

4. From the mesial wall of the Wolffian ducts on either side the buds which eventually give rise to the ureters, pelves, and the tubuli recti take origin. The glomeruli and the other parts of the uriniferous tubules are derived from the renal blastema, which is in continuity with the blastema of the mesonephros. Thus there is no fundamental difference between mesonephros and metanephros.

5. There is in the early stages of development a large entodermal cloaca, continuous with a well-developed tail gut.

6. The entodernal cloaca is divided throughout its whole length into two parts by a septum which reaches the surface and forms the primary perineum.

7. The permanent cloaca is a new formation. The primary perineum, with the openings in front and behind, withdraw, carrying with them a pouch of ectodermal epithelium.

8. The urogenital sinus communicates with the urinary bladder by means of a narrow passage, and the cephalic end of the sinus widens out to form the genital pouches. Into these pouches the Wolffian and Müllerian ducts open on the summits of well-marked papillæ. The ureter opens into the passage between the sinus and the bladder, the place being indicated by a well-marked papilla, from which the urine drops directly into the bladder.

9. Cowper's glands are ectodermal in origin, and their muscles are derived from the skin muscle.

10. The muscles of the cloaca and the retractor penis are so derived from the skin muscle.

11. The rudiment of the gall-bladder is at first bilobed.

12. There are two ventral and one dorsal pancreatic buds, and all three give rise to pancreatic tissue. The two ducts of the ventral buds unite to form the duct of Wirsung. The duct of the dorsal rudiment is rudimentary, but I have found it in all animals at the time of hatching, and in three adult animals which I have dissected.

13. The spleen is derived from the mesenchyma of the dorsa mesogastrium. It is quite independent of the entoderm and the dorsal pancreatic bud. The caudal part of the spleen becomes, later on, related to the mesentery of the end gut.

(6) Dr J. Cameron, in a contribution to *the Ontogeny of the Neuron in Vertebrates*, showed that the neuroblasts are really *nuclei*, possessing no cytoplasmic envelope whatever. The rudiments of the axis-cylinders arose in the form of protrusions from these nuclei.

The results, therefore, give support to the theories of His and Kölliker, and are, on the other hand, at variance with the theory of Hensen regarding the origin of nerve-fibres.

(7) *On the Skeletons from Short Cists found in the North-East of Scotland.* By A. Low.

The mode of burial and the pottery found along with the skeletons had characters usually assigned to the Bronze Age, and all implements found were of stone or flint. But I find that the skeletons have characters differing from those usually ascribed to Bronze Age skeletons in Britain.

I have detailed notes and measurements of 11 more or less complete skeletons, and the following summary will give some of the more important points. The crania are all very *broad*, for in the male skulls the cranial index varies from 81·1 to 92·3, with a mean index of 82·8. The mean index for 2 female skulls is 82·8. Of the 10 skulls, 6 are *hyper-brachycephalic.*

The *cubic capacity* does not fall much short of the average modern Scottish skull, the mean being 1460 c.c.

The skulls are also extremely *high*, the mean vertical index being 77·3.

Norma lateralis.—The nasion is somewhat depressed and the glabella fairly prominent, vault high, frontal arc big, but well forward.

Norma facialis.—The face is short and broad, and shows no trace of prognathism, the mean *gnathic* index being distinctly less than that of the average modern Scottish skull.

The *nasal aperture* is relatively wide, the mean nasal index being 50, and in most approximating to platyrhine.

The *orbits* in all are microseme, the mean index in five males being so low as 76·2.

Bones of trunk and extremities.—The vertebræ of one lumbar spine are preserved, and are peculiar in that the vertical depths of the five lumbar bodies is greater *behind* than in *front*, while the fifth is the only one which has the *anterior* depth markedly greater than the *posterior* depth, — characteristics of the lumbar spine in the dark races of man. The bones of the extremities are short, stout, and muscular-looking.

Stature.—The stature can be estimated with a fair degree of accuracy in six males, and averages 5 feet 3 inches, while one female must have been just under 5 feet in stature.

Contrasting these skeletons, then, with the ordinary type of Bronze Age skeleton, we note—(1) the low stature of 5 feet 3 inches instead of somewhere about 5 feet 8 inches; (2) the skulls are more broad and high.

The glabella and supraorbital ridges are not markedly developed; the malars are not prominent, they are not in any way prognathous. The orbits are narrow, and the *nasal aperture* distinctly broad, instead of long and narrow.

As to the affinities of this short-cist people I am in doubt. I take it they must be descendants from the short broad-head Alpine race that occupied Central Europe in late neolithic times. How they came to the north-east of Scotland it is difficult to say.

(8) *On the Metameric Structure of the Skin in Vertebrates.*

By Otto Grosser, Vienna.

Although the question of the metameric structure of the skin has been so ably dealt with in man and apes by Professor Sherrington and Mr Head, little or nothing has been done with regard to this important subject in lower vertebrates.

In reptiles, and especially in lizards, Rabl has found that it is possible to determine with a great degree of exactitude the number of vertebral segments, from a consideration of the number of scale-ranges on the abdomen and tail. Speaking generally, two ranges of scales correspond to one vertebra. There are, it is true, certain exceptions to this rule, especially in the neighbourhood of the limits of the trunk.

The correspondence of vertebræ and scales is far more striking in the tail of the alligator and the uromastix, where one range corresponds to each vertebra. At the same time, the tail of the alligator shows that the colour of these metameric scales is independent of segmentation, the transverse yellow bands of the tail not being limited to a fixed number of scales, nor being separated from each other by regular intervals.

The best specimens of segmentation in reptiles are afforded by the snakes, the abdomen of which is covered with broad transverse scales, forming a single longitudinal row. Dissection shows, in Tropidonotus for instance, that every scale corresponds to one vertebra and one metameric nerve, the innervation forming the best test of the really segmental character of the disposition of the epidermal derivates. The same may be seen on a section through a somewhat advanced embryo of Tropidonotus, in which the hæmalapophyses of the vertebræ, the nerves, and the scales are visible in the same section.

As for the segmental character of stripes and lines on the fur of mammals, we are reduced to the study of the innervation. We know that the dermal segments, the dermatomes, preserve their original character as transverse bands or girdles only in the region of the trunk, but without corresponding to the segments of the skeleton. They are broader than these, and situated more caudad. In the region of the extremities they assume a perfectly different shape, the so-called middle lines of Sherrington being perpendicular to the vertebral axis.

Sherrington himself has pointed out that in the tiger the stripes of the thorax correspond to the dermatomes in respect of their *direction*; that the hind-limb of the same shows the dorsal middle line; that in the zebra, only on the anterior half of the body does the direction of the stripes correspond to the direction of the dermatomes; and that in the ass, the colour of the skin shows the dorsal middle line of the fore-limb on the shoulder. But an exact statement of a correspondence of these stripes with the innervation, though highly probable, has not yet been made.

Winkler and Rynberk mention the occasional correspondence of the spots of cattle on the base of the extremities with the form of the dermatomes.

Finally, Haacke has published a paper on metameric formations in mammalian fur. He found that the transverse stripes on the back of *Hapale*, of *Herpestes fasciatus*, and of *Suricata tetradactyla* corresponded exactly with the vertebræ, and that they were consequently metameric.

But objection may be taken to this statement, since we know that the dermatomes do not correspond to the skeleton. In one specimen of *Herpestes* which I dissected myself, I found that corresponding to 15 vertebræ there were only 12 stripes. Further, on studying the distribution of the nerves, it was seen that to the area of 11 nerves there were only 10 stripes. And finally, that the stripes were also developed in the area of the sacrum and on the back of the thigh, where the dermatomes differ considerably in form. Consequently, I cannot agree with Haacke in admitting that the skin in the animals mentioned exhibit a metameric structure, a condition to which Haacke gave the name of 'trichomerie.'

Another question, rather of more practical interest, is the segmental distribution of the arteries of the skin in man. Since the investigations of Manchot (who determined their metameric character, and their relation to the skeleton instead of the nerves), it may be admitted that generally the arteries of the back (rami posteriores arteriarum intercostalium), together with the lateral branches of the intercostal arteries, are segmentally arranged. Manchot, however, remarked that they are frequently irregular, and my own researches confirm this observation. Frequently arteries of certain segments are missing, and vessels are furnished by those of other segments, which then show a greater development than usual. Frequently arteries join the nerve of the more cranial segment. Speaking generally, arteries, unlike the nerves, try to find the shortest way to the skin, and an apparently segmental lesion of the skin, produced by alteration of the circulation, must be stated with much greater caution and diffidence than a lesion produced by an affection of the nerve.

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PROCEEDINGS OF THE

ANATOMICAL SOCIETY OF GREAT BRITAIN AND IRELAND.

NOVEMBER 1904.

The Annual General Meeting of the Society was held at St Thomas's Hospital Medical School on 18th November 1904. The President, Professor J. Symington, F.R.S., in the chair. There were sixteen members and fourteen visitors present.

The minutes of the last meeting were read and confirmed.

The following gentlemen were elected the officers and council of the Society for the ensuing year:—*President*—J. Symington, M.D., F.R.S. *Vice-Presidents*—J. Yule Mackay, M.D.; *B. C. A. Windle, M.D., F.R.S.; *A. Keith, M.D. *Treasurer*—F. G. Parsons. *Secretaries*—*C. Addison, M.D. (England); R. J. A. Berry, M.D., F.R.S.E. (Scotland); R. A. Stoney, M.B. (Ireland). *Council*—A. Birmingham, M.D.; T. H. Bryce, M.D.; D. J. Cunningham, M.D., F.R.S.; A. F. Dixon, M.B.; *W. McAdam Eccles, M.B., M.S.; E. Fawcett, M.B.; R. J. Gladstone, M.D.; T. Wardrop Griffith, M.D.; A. Macalister, M.D., F.R.S.; J. Musgrove, M.D.; A. M. Paterson, M.D.; C. J. Patten, M.D.; W. G. Ridewood, D.Sc.; Arthur Robinson, M.D.; G. D. Thane; *Peter Thompson, M.D.; *Arthur Thomson, M.B.; *H. W. Marett Tims, M.D.; H. J. Waring, M.S.; A. H. Young, M.B.

Dr Keith proposed, and Mr Parsons seconded, that "the best thanks of the Society be accorded to Dr Peter Thompson for so ably discharging the duties of Secretary during the past three years." The President expressed his cordial agreement with the resolution, which was carried unanimously.

The Treasurer's Report, as circulated to the members, was received and adopted. On the motion of the Treasurer, the question of the

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* An asterisk denotes that these members did not fill a similar position during the preceding year.

Society's providing material for the International Catalogue of Scientific Literature was referred to the Committee of Management, with power to make what arrangements were thought desirable.

The following gentlemen, recommended by the Committee of Management, were unanimously elected members of the Society:—Seymour Sewell, B.A., Christ's College, Cambridge; Hugh Lett, F.R.C.S., Demonstrator of Anatomy, London Hospital Medical College; Charles Gibbs, F.R.C.S., 48 Queen Anne Street, Assistant Surgeon, Charing Cross Hospital; Sidney Boyd, M.R.C.S., L.R.C.P., Demonstrator of Anatomy, Charing Cross Hospital Medical School; Thomas Jefferson Faulder, B.A. (Cantab.), M.R.C.S., Junior Demonstrator of Anatomy, St Bartholomew's Hospital; C. Gordon Watson, F.R.C.S., Junior Demonstrator of Anatomy, St Bartholomew's Hospital.

The following communications were then made to the Society:—

(1) A paper by Professor A. H. YOUNG, containing observations on the *lumbar arteries*, was read by Professor ARTHUR ROBINSON.

The paper points out that the lumbar arteries are somatic segmental branches of the abdominal aorta.

In each segment a pair of arteries (right and left) is given off, and four or five segments are represented.

The lowest of the lumbar arteries are by many authors regarded as branches from the middle sacral artery (the so-called continuation of the aorta) rather than from the abdominal aorta itself.

Mr Young holds an entirely different view, and suggests that when the middle sacral artery appears to give off either one or both of the lowest pair of lumbar arteries it is, as a matter of fact, just the reverse—the middle sacral artery arises from one or both of the lowest lumbar vessels.

Preparations and specimens were shown to illustrate this view, and they are recorded in the paper.

The paper will be published *in extenso* in the April number of the *Journal of Anatomy and Physiology*.

Dr ARTHUR KEITH and Dr BLACK joined in the discussion.

(2) Dr ARTHUR KEITH gave a demonstration of the *development and morphology of the diaphragm*.

The chief points demonstrated were:—

1. Through the pericardium the central tendon of the diaphragm is intimately bound to the heart and roots of the lungs in man and the anthropoid apes. Hence all these parts necessarily undergo a corresponding movement in respiration.

2. The muscular fibres of the *spinal segment* of the diaphragm—those fibres which arise from the spine and arcuate ligaments—ascend in an approximately vertical direction to their insertion on the central tendon of the diaphragm, and therefore, during an inspiratory

contraction, they tend to draw the central tendon, heart, and roots of the lungs in a downward direction.

3. The muscular fibres of the costal segment of the diaphragm—the fibres which arise from the ribs and sternum—ascend upwards and backwards, and tend to pull the central tendon forwards and downwards during inspiration.

4. On inspiration, as can be seen with X-rays, the heart moves forward and downward, the extent and direction of the movement depending on the type of respiration. In the abdominal type the *descent* of the heart is greater than its *advance*, in the thoracic type the advance is greater than the descent.

5. The opinion generally held that the roots of the lungs are fixed and immobile parts is erroneous; so intimately are the roots bound to the heart that it is impossible to conceive that the one can move without the other.

6. Where an azygos lobe separates the central tendon from the pericardium, as is the case in most mammals, the respiratory movement of the heart and pulmonary roots is less in extent. In such animals the inferior vena cava is extremely elastic (it can be stretched to two times its length in relaxation) to permit the central tendon moving independently of the heart.

7. The respiratory movement of the pulmonary root is necessary, because the *dorsal wall* of the mammalian thorax—that wall formed by the bodies of the dorsal vertebræ and by the ribs from their heads to their angles—undergoes no expansion during inspiration. As far as the capacity of the thoracic cavity is concerned, this is a stationary wall in mammals. If the pulmonary roots were fixed, then all that part of a lung which is situated between the dorsal wall and the root could be only imperfectly expanded.

8. The movements of the pulmonary roots appear to be essential, and it is conceivable that the diaphragm arose not as a complete partition in the body cavity, but as two symmetrical bands of muscle (dorsal and ventral), which acted on the roots of the lungs. In a search for the origin of the diaphragm one had to seek for dorsal muscular bands rising from the spine and ending on the roots of the lungs, and two ventral bands rising from the ventral wall of the body and ending with the dorsal bands on the roots of the lungs.

9. The search for such muscular bands in birds and reptiles proved negative, but in the amphibia such bands were found. In Xenopus (a large African toad) and *Pipa Americana* such bands occur, some of which have been already described by Beddard.

10. The dorsal of these bands (representing the spinal segment of the diaphragm) was found to be derived from the anterior part of the transversalis muscle.

11. The ventral bands, which end on the pericardium as well as the roots of the lungs, are derived from a deep layer of the rectus abdominis, the segment immediately in front of it entering into the formation of the sterno-thyroid. The ventral bands represent the costo-sternal segments of the diaphragm.

12. The nerves which supply these muscular bands agree with the phrenic nerves in the following points:—(1) they are the most ventral branches of the spinal nerve from which they arise; (2) they lie on the lateral aspect of the superior vena cava (duct of Cuvier); (3) they are distributed on the hepatic aspect of these muscular bands.

13. When the pleuro-peritoneal opening is unclosed, owing to the presence of a hernia, the diaphragm is seen to be a band-like muscle, made up of three parts—a central tendinous part, a ventral muscular part, and a dorsal muscular part. The inner margin of the pleuro-peritoneal opening is formed by the lateral crescentic border of the diaphragm; the lateral boundary of the opening is formed by the thoracic wall. Since the central tendon of the diaphragm separates the pleuro-peritoneal opening of one side from that of the other, it must necessarily be formed within the mesentery of the foregut, the partition which separates the right and left halves of the cœlom.

14. The mammalian pleural cavity is essentially a space formed in the body wall, the deepest muscular layer of the parietes forming the diaphragm. Whereas the mammalian testis, when extruded from the abdominal cavity, passes through all three of the primary muscular layers of the body wall, the lung is produced, during development, as a hernia into a space between the inner and middle of these layers at the anterior end of the trunk. In amphibia, and the same is the case in reptiles, the lungs grow out within the abdominal cavity, but in mammals, as the researches of Mall, Piper, and Broman show, the lung, although it first appears within the abdominal cœlom, is developed outwards and forwards over the duct of Cuvier and pericardium, anterior and dorsal to the abdominal cavity.

Dr Marett Tims, Dr Ridewood, Professor Robinson, Mr Parsons, Dr W. Harris, and the President joined in the discussion, to which Dr Keith replied.

This paper will be published at length in the April number of the *Journal of Anatomy and Physiology.*

(3) Dr W. Harris showed some drawings of careful dissections of the *brachial plexus in anthropoid apes*, and discussed the causation of high and low forms of the plexus.

(4) Mr F. G. Parson's paper on the *articular epiphyses of the long bones* was postponed to the next meeting.

PROCEEDINGS OF THE
ANATOMICAL SOCIETY OF GREAT BRITAIN AND IRELAND.

FEBRUARY 1905.

A MEETING of the Society was held at the London Hospital Medical School on Friday, February 17th, 1905. There were fourteen members and twenty visitors present. In the absence of the President, the chair was taken by Dr ARTHUR KEITH (Vice-President).

The minutes of the previous meeting were read and confirmed.

The Chairman referred to the great loss the Society had sustained since its last meeting in the death of two very distinguished and most respected members, namely, of Professor G. B. Howes and of Professor Ambrose Birmingham. On the motion of the Chairman, it was unanimously resolved that "This meeting of the Anatomical Society of Great Britain and Ireland desires to offer its respectful condolences to the families of those bereaved in the deaths of Professor Howes and of Professor Birmingham, and at the same time to record its deep sense of the loss therein sustained, not only by the Anatomical Society, but by the Science of Anatomy."[1]

The proposal to erect a bust of Professor Carl Gegenbaur at Heidelberg was then considered, and referred to the Committee of Management to make inquiries, and to subscribe such an amount as it considered the funds of the Society would allow.

The attention of the members of the Society was drawn to the proposal to have a dinner of the members after the meeting in May.

The following gentlemen, recommended by the Committee of Management, were unanimously elected members of the Society:—William Gordon Taylor, M.D., M.B., B.Sc. (Lond.), the Middlesex Hospital, Cancer Department; W. H. Clayton Greene, M.B., B.C. (Cantab.), F.R.C.S., Demonstrator of Anatomy, St Mary's Hospital; Victor

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[1] Short obituary notices will be found at the end of the Proceedings.

Bonney, M.D., M.S., B.Sc. (Lond.), F.R.C.S., M.R.C.P., Lecturer on Practical Midwifery, the Middlesex Hospital.

The following communications were then made to the Society:—

(1) Mr F. G. Parsons read a paper on *the Articular Epiphyses of the Long Bones*, which will be published later in the body of the *Journal*. He dealt with these structures from three points of view:—(1) How they come. (2) What use they are. (3) Why they come. Under the first heading their morphology in the different classes of the Vertebrata was discussed, and their mode of appearance in the Mammalia described. Under the second heading the various suggestions which have been made as to their use were dealt with, and Mr Parsons was of opinion that no satisfactory explanation of their utility had as yet been brought forward. Under the third heading two possible mechanical causes of their appearance were brought forward and discussed: firstly, pressure; and secondly, want of nutrition in the centres of the cartilaginous ends of the long bones, leading to a deposit of calcification, which later on attracted blood-vessels, and so became ossified. The two chief points in favour of this latter theory were, that in the higher vertebrates the epiphysis always starts in the centre of the cartilaginous end of the bone, and that the largest cartilaginous masses are those which first begin to calcify and ossify. The direction of the nutrient artery was referred to, and details of its direction in the lower mammals were brought forward to show that it has no constant relation to the epiphysis which appears first, or to the knee or elbow joints.

(2) Professor E. Fawcett described *the Early Stages of the Ossification of the Pterygoid Plates of the Human Sphenoid.* He exhibited sections of the heads of human fœtuses of the ages of eleven weeks and three months.

The former showed the internal pterygoid plate to be already ossified, although it is described as ossifying quite late (4th month). The same section showed the external pterygoid plate to be membranous, *i.e.* not a continuation of the cartilaginous greater wing of the sphenoid.

The section of fœtuses of three months showed that the hamular process becomes cartilaginous before ossification, at the same time as a bony centre appears in the neighbourhood of (below) the foramen rotundum in the great wing. They also showed that the external pterygoid plate is ossified in membrane—not cartilage, as universally implied, if not actually stated.

No question of the morphology of the cartilage in the hamular process—if it have any morphological significance—was raised; facts, as observed, being alone stated. These being—

1. That the internal pterygoid plate is ossified earlier than any other part of the sphenoid bone (probably 9th or 10th week).
2. That its hamular process is ossified in cartilage, which appears during the 3rd month.

3. That the great wing is ossified at the same time as the external pterygoid plate, viz., at the 3rd month, the former being ossified in cartilage, the latter in membrane.

(3) Dr William Wright drew attention to *a hitherto undescribed Groove on the Atlas.* He said: The groove which, so far as I can ascertain, has escaped recognition and mention by writers on the Atlas, is situated almost directly behind the superior articular facet. It is present in more than 50 per cent. of the atlases that I have examined; it is well marked, and directed upwards and slightly outwards. In the recent state it is bridged across by a ligament, and is thus converted into a foramen. It transmits a vein from the intraspinal venous plexus below the atlas to the vertebral vein as it lies in a plexiform manner round the vertebral artery on the superior surface of the posterior arch. The vein, in its course, crosses the anterior primary division of the suboccipital nerve. The groove when present is usually bilateral; it is well shown in the accompanying figure, for which I am indebted to my friend Mr D. Priestley Smith.

(4) Mr Wallace Ashdowne read a paper on *the action of the Flexors and Extensors of the Carpus, and their association with the Flexors and Extensors of the Fingers.* He said: Authorities differ upon some points in connection with the action of the flexors and extensors of the carpus and of their association with the flexors and extensors of the fingers; and the following observations have been made with a view, if possible, of reconciling and explaining the differences.

My work has been—

1. To determine from the relations of the tendons to the axes and paths of movement of the joints what actions the muscles are capable of producing.
2. To examine by radiographs and the luminous screen the alteration in the relations of the bones to one another in the different positions and movements of the hand on the forearm.

3. To observe in the living subject the muscles which act in producing these under varying conditions.

Henke[1] has given an admirable account of the movements which take place at the wrist. The principal movements occur at the radio-carpal and transverse carpal articulations, but subsidiary ones occur between the individual bones of the first row of the carpus. Movement of the radius will affect movements at the wrist, although I think we may neglect these in considering the action of the muscles.

The radio-carpal and transverse carpal articulations move on oblique axes forwards and backwards.

The axis of the radio-carpal articulation passes from a point close to the styloid process of the radius (see figs. 1, 2), and immediately in front of the tendon of the extensor carpi radialis longior at the back through the scaphoid to the pisiform bone in front.

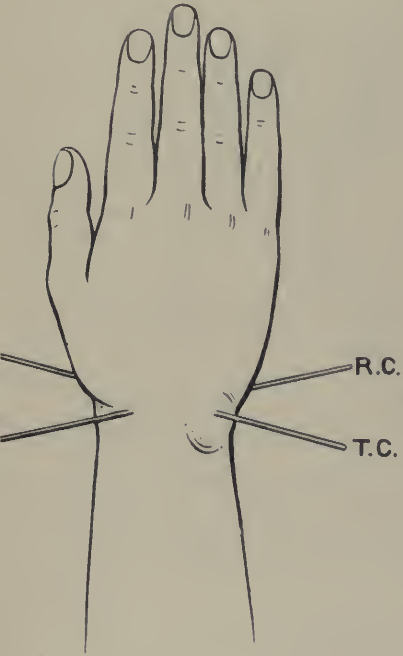

Fig. 1.

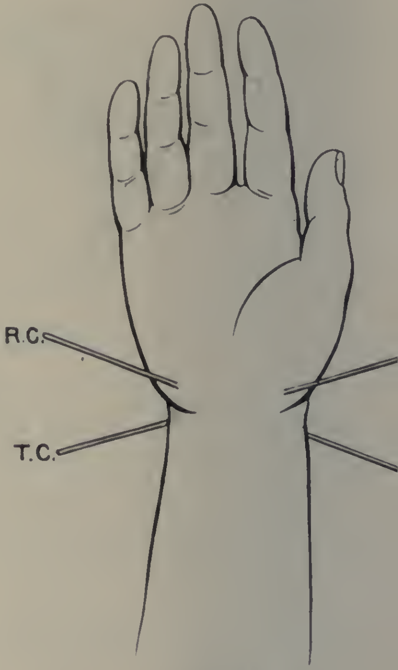

Fig. 2.

That of the transverse carpal from a point in the dorsal aspect of the unciform near its upper extremity to the anterior part of the tuberosity of the scaphoid.

Flexion of the radio-carpal joint gives flexion with radial deviation.

Extension of the radio-carpal joint gives extension with ulnar deviation.

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[1] *Handbuch der Anatomie und Mechanik der Gelenke*, 1863.

Flexion of the transverse carpal joint gives flexion with ulnar deviation.

Extension of the transverse carpal joint gives extension with radial deviation.

In flexion and extension of both joints the lateral deviation is balanced.

Movement of both joints in opposite directions will give movements to one side or other, *i.e.* radial abduction or ulnar adduction.

A consideration of the relations of the tendons to these axes gives the following information as to their possible action :—

The extensor carpi radialis longior and brevior can extend both joints.

The extensor carpi ulnaris can flex the transverse carpal and extend the radio-carpal articulation.

The flexor carpi ulnaris can flex both joints.

It will be observed, however, that the amount of movement which can be produced will vary according to the position of the tendon.

The muscles which can act to the greatest advantage upon the transverse carpal articulation are the extensor carpi radialis longior, the extensor carpi ulnaris and the flexor carpi ulnaris.

Those which act to the greatest advantage upon the radio-carpal joint are the flexor carpi radialis and the extensor carpi radialis brevior, although both these muscles can also act upon the transverse carpal articulation.

The flexors and extensors of the fingers are more favourably situated to act upon the radio-carpal than upon the transverse carpal joint, the flexors less so than the extensors.

The flexor and extensor carpi ulnaris are not favourably situated to act upon the radio-carpal joint.

In considering the action of the flexor carpi ulnaris, its insertion into the pisiform, which is movable on the cuneiform bone, and the attachment of the former to the unciform and 5th metacarpal by means of the pisi-uncinate and pisi-metacarpal ligaments must be taken into consideration.

Fixation of a joint can be effected by the muscles which produce movement in opposite directions.

Fixation of the transverse carpal joint can be effected by the extensor carpi radialis longior, the extensor carpi ulnaris and the flexor carpi ulnaris.

Fixation of the radio-carpal joint is effected by the extensor carpi radialis brevior and the flexor carpi radialis.

The movements of radial abduction are performed in the living subject by the extensor carpi radialis longior and the flexor carpi radialis.

If the flexor carpi radialis acts alone it flexes both joints, but if its action upon the transverse carpal joint is opposed it acts as a flexor of the radio-carpal joint only.

The flexor carpi radialis acting alone is a flexor of both joints, but in conjunction with the extensor carpi radialis longior it takes part in the movement of radial abduction.

In studying the movement of ulnar adduction it is necessary to do it first with the fingers flexed, and then in the extended position, since the muscles which act are different in the two cases.

With the fingers flexed, the muscles acting are the extensor carpi radialis brevior and the extensor carpi ulnaris. When the fingers are extended they are the extensor carpi ulnaris, the extensors of the fingers and the flexor carpi ulnaris. In each instance the extensor carpi ulnaris acts with an extensor of the radio-carpal joint, but in the latter the flexor carpi ulnaris also acts. This latter muscle acts when the hand is placed in line with the forearm with the fingers extended, perhaps to fix the pisiform bone, to allow the abductor minimi digiti to act efficiently. When the hand is adducted the pisiform bone approaches the ulna, as seen by radiograph and screen, and the muscle may act in this movement to keep the pisiform fixed. As it does not act when the fingers are flexed, I do not think it is essential to the movement of adduction.

As in each instance the extensor carpi ulnaris is associated in this movement with an extensor of the radio-carpal joint, this muscle acting alone cannot extend that joint. It can bring the ulnar border of the hand to a level with the forearm, but not beyond.

The association between the flexors of the carpus and the extensors of the fingers is of such a nature that when we flex and extend the hand upon the forearm with the fingers extended, flexion is performed by the flexors of the carpus and extension by the extensors of the fingers.

When the fingers are flexed so as to form a fist, if the hand is extended on the forearm the work is done by the three extensors of the carpus. If, in the course of this extension, the fingers are suddenly extended, the extensor carpi radialis brevior relaxes, the flexors of the carpus contract. The extensor carpi radialis longior and the extensor carpi ulnaris, although they may momentarily relax, again contract, and remain contracted during the time the fingers are extended So that in movements of flexion and extension of the hand on the forearm with the fingers extended the muscles acting are the flexors of the carpus, the extensors of the fingers, and the extensor carpi radialis longior and the extensor carpi ulnaris, and the question arises, Why do these muscles act? The explanation is, I think, as follows. The flexors of the carpus flex both transverse carpal and radio-carpal joints; the extensores carpi radialis longior and carpi ulnaris by their contraction fix the transverse carpal joint in this position, and the extensors of the fingers and the flexors of the carpus alternately contract and relax to extend and flex the radio-carpal joint. Movement is confined to this joint.

Duchenne[1] first pointed out that the reason the flexors of the carpus contracted was to elongate the extensors of the fingers to augment their dynamical power; but Beevor,[2] admitting that this is so, thinks that the purpose is to fix the wrist, so as to give the extensors of the fingers a secure basis to work upon.

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[1] *Physiologie des Mouvements*, 1867.

[2] *Croonian Lectures*, 1903.

Extension of the hand on the forearm with the fingers in this position is limited by tension of the flexors of the carpus and fingers; and if attempts are made to overcome this, the extensor carpi radialis brevior tendon will stand out prominently, without, however, producing further extension. Beevor [1] considers this proof that the extensor carpi radialis brevior is assisting the extensors of the fingers in extension, although I think it is possible to explain it in another way.

If we extend the hand on the forearm with the fingers flexed the extensors of the carpus contract, and the flexors give way so that both transverse carpal and radio-carpal joints are extended, and it is possible in this way to extend the hand on the forearm to a greater degree than when the fingers are extended. So that when we try to obtain the greatest amount of extension of the hand on the forearm with the fingers extended, the extensor carpi radialis brevior attempts to extend both joints, but is prevented from doing so by the contracted flexors of the carpus. There is antagonism between the extensor carpi radialis brevior and flexors of the carpus, due to the fact that we are trying to produce two opposite effects at one and the same time.

The following experiment, explained by diagram A, tends to confirm this:—

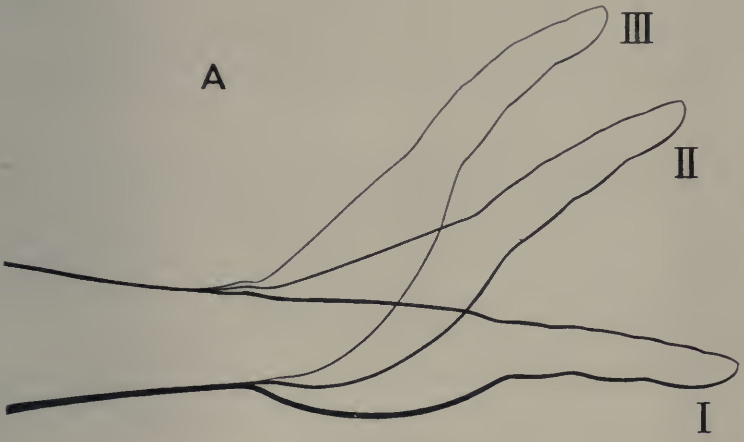

Diagram A.

1. Extend the fingers and hand forcibly so that they are in a line with the forearm (tracing I.).

2. From this position extend the hand on the forearm to the greatest extent possible, keeping the fingers in forced extension (tracing II.).

3. Now flex the fingers, extend the hand on the forearm as far as possible, and from this position extend the fingers (tracing III.).

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[1] *Loc. cit.*

It will be noticed that in position 2 extension is limited by tension on the flexor aspect, whereas in position 3 the difficulty arises in extension of the fingers, owing to the approximation of the attachments of the extensors of the fingers.

The association between the extensors of the carpus and the flexors of the fingers is of a similar nature. When the fingers are flexed, as in grasping, the flexors of the carpus give way and the extensors contract to extend both radio-carpal and transverse carpal joints; the latter is fixed in that position by the extensores carpi radialis longior and carpi ulnaris with the flexor carpi radialis. Movements of flexion and extension are now performed by the flexors of the fingers and extensors of the carpus, and they take place at the radio-carpal joint.

If great efforts are made to flex the wrist with the fingers in this position, the flexors of the wrist contract more forcibly, but without obtaining increased flexion, owing to the opposition of the extensors of carpus and fingers, the latter being tightly stretched. If, on the other hand, the wrist is flexed to its utmost with the fingers extended, and the fingers then flexed, a greater amount of flexion of the hand upon the forearm is obtained, but it is difficult to flex the fingers (see diagram B,—I., II. and III.).

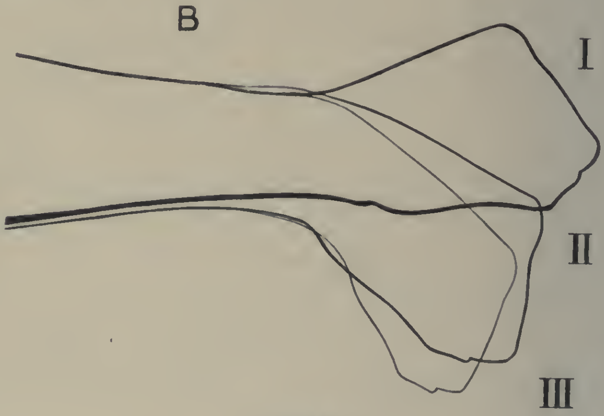

Diagram B.

As a result of these observations I conclude—

1. That the flexor carpi radialis is not an abductor, but a flexor of the hand upon the forearm. It acts, however, with the extensor carpi radialis longior in producing abduction.

2. The flexor carpi ulnaris is not an adductor, but a flexor of the hand upon the forearm. In the movement of adduction and flexion it acts with the extensor carpi ulnaris. It acts whenever the abductor minimi digiti is acting to fix the pisiform bone. It is not a strong flexor of the hand on the forearm, and acts best in extreme flexion.

3. The extensor carpi ulnaris is an adductor of the hand, but in this action it has to be associated with an extensor of the hand on the forearm. Acting alone it cannot extend the hand on the forearm.

4. The extensors and flexors of the carpus do not assist in extension and flexion of the hand upon the forearm, when that movement is performed by the extensors and flexors of the fingers with the fingers in forced extension and flexion respectively.

(5) Dr WALTER KIDD read a paper on *Imbrication of the Papillary Ridges in Man*, in which the normal arrangement of these separate ridges was shown to be one in which each ridge rises from the furrows on either side of it at an equal angle. This is the rule on the palmar and plantar surfaces in man, and on all those of eight species of monkeys examined, and on the digits of those species. In man the terminal phalanges of the hand show an imbricated arrangement, by which a slightly raised surface of each ridge meets any opposing surface when the hand is passed in a distal direction. This imbrication can be seen on the living subject in a very strong light when the ridges are taken in profile and a strong lens is used. It was also shown in sections of the skin under the microscope, and in certain of these the tactile corpuscles were also shown with the same forward or distal inclination as the epidermal ridges themselves. This is found in a less, and varying degree, on the proximal and middle phalanges. It was held to be an adaptation peculiar to the human hand and its digits, subserving the higher sense of touch. It is not found on the digits of the foot.

(6) Mr G. J. JENKINS gave an account of an investigation of *the topographical anatomy of the Brain* by the photographic method.

The brain was hardened *in situ* by formalin.

An apparatus was used to firmly fix the head so that the rays from the centre of the lateral aspect of the cranium to the lens would be at right angles to the sagittal plane. The lens was placed 15 feet from the subject. Six heads were so examined.

It was found that the fissures of the brain were fairly accurately indicated by the surface markings of Thane and Godlee, Anderson, Makins, and Chiene, the method described by Thane and Godlee giving the most satisfactory results.

In all cases the island of Reil and lateral ventricle were found in a position considerably posterior to that given in the text-books.

The anterior limit of the ventricle was in most cases posterior to the coronal suture.

The superior limit was in the average of the six cases 7·25 cm. above the zygoma.

The junction of the body with the descending and posterior horn was found to be accurately marked by a point 5 cm. above and 3 cm. behind the external auditory meatus.

The foramen of Monro lay very constantly in the pre-auricular line at the squāmo-parietal suture.

The superior surface of the corpus callosum corresponded to the superior limit of the lateral ventricle; its anterior extremity at the coronal suture, and posterior extremity at the point given for the junction of the body with descending and posterior horns.

(7) Dr WATERSTON showed lantern slides from photographs to illustrate a case of *extreme displacement of the stomach* in a female subject. The stomach, instead of being more or less horizontal in position, lay almost vertically, and exemplified in an extreme degree a condition found fairly often, especially in female subjects, and usually ascribed to constriction of the upper part of the abdominal wall. The cæcum and first part of the colon were greatly distended, and some discussion took place as to the ætiology of this condition, and especially as to whether or not it was primarily due to tight-lacing.

Dr A. KEITH and Dr C. ADDISON joined in the discussion, to which Dr Waterston replied.

(8) Dr A. KEITH gave an *exhibition of thirty malformed human Hearts*, from the London Hospital Medical College Museum.

Twenty of the specimens showed varying degrees of mal-development of the infundibular part of the right ventricle (conus pulmonalis). Through the courtesy of various authorities, Dr Keith had been able to inspect all specimens of malformed hearts in the medical museums in London, so that, including the series now shown, he had examined 185 specimens. Of that large series, 113 showed various degrees of mal-development of the conus pulmonalis; thus it will be seen that this part of the heart is by far the most liable to developmental error. When, to the 113 instances of mal-development of the conus pulmonalis, were added 22 cases in which there was merely a congenital stenosis of the pulmonary valves, it is found that over 70 per cent. of the congenital lesions in this series of hearts occurred near the root of the pulmonary artery.

The series of hearts exhibited to the Society threw light on the following points:—

1. On the origin of the right ventricle of the mammalian heart by the fusion of two distinct chambers, viz., by the fusion of part of the common ventricle with the bulbus cordis. The sinus of the right ventricle is derived from the common ventricle; the conus or infundibulum from the bulbus.
2. On the nature of certain muscular bands on the septal wall of the conus (see A, B, figs. 1, 2, 3, 4).
3. The manner in which the interventricular foramen is closed.
4. The manner in which congenital pulmonary stenosis is produced.

The specimens of mal-development of the bulbus might be grouped into the following five classes, the separation of the one class from the other being somewhat artificial, for they grade into one another:—

1. *Where the line of fusion of the two parts of the right ventricle is*

marked by a fibrous ring or thickening of the endocardium (see fig. 2). The ring represents the *ostium bulbi* or opening of the bulbus cordis into the primitive ventricle. Only 3 specimens of this condition were found—one at Middlesex Hospital, one at St George's, and one at St Bartholomew's.

2. *Where the two parts communicate by a narrow opening* (ostium bulbi), varying from 6 to 20 mm. in diameter (see fig. 3). Two specimens of this were shown, one of which was described by Dr John Hay, of Liverpool, to whom the exhibitor was indebted for the opportunity of showing it to the Society. The other was from a man who died recently in the London Hospital. There were 11 similar specimens in London museums. The ostium bulbi was surrounded by a fibrous orifice. The interventricular foramen was situated just below the ostium bulbi. In some of the cases the interventricular foramen was closed.

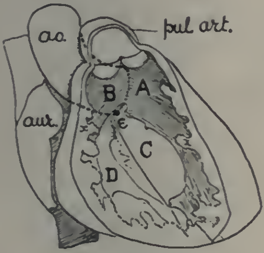

FIG. 1.

FIG. 2.

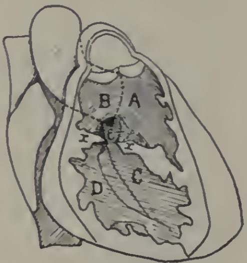

FIG. 3.

FIG. 1.—Diagram of the right aspect of the normal human heart with the lateral wall of the right ventricle removed.

A, septal band of infundibulum, corresponding to a muscular septum in the reptilian heart, which separates the conus pulmonalis from the common ventricle.

B, septal band peculiar to mammals. Between A and B is seen the 'infundibular raphe' corresponding to the margin of the aortic root. The position of the interventricular foramen is indicated above E.

C, on the septal wall of the sinus of the right ventricle.

D, on tricuspid valve.

x, *x*, the junction of sinus and infundibulum.

FIG. 2.—Diagram illustrating the condition described as class I. of the malformations of the infundibular region of the right ventricle. E, rugose thickening of endocardium marking the ostium bulbi.

FIG. 3.—The condition described as class II. E, the fibrous margin of the ostium bulbi. The interventricular foramen is indicated above E.

3. *Where the part derived from the bulbus remains small*, and is lined by a thick layer of endocardium (fig. 4). From the very thorough research of A. Greil into the development of the reptilian heart (*Morph. Jahrb.*, 1903, Bd. xxxi. p. 123) it may be safely inferred that in the hearts of all vertebrates which stand above Amphibia the bulbus cordis is submerged by the upgrowth of the musculature of the ventricle, its own musculature being replaced by that of the common ventricle. By the expansion of the cavity of the bulbus within the musculature of the ventricle the infundibular part of the

right ventricle is developed. In the present class of specimens the process of expansion, by the action of some unknown cause, has been arrested. The pulmonary valves are commonly more or less fused, but may remain free. The interventricular foramen is almost invariably open. Of the whole series examined, 39 belonged to this class.

4. *Where the part derived from the bulbus is merely represented by a fissure within the ventricular wall*, or may be absolutely obliterated (fig. 5). The pulmonary artery may be developed or completely absorbed. 50 specimens belonged to this class. The interventricular foramen is always large (see fig. 5). In a number of these specimens there was partial or complete obliteration of the sinus of the right ventricle.

5. *Where the part of the right ventricle derived from the bulbus is developed, but where the sinus is either obliterated or unseparated from the common or primitive ventricle* (see fig. 6). There were 8 specimens belonging to this class in the whole series. The bulbus is seen to communicate with the common ventricle by the ostium bulbi (fig. 6). In at least 2 specimens of this class the ostium bulbi was closed, the orifice present being the interventricular.

FIG. 4.

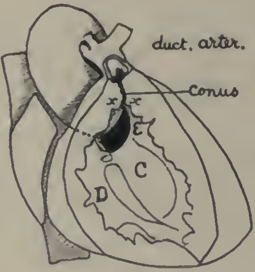

FIG. 5.

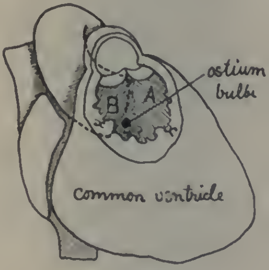

FIG. 6.

FIG. 4.—The condition described as class III., x, x, margin of ostium bulbi; interventricular foramen above E.

FIG. 5.—The condition described as class IV.

FIG. 6.—The condition described as class V.

The left ventricle is wholly derived from the proximal part of the common or primitive ventricle. The part of the bulbus arteriosus corresponding to the aorta becomes atrophied and absorbed during the developmental changes of the second month. In 3 specimens of the series there was present a distinct remnant of this part of the bulbus as a rugose endocardial ring or fringe, situated just below the fundi of the aortic semilunar valves; and in cases recently reported in the medical press it is evident that this remnant is frequently mistaken for a pathological product of adult endocarditis.

In a certain number of cases (at least 18 of the present series) the part of the bulbus which forms the conus pulmonalis became associated with the aorta instead of the pulmonary artery, giving rise to an apparent transposition in the origins of the aorta and pulmonary artery.

There are three features in the septal wall of the infundibular portion of the right ventricle, little noticed by anatomists at the present time, which are partly explained by a series of hearts showing stages of arrested development of the conus pulmonalis. These three features are (see fig. 1, between A and B)—(1) a line or furrow, more or less distinctly marked, running on the septal wall of the infundibulum from the angle between the septal[1] semilunar pulmonary valves to the position of the interventricular foramen (pars membranacea septi); (2) the muscular band A, representing the septal wall of the conus pulmonalis of the reptilian heart; (3) B, a strong muscular band, which in its size and arrangement is peculiar to the mammalian heart.

The infundibular raphe or furrow, which corresponds exactly to the terminal margin of the adjacent part of the aorta (see fig. 1), represents a fusion of the two lips of the primitive ostium bulbi. The orifice between the two parts of the right ventricle, which is here named ostium bulbi, represents the right extremity of the primitive ostium; the left extremity is represented by the aortic orifice of the left ventricle; and the raphe just described is the intermediate part, which has become closed by the fusion of its lips. In the series of specimens examined, several showed a greater or less opening up of this raphe, and partial attempts at a restoration of the complete primitive ostium bulbi.

The expansion of the conus pulmonalis and the separation and action of the septal band of musculature (B in fig. 1) have much to do with the closure of the interventricular foramen.

In the reptilian heart, the conus pulmonalis, the part derived from the bulbus cordis, is the part of the heart which acts as a pump for the lungs. The common ventricle, although nearly completely separated into right and left chambers, is constructed and designed to throw blood within the aorta. With the great expansion of the conus pulmonalis in the mammalian heart, its complete fusion with the right compartment of the common ventricle, and the development of the septal band 'B,' the whole design of the right heart is so altered that it can pump with advantage only through the pulmonary artery. In nearly every case in which there is a maldevelopment of the infundibular portion of the right ventricle it will be found that the ventricular fibres have assumed a more primitive arrangement, and are adapted for pumping through the aorta rather than through the pulmonary artery. When the infundibular cavity remains unexpanded and a mere fissure, the musculature of that part of the right ventricle forms in its action simply a part of the left ventricle, and helps to expel the blood from that chamber.

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[1] It will prevent confusion if the use of this word is justified. The position of the cusps as regards right and left, anterior and postérior, is variable. By 'septal' is meant those two cusps in the aorta and pulmonary artery which are adjacent, and which were continuous until the interaortic septum was formed.

PROFESSOR G. BOND HOWES.

By the death of Professor G. Bond Howes the Society has lost one of its most active supporters. At the first meeting of the Society, held in the rooms of the Medical Society, London, on July 7th, 1887, he was elected a member of the Committee of Management —his colleagues on that committee being Professor Macalister, Professor Curnow, Mr John Langton, Professor G. D. Thane, and Mr J. Davies Colley. In November 1890 he was elected Honorary Treasurer to the Society, in succession to Professor Charles Stewart, a post which he filled with ability and zeal until November 1903, when the commencement of an illness, which ultimately proved fatal, necessitated his handing over the finances of the Society to a successor, Mr F. G. Parsons. His services to the Society were then acknowledged by a special vote of thanks, proposed by the original secretary of the Society, Mr C. B. Lockwood.

His first appearance in the scientific business of the Society was at a meeting held in the library of St Bartholomew's Hospital in April 1888, when he took part in discussing a paper by Professor Arthur Thomson on "The Pterion in different Races of Men." Then and on many subsequent occasions he placed a very wide and minute knowledge of vertebrate anatomy at the disposal of the Society. A paper read at a meeting in November 1888 on "The intranarial position of the Epiglottis" gave rise to a prolonged discussion, and called forth a number of papers on the same subject. The last paper he contributed to the Society was on the "Pelvis of Mammalia" in May 1893; after that date the Linnæan and Zoological Societies had special claims on the work he published, but he still continued to take an active part in the discussions of the Society until his fatal illness set in.

To the younger members of the Society he manifested the greatest kindness and consideration. Perhaps he was too unselfish towards them: he gave his time, knowledge, labour, and material freely to whoever asked. His home at Chiswick was freely open to the younger men.

He was born in London, September 7th, 1853; he died at Chiswick on February 4th, 1905. The thirty years of his active scientific life were spent in the biological laboratories of the Royal College of Science, South Kensington. The first decade was spent as pupil and assistant to Huxley; the second decade was spent nominally as assistant but really as successor to Huxley; the third decade was spent as Professor of Zoology. He was an enthusiastic disciple of Huxley. In 1897 he became F.R.S.; in 1898, LL.D. (St Andrews); in 1902, D.Sc. (Victoria).

PROFESSOR AMBROSE BIRMINGHAM.

The Catholic University of Ireland, the Anatomical Society of Great Britain and Ireland, and Anatomical Science have to deplore the death, at the early age of forty-one, of Professor Ambrose Birmingham, which occurred in Dublin on the 23rd January 1905.

Professor Birmingham was born in the West of Ireland, and belonged to a family in which five brothers became members of the medical profession. He had a very distinguished career as a student in the Catholic University School of Medicine, Dublin, and graduated in medicine with first-class honours in the Royal University of Ireland in 1887. After working for a short time with Sir William Turner in the University of Edinburgh, he was appointed Professor of Anatomy and Registrar in his own school, and a Fellow and Examiner in Anatomy in the Royal University of Ireland. From the time of his appointment to the Chair of Anatomy he devoted himself with ceaseless energy and great ability to the organisation of the Catholic School of Medicine, and gained a great reputation as a teacher of anatomy. His numerous and arduous official duties did not deter him from undertaking numerous anatomical investigations, and in making valuable contributions to anatomical science. He was frequently present at the meetings of the Anatomical Society, and took an active part in its proceedings. He was a member of Council of the Society at the time of his death, Secretary, for Ireland, 1893–5, and Vice-President, 1898–1900.

His genial personality, ready wit, and sterling honesty made him a universal favourite, and he bore his long and painful illness with a bravery and a fortitude which were truly heroic. His early death is a great loss to the cause of Irish medical education, as well as to anatomical science. Most of his anatomical work appeared in the *Journal of Anatomy and Physiology*, or in Professor Cunningham's *Text-Book of Anatomy*, and is so well known to the members of our Society that any detailed analysis of it is unnecessary. The most important of these contributions dealt with the Topographical Anatomy of the Abdomen and of the Mastoid Region of the Skull, and they contain permanent and valuable additions to our knowledge of the subjects.

PROCEEDINGS OF THE

ANATOMICAL SOCIETY OF GREAT BRITAIN AND IRELAND.

MAY 1905.

A meeting of the Society was held at the Middlesex Hospital Medical School, on Friday, 19th May 1905, at 2.30 p.m. The President, Professor J. Symington, F.R.S., in the chair. There were nineteen members and sixteen visitors present.

The minutes of the last meeting were read and confirmed.

The following gentlemen were elected members of the Society:—Frank Poole, B.A., Sidney Sussex College, Cambridge; W. Warren Low, M.D., F.R.C.S., 27 Queen Anne Street, Cavendish Square, W.; J. V. Blachford, M.D., Bristol Asylum, Fishponds, Bristol.

An exhibition of naked-eye and microscopical preparations was held in the dissecting room from 2 to 2.30 p.m. The exhibits related to the various papers to be read before the Society, and, in addition, there were skiagraphs of the hands of the Russian giant, Manichow. During the tea interval a collection of old medical books—kindly lent by members of the hospital staff—was shown in the museum.

The following communications were made to the Society:—

(1) Professor Peter Thompson and Mr Gordon Taylor exhibited and described specimens of the *Liver* showing the *processus pyramidalis.*

Professor Ruge[1] had already described this process in the liver of a number of primates, and the demonstration given by Dr Thompson and Mr Taylor was intended to illustrate the view that the process was not confined to the primate liver, but was represented in other groups of mammals. Specimens of the liver of the marsupial mole, the cat, the rabbit, the guinea-pig, the phalanger, and a number of

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[1] "Die ausferen Formverhältnisse der Leber bei den Primaten," *Morph. Jahr.*, Feb. 25, 1902, and Sept. 12, 1902.

primates were exhibited, together with a number of human livers obtained from the post-mortem room and the dissecting-room.

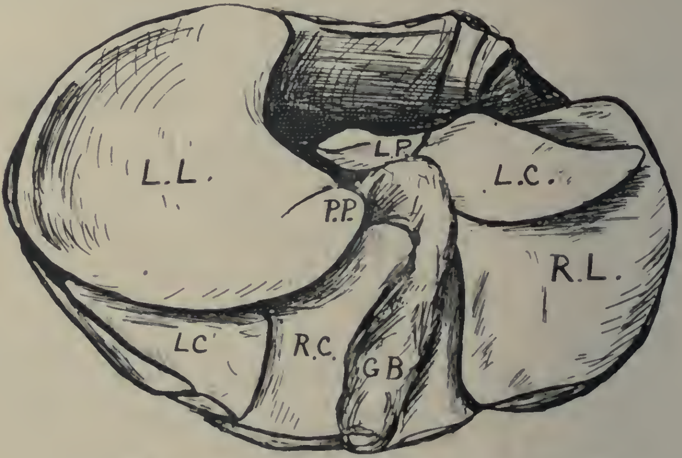


FIG. 1.—Liver of Macacus sinicus, hardened *in situ.* Visceral surface. L.C., l. caudatus; L.P., l. papillaris; R.L., right lateral lobe; G.B., gall bladder; R.C., right central lobe; L.C., left central lobe; L.L., left lateral lobe; P.P., processus pyramidalis.

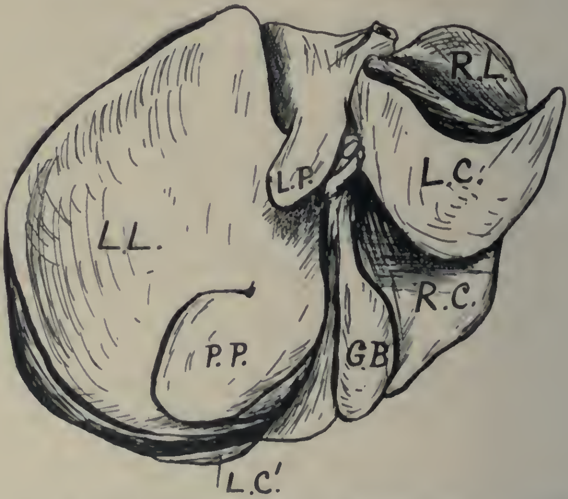


FIG. 2.—Liver of the cat, hardened *in situ.* Visceral surface. Lobes named as in preceding figure. Note the hook-like form of the pyramidal process and its extension downwards.

The origin of the process was quite constant. It always appeared as a prolongation of the ventral part of the left lateral lobe towards the longitudinal fissure. In some forms, as in *Cebus* and *Lepus*, it extended right across the fissure towards the right central lobe, and came into relation with the gall-bladder. In others, as in the cat, it extended downwards towards the ventral margin of the liver.

In form it varied considerably. In the macaque monkey, in *Cebus*, and in the marmoset, it was an attenuated and flattened process of liver-substance, often partially separated from the rest of the left lateral lobe by a well-marked fissure. In the domestic cat, it may present a hook-like appearance, with a deep fissure; in *Felis catus* the

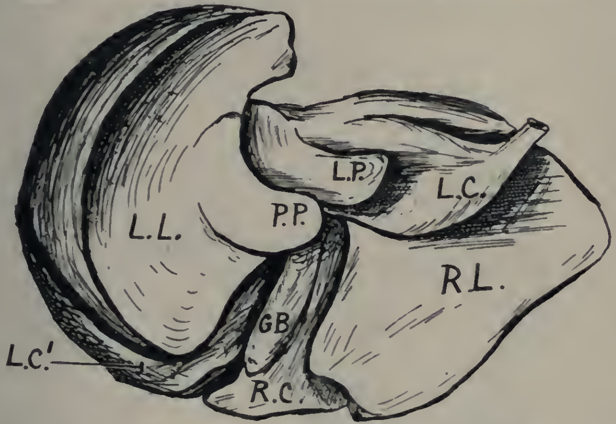


Fig. 3.—Liver of Cebus fatuellus. Pyramidal process (P.P.) well marked and extending across the umbilical fissure to the gall bladder (G.B.). Lobes named as before.

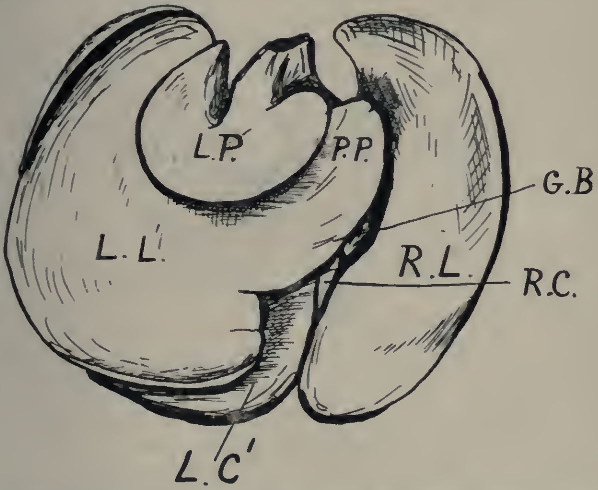


Fig. 4.—Liver of Lepus cunieulus, hardened *in situ*. Caudate lobe removed to show the pyramidal process (P.P.) extending to the right towards the umbilical fissure and gall bladder.

process was well marked but not hook-shaped, whilst in *Felis eyra* it may be pyramidal in form. In *Lepus cuniculus* the process was considerably elongated and extended some distance towards the right lateral lobe, and covered the gall-bladder.

It was interesting to note the relationship of the processus pyramidalis to the so-called lobus dorsalis. The latter was in most mammals of considerable size, and could be divided into (*a*) the lobus caudatus, or lobus descendens, and (*b*) the lobus papillaris. The latter, described also as the lobus omentalis, was situated above the portal fissure, and was in relation with the lesser sac of the peritoneum. The processus pyramidalis of the liver was placed ventrally to the lobus papillaris, and was thus prevented from extending dorsalwards. Expansion could, however, take place either towards the right side, or downwards towards the ventral border. The pyramidal process appeared, in fact, to be produced as the result of the pressure and moulding to which the left lateral lobe was subjected by adjacent viscera, and its extension was in most cases in the direction of the lesser sac of the peritoneum. In the cat, as already stated,

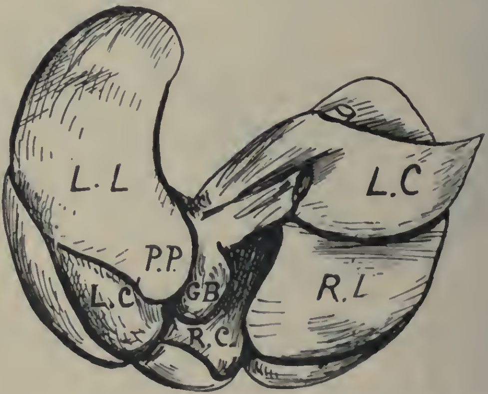


Fig. 5.—Liver of Marmoset. Visceral surface. Pyramidal process in relation with gall bladder.

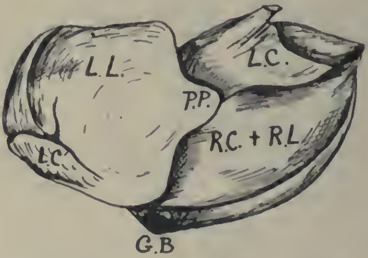


Fig. 6.—Liver of Notoryctes typhlops, showing well-marked pyramidal process (P.P.).

(fig. 2), the line of this extension was downwards instead of to the right, and it approached the ventral border.

In several specimens of the human liver which were exhibited, a process was present in the position of the omental tuberosity, and it was suggested that this represented a form of pyramidal process. In some cases it projected as a distinct, flattened, elongated structure, with a free extremity. In others, however, it was continued across the posterior end of the umbilical fissure and joined with the quadrate lobe, forming, indeed, a true pons hepatis.

If this process in the human liver corresponded to the processus pyramidalis of lower mammals, then the pons just referred to was a bridge uniting the representative of the left lateral lobe with the representative of the right central lobe. Situated near to the portal fissure, it was described as the posterior type of pons hepatis.

There was another form of pons hepatis crossing the umbilical fissure nearer its anterior end, which might be considered as a bridge joining the representative of the left central lobe to the representative of the right central lobe. This was an anterior type of pons hepatis, and in some specimens the two were continuous.

A specimen of the liver of *Macacus rhesus* was shown in which the second form of liver bridge was present, clearly uniting the left central with the right central lobe.

(2) Dr R. J. Gladstone showed a specimen of an *acardiac fœtus* (acephalus omphalositicus); the fœtus was one of triplets, all of whom were male. The umbilical vessels of one of these were connected directly with the umbilical vessels of the acardiac fœtus, or omphalosite, without traversing the capillary system of the placenta. The umbilical arteries of the autosite carried the blood coming from it into a single umbilical artery belonging to the cord of the omphalosite; this was continued into the right internal iliac artery of the latter. The blood thus passed upwards to the aorta, by which it was carried to the upper or thoracic end of the fœtus; it there bifurcated into two vessels, which appeared to anastomose with the radicals of the umbilical vein, which commenced in a mass of œdematous tissue in the thoracic region, and passed downwards to the umbilicus, and from thence to the placenta and umbilical vein of the autosite. The blood current through the omphalosite was thus, most probably, reversed.

The head and neck were entirely absent, as were also the thoracic organs, and the upper part of the alimentary canal with its associated glands. The small intestine commenced blindly outside the fœtus in an umbilical hernia, which contained also the cæcum and the appendix. The rectum terminated in a blind extremity within the pelvis. The genito-urinary organs were well developed, and appeared normal.

The upper limbs were rudimentary, and there was a complete absence of the three outer toes of the feet, which were in the position of marked "talipes varus."

Dr Gladstone considered that the absence of the head and thoracic viscera was due to a primary defect in development, and that the failure in their development was not secondary to a defective blood supply.

Professor A. Robinson, Dr Keith, and the President joined in the discussion.

The paper will appear in full in the *Journal of Anatomy and Physiology.*

(3) Mr D. Douglas-Crawford showed a brain in which the corpus callosum was represented by a round bundle of fibres ½ inch in diameter, placed in that portion of the "commissure bed" immediately anterior to the anterior pillar of the fornix and dorsal to the anterior commissure.

Both hemispheres were richly convoluted, but many of the sulci were markedly irregular; some of these sulci, especially on the left hemisphere, radiated from a point just behind the posterior limb of the fissure of Sylvius, an arrangement said to be especially characteristic of such brains.

Upon the mesial surface, the calloso-marginal sulcus ended posteriorly at a point corresponding to the precentral sulcus.

The anterior and posterior limbs of the right calcarine fissure were completely separated by the cuneo-lingual gyrus appearing upon the surface.

The left hemisphere showed upon dissection the presence of a complete primitive limbic lobe, the posterior limb presenting a well-marked Balken winding.

The fornix was complete upon both hemispheres, but their bodies were not united across the middle line. Fibres of the anterior pillar passed in front of the anterior commissure into the precommissural area.

The anterior commissure was normal in size and connections.

Coronal sections of the left hemisphere did not indicate any increase in size of the ventricles.

Unfortunately no clinical history of the case was obtainable, the brain having been removed from an elderly male subject in the dissecting room.

Dr Keith, Professor P. Thompson, Mr Bishop Harman, Dr Black, and the President joined in the discussion.

The paper will appear in full in the *Journal of Anatomy and Physiology.*

(4) Dr Alex. Low read a paper on *the Development of the Lower Jaw in Man.* Serial sections of human and mammalian lower jaws were also exhibited under the microscope.

The following is an abstract of Dr Low's paper. He said that the developing mammalian lower jaw had frequently been the subject of research both by histologists and anatomists; histologists finding in it different types of ossification; anatomists mostly regarding the lower jaw as a compound bone and trying to find homologies for its different elements in the jaw of lower vertebrates.

The researches of *Spix*, *Meckel*, *Magitot and Robin*, *Rambaud and*

Renault, *Callander*, *Parker*, *Brock*, *Baumuller*, *Sutton*, *Schaffer*, and *Fawcett* were briefly reviewed. Especial note was taken of a recent paper by *Professor Karl von Bardeleben*, in which he argued that the chin in man and mammals was a special and distinct skeletal element—the os mentale—and that there were also found in the lower jaw, condyloid, coronoid, angular, marginal and dentale as separate elements (*Anatomischer Anzeiger*, Bd. xxvi., Feb. 1905). Dr Low then demonstrated, by means of the lantern, microphotographs of sections showing the various developmental stages of the human lower jaw.

He said that in the human embryo by the fifth week Meckel's cartilage had passed forwards to the middle line, meeting but not fusing with its fellow of the opposite side. By the sixth week ossification was present as a delicate lamella of membrane bone on the outer aspect of Meckel's cartilage, and extending right forward to the symphysis. The inferior dental nerve passed forward between this lamella and Meckel's cartilage, and its dental branch passed over a notch on the upper border of the lamella.

At the beginning of the eighth week ossification had extended, so that each half of the lower jaw was mapped out as one complete membrane bone, and from its mesial aspect a dental shelf had commenced to grow inwards so as to overhang Meckel's cartilage from the outside.

At the tenth week these appearances were still better defined (fig. 1).

At this stage the condyle, coronoid, and angle were well defined, and shown to be formed by membrane bone quite continuous with the body of the lower jaw. Ossification was now commencing in Meckel's cartilage at a point between the first and second tooth germs, where the cartilage was in close relation with the membrane bone. The lamella of bone usually described as a distinct splenial element arose as an extension from the body of the bone.

By the beginning of the third month a cartilaginous nucleus or mass had appeared in the condyle, and this grew rapidly, so that by the middle of the third month this cartilaginous nucleus, as seen in sagittal section, was wedge-shaped, with its base at the condyle and its apex extending forwards below and in front of the coronoid process. Into this cartilaginous nucleus ossification was extending from the surrounding membrane bone. Traces of this cartilage persisted until full time. In a fœtus at three and a half months there was a distinct cartilaginous nucleus in the coronoid process into which ossification also extended from the surrounding bone. The cartilage in the coronoid process had practically disappeared by the sixth month. The condylar cartilaginous nucleus was present in all mammalian fœtal jaws examined, but a coronoid nucleus might be present and no angular nucleus, or *vice versâ*. In the pig embryo there was a distinct angular cartilage, which at one stage was continuous with the condylar. In the jaw of the fœtal deer and mole all three cartilages were present, and were especially distinct in the latter. Dr Low considered that these cartilaginous nuclei did not indicate separate elements, but that they were an adaptation to the growth of the jaw.

As to Meckel's cartilage, ossification commenced in it at a point opposite the interval between the first and second tooth germs. By the third month this part of Meckel's cartilage had passed from below upwards into the inner alveolar margin, and by three and a half months was rapidly ossifying to help to form the alveolar margin here. Behind this point Meckel's cartilage gradually

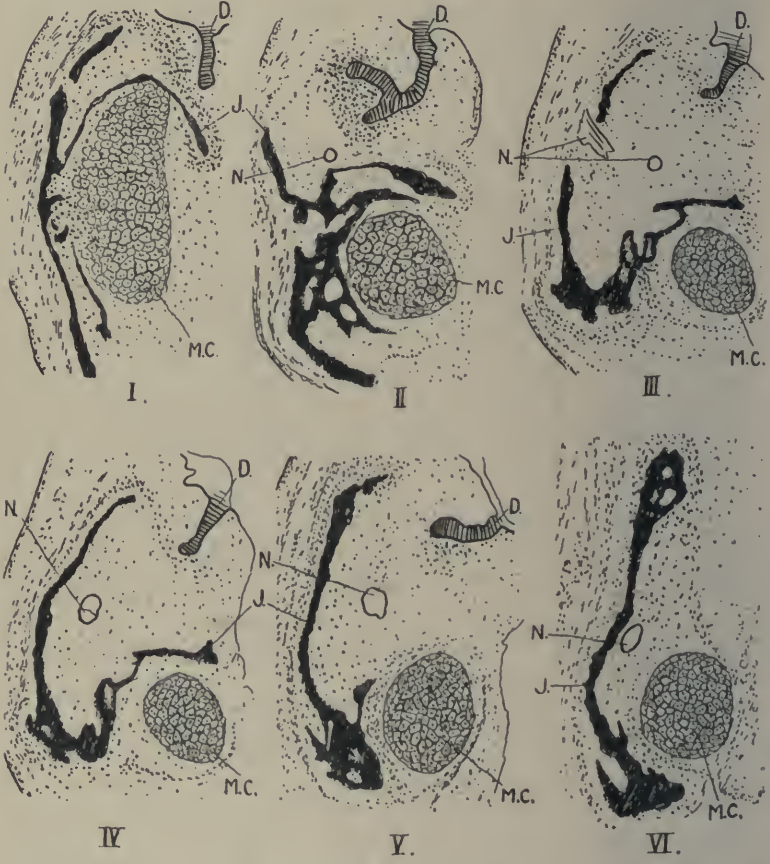


Fig. 1.—Transverse sections of lower jaw of a ten weeks human fœtus (from micro-photographs). I. is between first and second tooth germ; II. through the second tooth germ; III. at the mental foramen; IV. through middle of body of jaw; V. through posterior part of body; VI. through the coronoid process. J., lower jaw, a continuous sheet of membrane bone; M.C., Meckel's cartilage; D., dental lamina and germs; N., inferior dental nerve.

atrophied except in so far as it helped to form the internal lateral ligament and the malleus. Behind the symphysis the anterior extremity of Meckel's cartilage did not enter into the formation of the jaw, but usually persisted throughout fœtal life as one or two small rounded cartilaginous masses. It was possible that sometimes these might become ossified and form the accessory ossicles which some observers had noted here.

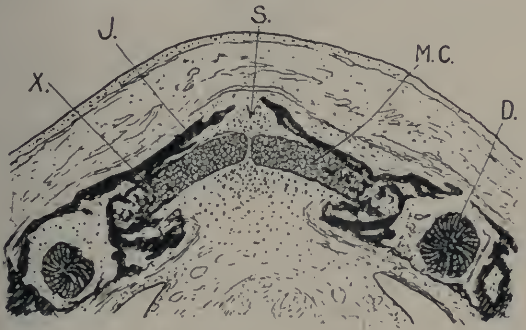


FIG. 2.—Horizontal section through the symphysis of the lower jaw of a human fœtus at the third month (from a micro-photograph). S., symphysis; J., membrane bone of jaw; M.C., Meckel's cartilage, its anterior extremities unossified; D., second tooth germ.

Dr Low's conclusions were:—

1. That the human lower jaw was developed in membrane as a single skeletal element.

2. That in connection with the condyle and coronoid, cartilaginous masses were developed at a comparatively late stage, that these did not indicate separate elements, but were an adaptation to the growth of the lower jaw.

3. That Meckel's cartilage became ossified and incorporated with the inner alveolar margin in a region opposite the first and second incisor tooth germs, and that proximal and distal to this point it took no part in lower jaw formation.

Many members, including Professor FAWCETT, Dr KEITH, and the PRESIDENT, joined in the discussion, and congratulated Dr Low on his work.

(5) Dr JAMES MILLER read a paper on *the Arrangement of the Elastic Fibres in the Bronchi and Lungs.*

In the bronchi the elastic fibres are arranged in four distinct layers—a thin layer of fine intersecting fibres under the homogeneous basement membrane, a longitudinal layer of closely-set thick fibres, a circular layer corresponding to the muscularis mucosæ, and a circular layer enveloping the cartilage nodules.

These layers are gradually lost as the air-tubes become smaller, till in the terminal bronchioles and alveolar passages the longitudinal layer is the only one left.

In the alveolar walls and interalveolar septa the fibres are arranged in an irregular manner. There is a gathering together and thickening of the fibres at the openings of the alveoli into the infundibula and alveolar passages.

In the pleura the fibres are arranged as a layer immediately under the endothelium in the form of a close network. This layer is frequently duplicated. In the interlobular septa there are no fibres apart from the presence of large vessels.

The smallest pulmonary vessels show a single layer of very fine longitudinal fibres. As the vessel becomes larger this layer is duplicated, and a circular layer corresponding to the middle coat appears.

Professor ROBINSON, Drs KEITH, ADDISON and GOODALL, and the PRESIDENT joined in the discussion.

This paper will appear in full in the *Journal of Anatomy and Physiology*.

(6) Professor FAWCETT and Dr BLACKFORD presented a Report on 700 specimens of the *Circle of Willis*.

The paper will appear in full in the *Journal of Anatomy and Physiology*.

(7) Dr WILLIAM WRIGHT read a paper on *the Human Fibula, its adaptation to the erect posture*.

Through the kindness of Professor Macalister, I was able to examine, last summer, a large number of fibulæ in the Anatomical Department of the University of Cambridge. In my examination I paid particular attention to variations and to features which usually escape mention in the text-books. By means of comparative osteology and dissections I sought to discover the reasons for their presence; at the same time I enquired into the manner in which the fibula has adapted itself to the erect posture.

Upper Extremity.—The cubical shape of the head of the fibula is peculiar to man, although there is an approximation to it in the anthropoid apes and slightly in the kangaroo. In most animals the head is flattened laterally. The modification of shape in the animals specified above, I correlate with the assumption of the erect or semi-erect posture and the bipedal mode of progression, in consequence of which a larger area for the attachment of certain muscles, particularly the soleus and biceps, becomes necessary.

The head varies in its relation to the shaft; it may be square to it, diagonal to it, or it may occupy any intermediate position. The head being moulded to shape by the muscles attached to it, I attribute any variation in the relation of head to shaft to unequal development of those muscles.

The facet for the tibia varies in position, shape, and size. It usually extends on to the styloid process, and is largely internal to a diagonal line drawn from the styloid process to the peroneal tubercle. In other animals the facet occupies practically the whole of the superior surface of the head—a difference which I attribute to the enlargement of the head in man for muscular attachment.

The styloid process is better marked in man than in any animal above the monotremata and marsupialia. In the ornithorhynchus and echidna the process is very long, and is obviously for the attachment of muscles. In several of the marsupials the process is well developed, flattened superiorly, and surmounted by a sesamoid bone. The view that such a styloid process with its sesamoid bone might represent the pointed human styloid process suggested itself to me, and it seemed to be supported by the fact that the sesamoid bone is in the short external lateral ligament, and that in man this ligament is attached to the tip of the styloid process. A brief consideration, however, showed that this could not be, for the short external lateral ligament in marsupials is, as Parsons has pointed out, the separated tendon of the popliteus. In man the tendon of the popliteus is continuous with its muscular portion, and I regard the short external lateral ligament in him as due to the thickening of the fascia between the outer head of the gastrocnemius and the popliteus, partly, it may be, in consequence of strain due to the adoption of the erect posture, and partly to bridge over the inferior external articular vessels and nerve. If the sesamoid bone of marsupials is ever represented in man, it would be as a sesamoid bone in the tendon of the popliteus, as it is in the cat and the squirrel. Having, therefore, eliminated the sesamoid bone as an element in the styloid process, I came to the conclusion that the styloid process of the human fibula is homologous with the blunt styloid process of the kangaroo and the wombat. The explanation of its presence in those animals which possess it, is, I consider, to afford a greater area for the origin of muscles for, in man, the soleus. This view is supported by the fact that the upper end of the process is frequently reverted, as though from the pull of the soleus. It might be asked, Is it not present in order to prevent dislocation? In the kangaroo it certainly has the appearance of being able to serve such a purpose, but not in any of the other animals which possess it. In man I don't believe that dislocation is prone to occur at the superior tibio-fibular articulation or that the styloid process would be effective in preventing it, for it is situated external to the facet and to some extent to the tibia.

Immediately external to the styloid process a shallow groove is sometimes seen passing downwards and then forwards; it is for the peroneal nerve.

On the outer aspect of the head there is an area, like a thumb impression, from which a ridge passes down to the shaft. The area is well marked in the anthropoidea; it is for the insertion of the biceps and for the passage of the external lateral ligament, which can frequently be traced to the aforesaid ridge.

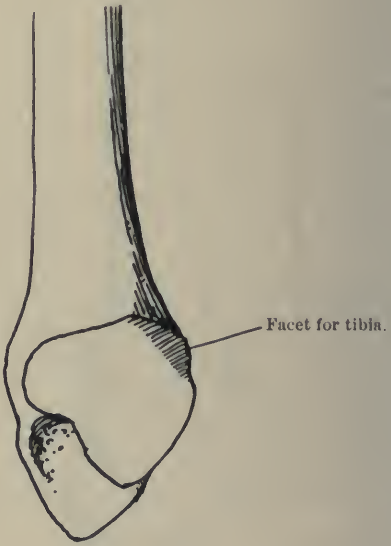
The Shaft.—Being primarily for the attachment of muscles, it is only to be expected that there should be great variation in shape, in accordance with the varying development of the muscles. Some bones are more or less cubical on section, others, due to the narrowness of the anterior surface, have the shape of a malacca cane. Some are channelled, the channelling affecting as a rule the external or internal surface; a few are so flattened as to resemble a knife, and I suggest 'coultered fibula' as a suitable designation for such. The shaft of a coultered fibula is bellied like a knife and flattened in such a way that the external and posterior surfaces form broad surfaces, whereas the anterior and inner surfaces are narrow; further, the external surface is antero-external, and the anterior surface looks inwards and forwards. The fibula, so far from being a disappearing bone, is larger in proportion to the tibia in man than in the great majority of other animals. It is characterised by unusually distinct and sharp borders for the attachment of the fibrous septa and the interosseous membrane which serve for the origin of muscles. This condition of the shaft is to be associated with the erect posture and with the powerful muscles responsible for the maintenance of the arch of the foot. Certain muscles, particularly the soleus, are accountable for asperities on the shaft. Two well-marked tubercles are situated, one below the other, on the postero-internal border. They are for the origin of certain tendinous fibres of the soleus; they are separated from each other by a smooth area over which the superior fibular artery passes. The area for the tibialis posticus muscle is often clearly defined by oblique limiting ridges, from the upper of which fibres of the soleus get origin. The area is almost invariably marked by an oblique line, directed downwards and backwards for tendinous fibres of origin of the muscle. In a few instances a ridge for the intermuscular septum between the peroneus longus and brevis is discernible. A large number of bones show a series of three or four well-marked grooves on the postero-external border, an inch or more apart, for branches of the peroneal artery. In the rough area above the facet for the astragalus a smooth line is occasionally seen for the anterior peroneal artery, which apparently sometimes passes forward through the upper portion of the inferior interosseous tibio-fibular ligament.

Lower Extremity.—The three fasciculi of the external lateral ligament are attached to areas which are usually circumscribed and easily recognisable. The middle fasciculus is attached to a portion which passes as a groove round the inferior border of the external malleolus a little in front of its tip. It is not attached to the tip, as is usually stated. The groove is continued round the malleolus to the area for the posterior fasciculus. This groove and the depression for the latter ligament have a practical interest, for they constrict and weaken the bone and occasion a liability to fracture along a line passing upwards and backwards from the groove on the lower border of the external malleolus. A fracture here might be produced by direct violence on the lower and back part of the malleolus, a part which is not supported by the astragalus, or by indirect violence from a twist of the ankle whereby the middle and posterior fasciculi being stretched the posterior part of the malleolus might be torn off. That such a fracture occurs was first mentioned to me by Dr Denyer of Cambridge. Professor Jordan Lloyd tells me that they are quite common, and there is an example of the fracture, partially united, in The Royal College of Surgeons Museum (No. 1077 Hunterian Collection). Immediately in front of the groove for the middle fasciculus, on the outer surface, is a facet of variable distinctness for the anterior fasciculus.

The groove for the tendons of the peroneus longus et brevis is more posterior in man than in other animals. In carnivora the groove is double, that for the peroneus brevis being anterior to that for the longus, which is in keeping with the origin of the brevis in front of that of the longus. The peroneus brevis has gradually moved backwards until it lies under the longus, and there is now in the anthropoid apes and man a single groove for the two tendons. I correlate this change with the assumption of the erect posture. The peroneus brevis, by moving backwards, is able not merely to evert the foot, but also to maintain the outer portion of the osseous arch of the foot, for it should be remembered that the skeleton of the foot is arched both on the inner and outer sides in consequence of the longitudinal axis of the os calcis being directed upwards as well as forwards.

From the migration backwards of the peroneus brevis, and from the addition of the peroneus tertius, the triangular subcutaneous area on the outer aspect of the lower end of the fibula has become more external and less anterior or antero-external.

As to the size of the external malleolus in man, although it is large and possessed of considerable vertical length in order to prevent lateral displacement at the ankle joint, it is no larger in proportion to the internal malleolus than is the case, say, in the pig, and it is a less effective arrangement for the purpose than that which obtains in such animals as the crocodile, kangaroo, elephant, and pig, in which the external malleolus projects down to articulate with a strong process from the calcaneum.



The rough area above the facet for the astragalus is unusually well marked in man, and at its posterior angle is often a prominent tubercle for the attachment of the transverse ligament.

In connection with the lower articular facet of the fibula, there is occasionally found at the antero-superior angle a shelf-like facet for the tibia. As is well known, the lower end of the tibia overhangs the astragalus antero-externally. In consequence the fibula, that it may articulate with the astragalus, has to pass to a certain extent under the tibia—hence the facet. It is of interest that an examination of the facets in other animals shows that this somewhat horizontal facet for the tibia is the one usually met with: typical examples of it are to be found in the anthropoidea and in carnivora. In such ungulates as the deer the only portion of the fibula which persists is the small portion round this facet and the facet for the astragalus. The vertical facet for the tibia seems to be confined to man, and to be not always present in him.

The fibulæ which I examined at Cambridge were chiefly Egyptian, but I also examined fibulæ of Bushmen, Negroes, Australians, and of natives of Jamaica and Sarawak. I have also examined a large number of fibulæ of Europeans. I have found the shelf-like facet for the tibia less frequent among Europeans than among other races; channelling of bones is a common feature of the fibulæ from Jamaica and Sarawak. With these exceptions I found nothing of interest from an anthropological point of view.

In conclusion I should like to express my indebtedness to Professor Macalister and Dr Barclay Smith for so kindly granting me every facility, and for favouring me with helpful suggestions and criticism. I am indebted to my friend Mr D. S. Smith for the illustrations.

(8) Mr GORDON TAYLOR and Dr W. VICTOR BONNEY read a paper on *the Homology and Morphology of the Popliteus Muscle.*

Attention was drawn to the fact that the popliteus belonged to the same stratum as the flexor tibialis and flexor fibularis, and not to the deep peroneo-tibial layer.

Moreover, it was pointed out that in certain animals the lowest and most external fibres of the popliteus muscle pass uninterruptedly into the tibialis portion of the deep flexor of the pedal digits, and it was suggested that these fibres represented the condylo-radialis of Windle, found in the anterior extremity. The name of condylo-tibialis was suggested for this slip. The slip is by no means constant in the various mammalian orders; but it was present in four marsupials examined—in Dasypus among the edentates, in atherura africana, in some specimens of felis domestica, and in suricata tetradactyla. It was also found in cebus fatuellus, macacus rhesus, and papio porcarius.

Certain other conclusions were also drawn regarding the popliteus:—

(i) The superficial portion of the pronator radii teres is homologous in the lower limb with a portion of the gastrocremius mass.

(ii) The deep portion of the pronator radii teres is homologous with the popliteus in the lower limbs.

(iii) The deep portion of the pronator radii teres and the popliteus arose primitively from the head of the ulna and head of fibula respectively.

(iv) That as movement between the tibia and fibula, and radius and ulna respectively, ceased to exist, the upper origin of the popliteus certainly, and the deep portion of the pronator radii teres probably, ascended to the external femoral and internal humeral condyles respectively.

(v) That in the upward migration they carried with them certain fibres of the flexor tibialis and flexor radialis respectively.

(vi) That these fibres exist as the condylo-tibialis and condylo-radialis respectively.

(vii) That in the lemur, where movement between the tibia and fibula has reappeared, the popliteus appears to be descending to its primitive fibular attachment.

(viii) That in man, and to an extent in the anthropoid apes, in whom movement between the radius and ulna has reappeared, the deep portion of the pronator radii teres has descended to its primitive ulnar attachment, carrying with it the condylo-radialis.

(ix) That the fibrous arch from which the soleus arises in man is identical with the similar structure to which, in ungulates, a large portion of the popliteus is attached, and is to be regarded as indicating the original line of the fibular origin of the popliteus.

Mr PARSONS, Professor P. THOMPSON, Dr WRIGHT, Dr KEITH, and the PRESIDENT joined in the discussion.

The paper will appear in full in the *Journal of Anatomy and Physiology.*

(9) Mr SIDNEY SCOTT described a new method of demonstrating the *Topographical Anatomy of the Human Skull.*

The method is that of graphic representation by simple geometric figures on reconstructive principles. It is based upon the constant topographical relations of some of the chief foramina and processes of the skull.

Mr SCOTT gave illustrations of the norma basilaris, norma frontalis, and norma lateralis, reproduced by the method devised.

The advantages of the system are that it is simple and yet can be indefinitely elaborated.

It enables anyone unskilled in linear or serial perspective to accurately delineate the typical human skull in all direct aspects.

The data for this demonstration were obtained from twenty skulls. The comparatively small number, Mr Scott thought, was counterbalanced to some extent by the varied selection of the races to which the skulls belonged—viz., European, ancient and recent, Asiatic, African, South American, and Australasian races. Some four hundred measurements in millimetres were taken, and these have been charted, and are included in the appendix to the communication, which will be published *in extenso* in the *Journal of Anatomy and Physiology.*

Professor SYMINGTON, Dr CHRISTOPHER ADDISON, Dr ARTHUR KEITH, Professor FAWCETT, Dr BLACK, and Mr RAWLING admitted the usefulness of the method.

(10) Mr FRANK S. POOLE, B.A., of Sidney Sussex College, Cambridge (introduced by Dr Marett Tims), read a paper on *a Method of recording Osteometric Indices.*

This communication was intended as a preliminary account of a graphical method for computing and recording osteometric indices, which differs from those hitherto published. Various devices have been introduced to lessen the labour associated with the calculation of the indices of an extensive series of measurements. An example is an instrument introduced in 1899 by D. Waterston (*Journ. of*

Anat. and Phys. vol. xxxiii. p. 301), which consists of a graduated quadrant, with a movable arm, the position of the latter being adjusted and the index being read off along its upper or lower edge. This instrument seems to present no particular advantages on the ordinary slide rule, which is very much more generally applicable to calculations of all sorts. A second method is one introduced by Flower, and published by him in Part I. of the Catalogue of Specimens in the Museum of the Royal College of Surgeons (1879). It consists of a number of tables, from which the numerical value of the index can at once be read off by reference to the required horizontal and vertical columns. Neither of these methods, however, affords any means of recording the indices, and recourse must be had to the ordinary statistical methods.

The present method consists of a number of charts, which can be drawn by the aid of ordinary logarithmic paper. Unfortunately it is only possible to reproduce one of these charts, the most general one, but it will be shown how other charts for more definite purposes can be obtained.

The working of the chart depends upon a series of diagonals, whose construction depends upon the fact that all points which represent the same index, as given by the equation

$$I = \frac{100y}{x},$$

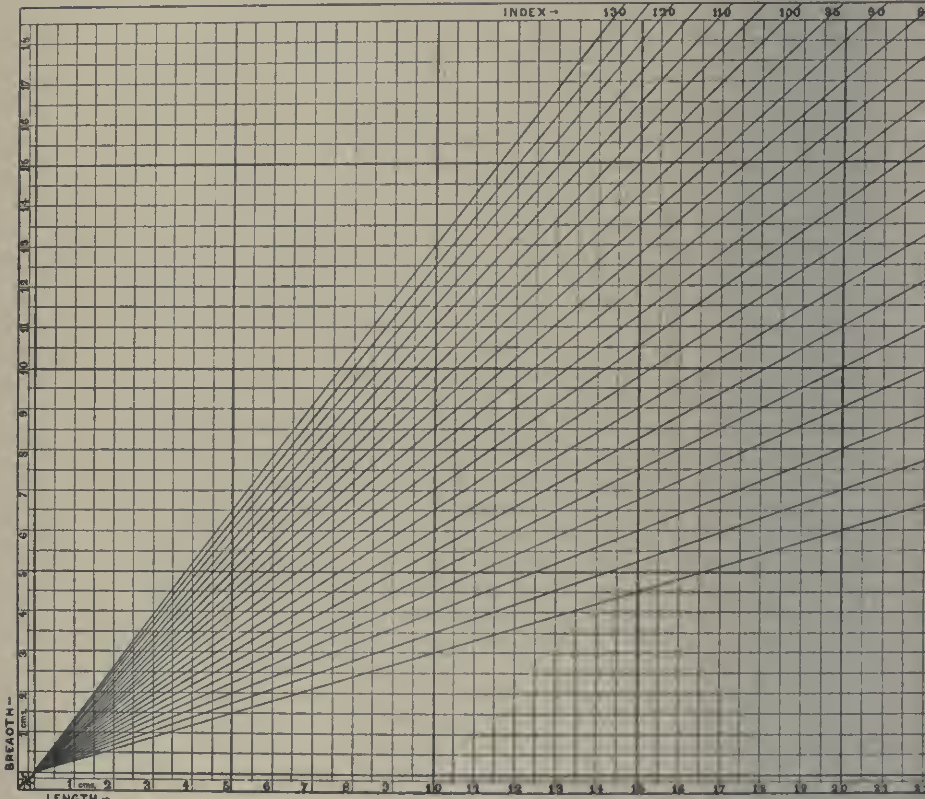
when x and y are length and breadth respectively, lie on a straight line, and, moreover, that each particular value of the index, I, can be represented by a fixed and definite straight line on the chart. The mathematical proof of this need not be entered into.

In the chart, reproduced, it is easy to see that all the diagonals must pass through the zero point, for if any one did not, but cut the line when either x or y equal zero, I would at that point have the value of either zero or infinity, and would not fulfil the condition of constancy. Now to define a line, only two points on it are necessary, and here one is fixed already, the zero point, so that to draw a line to represent any index only one other arbitrary point is required For convenience this point has been chosen to lie on the line when $x = 10$, for here the equation resolves itself into

$$I = \frac{100y}{10} \qquad \text{or} \qquad y = \frac{I}{10}.$$

It is only necessary, therefore, to mark points on this line for values of y corresponding to required values of I, and to join these to the zero point to complete the chart. If the chart be examined it will be seen that where the series of diagonals 35, 40, 45, etc., cut the line $x = 10$ (*i.e.* length = 10), y has the values 3·5, 4·0, 4·5, etc., respectively in accordance with the formula given. It remains to be mentioned that though the unit of measurement is taken to be the centimetre, the unit is arbitrary, and the same chart may also be used for volumetric, and even angular, measurements.

It is obviously impossible on such a chart to draw diagonals for every index, and to make the parts of the chart devoted to the larger measurements more useful these parts may be enlarged within certain limits to suit more definite requirements, and charts may be drawn to suit the cephalic, alveolar, nasal, or any other particular index. This is conveniently done on logarithmic paper, on which every fifth line is of double thickness, these lines being made to correspond



Nº 1 GENERAL CHART FOR OSTEOMETRIC INDICE

with the thin lines on the present chart, the unit by this means being converted into the millimetre. The indices lines as found on the general chart may be sketched in, and the intermediate ones added to make the parts of the chart complete.

The method of using the chart is probably obvious, but may be briefly set forth as follows:—The two dimensions, being known, are measured horizontally and vertically on the chart; a point is arrived at, which, lying on or near one of the diagonals, gives the index by inspection.

Lastly, these charts may be used not only for computing the index of a single pair of measurements, but also for recording a series of such measurements. Each member of the series may be represented on the chart by a point, or more definitely by a number, and not only the index, but also the actual dimensions, read off at any time. It is necessary to mention here that such a device occurs in a paper by Atkinson (*Journ. Anthr. Inst.*, 1879), where he records a number of measurements on logarithmic paper, and even indicates certain indices, but not, it appears, with any particular attempt at accuracy.

It is hoped that at a future date a fuller series of these charts may be published, as owing to their double use, and the ease with which they can be duplicated, it is probable that they may be useful to those who frequently make use of indices for comparative purposes, and who wish to avoid the ordinary statistical methods.

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