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OF THE

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I.—**On the Leaf-Trace in some Pinnate Leaves.** By **R. C. Davie**, M.A., D.Sc., Lecturer in Botany in the University of Edinburgh. *Communicated by* Dr R. Kidston, F.R.S. (With One Plate.)

(Read February 7, 1916. MS. received February 25, 1916. Issued separately February 16, 1917.)

In a general survey of the pinna-traces of Ferns (Davie, '14), the results of which have been summarised in tabular form (*loc. cit.*, p. 354), two main types of pinna-trace were described and contrasted. In the one—the "extramarginal"—the pinna-trace leaves the back of the hook formed by the incurved edge of the leaf-trace; in the other—the "marginal"—the outwardly directed margin of the leaf-trace is simply nipped off as the pinna-trace. The more primitive Ferns in the evolutionary scale, and the first leaves of both primitive and advanced Ferns, exhibit the marginal type of pinna-trace; the extramarginal type of pinna-trace is found in those Ferns which stand midway between the extreme types in the system of classification, and in some advanced forms. There is little doubt that the type of pinna-trace is in some degree dependent on the systematic position of the Fern which possesses it (*ibid.*, pp. 354, 362). On the other hand, there is apparently a relationship between the type of pinna-trace and the size and degree of division of the lamina of the leaf in which it occurs (*ibid.*, pp. 369, 372, 376). Further, the same type of pinna-trace seems regularly to occur in the species of any genus of Ferns (*ibid.*, p. 354). That there are a few exceptions to each of these generalisations (*ibid.*, *cf.* pp. 354, 372, and 373) made it desirable that a concise problem dealing with them all should be attacked in material grown under natural conditions. A visit to Brazil, in which I was aided by a Treasury grant, gave me the opportunity to collect species of the genera *Dryopteris*, *Aspidium*, *Polystichum* (which stand midway in the systematic grouping of the Ferns), *Polypodium*, and *Leptochilus* (which are "advanced" genera). Species of the genus *Polypodium* were found in such different natural conditions as the bed of a stream, the top of a wall, the exposed surface of a sandy strip of land near the sea, and the moist shaded depths of a dripping rain-forest. Short-leaved and long-leaved Polypodiums were found in these situations, and in more than one instance examples of the same species were found under different natural conditions. A paper recently published (Borkowski, '14) gives a description of the anatomy of the leaves of Colombian species of *Polypodium* grown in sharply contrasted natural surroundings, and has afforded the opportunity to extend the comparisons made among the Brazilian species. Plants of *Polypodium vulgare*, Linn., have also been collected in Scotland, at sea-level and at varying altitudes up to nearly 3000 feet above the sea, from rock-clefts, wall-tops, hedge-bottoms, stream-sides, and tree-trunks. And the comparisons made of the species of Ferns have been amplified and corrected by an examination of leaves of Cycads, Palms, and other Monocotyledons, and selected forms of Dicotyledons.

From the results of these investigations, which have been confined to pinnate leaves, but which have been spread over as wide a systematic field as possible, and which include a detailed examination of many forms of a single genus and of several types of a single species, it has been possible to draw conclusions regarding the factors which control the branching of the vascular system of the leaf in various groups of plants. I have throughout attempted to read results in relation rather to the physiological needs of the leaf than to its inherited tendencies. And such opinions as have been stated on questions of phylogeny have been printed only after the evidence seemed overwhelmingly in their favour. Vascular anatomy must at the best take a subsidiary place among the criteria which are valuable in the work of classifying plants. But the extraordinary parallelism which has been established for the Ferns between my results and the conclusions reached by the distinguished author of the *Index Filicum* has made worth mentioning a sphere in which anatomical characteristics may be usefully employed in confirmatory work.

I desire to acknowledge the assistance of a Government Grant,* which enabled me to visit Rio de Janeiro and São Paulo and to collect material in the vicinity of these cities.

Whilst in Rio de Janeiro I was given every facility to prepare my collections and to consult literature by Dr J. C. Willis, then Director of the Jardim Botanico, to whom I express my thanks.

I desire also to express my thanks to the Regius Keeper of the Royal Botanic Garden, Edinburgh, who supplied from the Garden collections much of the material described below; and to Professor F. O. Bower, F.R.S., who during the progress of the investigation made criticisms and suggestions which materially altered its scheme of construction and widened its field of inquiry.

The Brazilian Species of Polypodium.

Ten species of *Polypodium* were collected in natural situations in Brazil. One of these, *P. brasiliense*, Poir., was found on three separate occasions, under different natural conditions. It was found in the undergrowth of the rain-forest on the slopes of Monte Corcovado, which rises behind the city of Rio de Janeiro. Between the

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* Placed at my disposal by the Royal Society.

mountains and the sea, near Rio, there stretch narrow strips of sandy ground, known as "restingas" (*cf.* Ule ('01) and Hemmendorf ('12)), on which there grows a sclerophyllous vegetation (Loefgren, '14), never attaining any great height and affording scant shade from the sun's rays to a sparse undergrowth of straggling herbs. Next to the sea the restinga merges into loose sand, which supports a flora mainly composed of *Ipomæa biloba*, Forsk., *Remirea maritima*, Aubl., and a few Grasses (*cf.* Karsten and Schenck, '03). Among the loose sand, on the seaward edge of the restinga at Gavea Beach, a few miles south of Rio, *P. brasiliense* was found, in a situation fully exposed for the whole day to the sun and swept by the breezes from the Atlantic Ocean. It was found again in a rather cool, shaded position, with water dripping from above, on the rock-face of a narrow gorge, close to the sea, at Praia de Leblond, between Gavea and Rio. With *P. brasiliense* on the forest-slopes of Monte Corcovado there were found *P. loriceum*, Linn., and *P. decurrens*, Raddi. *P. catharinæ*, Langsd. et Fisch.—a species very closely resembling *P. loriceum*,—was collected on the restinga at Praia de Leblond; while *P. fraxinifolium*, Jacq., which is closely similar to *P. brasiliense*, was found in the very rich rain-forest at Alto da Serra, between São Paulo and the coast at Santos.

The other species collected were *P. serrulatum* (Sw.) Mett., a tiny, wiry-leaved form growing in the bed of a stream at Alto da Boa Vista, above Rio; *P. cultratum*, Willd., a flaccid Fern with small, delicate pinnæ, hairy on the under surface, found beside a stream at Alto da Serra, São Paulo; *P. lepidopteris* (Langsd. et Fisch.) Kze., and *P. plumula*, H. B. Willd., with firm pectinate leaves, from rocks and wall-tops near Petropolis and Therezopolis; and *P. polypodioides* (L.) Hitchcock, a small-leaved species from the bases of the Royal Palms in the Jardim Botanico at Rio.

The leaves of *P. brasiliense* from the loose sand on Gavea Beach had tough and leathery pinnæ, closely crowded on a leafstalk eight inches long (Plate, fig. 4); those from the gorge at Praia de Leblond were eighteen inches long and had narrow pinnæ placed about one and a half inches from one another (Plate, fig. 3); in the forest the leaves of this species had thinner, less leathery pinnæ, spread, at distances of about an inch and a half from one another, over a shorter length of rachis, the total length of the leaf being about fifteen inches (Plate, fig. 1).

P. fraxinifolium, which is very nearly related to *P. brasiliense*, and which was found in the depths of the forest on the mist-clad slopes above Santos, had leaves about two feet in length. The pinnæ were large, but more delicate in texture than those of *P. brasiliense* (even than those of the forest-grown form), and possessed "drip-tips" (Plate, fig. 2).

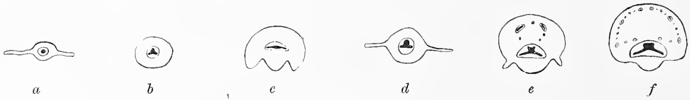
The Leaf-Traces and Pinna-Traces of the Brazilian Species of Polypodium.

In all ten species of *Polypodium* the margin of the leaf-trace nearest to the pinna to be supplied is simply nipped off and passes into the pinna. This has been found to prevail in every leaf examined, and occurs in relation to every pinna, from base to apex of the leaf. The leaf-traces of three leaves of *P. brasiliense* and a leaf of *P. fraxinifolium* are represented in the Plate, figs. 5, 6, 7, 8. Though the leaves from which the sections photographed were prepared were collected in very different surroundings, their pinna-traces were uniformly of the marginal type. This was to be expected if the results of the earlier investigation of some representatives of the genus *Polypodium* were to hold good for the whole genus. In a previous paper (Davie, '14, pp. 354, 358) it was shown for five species of *Polypodium* (including examples of *P. brasiliense*, grown in the Fern House of the Royal Botanic Garden, Edinburgh) that the pinna-trace always left the leaf-trace in marginal fashion. We are now able to conclude that the type of pinna-trace is not dependent, in the genus *Polypodium*, upon changes in the natural surroundings of a member of the genus. Different environments, as we shall see below, have a marked influence upon the leaf-trace in the genus: as far as we may conclude from the examination of a few species of *Polypodium* grown under natural and artificial conditions, the type of pinna-trace is independent of the environment of the leaf in which it occurs. This, certainly, is interesting in view of the admitted "naturalness" of the genus *Polypodium* (*cf.* Copeland, '07, p. 71). Transverse sections of the leaf-stalks of the forest, rock-face, and sand plants of *P. brasiliense* and of the leaf-stalk of *P. fraxinifolium* are figured in the Plate. These exhibit quite marked reactions to the conditions in which the plants were growing. In the plants found near the sea there is a greater number of strands in the leaf-trace than in those found in the forest, while the individual strands are larger in the former (*cf.* figs. 7 and 8 in Plate with figs. 5 and 6). The most curious feature of these sections, however, is in their adaxial vascular strands. In these strands in the Gavea Beach (Plate, fig. 8) and Praia de Leblond plants (Plate, fig. 7) the tracheides are rather more numerous than in those of the forest plants (Plate, fig. 5, and *cf.* fig. 6 of *P. fraxinifolium*). In the leaf-traces of the latter group, large water-storing cells are prominent, close to the lateral parts of the phloem surrounding the central group of tracheides (Plate, figs. 5 and 6). In the Gavea Beach and Praia de Leblond leaves the water-storing cells are replaced by ordinary parenchymatous cells, and the space devoted to them in the forest leaves is taken up by a greater development of tracheides (Plate, figs. 7 and 8).

An exactly similar contrast occurs between the leaf-trace strands of *P. loriceum*, which was found growing in the forest, and those of *P. catharinæ*—a Fern so similar to *P. loriceum* as to be almost indistinguishable from it,—which was found in exposed spots on the restinga at Praia de Leblond. The leaves from the restinga were perhaps slightly shorter; the individual pinnæ were a little longer, and were more closely crowded together. The water-storing tissue and the decreased amount of xylem in the forest leaves of *P. loriceum*, in contrast with the exposed leaves of *P. catharinæ*, are as conspicuous as in *P. brasiliense* and *P. fraxinifolium*.

The evidence of modification in the structure of the vascular strands in these Fern leaves in relation to their environment agrees as regards the xylem with what has already been described for various Angiospermic plants. VESQUE and VIET ('81) have shown that the vascular strands of Pea plants grown in a humid atmosphere are narrower than those of plants grown in a dry atmosphere. Similar results were obtained by KOHL ('86) and EBERHARDT ('03), while more recently GAIN ('95) and CANNON ('05) have made experiments on the influence of water in the soil upon the structure of some stems. CANNON found that "non-irrigated" desert plants have larger ducts and more of them per equivalent area of cross-section than "irrigated" plants. While this record agrees with the account of the forest and restinga Ferns, detailed above, no close comparisons are really permissible between the observations, because CANNON worked with the *stems* of plants which had an *annual increment* of growth. His explanation of the differences between the plants with which he made his experiments is not in any case applicable to the Ferns of forest and restinga, since he assigns the contrast between the irrigated and non-irrigated plants to differing rates of growth, the curve of growth for the non-irrigated plants being very similar to that of the yearly rainfall, while the irrigated plants grow evenly throughout the year. In the case of the Brazilian Ferns it certainly appears as if different rates of transpiration were responsible for the contrast between the forest and restinga types. No matter what may be the water-supply to the leaves, Ferns growing on the restinga or on the loose sand of the Brazilian beaches should lose much more water than those which grow in the moist depths of the forest. Rapid transpiration would involve the provision of a large amount of xylem in a leaf-trace, while the risk of desiccation on the hot wind-swept restinga might cause the employment of tracheides as water-storing elements, in place of thin-walled cells. This simple explanation would certainly fit the cases of the Ferns described above. Water-storage in tracheides is known in various groups of plants (see KRUGER, '83; KNY and ZIMMERMANN, '85; VESQUE, '86; VOLKENS, '86; GILG, '91; WARMING, '93; ROTHERT, '99), and might quite well occur in the leaves of these exposed Brazilian Ferns. The relative amounts of xylem in their leaf-traces form an interesting parallel to CANNON'S observations, which, however, have been subjected to criticism by GROOM ('10). In the absence of observations on the rates of transpiration in the two series of leaves and on the water content of the soil on the restingas and in the forest, we can merely record the results of the examination of these Fern-leaves. For the purpose of the present paper it is sufficient to note that the very different conditions, while they do markedly influence the structure of the leaf-trace, have no effect on the type of pinna-trace. In these leaves, as in the leaves of all the species of *Polypodium* which have been examined, the margins of the leaf-trace go off to supply the pinnæ. The marginal type of pinna-trace is found uniformly throughout the genus.

The leaf-traces of the ten species of *Polypodium* collected in Brazil are represented diagrammatically in text-fig. 1. Text-fig. 1*a* represents the leaf-trace of *P. serrulatum*, which has the smallest leaf of all the series and which has very tiny "pinnæ"—mere teeth projecting slightly from the sides of the rachis. In the leaf-trace there is a compact rod of xylem, the edges of which extend slightly and give off their margins below the pinnæ. In *P. cultratum*, the leaf-trace of which is represented in text-fig. 1*b*, the leaf is much longer than in *P. serrulatum*, but the pinnæ are small in proportion to the length of the leaf. The leaf-trace has a strong development of tracheides on its abaxial side. *P. polypodioides* has a short leaf, with relatively long pinnæ closely crowded together. Its leaf-trace, figured in text-fig. 1*c*, has long lateral extensions of xylem but little or no abaxial development. In *P. plumula* and *P. lepidopteris* the leaf is longer than in any of the species yet mentioned, and the pinnæ are short and very numerous. The leaf-traces, represented in text-fig. 1*d*, have only a slight development of the lateral extensions and a strong abaxial group of tracheides. The abaxial development of the leaf-trace becomes a system of separate vascular strands in the leaf-traces of *P. loriceum*, *P. catharinæ*, *P. brasiliense*, and *P. fraxinifolium*, the type of which is figured in text-fig. 1*e*. In these Ferns the leaf is longer than in any of the five species described above, while the pinnæ are larger than the pinnæ of these species, in relation to which the lateral extensions of the adaxial portion of the leaf-trace are prominent. *P. decurrens* has the longest leaf of the whole series; its pinnæ are larger than the pinnæ of any of the others; its leaf-trace, represented in text-fig. 1*f*, has a very extensive system of abaxial strands and prominent lateral extensions of the adaxial strand.



TEXT-FIG. 1.

We have thus, in the ten species of *Polypodium* examined, an increasing length of leaf and an increasing size of laminar surface. Apparently corresponding to the one there is an increasing development of the abaxial side of the leaf-trace, while in relation to the other there is an increasing extension of the lateral portions of the adaxial part of the leaf-trace.

As one follows in detail the changes in the leaf-trace in any member of the group *P. loriceum*, *P. catharinæ*, *P. brasiliense*, and *P. fraxinifolium*, from base to apex of a leaf, noting the relations of the various strands one to another, and especially the relation of the strands of the abaxial system to the adaxial strand, one finds that below the pinnæ, and prior to the departure of the margins of the adaxial strand as the pinna-traces, there is a movement of the strands of the abaxial system towards the adaxial strand and a fusion of those strands of the system which are nearest to the adaxial strand with the abaxial ends of that strand. There is in the type of leaf-trace shown in text-fig. 1*e* a reinforcement of the adaxial strand from the abaxial system of strands prior to the departure of a pinna-trace. In the case of the Gavea Beach example of *P. brasiliense*, which has large pinnæ closely crowded together on a short length of rachis (Plate, fig. 4) there is a double reinforcement of the adaxial strand below each pinna. Reinforcement of the adaxial strand may take place just after a pinna-trace has been nipped off, and again just before the next pinna-trace leaves the adaxial strand. Such a double reinforcement has been found only in this heavily-pinnate leaf.

The abaxial side of the leaf-trace makes its appearance in a relatively long leaf, becomes more prominent the longer the leaf in which it occurs, and is ultimately developed as a system of separate vascular strands. In leaf-traces with the abaxial system of strands, that system is commonly used to reinforce the adaxial strand before the pinna-traces depart from its margins. Where the pinnæ are large and closely set on the rachis, a double reinforcement of the adaxial strand from the abaxial system may occur.

In *P. decurrens* (text-fig. 1*f*) we have another use of the abaxial system in connection with the formation of the pinna-traces. Here the marginally-derived strand moving from the leaf-trace into a pinna is joined by another or by other two which come from the abaxial series of strands. The abaxial system is in this species employed directly to give vascular tissue to the pinnæ; in the other species of *Polypodium* it is employed to reinforce the strand which supplies the pinnæ with a vascular system and thus indirectly contributes to the supply of the pinnæ. In *P. decurrens* the abaxial ends of the adaxial strand are also affected during the process of departure of the pinna-trace. These ends give off small strands which unite with the strands linking the adaxial strand to the abaxial curve series (*cf.* text-fig. 1*f*). Each of these fused strands then gives off its outward tip to the pinna, this tip fusing with a small strand, derived from the corner strand of the abaxial curve series, to form the abaxial system of the pinna-trace.

It is worth noting here—the full discussion of the process will be found below—that the abaxial system of the leaf-trace is used directly to supply the pinna in this species only among the ten Brazilian species examined, and that in this species the individual pinnæ are larger than in any of the others.

Species of Polypodium from the Andes of Colombia.

The general conclusions which have been drawn from the Brazilian species regarding the relation between the length of a leaf and the size of its pinnæ on the one hand, and the degree of development of the abaxial portion of the leaf-trace on the other, find an interesting confirmation in the account recently published by Borkowski ('14) of the anatomy of some Ferns from the Colombian Andes. The leaf-trace of *P. crassifolium*, Linn. (*loc. cit.*, Taf. 1, fig. 14) shows the greatest development of the abaxial series of strands among the four species of *Polypodium* of which the leaf-traces are figured. And it has the longest leaf of all and the largest pinnæ. The leaf of *P. angustifolium*, Sw., is shorter and has smaller pinnæ; the abaxial development of its leaf-trace (*ibid.*, fig. 12) is less. *P. Mayoris*, Rosenstock, has as long a leaf as *P. angustifolium*, but it has small pinnæ. In the leaf-trace (*ibid.*, fig. 9) there is a prominent abaxial tongue. *P. murorum*, Hk., with the shortest leaf of the four, has little or no abaxial development of xylem in the leaf-trace (*ibid.*, fig. 10), though the rather broad pinnæ are probably the cause of the greater adaxial development than that in the leaf-trace of *P. Mayoris*.

The greater amount of xylem present in the petioles of *P. crassifolium*, *P. angustifolium*, and *P. murorum*, compared with that in *P. Mayoris*, is apparently related to the habitats of the Fern. The first three are xerophytes, growing on high, sunny, dry places (*loc. cit.*, p. 14); *P. Mayoris* is a mesophyte. Thus both in relation to habitat and to the size of the leaf these Colombian Ferns show close structural parallels to the series of Brazilian Ferns described above.

THE LEAF-TRACE OF POLYPODIUM VULGARE, Linn.

A more limited field than that afforded by the South American Polypodiums, but one which provides ample scope for testing the accuracy of the conclusions already stated, is given by *P. vulgare*, Linn. Plants of this species were collected in various situations and at different altitudes in several parts of Scotland. Some of these plants had leaves only two inches long; in others the leaves were as long as eighteen inches. Some leaves were leathery, others much less so. Plants were collected from wall-tops, rocks, hedge-rows, stream-sides, tree-trunks, the depths of woods, the open hillside, the sea-coast. The types of leaf-trace found in these plants are diagrammatically represented in text-fig. 2. In short leaves the tracheide-group forms a narrow plate stretching from one side of the petiole to the other (text-fig. 2*a*); in longer leaves it becomes an isosceles triangle (in section) with the apex on the abaxial side of the petiole (text-fig. 2*b*); the triangular outline appears also in some of the longest leaves (text-fig. 2*d*, *f*). But in some others two separate strands low down in the petiole unite below the first pinnæ to make an inverted V (text-fig. 2*c*); or two groups remain separate from each other until far up the rachis—one a large wide plate towards the adaxial side, the other a small round group towards the abaxial face (text-fig. 2*e*). In passing from the shortest leaves to the longest, through a series of intermediate forms, there is a gradual appearance of an abaxially-directed tongue in the leaf-trace (*cf.* text-fig. 2*b*, *d*, *f*). Such a tongue we have already seen becoming more prominent the longer the leaf, and finally being replaced by a system of separate strands along the abaxial curve of the petiole, in the species of *Polypodium* from Brazil and Colombia. Within the narrow limits of one species of *Polypodium*—a species very variable, however, in its habitats—there is the same variation in the form of the leaf-

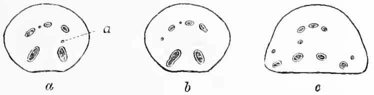
TEXT-FIG. 2.

trace as there is in different species of the same genus. Throughout the genus there is a strict adherence to one method of nipping off the pinna-trace; there is a gradual rise and development of an abaxial system in the leaf-trace as one passes from shorter to longer types of leaf; the abaxial system is as a rule used indirectly in the supply of the pinna vascular system, being employed to reinforce the strands from which the pinna-trace is nipped off; in leaves with very large pinnæ the pinna-trace is itself provided with an abaxial system derived directly from the abaxial system of the leaf-trace.

We must now see how far the canons thus established for the genus *Polypodium* are applicable to other genera of Ferns. Leaves of some species of other genera were collected in Brazil in the localities which supplied the ten species of *Polypodium* described.

The Leaf-Traces and Pinna-Traces of Aspidium martinicense, Spr. and A. trifoliatum (L.) Sw.

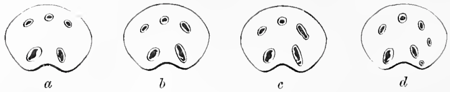
In *Aspidium martinicense*, Spr. and *A. trifoliatum* (L.) Sw., large-leaved Ferns found in the rain-forest on the Serra da Carioca, near Rio de Janeiro, the leaf-trace is composed of two adaxial and three or four abaxial strands (text-fig. 3*a*, *c*). The adaxial strands are unhooked. The pinna-trace comes partly from the margin of the adaxial strand (text-fig. 3*b*) and partly from the strand of the abaxial series nearest to the pinna to be supplied. The portion of the pinna-trace from the abaxial system is nipped off first (text-fig. 3*b*), and moves towards the adaxial corner of the petiole, where it is joined by the strand derived from the margin of the adaxial strand (text-fig. 3*c*). (Occasionally the abaxially-derived strand may join the adaxial strand on its abaxial face in a common endodermis.) Then it moves out into the base of the pinna, and is followed by the margin of the adaxial strand. The latter commonly divides into two strands, making with the abaxially-derived strand a three-stranded pinna-trace. The double derivation is evident even in the supply to the terminal pinnæ. The small strand *a* of text-fig. 3*a* is derived from the abaxial end of the adaxial strand. After the pinna-trace goes off (text-fig. 3*c*), or sometimes even while the pinna-trace is being separated from the parent strands (text-fig. 3*a*, *b*), it moves from the adaxial strand towards the corner strand of the abaxial curve and fuses with it. Such a reinforcement, however, is not always found in the two species. It is most pronounced in the petiole of the longest and most heavily-pinnate specimen of *A. martinicense*; only traces of it appear in the leaves of *A. trifoliatum*; it is absent in the shorter leaves of *A. martinicense*, which have pinnæ rather smaller than those of the long leaves.



Text-fig. 3.

THE LEAF-TRACE AND PINNA-TRACE OF LEPTOCHILUS GUIANENSIS (Aublet) C. Chr.

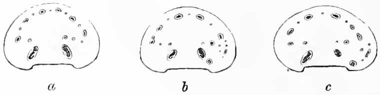
Another Fern of the rain-forest on the Serra da Carioca to show the combination-type of pinna-trace is *Leptochilus guianensis* (Aublet) C. Chr. This is a climbing Fern, with a long and wiry stem and rather short, simply pinnate leaves of the Stenochlæna type. The leaf-trace consists of five strands (text-fig. 4*a*)—two on the adaxial, three on the abaxial side of the petiole. The adaxial strands are, in the lower portion of the petiole, unhooked. But near the insertion of the first pinnæ their edges loosen out and become hooked (text-fig. 4*b*, *d*). Then the hook separates off, leaving one tracheide behind, close to the inner face of the parent strand, with which it presently coalesces. Meanwhile the abaxial strand nearest to the pinna to be supplied has extended its margin towards the pinna. There is no development of a hook on this strand; its margin is simply nipped off (text-fig. 4*c*) and moves out to the pinna with the arc derived from the adaxial strand (text-fig. 4*d*).



TEXT-FIG. 4.

THE LEAF-TRACE AND PINNA-TRACE OF POLYSTICHUM ADIANTIFORME (Forst.) J. Sm.

Polystichum adiantiforme (Forst.) J. Sm. is common on the loose sand of the *Ipomæa biloba* zone on the restingas and on the tops of the cliffs which intervene between the restingas. It has a leaf about a foot long with a firm petiole and repeatedly-divided leathery pinnæ. The leaf-trace is represented in text-fig. 5. There are two prominent hooked strands on the adaxial side of the petiole and a varying number of small strands on the abaxial curve. Below the first pinna one of the hooked adaxial strands extends its back towards the pinna, while it stretches out its abaxial end as a tongue towards the abaxial curve series (text-fig. 5*a*). At the same time the corner strands of the abaxial curve series also move out towards the pinna, dividing and fusing repeatedly among themselves as they do so (text-fig. 5*b*, *c*). The tongue stretched abaxially from the adaxial strand is nipped off as a small strand which sometimes takes its place with those which reform the abaxial curve. The pinna-trace is thus composed partly of the back of the hook of an adaxial strand, partly of strands derived from the series on the abaxial curve of the leaf-trace. The process of supplying the pinna-traces to the subsequent pinnæ is

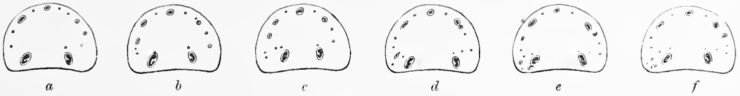


TEXT-FIG. 5.

similar to this, but the abaxial curve gradually dwindles and ultimately disappears in supplying the reinforcement to the second last pinna. The terminal pinna is supplied partly from the back of the hook of the adaxial strand, and partly from the abaxial tongue of this strand. The two portions move out independently of each other; that coming from the hook soon divides into two strands by simple antero-posterior fission; the other remains undivided, and the pinna-trace moves into the pinna as three strands. The process of supplying the pinnæ is very similar from one pinna to another along the length of the rachis; but the last pinna has its abaxial strand derived from the adaxial strand of the rachis, while the earlier pinnæ derive their abaxial curves from the abaxial curve of the leaf-trace. The pinna-trace of every pinna, however, resembles those of all the others in this respect, that its adaxial strands, derived extramarginally from adaxial leaf-trace strands, are *reinforced* by an abaxial system variously derived from the leaf-trace.

THE LEAF-TRACE AND PINNA-TRACE OF DRYOPTERIS GRANDIS (Pr.) C. Chr.

Dryopteris grandis (Pr.) C. Chr. grows in the rain-forest on the Serra da Carioca. Its leaves are about eighteen inches long, with pinnatifid pinnæ. The process of pinna-supply is very similar to that in *Polystichum adiantiforme*. The adaxial strand and the corner strand of the abaxial curve series both contribute to the pinna-trace (text-fig. 6*b*, *c*, *d*, *e*). And from the abaxial end of the contributing adaxial strand there is nipped off a small strand, before the back of the hook is separated (text-fig. 6*b*). This strand may divide into two (text-fig. 6*c*). One of these usually unites, wholly or in part, with one of the strands of the group derived from the corner of the abaxial curve series (text-fig. 6*d*). The remaining strand or strands come into position between the adaxial corner of the abaxial curve series and the abaxial end of the adaxial strand (text-fig. 6*e*, *f*). Above the second last pinna the strand derived from the abaxial end of the adaxial strand fuses again with the adaxial strand, then separates again and passes out into the terminal pinna with a strand derived from the other extremity of the adaxial strand. Thus *D. grandis* corresponds closely with *Polystichum adiantiforme* with regard to the portions of the leaf-trace which branch to supply the pinna traces. The hooked back of the adaxial strand and the corner strand or strands of the abaxial curve series take part in the supply of the pinna. The abaxial tongue of the adaxial strand in *Polystichum adiantiforme* is used only to repair the abaxial curve series as the pinna-trace departs and to prepare for the nipping off of the next pinna-trace. In *D. grandis* this



TEXT-FIG. 6.

function is performed by part only of this abaxial tongue; the remainder of it goes directly to supply the pinna-trace. The supply for the last pinna originates in the same fashion in the two Ferns—both ends of the adaxial strand give a contribution to the pinna-trace.

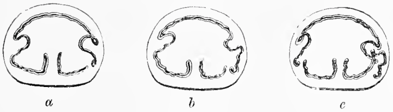
GENERAL DISCUSSION AND CONCLUSIONS.

The examination of the leaves of *Aspidium martinicense*, *A. trifoliatum*, *Polystichum adiantiforme*, and *Dryopteris grandis* has confirmed the opinion stated above (p. 9) as a result of the comparison of the leaf-traces of species of *Polypodium*, that the outline of the Fern leaf-trace is directly related to the length of the leaf, and that the type of pinna-trace is partly dependent on the size of the pinnæ. The only species of *Polypodium* of the series examined with a leaf comparable in length to those of the four species just named is *Polypodium decurrens*. The leaf-trace of *P. decurrens* has a strongly developed series of strands on the abaxial curve (text-fig. 1*f*), a feature which we have seen to be prominent in the leaves of the species of *Aspidium*, *Polystichum*, and *Dryopteris* (text-figs. 3, 5, and 6). Similarly, in *Polypodium decurrens* and in these four species the pinnæ are larger than in any of the other Ferns described. It is in these largely-pinnate forms that the abaxial curve of the leaf-trace is employed to supply a part of the pinna-trace, additional to that which comes from the adaxial strand.

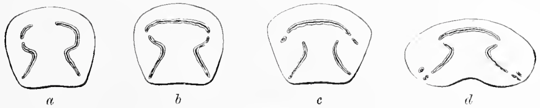
From these Ferns we may conclude that the abaxial portion of the Fern leaf-trace is directly related to the length of the leaf and becomes more prominent the longer the leaf. This is confirmed by the comparisons of the Fern leaf-traces figured by BORKOWSKI (above, p. 7) and of the leaf-traces of leaves of *Polypodium vulgare* grown under differing conditions (text-fig. 2).

That the abaxial curve of the leaf-trace may be used directly in the formation of the pinna-trace is shown by the largely-pinnate species *Aspidium martinicense*, *A. trifoliatum*, *Polystichum adiantiforme*, and *Dryopteris grandis*.

But we find the abaxial curve of the leaf-trace directly used in the pinna-supply in *Leptochilus guianensis* (text-fig. 4), which has relatively small pinnæ. Such a coincidence raises at once the idea that there may be in certain groups of Ferns an hereditary tendency to employ the abaxial portion of the leaf-trace in the formation of the pinna-trace. It has already been shown (DAVIE, '14, pp. 369–373) that while the extramarginal type of pinna-trace appears to occur regularly in Ferns with large leaves, it occurs also in small-leaved Ferns, *which are closely related to the large-leaved types* (*loc. cit.*, p. 354). Three species of *Leptochilus* have been examined. The leaf-trace of *Leptochilus guianensis* is described above (p. 10 and text-fig. 4); that of *L. cuspidatus* (Pr.) C. Chr. was described in a former paper (DAVIE, '14, p. 352 and text-fig. 2); that of *L. triscuspis* (Hk.) C. Chr. exhibits a simpler form than those of the other two species: it, like them, possesses the "combination-type" of pinna-trace, but the ends of the adaxial and abaxial strands only are nipped off to form this pinna-trace. The segments of the leaf are much larger in *L. cuspidatus* and *L. tricuspis* than in *L. guianensis*, but in *L. guianensis* the combination-type of pinna-trace is just as marked as in the other two. The resemblance of the method of pinna-supply in *L. cuspidatus* to that in most of the Cyatheaceæ has already been noted (Davie, '14, pp. 352, 353). In the Cyatheaceæ the pinna-trace comes partly "from the point where the adaxial arc or the xylem hook joins on to the abaxial curve," and partly "from the abaxial curve itself at the point where it is folded inwards" (Gwynne-Vaughan, '03, p. 724). This is exemplified by the pinna-trace of *Cibotium barometz* (L.) J. Sm. (text-fig. 7*a*, *b*, *c*). The adaxial portion of the leaf-trace in this Fern gives off its contribution to the pinna-trace in extramarginal fashion (text-fig. 7*a*), just as does the adaxial portion of the leaf-trace of *Leptochilus cuspidatus* (Davie, '14, text-fig. 2, p. 353), and, in much less marked degree, that of *L. guianensis* (above, p. 10, and text-fig. 4*c*). There is little doubt that in the Cyatheaceæ the long leaf and large pinnæ have involved the development of a leaf-trace of complex outline (see Tansley, '08, pp. 117, 126), and perhaps also the provision of the combination-type of pinna-trace. That the combination-type of pinna-trace does not invariably occur in the genera of the Cyatheaceæ is shown by the example of *Balantium culcita* (L'Hérit.) Klf. (Davie, '14, text-fig. 1, p. 351), in which a modification of the marginal type of pinna-trace is found. But in genera probably nearly related to some of the Cyatheaceæ, *e.g. Hypolepis tenuifolia* (Forst.) Bernh., the combination-type of pinna-trace appears (Davie, '14, p. 358). It occurs, too, in Ferns related to the Pterideæ, *e.g.* in *Histiopteris incisa* (Thbg.) J. Sm., and *Pteris* (*Litobrochia*) *macilenta*, A. Rich., though not in many species of *Pteris* itself (Davie, '14, p. 358). The leaf-trace of *Lonchitis pubescens*, Willd., a species apparently related to the Pterideæ and probably also to the Cyatheaceæ, is represented in text-fig. 8. There the pinna-trace is derived partly from the outwardly-turned margin of the antero-posterior flank of the leaf-trace, and partly from the margin of a strip which extends across the abaxial face of the petiole from side to side (text-fig. 8*c*, *d*). This recalls the processes found in *Hypolepis tenuifolia*, *Pteris macilenta*, *Histiopteris incisa*, and *Leptochilus tricuspis*. On grounds



Text-fig. 7.



Text-fig. 8.

unconnected with the anatomy of their leaves, the genera to which these species belong appear to be more or less related to one another and to the Cyatheaceæ on the one hand and the Pterideæ on the other (Bower, '08, pp. 615, 616). It is tempting to conclude that the appearance of the combination type of pinna-trace in these genera and in *Lonchitis* is dependent on a strongly-impressed hereditary tendency (probably originating in large-leaved forms of the Cyatheaceæ), and is not directly related to the size of the pinnæ in individual leaves. But this by no means invalidates the conclusions already reached regarding the factors which control the form of the Fern leaf-trace and the method of separation from it of the pinna-trace. The general principles seem clearly established from the examination of the members of the genus *Polypodium*, and from the comparison of the species of *Aspidium*, *Polystichum*, and *Dryopteris*. The leaf-traces and pinna-traces of *Balantium culcita* and *Leptochilus guianensis* are difficult to explain on these general principles. But that the two latter species (both of which have leaves relatively small in comparison with those of nearly related species) show modifications of the normal types of pinna-supply seems to suggest that their divergences may be explained from hereditary tendencies, acting in a circle of affinity where heredity has a powerful influence. That there has been, more than once in the course of evolution, a change from the extramarginal to the marginal type of pinna-trace is shown by a glance at the tabular scheme of the methods of pinna-supply among the Ferns (Davie, '14, p. 354). The change has occurred in the Cyatheaceæ, where we usually have the extramarginal type but find the marginal in *Balantium culcita*. It has occurred in the Davallieæ, where *Dennstædtia*, *Microlepia* (except *M. hirsuta*) and *Leptolepia* have the extramarginal type, and *Nephrolepis*, *Lindsaya*, and *Davallia* have the marginal type. It appears again in the Aspidieæ, *Dryopteris*, *Didymochlæna*, and *Polystichum* having extramarginal pinna-traces, while *Aspidium* has the marginal type. And in the genera mentioned above, related on the one hand to the Cyatheaceæ and their derivatives, and on the other to the Pterideæ, while the combination type of pinna-trace is prevalent, it is sometimes a combination of a "reinforcement" with an extramarginally-derived strand (*Cyathea*, *Alsophila*, etc.), sometimes of a "reinforcement" with a strand derived marginally (*Hypolepis*, *Histiopteris*, *Lonchitis*). Thus sometimes in a natural circle of affinity we find the extramarginal derivation retained and the "reinforcement" discarded (*e.g.* in the Cyatheaceæ, in the species of the genus *Cibotium*, and in *Dicksonia antarctica*, Lab.); sometimes the "reinforcement" is retained and the extramarginal derivation exchanged for the marginal (*e.g.* in *Hypolepis*—and its derivatives—in the circle of the Dennstædiinæ); sometimes both reinforcement and extramarginally derived strand are lost and a modified type of marginal pinna-trace replaces them (*e.g.* in *Balantium culcita* in the Cyatheaceæ). It is therefore evident that in drawing general conclusions regarding the types of pinna-trace among the Ferns, and in comparing the methods of branching found among their leaf-traces, we must not neglect the possible influences of heredity, though we have already seen that the main controlling factors are the length of the leaf and the size of the pinnæ.

In close dependence upon this qualifying generalisation there has been established a striking parallelism between the grouping of Ferns according to the types of pinna-trace found in them and that adopted by CHRISTENSEN in the *Index Filicum*.

A convincing example of this is connected with the genera *Aspidium* and *Polystichum*. These are generally admitted difficult of delimitation and definition. But such Ferns as *Nephrodium macrophyllum*, Baker (with marginal pinna-trace), on the one hand, and *Aspidium capense*, Willd. (extramarginal), and *Aspidium falcatum*, Sw. (extramarginal), on the other, differ altogether in the features of leaf-trace and pinna-trace from *Nephrodium Filix-mas*, Rich. (extramarginal), and *Aspidium polymorphum*, Wall. (marginal), yet fall at once into line with the other species of their genera when named, as CHRISTENSEN names them, *Aspidium martinicense*, Spr., *Polystichum adiantiforme* (Forst.) J. Sm., and *Polystichum falcatum* (L. fil.) Diels.

The case of *Microlepia hirsuta* (J. Sm.) Pr., referred to above, provides one of the few exceptions to the rule that the species of any genus of Ferns in the *Index Filicum* have all the same type of pinna-trace. And a note by Professor BOWER (GWYNNE-VAUGHAN, '03, p. 732) refers to the divergence of this plant from the type of *Microlepia*; it is one of the Mixtæ!

Thus it should be worth while for a systematist, when working with critical groups of Ferns, to pay some attention to the forms of leaf-trace and pinna-trace.

In the Ferns the portion of the pinna-trace derived from the adaxial part of the leaf-trace is always nipped off, for the basal and lower pinnæ, in the same way *within a genus*,* irrespective of the habitat of the Fern. The outline of the leaf-trace is constant within a species, though the degree of elaboration of the abaxial part of the leaf-trace is directly dependent on the length of the leaf and on the size and number of the pinnæ. The abaxial portion of the leaf-trace in "broken" leaf-traces is employed to reinforce the adaxial strands between the pinnæ, and, where the pinnæ are large, directly to give them a series of strands additional to that derived from the adaxial strand of the leaf-trace.

THE LEAF-TRACES AND PINNA-TRACES OF THE CYCADS.

The anatomy of the leaf in the Cycads has been the subject of numerous papers (VON MOHL, '32; METTENIUS, '61; KRAUS, '65; BERTRAND and RENAULT, '87; NESTLER, '95; CARANO, '03; MATTE, '03 and '04; WORSDELL, '06; SOUTH and COMPTON, '08; THIESSEN, '08; PAVOLINI, '09; COULTER and CHAMBERLAIN, '10; LE GOC, '14; and MARSH, '14). NESTLER, MATTE, and PAVOLINI give detailed accounts of the arrangements of the strands in the leaf-traces of many genera and species, and follow the courses of the strands throughout the leaves; but the majority

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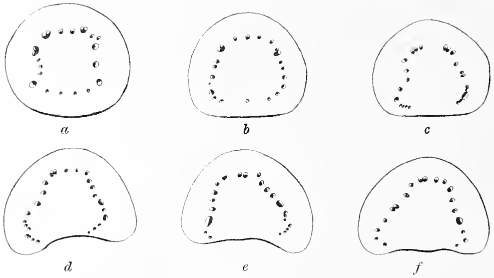
* Recognised as such by CHRISTENSEN in the *Index Filicum*.

of the recent papers deal mainly with the centripetal and centrifugal developments of the xylem in the individual strands. In many Cycads, as is well known, the outline of the leaf-trace is very elaborate. It has been found that in most of the genera the *pinna-traces* are simple and simply developed (*cf.* PRANTL, '89).

Stangeria paradoxa, T. Moore.

The genus with the simplest leaf is *Stangeria*. *Stangeria paradoxa*, T. Moore, has a rather short leaf bearing a few simple pinnæ at considerable distances from one another. At the base of the petiole the leaf-trace has the outline shown in text-fig. 9*a*. There the adaxial face of the petiole is lined by several small strands. As they pass up the petiole they move right and left and take up their positions on the adaxial corners of the antero-posterior flanks of the leaf-trace, sometimes fusing among themselves, sometimes with the strands at the corners of the petiolar system. A small strand remains for some time in the median position on the adaxial face of the petiole (text-fig. 9*b*). It comes from the series shown on the adaxial face in text-fig. 9*a*. The strands of this series, before moving to the margins of the antero-posterior flanks of the leaf-trace, link up together irregularly and separate again before leaving this odd strand in the middle of the adaxial face of the petiole. This median strand at first possesses both xylem and phloem. The xylem dies out first, as the strand, without moving to right or left, runs up the petiole; then the phloem also disappears into the ground tissue.

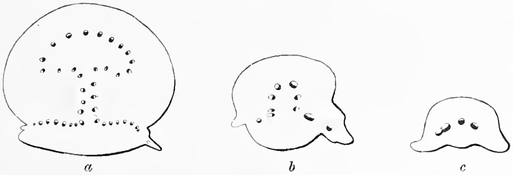


TEXT-FIG. 9.

Meanwhile, as the leaf-trace approaches the level of the first pinna, the strands on one margin of its antero-posterior flanks (consisting in part of half of the series of strands originally occupying the adaxial face of the petiole) divide off several small strands, of which four at the extreme tip move out towards the pinna (text-fig. 9*c*, *d*). Then from the opposite flank a similar group moves from the margin into the second pinna (text-fig. 9*d*, *e*). Above the lowest pinnæ the leaf-trace is widely open on the adaxial face and narrowed on the abaxial curve (text-fig. 9*f*), the succeeding pinnæ being supplied, like the earliest, from the adaxial margins of the series of leaf-trace strands.

Cycas revoluta, Thunb.

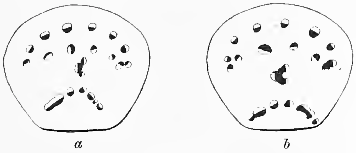
In the other genera of the Cycads the leaf-trace has a more complex form. The outline of that of *Cycas revoluta*, Thunb., is well known. In text-fig. 10*a* the leaf-trace below the first pinna is shown. The abaxial curve, which is prominent, is linked to the adaxial arcs by a double row of strands on the antero-posterior line. The abaxial curve runs up almost unchanged until near the tip of the rachis, though it shrinks gradually (text-fig. 10*b*), and is markedly reduced below the terminal pinnæ (text-fig. 10*c*). The strands of the abaxial curve fuse among themselves and with the strands connecting the curve with the adaxial arcs, while the adaxial arcs are reduced in size as they ascend the rachis. The pinna-traces are derived wholly from the outwardly-turned margins of the adaxial arcs, the marginal strands of which pass directly into the pinnæ. This is the process below the basal pinnæ, as well as below the terminal pair. As the marginal strands pass out into the pinnæ, neighbouring strands take their place, and the strands of the antero-posterior line and those of the abaxial curve are gradually moved towards the adaxial face of the petiole, to replace the departing strands of the adaxial arcs, until below the ultimate pinnæ the leaf-trace is reduced to three strands only (text-fig. 10*c*).



TEXT-FIG. 10.

Zamia Lindeni, Regel.

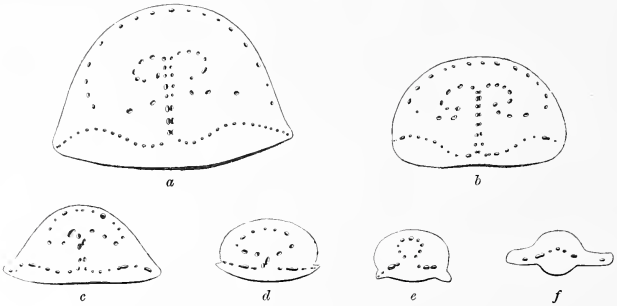
A similar process takes place in the leaf of *Zamia Lindeni*, Regel, the pinna-traces being given off from the margins of the adaxial portion of the leaf-trace (text-fig. 11*a*, *b*), while the abaxial curve is employed again to make good the drain on the adaxial strands. The leaf-traces of *Ceratozamia Kuesteriana*, Regel, and *Macrozamia Denisonii*, F. Muell., are similar in outline to that of *Zamia Lindeni*, and supply their pinnæ in the same fashion.



TEXT-FIG. 11.

Dioon spinulosum, Dyer.

In *Dioon spinulosum*, Dyer, the leaf-trace has an outline resembling that of *Cycas revoluta*, but the abaxial curve is folded inwards on itself as it joins the antero-posterior series of strands (text-fig. 12*a*). The pinna-traces are given off from the margins of the adaxial extensions of the leaf-trace (text-fig. 12*b*, *c*, *d*, *e*). As in *Cycas revoluta*, the abaxial curve alters and simplifies its shape as it passes up the rachis, and its strands are drawn in to replace those that pass out to the pinnæ. The outline of the leaf-trace below the ultimate pinna (text-fig. 12*f*) is less simple than that of *Cycas revoluta* at the same level (see text-fig. 10*c*), but the supply of the pinna in the two cases is provided on the same system. The leaf of *Dioon spinulosum* is longer than that of *Cycas revoluta*; its pinnæ are larger and more numerous. Both plants have leaves longer than those of *Stangeria paradoxa*, which also possesses a much smaller number of pinnæ. The pinna-traces are given off in exactly the same fashion in all three. The differences in the leaf-traces are in the abaxial curves and their elaborations. A comparison of text-figs. 9, 10, and 12, made in view of the different lengths of the leaves of the three genera, makes it difficult to resist the conclusion that the abaxial developments in the Cycad leaf-trace are related to the length of the leaf. In the Cycads, the longer the leaf the more elaborate is the system of vascular strands on the abaxial curve of the leaf-trace.

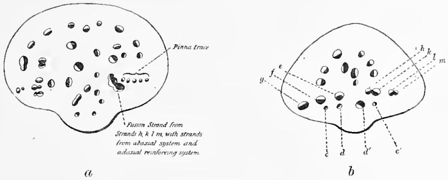


Text-fig. 12.

At this point in the consideration of the features of the leaf-trace and pinna-trace among the Cycads, we stand in the position corresponding to that which we reached in the discussion of the Fern leaf-trace at the close of the account of the genus *Polypodium*. From the information which we have obtained from the study of the genera described above, we may draw conclusions which are generally applicable to the leaf-traces of the Cycads as a whole, but which require to be supplemented in order that they may apply to two genera, of which we have not yet considered any examples. These genera are *Encephalartos* and *Bowenia*.

Encephalartos Altensteinii, Lehm.

Encephalartos Altensteinii, Lehm., which has a leaf of the same length as that of *Dioon spinulosum*, has fewer pinnæ (about half the number) than that species, but its pinnæ are twice as broad. The abaxial curve of the leaf-trace in *Encephalartos* (text-fig. 13) is more of the type of *Zamia* (text-fig. 11) than of that of *Cycas* or *Dioon*. On the adaxial face there is a system of additional strands (text-fig. 13*a*) forming a miniature replica-in-reverse of the normal Cycad system (*cf.* the leaf-trace shown in text-fig. 12*d*, *e*, with the adaxial portion in text-fig. 13*a*). Between this adaxial system and the abaxial curve there stretches a line of strands across the petiole from side to side (text-fig. 13*b*, strands *g*, *f*, *e*, *h*, *k*, *l*, *m*). It is from the tips of this line that the pinna-traces go off. The strands of this line are reinforced below the pinnæ from the strands on the antero-posterior line [*] (which are in close connection with the strands of the abaxial curve) and from the strands forming the adaxial system. The strands of the antero-posterior line give their reinforcement to strands *e* and *h* (text-fig. 13*b*), while those of the adaxial system join strands *f* and *k*. Then (to take the supply for one side only) the fusion strands at *h* and *k* fuse together, and strands *l* and *m* fuse with them. From this fusion strand several small strands are nipped off in quick succession and pass out together into the pinna (text-fig. 13*a*). The abaxial and adaxial reinforcing systems are gradually drawn in towards the pinna-supplying system as one ascends the rachis, until below the pair of pinnæ sixth from the tip of the leaf the leaf-trace has the outline shown in text-fig. 13*b*. Just above the point represented in text-fig. 13*b*, and just below the sixth last pair of pinnæ, strand *c* joins strand *f* and strand *c′* joins strand *k*. Strands *d* and *d′* then remain as the representatives of the adaxial system below the fifth last pair of pinnæ; strand *d* joins strand *e* and strand *d′* joins strand *h* prior to the formation of the pinna-traces for that pair of pinnæ. Above the fifth last pair of pinnæ, one strand, apparently derived from the strand *d′*, remains to reinforce the pinna-supplying system. Above the fourth last pair the adaxial system disappears, and to the last three pairs the pinna-traces go off simply from the outwardly-turned margins of the series of strands now nearest to the adaxial side of the rachis.



TEXT-FIG. 13.

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[*] And below some of the pinnæ (the pair twelfth from the tip of the leaf and other pairs below it) from the strands at the ends of the abaxial curve.

Bowenia spectabilis, Hook.

The leaf-trace of *Bowenia spectabilis*, Hook., has been the subject of a memoir by MATTE ('05), in which he compares the anatomy of the leaves of a young plant growing in the Botanic Garden at Caen. In this account he shows that the usually complex leaf-trace in *Bowenia* is an elaboration of a system with an abaxial curve of separate strands and a reinforcing strand on the adaxial face. In his specimens (*loc. cit.*, fig. 3) the reinforcing strand is composed of three portions, one going to each of the two large pinnæ and the third forward to the remaining part of the leaf. The appearance of a reinforcing system in this species, which has a bipinnate leaf, is a remarkable parallel to the occurrence of a similar system in *Encephalartos Altensteinii*,* with its long, wide pinnæ. There is thus little doubt that the Cycads employ the *adaxial* elaborations of the leaf-trace in relation to heavy pinnæ. MATTE calls attention to the appearance of this adaxial reinforcing system, and adds (*loc. cit.*, p. 415) that it develops in connection with an increasing area of lamina in the pinnules or in parts of them.

The Cycads thus resemble the members of the genus *Polypodium* among the Ferns in developing the abaxial curve of the leaf-trace in relation to the length of the leaf. They differ from them in using the adaxial side of the leaf-trace to develop a reinforcing system.

The reinforcing system in the Cycad leaf-trace is, as in the Fern leaf-trace, connected with the presence of large pinnæ in the leaf. A resemblance between the Cycads and the Ferns appears in the use, common in the Ferns but found only in *Encephalartos* among the Cycads, of the ends of the abaxial curve to form a part of the pinna-trace. This (see above, p. 19) occurs in the supply of certain of the pinnæ in *Encephalartos Altensteinii.* The amount of vascular tissue which passes from the edge of the abaxial curve strands into the pinna-trace is quite small in this species, and the method of employing the abaxial curve is confined to a few of the pinnæ. But the process is interesting, since it occurs in a leaf with large pinnæ and in a genus which has, as a whole, the largest, if not the longest, pinnæ among the Cycads. And it is in Fern plants with long leaves and large pinnæ that the abaxial curve of the leaf-trace is employed directly to provide a part of the pinna-trace. In general, then, the Cycads agree with the Ferns in developing in the leaf-trace an abaxial system to carry forward water for a long leaf. From this abaxial system the pinnæ are supplied indirectly, or (very occasionally in Cycads though frequently in Ferns) directly with some of their vascular strands.

The Cycads, in the genera *Encephalartos* and *Bowenia*, where the pinnæ are large, diverge from the great majority of the Ferns in supplying part of the pinna-trace from an accessory adaxial system.

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* MATTE ('03, '04) states that in *Encephalartos* (but in other species than *E. Altensteinii*) the adaxial reinforcing system is related *directly* to the pinna-traces in some leaves.

This method may be due simply to lack of space on the abaxial side of the leaf-trace, or, more probably, to the basipetal sequence of development in the pinnæ. Apparently a fair proportion of the Cycads (including species of *Encephalartos*) develop their pinnæ in basipetal succession (Bower, '84). Where the pinnæ which develop late are large it is quite likely that the vascular system which sufficed for those near the tip of the leaf may be unable to provide strands enough for them. For these pinnæ a new reinforcing system is required. Such a system could find room only on the adaxial face of the leaf-trace, since the abaxial side is quite fully occupied by the folds of the abaxial curve. It would seem as if in *Encephalartos Altensteinii* the abaxial curve is used directly to supply reinforcement for a few pinnæ well below the tip of the leaf while the new reinforcing system on the adaxial face is being elaborated to meet the needs of the larger pinnæ which occur successively lower on the rachis.

The adaxial reinforcing system does not appear in every Cycad leaf in which there is a basipetal sequence of pinnæ, but its appearance in the leaf of *Encephalartos Altensteinii* and in other species of the genus *Encephalartos*, where *large* pinnæ are found, certainly suggests a connection between the size and sequence of the pinnæ on the one hand and the construction of the leaf-trace on the other.

There is among the Ferns an interesting analogy to this in the Marattiaceæ. The leaf-traces of *Angiopteris*, *Marattia*, and *Archangiopteris* stand aloof from the type which prevails among the Filicales both in general construction and in the method of branching below the pinnæ (Gwynne-Vaughan, '05; Davie, '14), though they show some resemblance to those of some of the Ophioglossales. In the formation of the pinna-traces the strands at the corners of the leaf-trace nearest to the pinna are employed together with some of the strands situated directly on the adaxial side of the rachis. This is found, for example, in *Archangiopteris* (Gwynne-Vaughan, '05, p. 265). Both in this genus, however, and in *Angiopteris* the details connected with the formation and use of the adaxial reinforcing system differ entirely from those in *Encephalartos*.

But the suggestion of an analogy is strengthened when it is recalled that in *Angiopteris* the apical growth of the leaf is arrested at an early stage (Bower, '84, pp. 581, 605).

The aloofness of the type of leaf-trace in *Encephalartos* from that of the rest of the Cycads (except *Bowenia*, which no doubt owes its isolation to its practically unique form of leaf) is thus parallel to the aloofness of the Marattiaceæ from the rest of the Filicales.

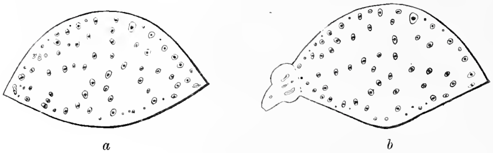
One can merely note the *analogy* between the Marattiaceæ and the Cycads in connection with some of the features of the leaf-trace; but from both we may conclude that there is some relation between the construction of the leaf-trace and the mode of growth of the leaf.

THE LEAF-TRACE IN THE MONOCOTYLEDONS.

Among the Monocotyledons the leaf-traces are composed of large numbers of vascular strands (*cf.* DRUDE, '89). In the smaller and shorter leaves the strands are less numerous than in the long leaves, especially if these have large pinnæ.

Cocos campestris, Mart.

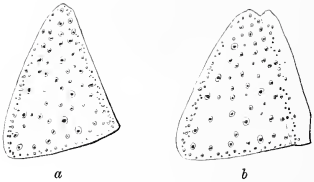
The leaf-trace of *Cocos campestris*, Mart., a short-leaved plant with small pinnæ, has a pair of wide curves, formed of larger strands, crossing from side to side, some scattered strands of the same type, and a large number of smaller strands round the periphery (text-fig. 14*a*). The rachis is roughly triangular in outline, and the pinnæ are inserted at the adaxial corners of the triangle. The pinna-trace is composed partly of some of the smaller strands of the peripheral series and partly of a few of the larger strands from the ends of the two prominent curves (text-fig. 14*b*).



TEXT-FIG. 14.

Phœnix dactylifera, Linn.

In *Phœnix dactylifera*, Linn., the petiole is larger and the pinnæ are longer than in the preceding example. The vascular strands are scattered irregularly in the rachis, the smallest being again close to the periphery, the larger ones in the centre (text-fig. 15*a*).



TEXT-FIG. 15.

The pinnæ are inserted along the whole width of the lateral faces of the rachis, and are supplied partly by the small peripheral strands along the faces and partly by larger strands derived from the larger series of the inner region (text-fig. 15*b*).

Caryota urens, Linn.

In *Caryota urens*, Linn., the pinnæ are pinnate and larger than in the two species described above. The leaf-trace is composed here also of larger and smaller strands, scattered respectively in the centre and round the periphery of the rachis. The pinnæ are inserted on cushions, to which the adjoining strands of the leaf-trace give off a line of large strands, preceded, accompanied, and followed by an indefinite number of the small peripheral strands, which pass out in no regular sequence but quite sporadically.

In these three examples from the Palms there is given off from the portion of the leaf-trace which is nearest to the pinnæ a series of larger and smaller strands, which are nipped off from the central and peripheral series respectively of the leaf-trace strands.

Philodendron Selloum, C. Koch.

In *Philodendron Selloum*, C. Koch, a large-leaved Aroid with two large basal pinnæ and an imperfectly-segmented laminar region beyond them, the strands of the leaf-trace are very numerous and are scattered at more or less equal distances from one another through the tissue of the petiole and rachis. The basal pinnæ are inserted at the same level, and are supplied from the peripheral, intermediate, and central regions of the rachis on the sides directed towards them. Many strands come from the periphery and from the intermediate region, and a few from the centre of the rachis.

Philodendron with its large pinnæ draws on a greater area of the leaf-trace than do the Palms, and the central strands of the leaf-trace, which in the Palms are unaffected by the departure of the lower pinnæ, are here employed in some degree in connection with the first pair of pinnæ.

These examples from the Monocotyledons show in the outlines of the leaf-trace and in the method of supplying the pinnæ from it no resemblance to the Ferns or the Cycads. The portion of the leaf-trace nearest to the pinnæ gives off the pinna-traces from its strands by simple fission; there is no allocation of supplying duties to one series, of reinforcing duties to another, such as we find so prominently among the higher Ferns and the Cycads.

The less rigid organisation of the leaf-trace and the less stereotyped method of forming the pinna-trace are probably related to the system of scattered vascular strands which is found in the Monocotyledons.

Before proceeding to consider the features of the leaf-trace in the Dicotyledons we may summarise the results of the examination of the leaf-traces of the groups already examined.

In the Ferns the outline of the leaf-trace is dependent partly on the length of the leaf, partly on the size and number of the pinnæ, and partly on the systematic position of the Fern. In a close circle of affinity the adaxial portion of the leaf-trace is unaltered, but the size of the leaf may affect the development of the abaxial curve.

The method of giving off the part of the pinna-trace which comes from the adaxial side of the leaf-trace is constant within a genus, but the reinforcement supplied from the abaxial curve varies in accordance with variations in individual leaves.

In the Cycads the general outline of the leaf-trace is constant within a genus. The degree of development of the abaxial curve depends upon the length of the leaf and the size of the pinnæ. The method of forming the pinna-trace is constant in all the genera examined except *Encephalartos* and *Bowenia*, where the size of the pinnæ causes the development of an adaxial reinforcing system. There is some likelihood that in some leaves the presence of the reinforcing system is related to a basipetal sequence in the development of the pinnæ.

In the Monocotyledons the form of the leaf-trace is directly connected with the scattered bundle system characteristic of the group, and is independent of the size of the leaf or of the order of development of its segments.

The factors, therefore, which control the form of the leaf-trace in the groups which have been examined are (*a*) systematic position, (*b*) the length of the leaf and the size of its appendages, (*c*) the order of development of the pinnæ, and (*d*) the type of vascular system found in the stem.

We may now proceed to discover which of these factors are operative among the Dicotyledons, in which the forms of leaf-trace are more varied than in any other group of plants.

The Leaf-Trace in the Dicotyledons.

The earliest comparative papers are by Frank ('64), de Lanessan ('74), and de Candolle ('79). In 1888 Lignier pointed out the relationship between the vascular system of the stem, the type of leaf-trace, and the arrangement of the leaves on the stem. The position of leaf-trace structure among the criteria of value in systematic analysis was discussed by Vesque in 1882. From that period forwards there is a continuous increase in the number of contributions to our knowledge of the leaf-trace in different families of Dicotyledons. These have been made by van Tieghem ('84 and '93)—to whose inspiration most of this work is due,—Dumont ('87), Petit ('87), Thouvenin ('90), Parmentier ('96 and '97), Perrot ('98), Decrock ('01), Gaucher ('02), Jodin ('03), Viguier ('06 and '09), Pellegrin ('08), Guillaumin ('09), and Le Renard ('13). General questions have been discussed by Bonnier ('00), who dealt with the relation of form to function in the leaf-trace and its branches; Bouygues ('02), who described the distribution of meristems in petioles, showing the type of leaf-trace with strands arranged in a circle to be an advance on the type open adaxially; Chauveaud ('11), who contrasted the evolution of the Fern leaf-trace with that of the Phanerogams; and Parmentier ('96) and Sarton ('05), who estimated the value of anatomy in the delimitation of critical forms. An admirable and richly illustrated general account of petiolar anatomy has been given by Col ('04), who referred the variations in complexity of Dicotyledonous leaf-traces to slow or rapid growth of the leaves.

Descriptions of the various types of leaf-trace in the Dicotyledons have been given by Frank and de Candolle. The former contrasts leaf-traces which are open on the adaxial face with those which are closed all round. He notes the presence of intracortical and intramedullary strands, but does not give such an exhaustive account of the distribution of these as does de Candolle. The two authors agree in regarding the leaf-trace open on the adaxial side as more primitive than the closed type, and those with intracortical or intramedullary strands as more advanced than those which do not possess them. De Candolle gives a very extensive list of genera and species from many different natural orders, and shows how constantly a natural order preserves one type of leaf-trace.

In comparing the leaf-trace of the Dicotyledons with those of other groups, one is most impressed with its plasticity in reference to the supply of the branches of the leaf.

Achillea Millefolium, Linn.

For example, in *Achillea Millefolium*, Linn., the leaf-trace is made up of a series of separate strands arranged along the abaxial side of the petiole and rachis. In the petiole and in the lower part of the rachis there are five large strands and some smaller ones. Between the pinnæ the smaller strands link up with the larger and afterwards separate again from them. At the point where a pinna-trace is given off there is no sign of the smaller strands, as there they coalesce with some of the larger ones. The pinna-traces come from the extended margins of the strands at the ends of the series forming the leaf-trace, and are simply nipped off from them.

Tripterodendron filicifolium, Radlk.

Another type of leaf-trace is found in *Tripterodendron filicifolium*, Radlk. The xylem forms a closed system, roughly triangular in outline in a cross-section. Below a pinna the corner of this triangle nearest to the pinna becomes drawn out, and the narrow "V" thus formed is nipped off as the pinna-trace. A gap is left for a short distance above the pinna-trace, but this is soon repaired by the tissue on either side and the triangular outline is resumed.

This form of pinna-supply recalls the extramarginal type of the Ferns, while the method in *Achillea Millefolium* resembles that in the marginal Fern type.

There is, however, another common type, which is found in leaf-traces with intramedullary strands.

Brownea coccinea, Jacq.

The leaf-trace of *Brownea coccinea*, Jacq., may be taken to represent this type. Here the leaf-trace forms a closed system, in which a small strand is enclosed. The main system is roughly parallel to the surface of the petiole or rachis, being flattened on the adaxial side and curved abaxially. The enclosed strand repeats on a smaller scale the outline of the main system. Below a pinna the portion of the main system nearest to the pinna is thrown into two longitudinal folds, the curved "backs" of which nip off, join together, and become the pinna-trace. Then the edge of the smaller enclosed strand nips off and passes to that part of the main system from which the pinna-trace has just been given off, thus assisting in the formation of the longitudinal folds destined to supply the pinna next above the one just supplied.

The intramedullary strand thus acts as a repairing and reinforcing system, which helps to make good the drain on the main system caused by the departure of the pinnæ.

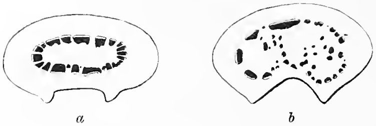
The three types of leaf-trace now described do not exhaust the types found among the Dicotyledons, but they are representative of the leaf-traces found in the great majority of Dicotyledons.

De Candolle (*loc. cit.*) has shown that the same type of leaf-trace does not invariably occur in all of the species of the same genus; the examples described above show that the complexity of outline of the leaf-trace is not directly related to the size or degree of division of the segments of the leaf, for the leaf of *Tripterodendron filicifolium* has compound pinnæ much larger than those of *Brownea coccinea*, which are simple in outline. The rules which we have found to apply to Fern leaf-traces are thus inapplicable to the leaf-traces of the Dicotyledons.

The leaf-traces of some species of the genus *Spiræa* throw an interesting light on the factors which control the form of the leaf-trace in the Dicotyledons.

Spiræa Aruncus, Linn.

The leaf-trace of *Spiræa Aruncus*, Linn., is composed of a large number of strands arranged in an ellipse (text-fig. 16*a*). Below the pinnæ the leaf-trace becomes extended laterally and from these extensions the pinna-traces are nipped off as replicas of the parent strand, which immediately resumes the elliptical form (text-fig. 16*b*).



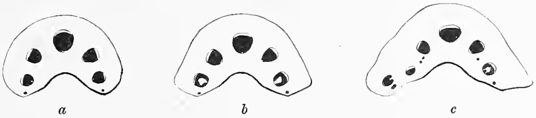
Text-fig. 16.

Spiræa sorbifolia, Linn., and *Spiræa Lindleyana*, Wall.

In *Spiræa sorbifolia*, Linn., and *S. Lindleyana*, Wall., the leaf-trace is more or less triangular in outline in cross-section. The pinna-traces leave the corners nearest to the pinnæ, while the leaf-trace quickly re-forms on their departure.

Spiræa lobata, Murray.

A different type of leaf-trace is found in *Spiræa lobata*, Murray, *S. Ulmaria*, Linn., *S. kamtschatica*, Matsum., and *Filipendula digitata* (W.) Freyn, var. *tomentosa* (Led.) Freyn. In *S. lobata*, Murray, the leaf-trace is composed of separate strands, usually of five large and a varying number of smaller strands, arranged along the abaxial side of the petiole and rachis (text-fig. 17*a*). Below a pinna the large strand nearest to the margin of the series becomes horse-shoe-shaped and gives off the "arch" of the horse-shoe to the pinna, leaving the tips to re-form the leaf-trace strand (text-fig. 17*b*, *c*). This process is repeated in *Spiræa Ulmaria* and *S. kamtschatica*. In *Filipendula digitata*, var. *tomentosa*, the "arching-up" of the horse-shoe is more pronounced than in the other species. The method of supplying the greater portion of the pinna-trace in these species is very like the extramarginal method in the Ferns, but here the small strand actually at the margin of the series forming the leaf-trace passes out with the larger strand as the pinna-trace (text-fig. 17*b*, *c*).



Text-fig. 17.

The species of *Spiræa* described above belong to three different sections of the genus (Wenzig, '88)—*Spiræa Aruncus* to the section *Aruncus*, Seringe; *S. sorbifolia* and *S. Lindleyana* to the section *Sorbaria*, Seringe; and *S. Ulmaria*, *S. kamtschatica*, and *S. lobata* to the section *Ulmaria*, Mönch. Focke ('94) raises these sections to generic rank, and separates *Aruncus* and *Sorbaria* somewhat widely from *Ulmaria*. But specific or even generic distinctions do not suffice to explain the differences in the leaf-traces described above. For in the genus *Astilbe* (which stands systematically further from *Spiræa* than do the genera *Aruncus* (Tourn.) Kostel and *Sorbaria* (Ser.) A. Br. from *Ulmaria* (Tourn.)) * the leaf-trace is exactly like that of *S. Aruncus*, and the pinna-traces are given off exactly as in that species and thus quite differently from the manner in *S. lobata*.

The Leaf-Trace of Astilbe.

In *Astilbe rivularis*, Ham., *A. rubra*, Hook. f. et Thoms., and in *A. Thunbergii*, Miq., the strands of the leaf-trace are rather less numerous than are those of *Spiræa Aruncus*, but they are arranged in precisely the same manner, though the distances between the adjacent strands are somewhat greater in *Astilbe* than in *Spiræa*. Text-fig. 16*b* represents exactly the method of formation of the pinna-traces in these species of *Astilbe*, the part of the ring of leaf-trace strands nearest to a pinna being extended towards the pinna and eventually nipped off as a pinna-trace.

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* Focke, *loc. cit.*, p. 12.

Within the genus *Spiræa* (in the wide sense employed above) there is a divergence in the method of development of the segments of the leaf. Acropetal development is the rule in *Spiræa sorbifolia* and *S. Lindleyana* (Trécul, '53, p. 251) and in *S. Aruncus* (Massart, '94, pl. ii. fig. 23); basipetal development occurs in *S. lobata* (Trécul, '53, p. 277). The order of development of the pinnæ has not been followed in every species of *Spiræa* described above, but the four just named give us representatives of the groups which are sharply contrasted in type of leaf-trace. One form of leaf-trace is found among the species whose leaves develop acropetally, another in those with basipetal development.

Professor Bower (*Phil. Trans.*, 1884, p. 607) has pointed out that "the arrest of the apical growth of the phyllopodium, and the tendency to develop the pinnæ in a basipetal succession, progress simultaneously" in Vascular Cryptogams and Gymnosperms, and adds: "It can hardly be doubted that the two phenomena are mutually connected." We have already seen in some of the Cycads that the tendency to develop the parts of the leaf in a basipetal succession has some effect on the structure of the leaf-trace. It is very probable that the differences in leaf-trace structure between the groups of species of *Spiræa* are to be related to the differences which we find to exist in the manner of development of their leaves.

But there is another factor which we must consider in dealing with leaf-trace differences among the Dicotyledons. The process of secondary thickening in the Dicotyledonous stem has no doubt an influence on the structure of the leaf-trace. And the degree to which secondary thickening is developed in the stem of any individual plant probably affects the outline of the leaf-trace. De Candolle ('79, p. 433) has shown how this appears in the leaves of a single plant, from the young to the adult state; he contrasts, too, the type of leaf-trace (the "closed" type) found in families with woody species with that (the "open" type) found in families with herbaceous species. Col ('04) has shown, however, that the "open" leaf-trace system does not always occur only in herbs; it appears, for example, in *Viburnum Opulus* (Col, *loc. cit.*, p. 132) and in *Pyrus Aucuparia* (de Candolle, '79, p. 429). From the list given by Eichler ('61) of plants whose leaves are developed in acropetal or in basipetal fashion, examples have been chosen* of herbaceous and woody plants.

In *Staphylea pinnata*, Linn., the leaf is developed acropetally (Eichler, '61, p. 18); the leaf-trace is of the "closed" type of *Spiræa Lindleyana*; the pinna-traces go off from the corners of the leaf-trace nearest to the pinnæ, on the adaxial side.

Basipetally-developed leaves are found in *Rosa arvensis*, Huds. (Trécul, '53, pp. 275, 276), *R. canina*, Linn., and *R. tomentosa*, Sm. (Eichler, '61, p. 18). The leaf-traces of all three are alike, open on the adaxial face; the pinna-traces are formed from the margins of the leaf-trace.

An exactly similar process appears in *Potentilla Anserina*, Linn., a herbaceous

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* Chiefly on account of their accessibility.

species with a basipetally-developed leaf (EICHLER, '61, p. 19), and in *Sambucus nigra*, Linn., the leaf of which is also developed basipetally (MASSART, '94, pl. iii, fig. 49). In *Heracleum Sphondylium*, Linn., and *Daucus Carota*, Linn., the leaves are developed in acropetal fashion (EICHLER, '61, p. 18); the leaf-trace has some nine separate strands forming a curve on the abaxial side and stretching towards the adaxial corners; two strands are present in the pith, on the antero-posterior line across the petiole. The intramedullary strands link up with all but the median abaxial strand when the pinna-traces are to be given off and assist the strands of the adaxial margins of the leaf-trace in giving the supply to the pinnæ.

Examples have now been described from woody and herbaceous plants with acropetally- and basipetally-developed leaves. In the woody plants with acropetally-developed leaves the leaf-trace is of the closed type; the pinna-traces come from its corners nearest to the pinnæ. In the woody plants with basipetally-developed leaves the leaf-trace is open on the adaxial side and the pinna-traces come from its adaxial margins.

Both types of leaf-trace are found among woody plants; the open type prevails among herbaceous plants.

In herbaceous plants with basipetally-developed leaves the leaf-trace is of the type found in woody plants with basipetally-developed leaves, and the pinna-traces arise just as in these plants. But in the two examples of herbaceous plants with acropetally-developed leaves there appear between the adaxially-directed arms of the leaf-trace curve additional strands which assist in the formation of the pinna-traces. We have thus:

Woody plants.	Herbaceous plants.
Rosa arvensis, Huds. ,, *canina*, Linn. ,, *tomentosa*, Sm. *Sambucus nigra*, Linn. *Spiræa Aruncus*, Linn. ,, *Lindleyana*, Wall. ,, *sorbifolia*, Linn. *Staphylea pinnata*, Linn.	*Daucus Carota*, Linn. *Heracleum Sphondylium*, Linn. *Potentilla Anserina*, Linn. *Spiræa lobata*, Murr.

Leaves acropetally-developed.	Leaves basipetally-developed.
Daucus Carota, Linn. *Heracleum Sphondylium*, Linn. *Spiræa Aruncus*, Linn. ,, *Lindleyana*, Wall. ,, *sorbifolia*, Linn. *Staphylea pinnata*, Linn.	*Potentilla Anserina*, Linn. *Rosa arvensis*, Huds. ,, *canina*, Linn. ,, *tomentosa*, Sm. *Sambucus nigra*, Linn. *Spiræa lobata*, Murr.

Closed leaf-traces.	Open leaf-traces with intramedullary strands.	Open leaf-traces.
Spiræa Aruncus, Linn. ,, *Lindleyana*, Wall. ,, *sorbifolia*, Linn. *Staphylea pinnata*, Linn.	*Daucus Carota*, Linn. *Heracleum Sphondylium*, Linn.	*Potentilla Anserina*, Linn. *Rosa arvensis*, Huds. ,, *canina*, Linn. ,, *tomentosa*, Sm. *Sambucus nigra*, Linn. *Spiræa lobata*, Murr.

We may therefore conclude that in the formation of the Dicotyledonous leaf-trace two factors are operative: (*a*) the degree of development of secondary thickening in the stem; (*b*) the mode of development of the leaf (whether acropetal or basipetal)—*cf.* Col, '04, pp. 264, 265.

The closed type of leaf-trace appears only in woody plants, and in them only if the leaf is developed in acropetal fashion; the open type of leaf-trace occurs especially in herbaceous plants, but also in woody plants whose leaves develop basipetally. A modified form of open leaf-trace is found in herbaceous plants with acropetally-developed leaves.

Factors which have been found to exercise an influence on the formation of the leaf-trace in Ferns and Cycads, *e.g.* systematic position and length of leaf and size of pinnæ, are apparently not operative among the Dicotyledons.

De Candolle's tabular summary (*loc. cit.*, pp. 455–478) shows that within a family, or even within a genus, intracortical or intramedullary strands may or may not appear in the leaf-trace. The examples described above from the genus *Spiræa* show an analogous variability, though it must be noticed that the types of leaf-trace are constant within the genera into which the most recent workers have divided the erstwhile genus *Spiræa*.

Similarly we have seen that an elaborate type of leaf-trace may appear in a relatively small and simple leaf, while a simpler type is present in a large and much-divided leaf. We may therefore set aside for Dicotyledons the first two of the four factors named* as those which operate in Ferns, Cycads, and Monocotyledons. In the Dicotyledons it is the second pair of factors which have been found to influence the form of the leaf-trace.

If we take the four factors—(*a*) systematic position, (*b*) the length of the leaf and the size of its appendages, (*c*) the order of development of the pinnæ, and (*d*) the type of vascular system found in the stem—we find that the first two operate, sometimes jointly, sometimes independently, on the Fern leaf-trace; the first three among the Cycads, (*a*) and (*b*) jointly in the majority of the genera, and (*a*), (*b*), (*c*) jointly in a few cases. The fourth factor apparently alone has an influence on the leaf-trace in the Monocotyledons; and the third and fourth apparently act jointly among the Dicotyledons.

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* On p. 24.

In the Ferns the lack of elasticity in the vascular system and the impossibility in most species of expanding vascular strands once formed, have involved a strict economy in the distribution of the vascular tissue in the leaf and its branches. Every strand appears, so to speak, to be ticketed and numbered; the supply given to any pinna is carefully measured in relation to the requirements of the pinna and in relation to the further development of the leaf as a whole. There never appears to be any vascular tissue to waste, but there rarely seems to be much to spare even for the needs of particular branches.

The Cycad leaf-trace is, on the whole, built on the same principles as that of the Ferns; it is just as provincially economical. In two genera a new method is adopted to meet a problem of size which is, in part at least, due to a departure from the method of development of the pinnæ which prevails in Vascular Cryptogams and in some Cycads.

The leaf-trace of the Monocotyledons is directly related to the form of vascular system found in the stem; it appears to be capable of indefinite expansion and elaboration; systematic position, size of leaf, sequence of appearance of pinnæ alike are without influence upon its form.

In Dicotyledons the vascular system of the stem seems greatly to influence the form of the leaf-trace, the outline of which is dictated in some measure by the degree to which secondary thickening is developed in the stem. But the manner of development of the leaf also has apparently an influence on the form of the leaf-trace, so that the type of leaf-trace found in any Dicotyledonous plant must be referred to the joint action of the two factors. The types of leaf-trace found in Dicotyledons are readily and easily adaptable to alterations in the size or shape of the leaf, and are capable of much expansion and elaboration.

The contrast between the types of leaf-trace found on the one hand in Ferns and Cycads, and on the other in Angiosperms, and especially in Dicotyledons, is very much one of slow and rapid growth; it may be partly due to the size of the leaf in relation to the size of the whole plant. Certainly, the much greater adaptability of the Angiospermic vascular systems must have been no small factor in the rapid spread of Angiosperms over the earth.

SUMMARY.

Plants of the genus *Polypodium* were collected in Brazil and Scotland in different situations; representatives of the same species of *Polypodium* were found growing under different conditions; the leaf-traces and pinna-traces of these species and of species of *Aspidium*, *Polystichum*, *Dryopteris*, *Leptochilus*, and other genera were examined and compared.

The habitat of the Fern was not found in any case to influence the type of leaf-trace or pinna-trace. In a few species of *Polypodium* the habitat was found to have an effect on the number of tracheides in the leaf-trace.

The type of pinna-trace is constant within a genus, recognised as such in Christensen's *Index Filicum*; the form of the leaf-trace is dependent on the length of the leaf and the size of the pinnæ.

The form of the adaxial portion of the leaf-trace is constant throughout a genus; the degree of development of the abaxial curve depends on the length of the leaf and the size of the pinnæ.

The leaf-traces of species of *Stangeria*, *Cycas*, *Zamia*, *Ceratozamia*, *Macrozamia*, *Dioon*, *Encephalartos*, and *Bowenia* have been compared with those of the Ferns. In the Cycads the abaxial portion of the leaf-trace is directly connected with the length of the leaf; the pinna-trace is, except in *Encephalartos* and *Bowenia*, supplied from the adaxial margin of the leaf-trace nearest to the pinna; in *Encephalartos* and *Bowenia* a reinforcing system is developed on the adaxial face of the leaf-trace. The adaxial reinforcing system is related partly to the size of the pinnæ and partly, in *Encephalartos*, to the mode of development of the leaf.

Species of *Cocos*, *Phœnix*, *Caryota*, and *Philodendron* have been examined; in them the forms of leaf-trace and pinna-trace are directly related to the type of vascular system found in the stem, and appear to be independent of the size of leaf and the manner of its development.

Two distinct types of leaf-trace, with their varieties, have been found in Dicotyledons, and have been studied especially in species of the genera *Achillea*, *Tripterodendron*, *Brownea*, *Spiræa*, *Astilbe*, *Rosa*, *Daucus*, and *Heracleum*.

The type of leaf-trace with strands forming a ring is found in woody plants, excepting those with basipetally-developed leaves; the type open on the adaxial face is found in herbaceous and woody plants with basipetally-developed leaves; in herbaceous plants with acropetally-developed leaves the "open" type of leaf-trace is provided with an intramedullary reinforcing system.

The factors which control the form of leaf-trace and its system of branching are:—

(*a*) Systematic position.
(*b*) The length of the leaf and the size of its appendages.
(*c*) The order of development of the pinnæ.
(*d*) The type of vascular system found in the stem.

(*a*) and (*b*) are operative among Ferns; (*a*), (*b*), and (*c*) among Cycads; (*d*) among Monocotyledons; and (*c*) and (*d*) among Dicotyledons.

LITERATURE CITED.

BERTRAND, C. EG., and RENAULT, B. ('87), "Remarques sur les faisceaux foliaires des Cycadées actuelles," *Archives Bot. du Nord de la France*, 1886–1887, p. 237.

BONNIER, G. ('00), "Sur la différenciation des tissus vasculaires de la feuille et de la tige," *Comptes rend. de l'Acad. des Sc.*, cxxxi, p. 1276.

BORKOWSKI, R. ('14), "Anatomisch-biologische Untersuchungen über einigen Pteridophyten der Kolumbischen Andenflora," *Bull. de la Soc. Neuchat. des Sc. Nat.*, Tome xl, pp. 1–73.

BOUYGUES, M. ('02), "Sur l'origine et la différenciation des méristèmes vasculaires du pétiole," *Comptes rend. de l'Acad. des Sc.*, cxxxiv, p. 438.

BOWER, F. O. ('84), "On the Comparative Morphology of the Leaf in the Vascular Cryptogams and Gymnosperms," *Phil. Trans. Roy. Soc.*, ii, pp. 565–615.

BOWER, F. O. ('08), *The Origin of a Land Flora.*

DE CANDOLLE, C. ('79), "Anatomie comparée des feuilles chez quelques familles de Dicotylédones," *Mém. de la Soc. de phys. et d'hist. nat. de Genève*, xxvi.

CANNON, W. A. ('05), "On the Water-conducting Systems of some Desert Plants," *Bot. Gaz.*, xxxix, pp. 397–408.

CARANO, E. ('03), "Contribuzione alla conoscenza della morfologia e dello sviluppo del fascio vascolare delle foglie delle 'Cicadacee,'" *Annali di Botanica*, i, fasc. 3, pp. 109–121.

CHAUVEAUD, G. ('11), "L'appareil conducteur des plantes vasculaires et les phases principales de son évolution," *Ann. des Sc. Nat., Bot.*, sér. 9, t. xiii, pp. 113–436.

CHRISTENSEN, C. ('06), *Index Filicum.*

COL, A. ('04), "Recherches sur la disposition des faisceaux dans la tige et les feuilles de quelques Dicotylédones," *Ann. des Sc. Nat., Bot.*, sér. 8, t. xx, pp. 1–288.

COPELAND, E. B. ('07), "The Comparative Ecology of San Ramon Polypodiaceæ," *Philippine Journal of Science*, ii, pp. 1–76.

COULTER, J. M., and CHAMBERLAIN, C. J. ('10), *Morphology of Gymnosperms.*

DAVIE, R. C. ('14), "The Pinna-Trace in the Ferns," *Trans. Roy. Soc. Edin.*, l, pp. 349–378.

DECROCK, E. ('01), "Anatomie des Primulacées," *Ann. des Sc. Nat., Bot.*, sér. 8, t. xiii, pp. 1–199.

DRUDE, O. ('89), "Palmæ": Anat. Verhalt. d. Blätter in ENGLER and PRANTL, *Natür. Pflanzenfam.*, ii, 3, p. 13.

DUMONT, A. ('87), "Recherches sur l'anatomie comparée des Malvacées, Bombacées, Tiliacées, Sterculiacées," *Ann. des Sc. Nat., Bot.*, sér. 7, t. vi, pp. 129–246.

EBERHARDT, PH. ('03), "Influence de l'air sec et de l'air humide sur la forme et sur la structure des végétaux," *Ann. des Sc. Nat., Bot.*, sér. 8, t. xviii, pp. 61–153.

EICHLER, A. W. ('61), *Zur Entwickelungsgeschichte des Blattes mit besonderer Berücksichtigung der Nebenblatt-Bildungen*, Marburg, 1861.

FOCKE, W. O. ('94), "Rosaceæ" in ENGLER and PRANTL, *Die natürlichen Pflanzenfamilien*, iii, 3, pp. 16, 40, 41.

FRANK, A. B. ('64), "Ein Beitrag zur Kenntniss der Gefässbündel," *Bot. Zeit.*, xxii, pp. 377–382, 411, and Taf. xiv.

GAIN, E. ('95), "Action de l'eau du sol sur la végétation," *Rev. gén. d. Bot.*, vii, pp. 15–26, 71–84, 123–138.

GAUCHER, L. ('02), "Recherches anatomiques sur les Euphorbiacées," *Ann. des Sc. Nat., Bot.*, sér. 8, t. xv, pp. 161–309.

GILG, E. ('91), "Beiträge zur vergleichenden Anatomie der xerophilen Familie der Restiaceæ," *Bot. Jahrb.*, xiii, pp. 541–606.

LE GOC, M. J. ('14), "Observations on the Centripetal and Centrifugal Xylems in the Petioles of Cycads," *Ann. of Bot.*, xxviii, pp. 183–193.

GROOM, P. ('10), "Remarks on the Œcology of Coniferæ," *Ann. of Bot.*, xxiv, pp. 241–269.

GUILLAUMIN, A. ('09), "Recherches sur la structure et le développement des Burséracées," *Ann. des Sc. Nat., Bot.*, sér. 9, t. x, pp. 201–301.

GWYNNE-VAUGHAN, D. T. ('03), "Observations on the Anatomy of Solenostelic Ferns," part ii, *Ann. of Bot.*, xvii, pp. 689-742.

Gwynne-Vaughan, D. T. ('05), "On the Anatomy of *Archangiopteris Henryi* and other Marattiaceæ," *Ann. of Bot.*, xix, pp. 259–271.

Hemmendorf, E. ('12), "Bilder aus der Restinga-Vegetation bei Rio de Janeiro," *Svensk. Bot. Tidskr.*, vi, pp. 889–902.

Jodin, H. ('03), "Recherches anatomiques sur les Borraginées," *Ann. des Sc. Nat., Bot.*, sér. 8, t. xvii, pp. 263–346.

Karsten, G., and Schenck, H. ('03), *Vegetationsbilder*, Heft 7, Tafn. 37–42.

Kny, L., and Zimmermann, A. ('85), "Die Bedeutung der Spiralzellen von Nepenthes," *Ber. deut. Bot. Gesell.*, iii, pp. 123–128.

Kohl, F. G. ('86), *Die Transpiration der Pflanzen und ihre Einwirkung auf die Ausbildung pflanzlicher Gewebe*, Braunschweig, 1886.

Kraus, G. ('65), "Ueber den Bau der Cycadeenfiedern," *Jahrb. f. wiss. Bot.*, Bd. iv, pp. 305–348.

Krüger, P. ('83), "Die oberirdischen Vegetationsorgane der Orchideen in ihren Beziehungen zu Clima und Standort," *Flora*, n.r., xli, pp. 435–443, 451–459, 467–477, 499–510, 515–524.

De Lanessan, J.-L. ('74), "Observations sur la disposition des faisceaux fibro-vasculaires dans les feuilles," *Comptes rend. de l'Acad. des Sc.*, lxxviii, p. 891.

Lignier, O. ('88), "De l'importance du système libéro-ligneux foliaire en anatomie végétale," *Comptes rend. de l'Acad. des Sc.*, cvii, p. 402.

Loefgren, A. ('14), "Ensaio para uma introducção da Ecologia Botanica," *Rev. d. Centro d. Sc. Let. e Art. S. Paulo*, xiii, pp. 1–22.

Marsh, A. S. ('14), "Notes on the Anatomy of *Stangeria paradoxa*," *New Phyt.*, vol. xiii, pp. 18–30.

Massart, J. ('94), "La récapitulation et l'innovation en embryologie végétale," *Bull. de la Soc. Roy. d. Bot. d. Belgique*, xxxiii, prem. part, pp. 150–205.

Matte, H. ('03), "Le mériphyte chez les Cycadacées," *Comptes rend. de l'Acad. des Sc.*, cxxxvii, pp. 80–82.

Matte, H. ('04), "Recherches sur l'appareil libéro-ligneux des Cycadées," *Mém. Soc. Linn. Normandie*, Caen, 1904.

Matte, H. ('05), "Compléments à la structure mériphytaire du *Bowenia spectabilis*, Hook.," *Assoc. Franc. pour l'Av. d. Sc.*, 1905, pp. 409–416.

Mettenius, G. ('61), "Beiträge zur Anatomie der Cycadeen," *Abh. d. kön. Sächs. Ges. d. Wiss.*, vii, pp. 565–609.

Von Mohl, H. ('32), "Ueber den Bau des Cycadeen-Stammes," *Abh. d. k. b. Acad. zu München*, i.

Nestler, A. ('95), "Ein Beitrag zur Anatomie der Cycadeenfiedern," *Jahrb. f. wiss. Bot.*, xxvii, pp. 341–368.

Parmentier, P. ('96), "Du rôle de l'anatomie pour la distinction des espèces critiques ou litigieuses," *Ann. des Sc. Nat., Bot.*, sér. 8, t. ii, pp. 1–36.

Parmentier, P. ('97), "Recherches anatomiques et taxinomiques sur les Onotheracées et les Haloragacées," *Ann. des Sc. Nat., Bot.*, sér. 8, t. iii, pp. 65–149.

Pavolini, A. F. ('09), "La *Stangeria paradoxa*, T. Moore," *Nuovo Giornale Botanico Italiano*, nuova serie, xvi, pp. 335–351.

Pellegrin, F. ('08), "Recherches anatomiques sur la classification des Genêts et des Cytises," *Ann. des Sc. Nat., Bot.*, sér. 9, t. vii, pp. 129–319.

Perrot, E. ('98), "Anatomie comparée des Gentianacées," *Ann. des Sc. Nat., Bot.*, sér. 8, t. vii, pp. 105–292.

Petit, L. ('87), "Le pétiole des Dicotylédones au point de vue de l'anatomie comparée et de la taxinomie," *Ann. des Sc. Nat., Bot.*, sér. 7, t. vi, pp. 342–354.

Prantl, K. ('89), "Cycadaceæ," Anat. Verhalt. in Engler and Prantl, *Natür. Pflanzenfam.*, ii, 1, p. 11.

Le Renard, A. ('13), "Rapports anatomiques du genre *Arfeuillea*," *Ann. des Sc. Nat., Bot.*, sér. 9, t. xvii, pp. 353–389.

Rothert, W. ('99), "Ueber parenchymatische Tracheïden und Harzgänge im Mark von Cephalotaxus-Arten," *Ber. d. Bot. Gesell.*, xvii, pp. 275–289.

Sarton, A. ('05), "Recherches expérimentales sur l'anatomie des plantes affines," *Ann. des Sc. Nat., Bot.*, sér. 9, t. ii, pp. 1–117.

South, F. W., and Compton, R. H. ('08), "On the Anatomy of *Dioon edule*, Lindl.," *New Phyt.*, vii, pp. 222–229.

TANSLEY, A. G. ('08), *The Evolution of the Filicinean Vascular System.*

THIESSEN, R. ('08), "The Vascular Anatomy of the Seedling of *Dioon edule*," *Bot. Gaz.*, xlvi, pp. 357–377.

THOUVENIN, M. ('90), "Recherches sur la structure des Saxifragacées," *Ann. des Sc. Nat., Bot.*, sér. 7, t. xii, pp. 1–174.

VAN TIEGHEM, PH. ('84), *Traité de botanique*, pp. 810–813, 826, 829.

VAN TIEGHEM, PH. ('93), "Recherches sur la structure et les affinités des Thyméléacées et des Pénéacées," *Ann. des Sc. Nat., Bot.*, sér. 7, t. xvii, pp. 185–294.

TRÉCUL, A. ('53), "Mémoire sur la formation des feuilles," *Ann. des Sc. Nat., Bot.*, sér. 3, t. xx, pp. 235–314.

ULE, E. ('01), "Die Vegetation von Cabo Frio an der Küste von Brasilien," *Bot. Jahrb.*, Bd. xxviii, pp. 511–528.

VESQUE, J., and VIET, CH. ('81), "De l'influence du milieu sur la structure anatomique des végétaux," *Ann. des Sc. Nat., Bot.*, sér. 6, t. xii, pp. 167–176.

VESQUE, J. ('82), "L'espèce végétale considérée au point de vue de l'anatomie comparée," *Ann. des Sc. Nat., Bot.*, sér. 6, t. xiii, pp. 5–46.

VESQUE, J. ('82), "Essai d'une monographie anatomique et descriptive de la tribu des Capparées (*Capparidées ligneuses*)," *Ann. des Sc. Nat., Boi.*, sér. 6, t. xiii, pp. 47–134.

VESQUE, J. ('86), "Études microphysiologiques sur les réservoirs d'eau des plantes," *Ann. Agronom.*, xii, pp. 449–473.

VIGUIER, R. ('06), "Recherches anatomiques sur la classification des Araliacées," *Ann. des Sc. Nat., Bot.*, sér. 9, t. iv, pp. 1–207.

VIGUIER, R. ('09), "Nouvelles recherches sur les Araliacées," *Ann. des Sc. Nat., Bot.*, sér. 9, t. ix, pp. 305–405.

VOLKENS, G. ('86), "Zur Flora der aegyptisch-arabischen Wüste," *Sitzber. d. k. Pr. Akad. d. Wiss. zu Berlin*, vi.

WARMING, C. ('93), "Note sur la biologie et l'anatomie de la feuille des Vellosiacées," *Bull. de l'Acad. Roy. d. Sc. et d. Lett. de Danemark*, 1893, p. 23.

WENZIG, TH. ('88), "Die Gattung *Spiræa*, L.," *Flora*, 1888, pp. 243–248, 266–274, 275–290.

WORSDELL, W. C. ('06), "The Structure and Origin of the Cycadaccæ," *Ann. of Bot.*, xx, pp. 129–159.

DESCRIPTION OF PLATE.

All the figures are from untouched photographs by Mr R. M. ADAM.

Fig. 1. Leaf of *Polypodium brasiliense*, Poir., from the rain-forest below Vista Chineza, near Rio de Janeiro.

Fig. 2. Leaf of *Polypodium fraxinifolium*, Jacq., from the rain-forest at Alto da Serra, above Santos.

Fig. 3. Leaf of *Polypodium brasiliense*, Poir., from cleft of dripping rock in the gorge near the sea at Praia de Leblond, south of Rio de Janeiro.

Fig. 4. Leaf of *Polypodium brasiliense*, Poir., from the loose sand on Gavea Beach, south of Rio de Janeiro.

Fig. 5. Transverse section of the rachis of a leaf from the plant of *Polypodium brasiliense*, Poir., a leaf of which is represented in fig. 1.

Fig. 6. Transverse section of the rachis of a leaf of the plant of *Polypodium fraxinifolium*, Jacq., another leaf of which is shown in fig. 2.

Fig. 7. Transverse section of the rachis of a leaf of the plant of *Polypodium brasiliense*, Poir., a leaf of which is shown in fig. 3.

Fig. 8. Transverse section of the rachis of a leaf of the plant of *Polypodium brasiliense*, Poir., another leaf of which is represented in fig. 4.

The transverse sections shown in figs. 5, 6, 7, 8 were cut at the same relative levels in the different leaves. A stage in the formation of the pinna-trace is shown in every section. All × about 30.

DESCRIPTION OF FIGURES IN TEXT.

Text-fig. 1. Diagrammatic representation of the leaf-traces of—

(*a*) *Polypodium serrulatum* (Sw.) Mett.
(*b*) „ *cultratum*, Willd.
(*c*) „ *polypodioides* (L.) Hitchcock.
(*d*) „ *plumula*, H. B. Willd., and
„ *lepidopteris* (Langsd. et Fisch.) Kze.
(*e*) „ *loriceum*, Linn.
„ *catharinæ*, Langsd. et Fisch.
„ *brasiliense*, Poir., and
„ *fraxinifolium*, Jacq.
(*f*) „ *decurrens*, Raddi.

Text-fig. 2. Diagrammatic representation of the forms of leaf-trace found in leaves of different length in *Polypodium vulgare*, Linn. The type shown in *a* is found in the shortest leaves; those in *b*, *c*, and *d* in longer leaves, and those in *e* and *f* in the longest leaves.

Text-fig. 3. Diagrams to show the formation of the pinna-traces in *Aspidium martinicense*, Spr., and *Aspidium trifoliatum* (L.) Sw.

Text-fig. 4. Diagrams showing the leaf-trace and the method of forming the pinna-trace in *Leptochilus guianensis* (Aublet) C. Chr.

Text-fig. 5. Diagrams illustrating the formation of the pinna-trace in *Polystichum adiantiforme* (Forst.) J. Sm.

Text-fig. 6. A series of diagrams to illustrate the method of forming the pinna-trace in *Dryopteris grandis* (Pr.) C. Chr.

Text-fig. 7. Diagrammatic representation of the development of the pinna-trace in *Cibotium barometz* (L.) J. Sm.

Text-fig. 8. Diagrams to illustrate the type of leaf-trace found in *Lonchitis pubescens*, Willd., and the method of forming the pinna-trace.

Text-fig. 9. Series of diagrams to illustrate the form of leaf-trace and the development of the pinna-trace in *Stangeria paradoxa*, T. Moore.

Text-fig. 10. Diagrammatic representation of the leaf-trace of *Cycas revoluta*, Thunb.,

(*a*) below the first pinna,
(*b*) near the tip of the rachis,
(*c*) below the terminal pinnæ.

Text-fig. 11. Diagrammatic representation of the leaf-trace of *Zamia Lindeni*, Regel.

Text-fig. 12. Series of diagrams illustrating the changes in the leaf-trace of *Dioon spinulosum*, Dyer, from below the first pinnæ to below the ultimate pinnæ.

Text-fig. 13. Diagrams illustrating the type of leaf-trace found in *Encephalartos Altensteinii*, Lehm., and the changes which it undergoes in connection with the formation of the pinna-traces.

Text-fig. 14. Diagrams to illustrate the form of leaf-trace and the pinna-trace in *Cocos campestris*, Mart.

Text-fig. 15. Diagrams showing the development of the pinna-trace in *Phœnix dactylifera*, Linn.

Text-fig. 16. Diagrams illustrating—

(*a*) the form of the leaf-trace, and
(*b*) the development of the pinna-traces in *Spiræa Aruncus*, Linn.

Text-fig. 17. Diagrams illustrating the leaf-trace and the formation of the pinna-trace in *Spiræa lobata*, Murr.

R. C. DAVIE: LEAF TRACE IN PINNATE LEAVES.

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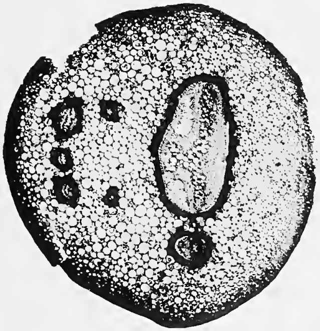

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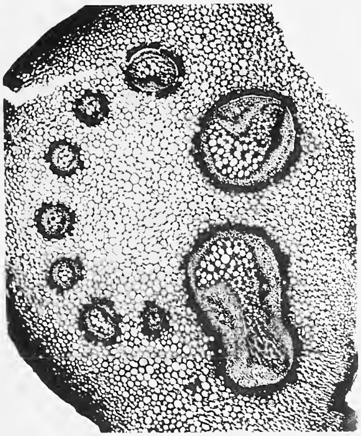

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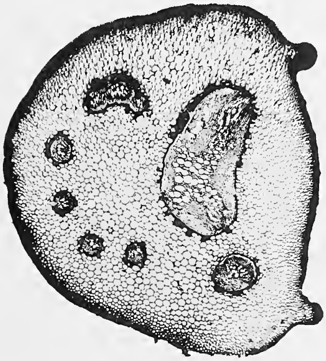

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II.—The Insect Association of a Local Environmental Complex in the District of Holmes Chapel, Cheshire.

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(MS. received March 16, 1916. Read May 1, 1916. Issued separately April 4, 1917.)

CONTENTS.

Introduction.

That there is a decided need for the ecological study of insects and other animals was first brought home to the mind of the author whilst engaged upon the subject of a "General Survey of the Insect Fauna of the Soil" (vide *Jour. Econ. Biol.*, vol. viii, part 3, 1913). Much information has been collected at various times by numerous authors, and especially those who have treated of the habits and behaviour of animals, but very little attempt has been made to systematise the data variously gathered, to explain the cause and effect of many obscure phenomena, or to make important observations accessible for the use of the animal ecologist. Thus, at present, we find ourselves on the threshold of practically a new and undisputed field, with opportunities for original and interesting research extending in innumerable directions. Dr C. C. Adams, now of Syracuse University, New York, who has written a most useful work,* "the outgrowth of the effort as it has developed in the study and teaching of animal ecology," in which is listed most of the literature applicable to the science, says (p. 10): "The associational is the phase of animal activity which may be considered as the form of animal behaviour which has developed into the human social relations," and concludes that, because of the social character of human society, those interested in matters pertaining to the welfare of mankind, such as the sociologist, the physician, the sanitarian, and the agriculturist, will ultimately participate in a keener appreciation of the associational aspect. In another place the same author indicates briefly the magnitude of the problems involved when he says (p. 15): "The aim of the ecologist is professedly genetic or explanatory, because it is the study of *responses* to all conditions of the complete

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* Adams, C. C., *Guide to the Study of Animal Ecology*, New York, 1913, 183 pp., 7 figs.

environment. But these responses must be described and the conditions influencing them as well, so that a descriptive aspect is an essential part in all phases of ecology. In the study of the responses of an individual, an order, or an association, pure description of the responses is necessary; but a description which will at once describe and show the working of the processes by which the results were produced is of quite a different order. This phase of explanation has been most concisely expressed and applied by the students of the physical sciences, and biologists may profit much from a study of their methods." Therefore, for the sake of accurate deduction, a method of measuring all the important factors of an environment which are likely to influence its *biota* is absolutely essential, and the reason why plant ecology is now quite a well-ordered and organised science is due to this very fact. It was almost essential that plant ecology should have precedence over animal ecology in point of time, because the latter involves a knowledge of the former, and, indeed, it will likely prove true, as VESTAL* has remarked (p. 13), that plant and animal associations are co-extensive and to a large extent interdependent, the animals being entirely dependent upon the plants, speaking broadly, and the plants being partly dependent upon the animals. This view-point has not been neglected in the present study, but the author recognises the difficulty of superimposing the structure of the insect association so as to show how it coincides exactly with that of the plant association. The problem might be tackled equally well from one of two standpoints:—

1. The insect proposition wherein, with a species, genus, family or order as the unit, an attempt is made to weave the web of which the physical and vegetational factors are the warp, the insect unit, its activities and behaviour, the woof.

2. The environmental aspect in which the unit is represented by the environmental factors of the habitat, and the relationships of all insects of various orders, family, genus, and species to these factors and to each other are discussed.

The first of these methods is perhaps the one most likely to be productive of detailed and accurate results. By multiplying the unit to include, say, every family represented in the habitat, our knowledge of any one is likely to be very exact. Necessarily, this method entails much application, besides time and labour. The second is more general, but has the advantage that by including all insect species in one study, it treats of the sum-total of biographical relationships and the interacting influences of every physical or other factor and the individual insect units. The latter of these is the method which has been adopted for this paper. But, either way, although the manner of attacking the subject may differ, the ultimate result would be the same.

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* VESTAL, A. C., "An Associational Study of Illinois Sand Prairie," *Bull. Ill. State Lab. Nat. Hist.*, 1913, vol. x, art. 1.

Physiography and Topography.

In so far as the locality of our investigations is representative of the conditions which prevail throughout the lower-lying reaches of the Dane valley, it may be considered as physiographically typical of the whole area. Terraces of a fairly wide sweep, composed of river gravel, extend along the greater part of the valley.* Westwards from the North Rode viaduct the river winds from side to side of a flat of an average breadth of a quarter of a mile, on each side of which rise hills of red marl capped by a few feet of sandy gravel, and the valley shows here and there traces of two or three terraces. The river runs in a deep channel cut through this old alluvium well down into the red marl below. The pebbles in the gravel are of all sizes, up to that of a man's fist, and there are sometimes beds of sand: the gravel is at times stratified, but is oftener just such a rude tumbled mass of pebbles and boulders as now lies in the bed of the river; it has doubtless been formed mainly from the waste of the Drift Sand and Gravel. As this gravel rests on red marl without any trace of boulder beds between, it is likely that the valley of the Dane has been greatly deepened since the Drift period. From Congleton, eight miles to the west, to Holmes Chapel and beyond, on the north-east side of the valley, a pair of terraces may be made out, but they have been much cut up by river denudation. They soon give place to a broad, well-marked flat about 15 or 20 feet above the river, with here and there a ledge some 10 feet lower.

The farmland of the Holmes Chapel Agricultural College stands at about 225 feet above sea-level, which represents the altitude of Glover's Meadow, covering an area of 1·633 acres (Pl. I; Pl. II, fig. 2). This name has been used throughout the paper to designate the grassland situated on the top of the wooded declivity, at the bottom of which the Alluvial Pasture of 4·658 acres (Pl. I; Pl. II, fig. 1) extends along the south side of the River Dane. The Farm Pasture, on which is situated the filtering tank of the College sewage system, is 4·09 acres, wheat field 6·94 acres, and potato field 5·86 acres, about one-tenth acre being sown in oats and a small strip planted with cabbages as represented in the diagram (Pl. I) taken from the survey map of the farm. As the study is mainly concerned with the two fields, Glover's and Alluvial, the latter of which is confluent with the higher-lying Farm Pasture, the importance of the adjacent fields and woods lies in the fact that the crops and trees which they bear supplied numerous species of insects which invaded our more limited area and so had to be considered as temporary invaders or migratory forms.

The Alluvial Pasture stands at a height of about 155 feet above sea-level. Its surface soil is derived from the Post-Glacial Drift, and consists of alluvium. This is in decided contradistinction to the surface soil of Glover's Meadow, which is

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* Hull, E., and Green, A. H., "The Geology of the Country round Stockport, Macclesfield, Congleton, and Leek," *Mem. Geol. Sur. Gt. Brit.*, London, 1866, p. 80.

derived from Middle Sand overlying Boulder Clay and Keuper Marl, evidences of which can be traced in the escarpment connecting the two meadows. Naturally, after a period of time, soils become modified by the accumulation of humus, which tends to make a soil " heavy." There is really very little difference to be found in the texture of the soils of the two meadows, although derived from such different sources, and very little variation in their water-content. That of Glover's Meadow, with its underlying strata of clay which prevents leaching, has a large retentive capacity for moisture. The Alluvial Pasture, by reason of its position on the banks of the Dane, does not dry readily, and its moisture content is continually being added to by the waters draining from the higher lands down the declivity on its southern side, so that at the base of the slope on the side distal from the stream the ground, even in midsummer, had almost always a tendency to be marshy. If anything, the soil of the Alluvial Pasture is the more friable when dry, that of Glover's Meadow tending to become compact and cloddy.

The Alluvial Pasture varies in evenness. It is flat on the west side and rises gradually at the east and south sides towards the escarpment (Pl. II, fig. 1.) Sundry undulations cause here and there the formation of moister hollows. The surface of Glover's Meadow is almost level, dipping slightly on one side towards the wood (Pl. II, fig. 2). The Farm Pasture is level for a great part, but its evenness is interrupted by the steep gradient leading down to the banks of the river.

It was not considered necessary to make chemical analyses of the soils of the habitat. A knowledge of the mechanical nature of the soil, its coarseness or fineness, is much more important for ecological purposes.* The texture of a soil determines and regulates its water-content, which is of far more importance to animal and plant life than its chemical composition. Mechanical analyses need not be too exact, and the measurement and separation of the particles according to definite units of size or variation represents a waste of effort. The results give no real clue to the nature of the soil as it actually exists, where the particles are all mixed up. Therefore, it is sufficient to know that the Alluvial Pasture soil is a dark-coloured loam, that of Glover's Meadow a reddish clay loam.

THE PLANT ENVIRONMENT AND ITS RELATION TO INSECTS.

With the assistance of Mr C. H. GADD, Lecturer in Biology at the Holmes Chapel Agricultural College, a thorough analysis was made of the dominant floral species. The vegetation is essentially of the mesophytic type. In Glover's Meadow the predominant herbage of the field consists of *Anthoxanthum odoratum* and *Holcus lanatus*. Among species which could be designated abundant, there were *Dactylis glomerata*, *Festuca ovina*, *Rhinanthus crista-galli*, *Rumex acetosa*, and *R. acetosella*, *Cynosurus cristatus*, *Ranunculus repens*, *Plantago lanceolata*, and

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* CLEMENTS, F. E., *Research Methods in Ecology*, Lincoln, Nebraska, 1905, pp. 15, 80.

Bromus mollis. A close matting of moss, *Brachythecium rutabulum*, covered the surface of the ground, obscured to casual observation by the taller plants. In addition to these species there were also present in greater or less abundance *Poa trivialis*, *Ranunculus acris*, *Veronica chamædrys*, *Trifolium repens*, *Chrysanthemum leucanthemum*, *Bellis perennis*, *Bunium flexuosum*, *Cerastium triviale*, *Potentilla anserina*. *Potentilla reptans*, *Lolium perenne*, *Agrostis alba*, *Agrostis vulgaris*, *Prunella vulgaris*, *Phleum pratense*, *Ranunculus ficaria*, *Trifolium pratense*, and *Draba verna*.

In the south-eastern corner of the same meadow, in the vicinity of a pond, the plant species were essentially hygrophytic, and included *Lychnis flos-cuculi*, *Carduus palustris*, *Spiræa ulmaria*, *Lotus corniculatus*, *Ajuga reptans*, *Anemone nemorosa*, *Primula vulgaris*, *P. veris*, *Cardamine pratensis*, *Trifolium pratense*, together with species of *Carex*, *Juncus*, and *Equisetum*. In the north corner of the same meadow, surrounded almost wholly by trees, bracken (*Pteris aquilina*) flourishes, interspersed by blue-bells and yellow pimpernel. On its westerly exposure Glover's Meadow is bounded by an intermittent hedge of hawthorn, elm, and willow, interrupted here and there by isolated trees of oak and alder. At the base of this hedge the following species were observed :—*Rubus fruticosus*, *Rosa canina*, *Urtica dioica*, *Digitalis purpurea*, *Teucrium scorodonia*, *Sarothamnus scoparius*, *Equisetum* spp., *Stellaria holostea*, *Lychnis diurna*, *Anthriscus sylvestris*, *Heracleum sphondylium*, and *Vicia sepium*.

The trees on the eastern side of the meadow (Pl. II, fig. 2), forming the upper limits of the wood which clothes the declivity, are a mixed assortment of sycamore, elm, oak, holly, ash, hawthorn, hazel, and elder.

The herbage of the Alluvial Pasture has as its predominant constituents *Holcus lanatus*, *Trifolium repens*, *Lolium perenne*, *Anthoxanthum odoratum*, *Festuca ovina*, *Agrostis alba*, and *A. vulgaris*. Other grasses present are *Poa trivialis*, *P. pratensis*, and *P. annua*, *Festuca pratensis*, *Cynosurus cristatus*, and *Dactylis glomerata*. The wood on the southern side (Pl. II, fig. 1) contains alder, ash, sycamore, beech, holly, hawthorn, elder, hazel, oak, willow, mountain ash, and elm. In the shade of the trees overhanging the meadow the *Urtica dioica*, *Lychnis diurna*, *Mercurialis perennis*, and *Arctium lappa*, each of these species occurring in great profusion in this particular location.

A summary of the weeds in the Alluvial Pasture showed that the following species were abundant :—*Urtica dioica*, *Rumex acetosa*, *Ranunculus repens*, *R. acris*, *Bellis perennis*, *Achillea millefolium*, *Cerastium triviale*, *Luzula campestris*, *Carduus arvensis*, *Rumex obtusifolius*, and *R. crispus*.

It has been considered necessary to detail the floral species in this way, not only because of the important relations which exist between plants and phytophagous insects directly, but also because of the action and interaction continually exerted between the vegetational type and the climatic factors so important to animal life, of which it serves as a general sort of index. Temperature, humidity, and wind velocity are each and severally modified by the particular kind of plant association, whether it be herbage, shrubs or forest, and each kind of association harbours its own kind of animal life, species which are characteristic of it and of no other. Often the line of demarcation between one association and another can be strictly delimited, so that species which may be introduced into an association which is alien to their habits react negatively to the prevailing physical factors of their new abode and tend to turn back. On the other hand, where two distinct associations are in juxtaposition and gradually merge into one another, as in the case of woodland and grassland, many species from both will intermingle, especially so at the places of transition. Thus the feeding habits of many larval forms will be actively pursued in the humus or decaying wood of forests, and will react negatively to light and to a dry atmosphere, whilst the winged adults will visit the herbage of meadows and pasture, bathing themselves in the rays of the sun. Migration, however, is more frequent from stratum to stratum, by which is meant the vertical divisions of a uniform area such as the subterranean, surface, plant, and aerial strata, for which VESTAL [*] has introduced the terms *subterricolous*, *terricolous*, *herbicolous*, and *aericolous* respectively. It is this process of interchange of either one individual or the same group of indivduals from one stratum to another that lends unity to the association. The process may be induced by changes of light intensity, or may be a direct response to the different needs and activities of an insect during different stages of its life-history. An analysis of migration reveals the presence of four factors, viz. motility, agency, proximity, and topography. Not all of these are present in every instance of migration, and in many cases where the proper distributive agent is lacking to eke out the motile powers of an organism, the effective operation of the two will be profoundly modified by distance and topography. In general, insects do not take long migratory flights except when there is some urgent necessity, such as lack of food due to enormous multiplication of a species, a phenomenon which occurs in the Rocky Mountain locust (*Schistocerca americana*). A curious example of migration, as yet unexplained, which the author had the opportunity of observing during a sojourn in America last summer, is that of two species of Salt Marsh mosquito, *Culex cantator* and *Culex solicitans*, which come off the extensive salt marshes bordering the New Jersey coast in enormous numbers. Specimens were taken in grasses and rank herbage as many as five to seven miles inland. Dr SMITH [†] first proved (1902) that the theory which maintained that mosquitoes do not fly far from the point where they breed, was not applicable to all the species of this family.

In a general way it is now recognised, as has been already remarked (p. 38), that

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[*] VESTAL, A. G., "An Associational Study of Illinois Sand Prairie," *Bull. Ill. State Lab. Nat. Hist.*, 1913, vol. x, art. 1, p. 67.

[†] SMITH, J. B. "Mosquitoes," *Rept. New Jersey State Agric. Exper. Station, Trenton, N.J.*, 1904, p. 5.

for a given terrestrial environment the animal and plant association is co-extensive, and that the boundaries of the one roughly coincide with the other, the whole forming what has been defined as a *biota* composed of animal and plant assemblages. This relationship, which must as yet be considered hypothetical when regarded broadly, has been here constantly kept in view, and the tables in which the various insect species have been listed are meant to indicate this basic principle. The plant ecologist recognises various kinds of association which have been designated by the name of the dominant type of vegetation, such as pine association, moorland association, etc. In our study the association which is recognised as rather heterogeneous belongs to the grassland + mixed wood type. Being a strictly local complex, the conditions must be referred to as dependent primarily on soil or edaphic, as contrasted with climatic factors which determine the kind of vegetation over wide areas, such as deciduous forest and steppe.

For the determination of the various species of an association, their abundance and grouping, the botanist has devised the *quadrat* method. By this means the most accurate information can be obtained of the facts as they exist within a definite square area. Although the space covered is minute, valuable data can be obtained, from which conclusions of a general nature can be deduced applying to the whole association of which the smaller area selected is representative. Such detail and thoroughness is scarcely required for our purposes, and only a general idea of the relative abundance of plant species has been attempted, expressed as common, fairly common, very common (*cf.* Tables X, XI).

By reason of their sessile habits the individuals of a plant association can be more easily studied than those of the more motile species of an animal association. It is often a very difficult matter to settle what species are peculiar to the association and what are merely invaders, temporarily or permanently. The clue to an insect's real habitat is the test of where it breeds. This may also be the situation where it feeds, but in a great many cases the two places are not the same. A knowledge of the larval habits is therefore essential as giving an indication of the animal's real habitat.

PHYSICAL FACTORS OF THE ENVIRONMENT.

The environment or habitat may be defined as the result of the action and interaction of the combined forces or factors present in any given region, and, according to VESTAL,[*] who quotes SCHIMPER, have been classified into two groups—climatic (geographic) factors which operate over very broad areas, and edaphic (local) factors which effect local modifications of the plant life (and the animal as well) within any such broad region. The composition of the animal association is primarily dependent upon the ecological type of the vegetation, which is again dependent upon various factors, enumerated by CLEMENTS[†] as water-content, humidity, light,

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[*] *Op. cit.*

[†] *Op. cit.* p. 18.

temperature, soil, wind, precipitation, pressure, altitude, exposure, slope, surface (cover), and animals. To these are added gravity and polarity, which are practically uniform for all habitats. In their total effect they represent the controlling forces of the environmental complex, and it is often difficult to attribute to each one its proper rank and value in determining the facies of the plant or animal association, on the latter of which they also have a more or less direct influence.

The water-content of any soil is in inverse ratio to its fineness of texture, and is also for any particular area dependent upon the degree of humidity which prevails and upon the amount of rainfall at any given time. The question of soil-moisture has been already discussed in a previous paper* with regard to its relationship to soil-inhabiting insects. The author indicated its importance as bearing upon their welfare. In the same connection the questions of temperature and soil ventilation were also amplified.

It is very doubtful whether such factors as altitude and pressure in any given region will be found to exert a measurable stimulus upon insect behaviour. In the first place, it is very difficult to analyse the real effects of altitude. To some extent it is associated with rainfall, but only in an indefinite degree. Clements, who has just been quoted, says (p. 18) that its influence, so far as the plant is concerned, is really pressure, and that, in consequence, its effect is exerted upon the climatic and not the edaphic factors of the habitat. Therefore so far as the present study is concerned, the consideration of altitude and pressure may be neglected. Daily records have, however, been kept of the barometric pressures. These have been averaged (*cf.* Table XII) for the various months during which the investigation lasted, in the hope that they might prove useful for comparison with the pressures prevailing in regions of lower or higher altitude. Thus, perhaps, an approximation to the proper value of pressure in influencing the composition of animal associations may be derived. It is a well-known fact that many insects inhabit only localities of high altitude, but as to whether this phenomenon can be directly assigned to the decreased density of the atmosphere is a matter of conjecture.

From the standpoint of the animal association the surface covering of the soil, its nature and density, is recognised to be of such importance that it is customary to speak of insects of forest, of grassland, of corn and other cultivated crops. Sometimes the mere fact that a particular type of vegetation offers a favourable means of shelter and protection from enemies will explain the presence of many insect species. Or it may be that predatory habits will induce them to frequent a particular locality in their search for food, other than the one in which they breed. This fact was boldly confronted in the present investigation.

Wind as a distributive agent is perhaps more important to the plant than to the animal association, and, naturally, where soils are light and loose it may be quite effective in modifying the surface topography. In the Holmes Chapel locality its

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* Cameron, A. E., "General Survey of the Insect Fauna of the Soil," *Journ. Econ. Biol.*, vol. viii, p. 189.

effect in this way is negligible. Many insects are anemotropic, and in moderate breezes will orient themselves head-on to the air-current, maintaining a seemingly motionless attitude on the wing for quite appreciable periods. Species of *Bibio* will often be observed maintaining their bodies headed to a gentle breeze, changing their position to the windward as the breeze veers in one direction or another. Many Anthomyiidæ, Syrphidæ, and Chironomidæ have a similar behaviour, and Folsom * quotes Wheeler as having observed *Empidæ* swarming in one spot every day for no less than two weeks, probably on account of some particular odour emanating from the ground which attracts and arrests the flies as they emerge from their pupæ. In this latter case, perhaps chemotropism determines their curious behaviour as much as anemotropism.

Many insects are undoubtedly carried before the wind from one association to another, and it may be of decided importance in migration and invasion. Otherwise it would often be difficult to explain why certain insects which belong to woodland associations are sometimes met with in grassland. During violent disturbances of the atmosphere winged insects generally seek shelter near the ground amongst the herbage.

The readings for the temperature, pressure, and rainfall were made each day at 9 a.m. Standard instruments were used. For accurate results in the study of biological phenomena, however, it is recognised that self-recording apparatus is essential, whereby the actual temperature fluctuations throughout the course of the day are obtained. The monthly averages of the soil-temperature records at Holmes Chapel show a seeming discrepancy, in that apparently the temperature at a depth of six inches at no time, during the fifteen months covering the investigation, rose above that at the depth of eighteen. This is, of course, erroneous, and due to the fact that the readings were made at a time (9 a.m.) when the soil at the uppermost layer of six inches has lost most of its heat during the night by radiation to the layers beneath and to the atmosphere, whilst the effect of the sun's rays have not yet reached sufficient strength to warm it up. In the summer months at midday, in bright warm weather, the surface layer is generally a few degrees warmer than the layers immediately beneath. In the winter months, during periods of frost and snow, the converse prevails.

The earlier months of 1914 were milder than those of 1913, as a glance at Table XII will show at once. Whereas, in January 1913, the average maximum air temperature was 42° F., in January 1914 it was as high as 58° F.; the average maximum for the same month of 1914 was 37° F. compared with 31° F. for the corresponding month of the previous year; the average minimum temperature on grass differed by 4° F., 31° F. in January 1913 and 35° F. in January 1914. The average soil temperatures for these same months also varied; at six inches depth, January 1913, 40° F., January 1914, 38° F., a drop of 2° F.; at eighteen inches below

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* Folsom, J. W., *Entomology: its Biological and Economic Aspects*, Philadelphia, 1906, p. 348.

the surface, January 1913, 38° F., January 1914, 44° F., an increase of 6° F. Analogous variations were recorded for February and March, with an increase of temperature in 1914 favourable to the earlier emergence of insect species from their hibernating quarters, a fact which was actually observed during the latter year.

The facts regarding the relationship of temperature to the hibernation, æstivation, and growth of insects are but inadequately known. Several workers have recently made notable contributions to the subject, of which those of TOWER, SANDERSON, HEADLEE, and DEAN in America, and BACHMETJEW in Europe are important.

SANDERSON[*] has endeavoured to determine the existence of physical laws upon which the time of emergence of insects from hibernation and the date upon which they begin oviposition, depends. In experiments with the brown-tail moth (*Euproctis chrysorrhœa*), the tent caterpillar (*Malacosoma americana*), and the codling moth (*Carpocapsa pomonella*), he has also endeavoured to establish a "thermal constant" governing the emergence of insects from hibernation. "Thermal constant" is defined as *that accumulation of mean daily temperature above the "critical point" of the species which will cause it to emerge from hibernation or to transform from any given stage.* Active metabolism in insect species as well as in plants only occurs at or above a certain temperature, probably specific for each kind or group, and this temperature has been designated the "critical point" for the species concerned. Heretofore 43° F. was generally accepted as being the universal temperature at or above which all temperatures were effective, but recent work has proved that it varies for different species.

It has generally been accepted that a lowering of temperature causes or is at least associated with the phenomena of hibernation, but SANDERSON (*loc. cit.* p. 58) and TOWER[†] have shown that insects have persisted in hibernating, or at least have their activities curtailed, in spite of being subjected to high temperature just previous to the normal time for hibernating. The latter author asserts that all the species of the genus *Leptinotarsa*, which includes the notorious Colorado potato beetle, have but two generations, when a period of rest, hibernation, or æstivation ensues, either of which exert the same effect on the life-history phenomena of the insect. During the period of rest the insect loses about 30 per cent. water, causing a concentration of its protoplasm and body fluids, by virtue of which it can the more readily resist the injurious effects of lower and higher temperatures.

SANDERSON[‡] in a later paper also draws attention to the fact that for some species moisture content is very important, and often more so than temperature, in determining the optimum for development; and therefore it is necessary for accurate work on the effect of temperature that moisture conditions should be kept constant.

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[*] SANDERSON, E. D., "The Relation of Temperature to the Hibernation of Insects," *Jour. Econ. Ent.*, vol. i, No. 1, pp. 56–65, 2 figs.

[†] TOWER, D. L., *Evolution in Chrysomelid Beetles of the Genus* Leptinotarsa, Carnegie Institution, No. 48, 1906.

[‡] SANDERSON, E. D., "The Relation of the Temperature to the Growth of Insects," *Jour. Econ. Ent.*, 1910, vol. iii, No. 2, p. 121.

This aspect of the question is emphasised in a paper by HENNINGS * on the relation of temperature and moisture to the development of the scolytid beetle *Tomicus typographus*, L., in which he says: "Dass nicht nur 'kalte' sondern 'nasskalte' Witterung die Entwickelung verlangsamt, hatten schon früher die Beobachtungen im Freien gelehrt; mein Bestreben ging dahin, den Einfluss der Luftfeuchtigkeit ebenso wie den der Temperatur zahlenmässig darzustellen." In a series of tables he shows the relation between temperature and moisture and the time occupied in the development of the various stadia of the insect. Perhaps the most exhaustive inquiry into the temperature-moisture relations of insects has been made by BACHMETJEW in two large treatises,† where he states that there is an optimum degree of humidity for insect development which differs for different species. DEWITZ ‡ has also carried out similar experiments with various Lepidoptera and Diptera, notably *Cochylis ambiguella*, *Œnophthira pilleriana*, *Eudemis botrana*, *Phalera bucephala*, and *Calliphora erythrocephala*, in order to determine the maximum temperature beyond which the activities of these insects are retarded, and after what period death ensues. Both the time and temperature factors were varied with interesting results, which depended upon the stage of development of the larvæ employed in the tests.

All of this work is of the utmost significance to economic entomology. It is absolutely essential to know the fundamental factors which govern the various phases of insect life, and as SANDERSON (*loc. cit.* p. 64) has remarked: "Entomology, as well as all biological science, must consider its relations to the more exact and fundamental sciences of physics and chemistry, if we are to have exact knowledge of the life with which we are dealing." This author, along with PEAIRS,§ has lately published a more detailed account of his researches in bulletin form.

There is, however, an objection to indoor experiments in temperature-moisture work. It is doubtful in how far one can base one's conclusions on results obtained under laboratory conditions, which are generally radically different from those that prevail outside. There are probably other physical factors besides temperature and moisture which must be considered, such as light intensity and atmospheric gases. To control all of these is by no means easy, but it appears to the author that no matter how unimportant any single factor may seem, it must be considered as contributing towards the changes which the insect undergoes in its progress towards maturity.

At the Philadelphia meeting of the American Association of Economic

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* HENNINGS, C., "Beiträge zur Kenntniss der die Insektenentwickelung beeinflussenden Faktoren," *Biologische Centralblatt*, 1907, vol. xxvii, p. 327.

† BACHMETJEW, P., (1) *Experimentelle Entomologische Studien: I. Temperature Verhältnisse bei Insekten*, Leipzig, 1910, p. 160. (2) *Experimentelle Entomologische Studien vom physikalisch-chemischen Standpunkt aus zweiter Band*, Sophia, 1907, pp. 999+cviii, pls. 31.

‡ DEWITZ, J., "Physiologische Untersuchungen auf dem Gebiet der Schadlingsforschung," *Naturwiss. Zeits. f. Forst- u. Landwirtschaft*, vol. x, pt. 7, pp. 539–549.

§ SANDERSON, E. D., and PEAIRS, L. M., "The Relation of Temperature to Insect Life," *Tech. Bull. No.* 7, *New Hampshire Coll. Agric. Exper. St.*, Durham, N.H., pp. 1–125.

Entomologists, December 1914, Dean and Nabours[*] described a new air-conditioning apparatus for maintaining a desired constant humidity and temperature within a reasonable degree of variation. If in nothing else, it does not lack elaborate structure. The principle seems to consist in passing a current of air through a spray chamber, where it acquires a certain degree of relative humidity depending on the temperature of the water. It then passes over a thermostat, where there is imparted to it the required change of temperature before entering the breeding chamber. Dr Headlee, with whom the author has had the opportunity of discussing the subject, described at the same meeting a simple apparatus for the same purpose, consisting of constant temperature and moisture incubators. It is his opinion[†] "that the response of insect protoplasm, as exhibited in variations of the rate of metabolism, appears to depend upon: (1) where in the particular insect's temperature range the temperature changes occur; (2) the type of metabolism characteristic of the insect, when the response (*to temperature change*) is taken; (3) the presence of any abnormal factor such as parasitism." The third of these is of peculiar interest, and, if neglected, might lead to an apparent discrepancy in the results. Quoting Davenport, he further emphasises (*loc. cit.* p. 416) the effect of moisture on insect metabolism, where, according as the amount of moisture is increased, growth increases until an optimum is reached. The quantity available does not determine the amount imbibed, which is rather controlled by the needs and habits of the species.

Shelford[‡] is of the opinion that the best and most accurate index of the varying physical conditions surrounding land animals wholly or partly exposed to the atmosphere, is the "evaporating power of air." The standard of measurement is expressed by the amount of water which the atmosphere, under different conditions of air-temperature, pressure, relative humidity, and average wind velocity, absorbs from a free water surface in a given time. Evaporation is greatest in open associations, as has been demonstrated by Transeau,[§] where the absence of dense vegetation permits of the more rapid removal of water vapour. By means of the porous cup atmometer, as devised by Livingston,[||] quantitative evaporation experiments can be successfully carried out.

The significance of the evaporation aspect is likely to prove so important that Shelford's[¶] conclusions, deduced from the results of a series of experiments on the reaction of various animals to atmospheres of different evaporation capacities, may

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[*] Dean, G. A., and Nabours, R. K., "A New Air-Conditioning Apparatus," *Jour. Econ. Ent.*, vol. viii, No. 1, pp. 107–111.

[†] Headlee, J., "Some Data on the Effect of Temperature and Moisture on the Rate of Insect Metabolism," *Jour. Econ. Ent.*, 1914, vol. vii, No. 6, p. 414.

[‡] Shelford, V. E., "Animal Communities in Temperate America," *Geog. Soc. Chicago*, Chicago, 1912, p. 161.

[§] Transeau, E. N., "The Relation of Plant Societies to Evaporation," *Bot. Gaz.*, pp. 217–231.

[||] Livingston, B. E., "The Relation of Desert Plants to Soil Moisture and Evaporation," Publ. No. 50, Carnegie Institution.

[¶] Shelford, V. E., *loc. cit.* p. 163.

be stated here: "(1) The animals studied react to air of a given high rate of evaporation whether the evaporation is due to moisture, temperature, or rate of movement; (2) the sign and degree of reaction to the given rate of evaporation are in accord with the comparative rates of evaporation in the habitats from which the animals were collected; (3) the animals of a given habitat are in general agreement in the matter of sign and degree of reaction; the minor differences which occur are related to vertical conditions and kind of integument, but no agreement between survival time and habitat when a number of members of a community are taken together."

The Insect Association.

A large number of the insect species which occur in meadows and pastures are not peculiar to them. The real index of an insect's habitat is where it breeds, and, although this may be the same as where it feeds during various of its life-history stages, there are innumerable instances where this is not so. If this fundamental principle be recognised, it is a very simple matter to distinguish between those forms which are proper or peculiar to an association (*endemic*) and those which are invaders (*polydemic*), provided always the larval habits are known. The second of these classes may be again subdivided into two groups, viz.:—1. Temporary invaders. 2. Permanent invaders. Only the first of these concern us. The second may be better considered in a discussion of the phenomena of *succession*. In any given area the physical conditions, climatic or topographical, may undergo such a change that its fauna or certain members of it can no longer exist within the environment. The new conditions may, however, be suitable to another set of organisms which invade the locality and make it their own. Thus a new order of things is established, lasting only so long as the fresh conditions do not vary to any great extent. Similar results may also be produced by a change of the biological conditions. In time, living organisms may render their surroundings toxic to their own kind by the accumulation of waste matter or excreta, or it may be that the food supply will give out. On the other hand, other organisms will thrive in just those conditions and replace their benefactors (SHELFORD, pp. 308, 309).* In the process of reduction and demolition of a felled log to humus one obtains a good idea of what is meant by succession, where the Scolytid and large Cerambycid beetles are followed by the larvæ of Elateridæ. With the advance of decay these forms give place to the larvæ of Muscidæ, Tipulidæ, Mycetophilidæ and attendant predaceous forms, such as the larvæ of Leptidæ, Xylophagidæ, Staphylinidæ, and Carabidæ. Ants will frequently rear their broods in the old burrows of the wood-boring forms. In the final stages, when fungus and moisture have aided materially in reducing the wood to pulp, earthworms enter and complete the processes of demolition.

We also recognise definite changes or succession of organisms from season to

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* *Op. cit.*

season. For any given locality the same changes in the same order occur year after year. It may merely be a succession of the various life-history stages of the individual species. Every collector and ecologist knows that many insects are only to be found on the wing for a certain, well-defined period of each year.

Apterygota.

It has not been considered necessary to draw up a detailed table of the various species of the Apterygota. In the first place, their numbers were comparatively few, and in the second, their habits are probably all alike, viz. : humus-feeders requiring fairly moist conditions. The following occurred :—

Campodea staphylinus, Westw.
Onychiurus fimetarius, L.
Onychiurus ambulans, L.
Isotoma viridis, Bourl.
Isotoma grisea, Lubb.
**Tomocerus tridentiferus*, Tullb.
Entomobrya nivalis, L.
Entomobrya albocincta, Templ.
**Lepidocyrtus curvicollis*, Bourl.
**Orchesella cincta*, Lubb.
**Dicyrtomina ornata*, Lubb.

The species marked * were found mostly among dead leaves on the boundary of Glover's Meadow near the wood (Pl. II, fig. 2), and in similar situations in the Alluvial Pasture (Pl. II, fig. 1). They are probably characteristic of forest floors. The remaining species occurred at the roots of grasses.

Plectoptera, Neuroptera, Mecaptera, Trichoptera.

Of the various species (Table VIII) only *Chrysopa vulgaris* and *C. perla* belong to the association. The others, except *Panorpa communis*, are members of aquatic communities. Only the proximity of their habitats, neighbouring ponds and the River Dane, will account for the occurrence of the adult forms in grassland. They were taken very frequently when attracted by artificial light. The larva of *P. communis* is a soil inhabitant generally found in moist, wooded areas. The male of the species possesses a curious clasping organ near the anus.

Diptera.

This order (Tables I, II, III) is especially well represented in grassland. In our particular locality the various species are referable to several distinct classes, chief among which are :—

1. Those peculiar to grassland and consisting mostly of species, the larvæ of which are predaceous either in the soil or other vertical strata, or truly phytophagous, depending chiefly for their subsistence upon grassland plants and weeds (Table I).
2. Those the larvæ of which are coprophilous or subsist on decaying animal or vegetable tissue. The imagines have generally the same habits or frequent flowers. Some may become pests of cultivated crops, e.g. *Dilophus*, *Bibio* (Table II).

3. Those species which are aquatic as larvæ. The adults frequent and shelter among grasses often in large numbers (Table III).
4. Those species which invade from adjacent wood and ruderal associations, *e.g.* *Chortophila brassicæ*. They have been indicated in the tables (*q.v.*).

The classes are not mutually exclusive, as many species might be equally well included in one or other. Primarily, the tables are meant to apply only to the area of our investigation, but as a basis of comparison for other similar areas the data will prove useful. Where the larval habits are not known it is impossible to relegate the species to its proper habitat with any degree of accuracy, but a knowledge of allied species will often furnish a clue.

An interesting case of unorthodox habits may be cited of one family of Diptera. It is considered by most students of Leptidæ that the larvæ are predaceous. Whilst this may undoubtedly be the case, the author had convincing evidence that this statement cannot be considered absolute. Almost mature larvæ of *L. scolopacea* and *L. tringaria* (Table I) were found well buried in decaying, pulpy (seed) tubers. They seemed suspiciously engrossed in satisfying a depraved appetite on the liquefying, evil-smelling mass. In some cases, it is true, they were associated with scavenging larvæ of Staphylinidæ, *Oxytelus* and *Stenus* (Table V), and also *Onychiurus*. The author was, however, successful in rearing the adults from larvæ in decaying potatoes where no other insects were present. On several occasions the larva of *L. scolopacea* has been taken among decaying vegetable matter, which would appear to be their true habitat.

It is not intended to enter into a lengthy discussion of the various species. The information which has been culled from the author's observations in the field, and supplemented here and there from well-known and authenticated sources, has been conveniently tabulated for the reader's reference. In all cases the authorities have not been quoted, not because of any pre-conceived idea of neglect, but because their very familiarity renders this unnecessary.

Coleoptera.

Practically the same classes (Tables IV, V) can be distinguished as in the case of Diptera. Although the consideration of the aquatic forms is quite relevant because of the proximity of field ponds and the river to our grassland association, yet they have been neglected, as the imagines are very rarely, if ever, found among herbage. In their behaviour they practically do not contribute towards influencing the constitution of the insects of the grassland association. They are best confined to a consideration of aquatic communities.

One point of significance was the occurrence of forms peculiar to moist localities. For instance, both in the Alluvial Pasture and in Glover's Meadow species of Coleoptera, besides Diptera, Lepidoptera, and Hemiptera, were taken, which are, as a rule, confined to humid places. The physical and vegetational conditions supply an indication of the fauna. Conversely, the composition of the latter will in a very general way be a reflex of these same factors.

Some species of Coleoptera that are pests of grassland are equally injurious to cultivated crops. Wireworms will adapt themselves to various root and graminaceous crops besides natural grasses. This accounts for the fact that rotation has very little effect in diminishing the numbers of this pest.

The Nitidulid beetle, *Epuræa æstiva* (Table V), is probably a scavenger feeding on débris in the nests of wild bees. According to Fowler[*] the species is said to have been reared in numbers by CHAPPELL from those of *Bombus lucorum*. Another member of the same family, *Rhizophagus bipustulatus* (Table IV), which the author has found under bark in the early part of the year, preys upon wood-boring larvæ. An allied species, *R. depressus*, has been recorded attacking the larvæ of the Scolytid beetle *Hylesinus*.

Those species which could be traced to habitats other than those of grassland have been indicated in the tables (IV, V) by means of symbols (*q.v.*).

Lepidoptera and Tenthredinidæ.

The night-flying moths of the family Noctuidæ (Caradrinidæ) are typical of grassland associations (Table VI). Their larvæ, surface-caterpillars or cutworms, burrow into the soil or hide beneath some ground-shelter during the day and feed on the surface at night. In general, those Lepidopterous species will occur in any given locality where their food-plant is at hand. Isolated trees of willow along the banks of the Dane and elsewhere in close proximity provided food for *Smerinthus populi*, *Earias çlorana*, and *Acronycta rumicis*. Quite a number were invaders from woodland, whilst ruderal species were not uncommon. The Pieridæ, for instance, affect cabbage (*Brassica*) principally, and several Agrotids have a like habit. In the north corner of Glover's Meadow, closely grown over with bracken (*Pteris aquilina*), *Pseudopanthera petraria* and *Melanchra pisi* occurred in fair numbers.

The nomenclature of MEYRICK[†] has been adopted in designating the various species recorded.

Of the Tenthredinidæ (Table VI) which have been included in the same table as the Lepidoptera because of the similar larval habits of both, the species and specimens were preponderantly of the genus *Dolerus*. They appear first in the late spring and fly lazily about among herbage on which their larvæ feed, never, seemingly, undertaking very extensive flights. The fully fed larvæ do not spin a cocoon, but pupate free in an earthen cell. *Allantus arcuatus* also occurred in great abundance. Species of *Selandria*, *Blennocampa*, *Fenusa*, and *Nematus* were taken occasionally.

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[*] FOWLER, C., *British Coleoptera*, 1899, vol. iii, p. 228.

[†] MEYRICK, E., *Handbook of British Lepidoptera*, London, 1895.

Hemiptera.

Although the various species of Aphididæ occurring in the association were not studied, their importance must not be lost sight of. The species of this important family are the prey of lace-wing flies, lady-bird beetles and the larvæ of hover-flies. As many of the predatory species seem to confine their activities to one or perhaps a few species of Aphids (*oligotrophic*), the presence and numbers of the latter are in great measure determinative of the abundance of the various species of their enemies.

Capsidæ are fairly well represented in the herbage of meadows. One species, *Pithanus Maerkeli*, rarely occurs in the fully developed form, and likewise the Reduviid bug, *Nabis limbatus*, was always micropterous. Of the Cimicidæ, two species of *Anthocoris* were quite common (Table VII).

. Cuckoo spits were abundant during the summer months, and, of the three species, *Philænus spumarius*, which occurred in great numbers, must exact quite a heavy toll from its host grasses.

Hymenoptera.

The parasitic species of this order represent one of nature's most efficient controls of injurious insects. Various species were taken in large numbers among herbage and, including those reared from hosts occurring in the association, there were in all thirty distinct species, without Chalcids. The host was not determined in each case, but in order to make Table IX (*q.v.*) fairly complete, the works of Morley [*] and Brischke [†] were frequently consulted, and probable hosts suggested. The extent of this indebtedness has been indicated in this table.

Other Hymenopterous species which frequent meadows and pastures are the anthophilous bees (Apidæ), of which *Andrena trimerana*, *Andrena fulva*, and *Andrena nitida* occurred commonly on the flowers of *Trifolium repens* and *T. pratense.*

Vespa vulgaris, which had its nest under the shady bracken in Glover's Meadow, —where the soil was rather light—was noted as especially busy in late summer frequenting the foliage of potatoes in the adjacent field. Its activities seemed to be related in some way with the potato-infesting aphis, probably gathering the sweet secretion which the latter exudes on the leaves.

The black variety of the fossorial wasp *Crabro quadrimaculatus* invades meadows from wooded areas. This species burrows in rotten wood and provisions its nest with gnats and other small Diptera, frequenting herbage in search of its prey. It is one of the most abundant species of the genus.

Ants occurred commonly in the Alluvial Meadow in midsummer. They seemingly all belonged to the same genus, *Myrmeca.* A black ant of larger size, *Lasius* sp., was found near the boundary of meadow and wood. It was evidently the same

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[*] Morley, C., *British Ichneumons*, 4 vols., 1903–11, Plymouth.

[†] Brischke, C. G. A., "Die Ichneumoniden der Provinzen West- und Ost-Preussen," *Schr. d. Naturfors. Ges. Danzig*, vol. iv, pt. 3, pp. 35–121 ; *loc. cit.*, vol. iv, pt. 4, pp. 108, 210 ; *loc. cit.*, vol. v, pt. 3, pp. 121–199.

species as the author found early this year (1915) hibernating in the larval galleries of *Rhagium bifasciatum* in a felled tree at Whaley Bridge, Cheshire.

SOIL-INSECT CENSUS.

The interest of an analysis of the insect numbers and species of definitely measured samples of soil first appealed to the author after perusing the data collected by various workers in their investigations upon the food of birds. In any given locality, a study of the relative abundance of the insect species and of the various birds which prey upon them, would be productive of much important information. Hitherto, most insectivorous birds have been classified as "useful," but one must discriminate between those which feed on pests and those which feed on insects that are themselves predaceous and therefore beneficial. It is extremely doubtful if a bird distinguishes between different insect species so far as to select one more than others as its prey. The fact that one species may predominate in a bird's diet, as shown in post-mortem dissection, merely demonstrates that at a given time the particular insect was either very abundant or the most accessible in the district from which the bird was taken. Necessarily, to be complete, the insects which belong to each of the vertical strata of an association should be considered. But for such birds as starlings, rooks, and lapwings, which are typically ground-feeders, only the surface and subterranean insect strata need be dealt with.

At the outset of the survey, whilst tentative efforts were being made to grasp the associational aspects of the insect complex, the very great abundance of Tipulid larvæ in the Alluvial Pasture and their practical non-existence in Glover's Meadow seemed to require explanation. In the case of wireworms, the facts were almost exactly reversed. Therefore, in order to ascertain whether there were similar or parallel phenomena with regard to other species due to the same or allied causes, the analysis assumed the form of a comparison between definitely measured samples of the two grasslands. It must be remembered that they differed principally as regards altitude and exposure, water-content of their soils, which were respectively alluvial and clay loams, and also in the texture of their soils, a fact which naturally depends on their different origins. In its ultimate composition, the flora did not differ greatly in the two. One field, however, the Alluvial, was grazed by cattle whilst Glover's was left undisturbed. As these points have already been dealt with in detail, this brief restatement will be quite sufficient here.

The method of procedure consisted in cutting out samples of soil of one cubic foot capacity. After the adhering plant-species had been determined, and, in a general way, their relative abundance, each sample was thoroughly and systematically investigated in the laboratory. As far as possible all insects, whether in the egg, larval, pupal, or adult condition, were enumerated. Tables X and XI represent briefly the results which this research produced. All insect specimens, whether they lived in the ground or merely inhabited the surface, are included in the two tables.

Although it may be argued that some of the species are not strictly soil insects according to the strict usage of the definition, viz. parasitic Hymenoptera (Table X, sample 1), yet it may just be possible that even they may be identified with the soil or with soil-inhabiting forms at some stage of their life-histories.

The census was carried out during the period extending from October to March (1913–14). The author recognises that, for completeness sake, the investigation should have covered a whole year. This, however, was not possible at the time, as the work was interrupted by his departure for America. Still, there is this much to be said in favour of a winter census, that the variation in the constitution of the subterranean and surface fauna is less at this season than during any other of the year. Most soil insects hibernate as larvæ and pupæ, and so the variation is reduced to one of size and development of the individual species. Many larval forms do not even vary to this extent, as, with a cessation of feeding and a general suspension of all activities consequent on the lowering of temperatures, there is an inhibition of growth. Before and after the two months stated, metamorphoses progress much more rapidly. From April to September many of the larvæ of the soil inhabitants have attained the imaginal stage, the adults now frequenting the aerial stratum. Therefore it may be justly contended that one is likely to get a much better idea of the soil-insect fauna during the winter than at any other season.

In passing, it may be worth while to draw attention to the fact that many of the insect larvæ which one commonly encounters in the soil have not as yet been adequately described, and some, indeed, not at all. Insufficient knowledge of the premature stages of an insect renders accuracy of identity oftentimes extremely difficult and uncertain. Where not otherwise possible, the species of the larva or pupa can only be determined with exactness by rearing the imago and having this identified. Where success did not always attend the rearing of a species, it was at least possible to indicate the family and sometimes also the genus.

Assuredly a wide field exists for the scientist who is willing to undertake life-history studies of either predaceous or phytophagous, soil-inhabiting insects. Especially is there a lack of information of the facts pertaining to the life-histories of species of Empidæ, Asilidæ, Therevidæ, Leptidæ, and Tabanidæ. As for the Stratiomyiidæ, the larvæ have been classified by LUNDBECK,* but the key must be used with reserve, as his examination did not exhaust the larvæ of all species. In the course of our investigations one or two larvæ of the family were collected, the characters of which would not fit with the descriptions of any in this author's list. The same lack of information applies to the larval forms of most other families and orders besides those of Diptera.

In point of number of species as well as of specimens, the orders most extensively represented in our soil census are Coleoptera and Diptera. Of Lepidoptera, there were a few surface caterpillars (Noctuidæ) which occurred in 4 of the 11 samples

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* LUNDBECK, W., *Diptera Danica*, Copenhagen, 1907, pt. 1, pp. 73–75.

taken from Glover's Meadow and in 1 of the 14 from the Alluvial Pasture. Three species of sawfly, 2 cocoons and 1 larva, 2 specimens of an adult Ichneumon (*Hemiteles necator*), and 1 specimen of an adult Braconid (*Blacus ruficornis*) represented the sum-total of Hymenoptera, all taken in 4 samples (Table X, examples 1, 3, 4, 7) from Glover's Meadow. Hemiptera, except for the occurrence of the remains of the 7 specimens of *Schizoneura* sp. in sample No. 6 of the Alluvial Pasture, were entirely lacking. This circumstance would tend to show that the grassland Hemiptera winter in the egg stage, which may have been overlooked. Of course, it is possible that they betake themselves to winter quarters elsewhere, or, perhaps, in an alternate form (*Aphidæ*), migrate to other plant species outside the grassland association. The Apterygota were fairly well represented, considering the location of the two fields and the size of the samples investigated. Being principally humus-feeders, the species of this order are generally associated with decaying vegetable substance. They occurred in 2 Glover's samples and in 6 of the Alluvial.

It was at first thought that some degree of relationship might be discovered between certain of the phytophagous soil insects of the two grasslands and some of the plant species existing therein; but for definite and conclusive results, it is recognised that a more restricted analysis would be necessary. In meadows and pastures, with their heterogeneous mixture of grasses and weeds, it is extremely difficult to diagnose the constancy, or otherwise, of the feeding habits of any one species, especially if it be graminophilous and also polytrophic. Again, many forms that find nourishment in the roots of grass will subsist equally well on those of various weeds.

The samples taken from the Alluvial Pasture, in which perennial rye-grass (*Lolium perenne*) predominated or was common, generally yielded several specimens of Cecidomyiidæ (*C. destructor*, *L. auricincta*), Bibionidæ (*B. Marci*), and Tipulidæ (*T. oleracea*); but, probably, according to the evidence as obtained from Glover's Meadow samples, *L. auricincta* is equally attached to sheep's fescue (*Festuca ovina*). General conclusions, however, are difficult to establish. In sample No. 4 (Table XI) none of the insect species of the families above mentioned were taken, and in sample No. 12 only 2 Cecidomyiidæ occurred. A greater or less degree of association could be traced between the numbers of species of these same families and the relative abundance of perennial rye-grass in Glover's Meadow, but in sample No. 1 (Table X), where the only grass was Yorkshire fog (*Holcus lanatus*), both Cecidomyiidæ and Tipulidæ are represented; whereas, in sample No. 5, with perennial rye-grass predominant, no specimens of either family were present.

It may be interesting to mention here that the larvæ of *Bibio Marci* and *Tipula oleracea*, especially the younger stage forms, more often than not occurred gregariously, which socialistic mode of existence—a phase of the phenomenon of what DEWITZ calls stereotropism*—seems to be the result of a response to the stimulus of contact between larvæ of the same species.

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* DEWITZ, J., "The Bearing of Physiology on Economic Entomology," *Bull. Ent. Res.*, vol. iii, pt. 4, p. 345.

Out of the 25 samples from both fields specimens of Neuroptera, cocoons of *Chrysopa vulgaris*, occurred only once in sample No. 7 of Glover's Meadow, selected from the western boundary adjacent to the wood. The larvæ had probably been feeding on tree-infesting aphids before descending to the ground to spin up the silken domiciles in which they spend their period of inactivity.

It will be at once evident by consulting Tables X and XI that the majority of the species of soil insects, according to our census, belong to the two great orders Coleoptera and Diptera. In the first of these orders, again, they are ranked for the great part in the families Carabidæ, Staphylinidæ, Silphidæ, Scarabæidæ, Sphæridiidæ, Lampyridæ, Telephoridæ, Elateridæ, and Curculionidæ. The kind of soil determines in great measure the species that may be present in any given locality; thus, many Carabid species will be found only in light soils, whilst others are more frequently met with in damp and heavy soils, e.g. *Anchomenus*, *Nebria* (Table IV). Similar selective habits hold good for Staphylinid species, e.g. *Tachinus*, *Tachyporus*, *Xantholinus Oxyporus* (*loc. cit.*), for many of which the presence of decaying vegetable matter or humus is essential. Some, for instance, are invariably associated with dead moist leaves on the forest or woodland floors and, being negatively phototropic, will retreat from more open conditions. Species of Sphæridiidæ, Silphidæ, and Scarabæidæ are associated with decaying animal and excrementitious matter, the species of Sphæridiidæ being chemotactic to dung, those of Silphidæ to putrefying flesh. The larvæ of Telephoridæ often occur in grassland soil where they also pupate. Their food-habits are believed to be predaceous, but it is the author's suspicion, engendered by observation and experience, that certain of them may also be vegetarian and even find nourishment in the products of decaying vegetable tissue. Lampyrid larvæ frequent moist localities, where they are most likely to find their terrestrial slug-hosts. As for wireworms, any sort of meadow seems to offer suitable conditions, provided it is not too damp, and our investigation shows that the higher-lying and drier situation of Glover's Meadow harboured these pests in far larger number than the fluviatile pasture below. But it is just possible that the proximity of the former to the ruderal associations of cultivated root crops, such as potatoes and mangolds,—where examination showed that wireworms were quite common—might adequately explain this difference of infestation. The imagines often migrate from cultivated crops to meadows and pastures and, being the nearer of the two, Glover's Meadow would be likely to receive the larger quota of migrants.

Among Diptera, the families most extensively represented in the soil—generally in the egg, larval, and pupal stages—are Cecidomyiidæ, Mycetophilidæ, Chironomidæ (a few), Bibionidæ, Tipulidæ, Stratiomyiidæ, Tabanidæ (in moist earth near water), Asilidæ, Therevidæ, Empidæ, Dolichopodidæ, Platypezidæ, Syrphidæ, Sarcophagidæ, Muscidæ, Anthomyiidæ, Cordyluridæ, Lonchæidæ, Sapromyzidæ, Sepsidæ, Borboridæ, and Phoridæ (a few). The larval habits vary. Some are predaceous and forage for their prey, such as those of Leptidæ, Asilidæ, Therevidæ, Empidæ, and Dolichopodidæ probably. In the majority of cases, dipterous larvæ are attracted to those soils which are rich in decaying vegetable or animal matter. Some, however, will attack healthy growing roots, as witness the depredations of *Tipula oleracea*, *Dilophus febrilis*, and *Chortophila brassicæ*. Many more examples of pest species might be cited, besides others suspiciously near the border line. Observations require to be made in order to ascertain to what extent an insect species is capable of adapting itself to new feeding habits in the absence of the accustomed diet—whether, indeed, there may not be a certain faculty of accommodation of taste for healthy or decaying animal and vegetable tissues or matter. The author has on one occasion taken an almost mature larva of *Tipula oleracea* at the roots of grass with a partly destroyed Anthomyiid larva in its jaws. Had it mistaken the maggot for a grass root? Surely a novel diet!

Those samples wherein the weed species were rather common—*Ranunculus repens*, *Trifolium repens*, and *Plantago lanceolata*—seemed to provide better conditions for the activities of predaceous soil-inhabiting larvæ on account of the lesser binding effect of their roots on the soil particles, than is the case with those grasses. So it was in these that species of Empidæ occurred most frequently, but at no time in any great abundance, like the phytophagous Bibionid and Tipulid larvæ. In those areas of the Alluvial Pasture which were sodden with moisture, they occurred not at all, but, otherwise, would be about equally represented in both fields.

The herbaceous perennials of grasslands, by the death and decay of their leaves and flowering parts, add annually to the soil an appreciable amount of rotting vegetable tissue and humus, which serve to attract numerous scavenging Diptera and Coleoptera. The component species were in this respect very similar in the two fields, a fact which applies with equal truth to the species of humus-feeding Apterygota for which moisture is essential. Seeing that the Alluvial Pasture was grazed by cattle whilst Glover's Meadow was undisturbed, one would have naturally concluded that coprophilous Coleoptera would have been scarcely, if at all, represented in the latter. As regards the larvæ, this was actually the case, but, as Table X shows (samples Nos. 5, 6, 11), the imagines of *Aphodius fimetarius* occurred fairly frequently; whereas, at the time of the census, no species of Scarabæidæ were taken in the Alluvial Pasture samples. As a matter of fact, *Aphodius fossor*, *A. fimetarius*, *A. contaminatus*, and *A. prodromus* occurred frequently at cow-droppings in the Alluvial Pasture. That *A. fimetarius* was taken in Glover's Meadow may be accounted for by the fact that it may have been merely an invader sheltering or resting amongst the herbage. But some specimens occurred beneath the surface of the ground where, on several occasions, the remains of this pretty Scarabæid were met with. It is just possible that after oviposition in the autumn, the adults may burrow into the soil near where the eggs have been laid, or they may wing their way to meadows further afield previous to their demise at the roots of grasses. The presence of *Sphæridium scarabæoides* in Glover's Meadow may be readily explained on the supposition that this species, besides being coprophilous, may also feed on humus and decaying vegetable matter.

Of Curculionidæ, species of *Sitones* were more numerous in the Alluvial Pasture, but the only two species of *Hypera* occurred in Glover's Meadow (*cf.* samples Nos. 2, 4). Larvæ of *Otiorhynchus sulcatus* were about equally distributed in both fields, but never very numerous.

Perhaps with such small numbers as our census represents, no really strict comparison should be drawn between the faunistic composition of the two areas. The physical-factor differences of the two were very restricted and confined mostly to those of soil, water-content, altitude, and exposure, to which is added the fact of the Alluvial Pasture being also grazed. Impartially, the facts as revealed by the census, in broad outlines, tend rather to indicate that, in this country at least, the soil-insect fauna of grassland in any given locality is not likely to vary to any great extent. Of one thing the author is convinced, and that is, large numbers of specimens must be treated of in order to throw minor differences due to variable local conditions into bold relief.

In addition to insects alive and dead, one encounters in the soil representatives of Araneida and Acarina, Annelida and Mollusca, not to mention fruits and seeds, all of which may form food for ground-feeding birds. In many cases they are definitely associated with insects, either preying on or being preyed upon by the latter. Spiders are quite prevalent, and mites of the genera *Gamasus*, *Trombidium*, and *Smaris* are not infrequent, as are likewise various species of worms. Generally, in those samples which bore a covering of moss on their surface, two species of shelled Mollusca, *Cochlicopa lubrica* and *Vitrea nitidula*, were quite common, as well as specimens of the slug *Arion circumscriptus*, and innumerable slug eggs. Earthworms of various species and their cocoons, as one would naturally expect, were abundant in almost every sample.

Soon after the work of the soil-insect census had been commenced, the author's attention was directed to a paper by M'Atee,* in which, from an enumeration of all the insects and other invertebrates, besides seeds and fruits, present in four square feet of forest floor near Washington, U.S.A., it was calculated that, for the particular locality specified, there were in each acre 1,216,880 animals belonging variously to Insecta, Arachnida, and other Arthropoda, Annelida, and Gastropoda, and 2,107,810 seeds and fruits. Truly formidable figures! which almost pale into insignificance in the light of this same author's calculation, on a similar basis, of the numbers in one acre of meadow land for the same locality, viz. 13,654,710 animals and 33,822,745 seeds!

Of course, these numbers only apply to the class of soil surface indicated and to the particular locality stated. As a basis for general conclusions they avail nothing. It would, further, be absurd to deny that these figures might not be

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* M'Atee, W. L., "Census of Four Square Feet," *Science*, N.S., 1907, vol. xxvi, pp. 447–449.

easily reversed. If an area of four square feet in a forest included a decaying tree with its myriads of Scolytidæ and other wood-borers, the figures which would be obtained would probably surpass any that could be derived from a census of any meadow area of the same size.

In conclusion, it is my privilege to be able to express here my gratitude to the following gentlemen who courteously assisted in the identification of much of the material, more particularly Diptera, Coleoptera, and Hymenoptera:—Mr F. E. Edwards, Natural History Museum, London; Mr J. E. Collin, Newmarket; Mr C. Morley, Natural History Museum, London; and Mr J. Ray Hardy, Manchester Museum. For the rest, the author found the entomological collections under the charge of the last-named of invaluable assistance, and they were constantly consulted.

SUMMARY.

1. In any given locality the composition of the insect association is determined by a complex of factors, which may be classified as follows, viz. physical, physiographical, topographical, and vegetational. Primarily, it is dependent upon the ecological type of the vegetation.

2. The most accurate index of the various physical factors surrounding animals is the "evaporating power of air."

3. The insects of a given association may not be strictly confined to it. It is therefore necessary to distinguish between those species which are peculiar or proper to an association, and those which owing to a response to varying stimuli, play the rôle of invaders.

4. In all cases the criterion of an insect's true surroundings or habitat is the place where it breeds. It must be also recognised that as the facies of a habitat changes so also will its fauna (phenomenon of *succession* of organisms).

5. A census of soil-inhabiting insects is of interest in relation to the problem of the food-habits of ground-feeding birds.

6. A comparison of the soil-insect fauna of two areas which differ radically as regards their soil-types and vegetational covering is of intrinsic importance in obtaining a solution to the question in what measure the faunistic differences can be explained by variations of edaphic factors.

7. In a restricted way the study of the two grasslands, Glover's and Alluvial, was productive of much information on differences of their soil-insect fauna. In this connection the food-habits of the various species rank as of primary consideration.

Correction.

It is necessary here to rectify an error which occurs in the explanation of the plates on p. 203 of the paper, "The Insect Fauna of the Soil," *Jour. Econ. Biol.*, vol. viii, pt. 3. Larva of *Rhyphus fenestralis* should read larva of Tipulid.

TABLE 1.

Diptera proper to the Association recorded from Alluvial, Glover's, and other Meadows and Adjacent Wooded Coppices.

In the first column the family name applies to all species opposite it and which follow it in column two. In the third column the numbers refer to the various months in which the adults were collected.

Abund. = abundant; v. com. = very common; com. = common; f. com. = fairly common; occ. = occasional; infreq. = infrequent; † indicates that the species has also been found in cultivated crops or ruderal associations; * in forest associations; ‡ generally found in moist situations.

Family.	Species.	Month.	Occurrence.	Remarks on Habits.
CECIDOMYIIDÆ	*Lasioptera auricincta*, Winn.	5	occ.	Larvæ and pupæ at roots of *Festuca ovina*.
	†*Cecidomyia destructor*, Say.	5, 8	com.	Pupa is the "flax-seed" in decaying grass; the species commonly attacks meadow grasses, *Triticum* and *Phleum*.
	†*Diplosis tritici*, Kirkby	5, 6	,,	Attacks *Triticum* besides cultivated graminaceous crops; fully fed larva, "Red-Maggot," pupates in the soil.
MYCETOPHILIDÆ	*Sciara Thomæ*, L.	10	occ.	Larvæ among grass at the base of the stems.
	,, *quinquelineata*, Mcq.	3	,,	Larvæ among decaying tubers.
	,, *pulicaria*, L.	10	,,	,, ,, ,,
BIBIONIDÆ	*Bibio Marci*, L.	3, 4	v. com.	Larvæ often in masses at roots of meadow grasses.
TIPULIDÆ	**Pachyrrhina histrio*, F.	6	occ.	Larvæ in rotten wood.
	† ,, *maculosa*, Mg.	5	v. com.	Larvæ infesting adjacent potato crop and also in meadow soil.
	Tipula nigra, L.	9, 10	occ.	A single larva taken at roots of grass pupated at the end of September.
	,, *lateralis*, Mg.	6, 8	com.	Larva infesting potato field.
	† ,, *oleracea*, L.	7, 8	abund.	Larva attacking root crops and meadow grasses.
	† ,, *ochracea*, Mg.	7	occ.	Larva probably similar to that of previous species.
LEPTIDÆ	†*Leptis scolopacea*, L.	4, 7	v. com.	Larva free in soil and also in decaying seed tubers.
	† ,, *tringaria*, L.	7, 8	com.	Larva in decaying seed tubers.
	,, *lineola*, Fab.	6	,,	Larva probably in the soil.
EMPIDÆ	‡*Rhamphomyia sulcata*, Fln.	7, 8	,,	Larva free in soil, adults on low herbage in moist places.
	,, *longipes*, Mg.	6	,,	Larva free in soil, adults on low herbage. Hitherto recorded mostly in the South of England, from the New Forest.
	Empis livida, L.	6, 7	abund.	Larvæ free in soil; adults frequent herbage to prey on smaller Diptera.
	,, *lutea*, Macq.	6	occ.	Habits probably similar to those of *E. livida*.
	,, *unicolor*, Brullé	8	,,	,, ,, ,, ,,
	Hilara maura, F.	8	com.	Larvæ according to BRAUER (p. 61)[1] in mole-burrows.
DOLICHOPODIDÆ	*Dolichopus griseipennis*, Stann.	8	occ.	Larvæ probably in decaying vegetation.
	Dolichopus atratus, Mg.	6, 8	,,	,, ,, ,, ,,
	‡*Pœcilobothrus ducalis*, Lw.	8	v. com.	Adults on low herbage in damp places.

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[1] BRAUER, F., "Die Zweiflügler des Kaiserlichen Museums zu Wien," *Denkschr. der Kais. Akad. der Wiss., math.-naturwiss. Classe*, Wien, 1883, vol. xlvii.

TABLE I—*continued.*

Family.	Species.	Month.	Occurrence.	Remarks on Habits.
DOLICHOPODIDÆ . (*cont.*)	‡*Gymnopternus metallicus*, Stan.	8	com.	Adults very active, living in communities in damp herbage.
	Porphyrops spinicoxa, Lw.	8	v. com.	Larva probably in soil as described by BELING (p. 226, 1882)[1] in the case of *P. crassipes*.
PLATYPEZIDÆ .	*Platypeza modesta*, Ztt. .	9, 10	occ.	Larva in humous soil in meadow land and may also be coprophilous.
SYRPHIDÆ . .	*Pipiza quadriguttata*, Mcq.	5, 6	,,	Larva aphidivorous, adult anthophilous like most Syrphids.
	Melanostoma mellinum, L.	6	infreq.	Larva aphidivorous, adult anthophilous like most Syrphids.
	Ascia podagrica, Fab. .	6	,,	Larval habits unknown; adults on low herbage.
TACHINIDÆ . .	*Siphona geniculata*, Deg. .	5, 6	com.	Larva probably parasitic on Lepidopterus larva.
ANTHOMYIIDÆ .	†*Chortophila brassicæ*, Bché.	6, 9	v. com.	Larva attacks cabbage roots; adult sheltering among herbage.
	Pegomyia bicolor, W. .	6–9	com.	Larva mines in leaves of *Rumex* spp.
	,, *nigritarsis*, Ztt. .	6–9	occ.	,, ,, ,,
	,, *hyoscyami*, Pz. .	6–9	,,	Larva mines in leaves of marigolds and other plants (CAMERON, p. 50, 1914)[2]; adults taken rarely, resting among herbage.
	Caricea tigrina, F. . .	7	infreq.	One specimen reared from larva at roots of grass; adults in moist meadow places.
	Cœnosia lineatipes . .	6	,,	One larva found and reared under similar conditions as the previous; probably both species are more often coprophilous.
MICROPEZIDÆ .	*Calobata petronella*, L. .	8	,,	Adults on low shrubs.
TRYPETIDÆ . .	*Spilographa zoë*, Mg. .	5, 8	occ.	Larva mines in leaves of *Senecio* spp.
OPOMYZIDÆ . .	*Balioptera tripunctata*, Fln.	7, 8	v. com.	Larva probably lives in stems of herbaceous plants; adults numerous in herbage.
	,, *combinata*, L. .	7, 8	,,	Habits similar to the previous species.
	Opomyza germinationis, L.	7, 8	abund.	Larva unknown; adults in herbage.

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[1] BELING, TH., "Beitrag zur Metamorphose der zweiflügeligen Insecten aus den Familien Tabanidæ, Leptidæ, Asilidæ, Empidæ, Dolichopidæ, und Syrphidæ," *Archiv für Naturges.*, Jahrg. 48, Heft 2.

[2] *Op. cit.*, 1913, vol. viii.

TABLE II.

Coprophilous and other Scavenging Diptera recorded in the Association, Intruders.

Abbreviations as in Table I. † indicates that the species is also a pest on cultivated crops; * indicates that the species is characteristic of forest or wood associations; ‡ the species is generally found in moist situations.

Family.	Species.	Month.	Occurrence.	Remarks on Habits.
BIBIONIDÆ .	*Scatopse notata*, L. . .	5-9	com.	Larvæ in cow-dung, humous soil and decaying vegetable matter.
	,, *inermis*, Ruthe. .	6-9	,,	Larval habits similar to the previous.
	†*Dilophus febrilis*, L. . .	6-10	v. com.	Larva in cow manure.
CHIRONOMIDÆ .	*Orthocladius stercorarius*, Deg.	...	occ.	Larva in cow-dung and humous earth.
PSYCHODIDÆ .	*Pericoma*, sp. . . .	6-9	com.	Larva in decaying vegetable substance.
TIPULIDÆ .	*‡*Poecilostola punctata*, Schrk.	8	occ.	Larva probably in rotten wood in marshy places.
	‡*Limnophila discicollis*, Mg.	6	,,	BRAUER (p. 54)[1] quotes PERRIS, who took the larva of an allied species, *L. dispar*, in the stems of *Angelica sylvestris*. *L. fuscipennis* has been reared from larvæ in rotten wood.
	Trichocera hiemalis, Deg. .	12-3	com.	Larva in decaying vegetation.
RHYPHIDÆ .	*Rhyphus fenestralis*, Scop.	6-9	,,	Larva in decaying vegetable substance.
STRATIOMYIIDÆ	*Chloromyia formosa*, Scop.	6, 7	infreq.	One specimen reared from larva found in meadow soil probably associated with humus or manure.
	Microchrysa polita, L. .	6-9	com.	Larva in decaying vegetable matter and in dung.
	,, *flavicornis*, Mg.	6, 7	infreq.	A single specimen reared from a larva found in meadow soil.
	Chorisops tibialis, Mg. .	...	rare	A single larva found in meadow soil.
XYLOPHAGIDÆ .	**Xylophagus* sp. . .	...	,,	Larvæ in rotten beech, 30.1.13.
LONCHOPTERIDÆ	*Lonchoptera lutea*, Pz. .	7, 8	abund.	Larvæ in decaying vegetable substance.
SYRPHIDÆ .	*Orthoneura elegans*, Mg. .	6	rare	The larvæ of all live either in decaying vegetable or animal matter; that of *P. albimanus* I have also observed feeding on Aphids. The adults frequent various meadow flowers, Compositæ and Ranunculaceæ.
	Liogaster metallina, Fab. .	7, 8	com.	
	Chrysogaster hirtella, Lw.	6, 7	,,	
	,, *viduata*, Fall.	6	occ.	
	Platycheirus albimanus, F.	5-8	v. com.	
	,, *clypeatus*, Mg.	5	com.	
	,, *scalaris*, Fab.	6	,,	
MUSCIDÆ .	*Onesia sepulcralis*, L. .	5, 9	,,	Larva in decaying vegetable and animal matter; adults, which frequent flowers, are said by GEOFFROY and ROBINEAU-DESVOIDY (SCHINER, vol. i, p. 576)[2] to be oviparous.
	Pollenia rudis, F. . .	9	,,	Larvæ in humous soil and in dung; adults sluggish and lazy often cluster on walls.
	Myiospila meditabunda, F.	9	,,	Larvæ in decaying vegetable substances.
	Pyrellia cadaverina, L. .	6, 9	,,	Larva in cow-dung.
ANTHOMYIIDÆ .	*Hyetodesia incana*, W. .	9, 10	,,	Larva in humous soil and decaying vegetable matter.
	,, *lucorum*, Fln. .	6	infreq.	,, ,, ,, ,,
	,, *errans*, Mg. .	6	occ.	,, ,, ,, ,,
	,, *signata*, Mg. .	9	com.	,, ,, ,, ,,
	Spilogaster duplicata, Mg.	8	occ.	Larva in cow-dung.

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[1] BRAUER, F., *loc. cit.*

[2] SCHINER, J. R., *Fauna Austriaca: Die Fliegen*, Wien, 1862, vol. i.

TABLE II—*continued.*

Family.	Species.	Month.	Occurrence.	Remarks on Habits.
ANTHOMYIIDÆ (*cont.*)	*Spilogaster depuncta*, Fln.	6	com.	Larva in cow-dung.
	Hydrotæa irritans, Fln.	8	,,	Larva in humous soil and cow-dung.
	,, *dentipes*, F.	6, 7	,,	Larva in manure.
	Hylemyia variata, Fln.	5, 8, 9	v. com.	Larva probably in decaying vegetable and other substances.
	,, *pullula*, Ztt.	8	infreq.	Habits of larva similar to the previous species.
	,, *strigosa*, F.	5, 9	com.	Larva in manure and fungi.
	†*Anthomyia radicum*, L.	5–11	v. com.	Larva in dung, humous soil; also attacks cabbage roots like *C. brassicæ*.
	,, *sulciventris*, Ztt.	8	occ.	Larval habit unknown; adults shelter among herbage.
	Chortophila striolata, Fln.	5, 8	com.	Larva in dung.
	† ,, *sepia*, Mg.	5	,,	Larva said to live in cornstalks (BRAUER, p. 71).[1]
	Homalomyia scalaris, F.	8	infreq.	Larva probably in manure.
	,, *canicularis*, L.	7–10	com.	Larva in manure, dung, decaying vegetable substance.
CORDYLURIDÆ	*Norellia spinimana*, Fln.	8	infreq.	This species said to have been reared from the larva of *Anthomyia versicolor*; larva also said to have been found in the stems of *Rumex aquaticus* (BRAUER, p. 93).[1]
	Scatophaga scybalaria, L.	7	com.	Larva in cow-dung; adults frequent herbage to prey upon other smaller insects.
	,, *stercoraria*, L.	6–10	abund.	
	,, *squalida*, Mg.	6, 7	com.	
HELOMYZIDÆ	‡*Helomyza pectoralis*, Lw.	9	occ.	Larva in fungi and decaying vegetable matter; adults frequent moist, shady places.
LONCHÆIDÆ	*Lonchæa chorea*, F.	5, 7	com.	Larva in manure.
	Lauxania ænea, Fln.	8	occ.	Larva said by WINNERTZ (BRAUER, p. 90)[1] to live in stems of *Viola tricolor*; probably live in manure.
SEPSIDÆ	*Sepsis cynipsea*, L.	7, 9	v. com.	Larva in decaying vegetable substance.
BORBORIDÆ	*Borborus nitidus*, Mg.	7, 8	,,	Larva in dung and refuse.
	,, *equinus*, Fln.	7, 8	,,	,, ,, ,,
	Limosina fontinalis, Fln.	7, 8	com.	Larva in decaying vegetable matter and dung.
PHORIDÆ	*Phora rufipes*, Mg.	6	infreq.	Larva in decaying vegetable matter; various authors record it as parasitic on other Diptera and Lepidoptera.

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[1] BRAUER, F., *loc. cit.*

TABLE III.

Aquatic Diptera recorded in the Association, Intruders.

Abbreviations as in Table I. † Indicates that the larval habits are not definitely known and only tentatively indicated.

Family.	Species.	Month.	Occurrence	Remarks on Habits.
SIMULIIDÆ .	*Similium maculatum*, Mg.	8	occ.	Adult in moist places in herbage.
CHIRONOMIDÆ .	*Chironomus annularis*, Deg.	8, 9	,,	,, ,, ,,
CULICIDÆ .	*Culex pipiens* . . .	7, 8, 9	,,	Adults rest among meadow grasses.
TIPULIDÆ .	*Ptychoptera albimana*, Mg.	8	com.	Larva in stagnant water.
	†*Rhypholophus nodulosus*, Mg.	5, 6	infreq.	Larva probably in marshy places or wet margins of ponds.
	†*Erioptera trivialis*, Mg. .	6	,,	Supposedly either wholly aquatic or mud-inhabiting in larval stage.
	†*Amalopis* sp. . . .	6	occ.	Larva of an allied species, *A. Schineri* (BRAUER, p. 54)[1] in spring water.
TABANIDÆ .	*Hæmatopota pluvialis*, L. .	5-7	com.	According to BRAUER (p. 60),[1] larva lives in earth ; more probable that it is aquatic.
LEPTIDÆ . .	*Atherix Ibis*, F. . .	8	occ.	The adult female lays her eggs on twigs overhanging ponds. The eggs are cemented together and to the body of the female by a sticky substance. Often whole masses of eggs and dead females may encrust a twig.
SYRPHIDÆ .	*Eristalis tenax*, L. . .	8	com.	The larvæ in stagnant water. *E. tenax* is cosmopolitan and will breed in drains and sewage systems. The larva is the reputed "rat-tailed" form.
	,, *horticola*, Deg. .	8	occ.	
	Helophilus pendulus, L. .	5	,,	
	,, *lineatus*, Fab. .	8	com.	
SCIOMYZIDÆ .	†*Neuroctena anilis*, Fln. .	6	occ.	Adults frequent moist meadows.
	†*Tetanocera lævifrons*, Lw. .	7	,,	Probably aquatic. Larva of *T. ferruginea* has been found under leaves of water weeds, *Lemna* and *Callitriche* (BRAUER, p. 84).[1]
EPHYDRIDÆ .	†*Hydrellia griseola*, Fln. .	10, 11	v. com.	Larvæ probably semi-aquatic, inhabiting leaves of water plants. Adults occur abundantly in moist places. *H. albilabris* occurs as larva and pupa in the leaves of *Lemna*. Other species are recorded from sap of trees by WILLISTON (p. 306).[2]

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[1] BRAUER, F., *loc. cit.*

[2] WILLISTON, T. W., *North American Diptera*, 3rd ed., 1908.

TABLE IV.

Coleoptera proper to the Association, recorded from Alluvial, Glover's, and other Meadows and Adjacent Wooded Coppices.

Abbreviations as in Table I. † indicates authenticated pests of trees or crops; ‡ indicates species frequenting damp places; * species which generally frequent woods or forests.

Family.	Species.	Month.	Occurrence.	Remarks on Habits and Habitat.
CARABIDÆ.	*Carabus nemoralis*, Müll.	9–12	f. com.	Several specimens found hibernating in Dec. under rubbish.
	Notiophilus aquaticus, L.	8–12	v. com.	Common everywhere in the locality.
	Leistus fulvibarbis, Dj.	10	occ.	In herbage.
	,, *ferrugineus*, L.	6, 7	infreq.	,,
	‡*Nebria brevicollis*, F.	7–11	abund.	The most frequently occurring Carabid; very general in moist places and especially so along banks of River Dane.
	‡ ,, *gyllenhali*, Sch.	7–11	infreq.	Often taken along with the previous species; not so general.
	‡*Loricera pilicornis*, F.	11–3	occ.	On the banks of the Dane, also at roots of trees; generally in moist places.
	Clivina fossor, L.	6–10	com.	Ubiquitous, in the soil.
	,, *collaris*, Hbst.	5–8	occ.	,, ,,
	Dyschirius sp.	4	...	Remains of a single specimen on banks of Dane.
	Bradycellus similis, Dj.	8–10	occ.	Usually in dry places in the meadows.
	†*Pterostichus madidus*, F.	6, 8	v. com.	Frequents cultivated as well as meadow land.
	,, *vulgaris*, L.	6, 7, 8	,,	Ubiquitous, in grass, under stones, cultivated land.
	‡ ,, *vernalis*, Pz.	4, 6	,,	Frequents marshy places, banks of Dane, and roots of grass.
	,, *striola*	6, 8	com.	Ubiquitous, but especially frequent amongst herbage.
	Amara apricaria, Pk.	6, 7	,,	In herbage.
	Calathus flavipes, Fourc.	8	infreq.	At roots of grass, in dry situations.
	Anchomenus angusticollis, F.	11, 5	v. com.	Abundant in grass and at roots of trees.
	,, *dorsalis*, Müll.	8, 5	,,	At roots of grass and trees.
	‡ ,, *parumpunctatus*, F.	11, 5	com.	Frequent in damp places; most specimens were collected in Glover's Meadow.
	‡*Bembidium littorale*, Ol.	6–12	,,	On banks of Dane and marshy places.
	‡ ,, *fluviatile*, Dj.	6, 12	v. com.	,, ,, ,,
	,, *lampros*, Hbst.	7, 9	occ.	Among meadow grasses.
	Trechus minutus, F.	5, 10	com.	In dry situations among meadow grasses.
STAPHYLINIDÆ.	*Homalota vicina*, Steph.	3–6	,,	At roots of grasses; this species was also taken among refuse.
	Tachyporus obtusus, L. var. *nitidicollis*, Steph.	7, 8	,,	All three species occurred in moss in Glover's Meadow.
	Tachyporus solutus, Er.	7, 8	occ.	
	,, *hypnorum*, F.	6, 7, 8	com.	
	‡*Quedius molochinus*, Gr.	7, 8	,,	At roots of grasses especially in moist places.
	Ocypus olens, Müll.	7, 9	,,	Larva frequently taken in herbage and in loose soil.
	,, *brunnipes*, F.	2	infreq.	A few specimens under stones in alluvial meadow.
	‡ ,, *cupreus*, Ross.	2	,,	Under stones and moist leaves.
	Philonthus politus, F.	8–10	com.	Occurred frequently in meadow soil.

TABLE IV—*continued.*

Family.	Species.	Month.	Occurrence.	Remarks on Habits and Habitat.
Staphylinidæ. (*cont.*)	‡*Othius fulvipennis*, F.	2	infreq.	In humous soil and moist leaves; also under bark of trees.
	Lathrobium fulvipenne, Gr.	10	,,	In moss in Glover's Meadow.
	*‡*Syntomium æneum*, Müll.	2	occ.	In moss in meadows; more frequent in leaves under trees.
Coccinellidæ	**Adalia bipunctata*, L.	6, 3	com.	Adults hibernate under wood; in summer they occur on trees, shrubs, and herbage.
	**Coccinella* 10-*punctata*, L.	7–12	f. com.	Adults hibernate under logs and leaves.
	**Halyzia* 14-*guttata*, L.	8, 2	infreq.	Adults occur on alder and other trees; hibernate as adults.
Nitidulidæ	*Brachypterus urticæ*, F.	6	com.	Adults on nettles.
	Meligethes rufipes, Gyll.	6	,,	On flowers of Ranunculaceæ.
	† ,, *æneus*, F.	6	abund.	On flowers of Compositæ, Cruciferæ, Ranunculaceæ.
	,, *difficilis*, Heer.	6	com.	On flowers of Labiatæ (*Lamium album*, *Stachys sylvatica*).
	,, *flavipes*, Stm.	6	,,	On flowers of Labiatæ, Umbelliferæ, and Compositæ (*Cirsium* sp.).
	**Rhizophagus bipustulatus*, F.	2	infreq.	Adults under bark; probably predaceous on wood-inhabiting larvæ.
Byrrhidæ	‡*Simplocaria semistriata*, F.	8	occ.	Adults in damp herbage, larvæ in decaying wood.
Elateridæ	‡*Cryptohypnus riparius*, F.	...	,,	Adults and larvæ in soil on banks of Dane.
	†*Athous hæmorrhoidalis*, F.	5	com.	Adults and larvæ in meadow soil as well as cultivated.
	†*Agriotes lineatus*, L.	5, 6	v. com.	,, ,, ,, ,,
	,, *pallidulus*, Ill.	5	com.	Adults in herbage.
	‡*Corymbites quercus*, Gyll	8	,,	In soil on banks of Dane.
	Campylus linearis, L.	7, 8	,,	Larvæ in soil at roots of grasses.
Telephoridæ	**Podabrus alpinus*, Pk.	5	occ.	On coppice, shrubs, oak, birch.
	Telephorus pellucidus, F.	5	freq.	On meadow flowers and on shrubs at the margins of meadow.
	,, *nigricans*, Müll.	5	com.	,, ,, ,, ,,
	,, *bicolor*, F.	5	f. com.	In grass and on flowers in meadow.
	Rhagonycha testacea, L.	5	com.	,, ,, ,,
	**Malthinus punctatus*, Fourc.	6, 7	infreq.	On oak, hazel, hawthorn.
	Malachius bipustulatus, L.	6	f. com.	In herbage and on flowers.
Chrysomelidæ	**Phyllodecta vitellanæ*, L.	6	com.	Adults on willows, hazel, and poplar.
	Longitarsus melanocephalus, De G.	9	,,	On herbage.
	†*Phyllotreta nemorum*, L.	7–9	v. com.	On cruciferous weeds.
	,, *vittula*, Redt.	7–9	com.	,, ,,
	,, *undulata*, Kuts.	7–9	occ.	,, ,,
	Aphthona sp.	2	...	One specimen hibernating under dead leaves.
	Plectroscelis concinna, Marsh.	9	com.	In herbage.
Anthicidæ	*Anthicus floralis*, L.	6	occ.	In herbage; a few were taken among vegetable refuse which is perhaps the true habitat of this species.
Curculionidæ	*Apion rubens*, Steph.	7–9	com.	On *Rumex acetosella*.
	† ,, *apricans*, Hbst.	7, 8	,,	On *Trifolium pratense*.
	,, *virens*, Hbst.	7, 8	,,	,, ,,
	†*Otiorhynchus sulcatus*, F.	5, 6	,,	Larva at roots of grasses in meadows; adults on surface of ground.
	**Strophosomus coryli*, F.	7	occ.	On hazel and oak.

TABLE IV—*continued.*

Family.	Species.	Month.	Occurrence.	Remarks on Habits and Habitat.
CURCULIONIDÆ (*cont.*)	*Phyllobius urticæ*, De G.	5	v. com.	On nettles.
	* ,, *argentatus*, L.	5	,,	On birches and young oaks.
	†*Barynotus obscurus*, F.	5, 6	occ.	Larvæ at roots of grasses, adults on surface of ground.
	Sitones hispidulus, F.	9, 10	com.	In pasture, larvæ at roots of clover, vetch.
	† ,, *lineatus*, L.	9, 10	,,	,, ,, ,, ,,
	,, *puncticollis*, Steph.	9, 10	,,	In pasture; larvæ at roots of clover, trefoil, and vetch.
	Hypera punctata, F.	9	f. com.	Larvæ at roots of clover.
	,, *polygoni*, L.	8, 9	com.	On *Leguminosæ*, *Polygonum*.
	,, *variabilis*, Hbst.	10	occ.	On *Leguminosæ*.
	Mecinus pyraster, Hbst.	9	,,	The larva lives in the galled flower-heads of *Plantago lanceolata*.
	Cœliodes quadrimaculatus, L.	5	com.	On the common nettle, *Urtica dioica*.
	Ceuthorhynchus hirtulus, Germ.	6	occ.	Larva in ovoid swellings at the base of the stem of *Draba* (*Erophila*) *verna* (Whitlow Grass).
	Ceuthorhynchus pollinarius, Först.	5	com.	On nettles.
	‡*Phytobius canaliculatus*, Fabr.	6	,,	On herbage in moist places.
SCOLYTIDÆ	*†*Scolytus destructor*, Ol	...	...	A single dead specimen taken in Glover's Meadow; its habitat is the elm tree.

TABLE V.

Coprophilous and other Scavenging Coleoptera recorded in the Association, Intruders.

Abbreviations as in Table I. The species represented are all more or less beneficial, being active in hastening the decomposition of organic substances and rendering it available as food for plants. * indicates species generally found in wood and forest.

Family.	Species.	Month.	Occurrence.	Remarks on Habits.
HYDROPHILIDÆ	*Sphæridium scarabæoides*, L.	2	...	Remains of a few specimens among grass in meadow.
	Cercyon depressus, Steph.	7	occ.	In decaying vegetation.
	,, *melanocephalus*, L.	7, 8	,,	In cow-dung.
STAPHYLINIDÆ	*Homalota æneicollis*, Shp.	2, 3	f. com.	In decaying leaves.
	,, *sodalis*, Er.	2, 3	,,	,, ,,
	Tachinus rufipes, De G.	3, 5	,,	Dung, also in moss.
	Quedius fulgidus, F.	8	occ.	In decaying vegetation.
	,, *cinctus*, Pk.	10	com.	Vegetable refuse and dung.
	,, *tristis*, Gr.	7	,,	Decaying vegetation.
	,, *picipes*, Man.	7	occ.	Decaying vegetation and wood, also in moss.

TABLE V—*continued.*

Family.	Species.	Month.	Occurrence.	Remarks on Habit.
STAPHYLINIDÆ (*cont.*)	*Quedius boops*, Gr.	3	com.	Decaying vegetation, roots of grass.
	Philonthus laminatus, Creutz.	7–9	v. com.	In dung.
	,, *varius*, Gyll.	8–10	com.	Dung and vegetable refuse.
	,, *ebeninus*, Ol.	2, 4	occ.	,, ,, ,,
	Xantholinus linearis, Ol.	9–11	com.	Vegetable refuse and in soil.
	,, *longiventris*, Heer.	9–11	,,	,, ,, ,,
	Platysthethus arenarius, Pk.	11, 3	,,	Vegetable refuse, dung.
	Stenus speculator, Lac.	9	,,	Larvæ and adults in decaying tubers and vegetation.
	,, *tarsalis*, Ljun.	6	,,	
	,, *similis*, Hbst.	9	,,	
	Oxytelus rugosus, F.	7, 8	,,	Decaying vegetable substance and dung.
	,, *nitidulus*, Gr.	7, 8	,,	,, ,, ,, ,,
SILPHIDÆ	*Choleva fusca*, Pz.	9	occ.	Decaying vegetation.
NITIDULIDÆ	*Epuræa æstiva*, L.	9	,,	Decaying vegetation. FOWLER, vol. iii, p. 228, says it has been reared from nests of *Bombus lucorum.*
MYCETOPHAGIDÆ	*Typhæa fumata*, L.	1, 2	com.	In vegetable refuse and flood rubbish on banks of Dane.
SCARABÆIDÆ	*Aphodius fossor*, L.	8, 9	,,	In dung.
	,, *fimetarius*, L.	8–10	,,	In dung; adults also in meadow grass.
	,, *prodromus*, Brahm.	5	infreq.	In dung.
	Geotrupes stercorarius, L.	4, 5	com.	Larvæ abundant in manure.
	**Serica brunnea*, L.	10	...	Remains of one specimen in meadow soil; adult generally on poplars and decaying birch.
ELATERIDÆ	**Melanotus rufipes*, Hbst.	5, 6	infreq.	Larvæ in rotten wood.

TABLE VI.

Lepidoptera and Tenthredinidæ recorded in the Association.

Abbreviations as in Table I. * indicates species which are invaders from adjacent woods; ‡ species frequenting damp localities; † species that are authenticated pests of cultivated crops and trees.

Order and Family.	Species.	Month.	Food Plant of Larva.
LEPIDOPTERA—			
PIERIDÆ	†*Pieris brassicæ*, L.	6, 8	*Brassica.*
	† ,, *rapæ*, L.	5–8	,,
	† ,, *napi*, L.	6–8	,,
SPHINGIDÆ	*Smerinthus populi*, L.	5, 6	*Salix* and poplar.
ARCTIADÆ	*Earias clorana*, L.	5, 6	*Salix.*
	‡*Lithosia griseola*, Hb.	7. 8	Lichens and dead leaves in marshy places.
	Diacrisia lubricipeda, Esp.	5, 6	*Rumex*, *Plantago.*
	,, *menthrastri*, Esp.	5, 6	,, ,,
HEPIALIDÆ	†*Hepialus humuli*, L.	6, 7	Roots of grasses, *Rumex*, *Urtica.*
OCNERIADÆ	*†*Euproctis chrysorrhœa*, L.	7, 8	Hawthorn, elm.
NOTODONTIDÆ	**Odontosia camelina*, L.	5, 6	Oak, beech, hazel.
	*†*Phalera bucephala*, Hb.	5, 7	Elm.

Table VI—*continued.*

Order and Family.	Species.	Month.	Food Plant of Larva.
Caradrinidæ	*†*Acronycta psi*, L.	5, 6	Birch.
	,, *rumicis*, L.	6	*Polygoni*, *Salix*, hawthorn.
	†*Diloba cæruleocephala*, L.	9	Hawthorn.
	†*Charæas graminis*, L.	8	Meadow grasses.
	Leucania comma, L.	7, 8	,, ,,
	‡*Caradrina micacea*, Esp.	8, 9	*Rumex*, *Equisetum*.
	,, *quadripunctata*, F.	7	Meadow grasses and corn.
	†*Melanchra brassicæ*, L.	6–8	*Brassica*, *Rumex*.
	† ,, *oleracea*, L.	6	,, ,,
	* ,, *thalassina*, Rott.	5, 6	Birch, *Polygonum*.
	,, *pisi*, L.	6	*Pteris*, scabious.
	Hadena nictitans, Bork.	8	Meadow grasses.
	,, *lithoxylea*, Fb.	7	,, ,,
	,, *basilinea*, Fb.	6	Meadow grasses and wheat.
	,, *gemina*, Hb.	7	Meadow grasses.
	†*Agrotis segetum*, Schiff.	6–8	Roots of *Brassica*, *Rumex*.
	† ,, *exclamationis*, L.	7, 8	Roots of *Brassica*.
	,, *corticea* Hb.	6, 7	*Chenopodium*, *Trifolium*.
	† ,, *tritici*, L.	8	*Plantago*, *Brassica*.
	,, *augur*, Fb.	7	Hawthorn, *Rumex*.
	,, *c-nigrum*, L.	7, 8	*Rumex*.
	,, *orbona*, Hufn.	7, 8	Roots of grasses, *Ranunculus*.
	† ,, *pronuba*, L.	6, 7	Roots of *Brassica*, *Rumex*, grasses.
	Orthosia ypsilon, Bork.	7	*Carex*, *Ranunculus*.
Plusiadæ	†*Plusia gamma*, L.	6, 9	*Urtica*.
	Panemeria tenebrata, Scop.	5, 6	*Cerastium*, seed capsules and flowers.
Selidosemidæ	*Ourapteryx sambucaria*, L.	7	Hawthorn.
	Opisthograptis luteolata, L.	6	Birch, hawthorn.
	Deileptenia abietaria, Hb.	7	Not discovered.
	Pseudopanthera petraria, Hb.	6	*Pteris aquilina*.
Geometridæ	**Geometra papilionaria*, L.	7	Birch.
	Nemoria viridata, L.	6	Hawthorn.
Sterrhidæ	**Leucophthalmia trilinearia*, Hb.	5, 6	Beech.
Hydriomenidæ	*Hydriomena albulata*, Schiff.	6	*Rhinanthus cristagalli*.
	Xanthorrhœ montanata, Bork.	6	Grasses, *Plantago*.
	,, *ferrugata*, Clerck.	6, 8	*Galium*.
HYMENOPTERA—			
Tenthredinidæ	**Allantus arcuatus*, Forst.	5–7	Alder, milfoil.
	Dolerus gonagra, Klug.	5–9	*Festuca*, *Poa*.
	,, *hæmatodis*, Klug.	5	*Juncus*, *Scirpus*.
	,, *niger*, Klug.	5	*Festuca ovina*.
	,, *coracinus*, Klug.	5	Meadow grasses?
	‡*Selandria serva*, Ste.	6, 7	Grasses in marshy places.
	Blennocampa sp.	6	...
	**Fenusa betulæ*, Zad.	6	Birch.
	Nematus sp.	8	...

Table VII.

Hemiptera[1] *recorded in the Association.*

† Indicates pest species.

Sub-Order and Family.	Species.	Month.	Occurrence.	Habitat.
HETEROPTERA—				
Reduviidæ . .	*Nabis limbatus*, Dahlb. .	11	com.	On herbage ; developed form rare.
Cimicidæ . .	*Anthocoris confusus*, Reut. .	7, 8	,,	On herbage.
	,, *nemorum*, L. .	8	,,	On shrubs.
Capsidæ . .	*Pithanus Mærkeli*, H. S. .	8	occ.	On herbage ; developed form rare.
	Leptopterna dolobrata, L. .	6, 7	com.	On grass in dry situations
	Pantilius tunicatus, Fab. .	9	occ.	Hazel, birch, and alder.
	Calocaris sexguttatus, Fab. .	6	freq.	On grass.
	Liocoris tripustulatus, Fab. .	8	com.	On nettles.
	Dicyphus pallidicornis, Fieb.	7	,,	On foxglove in wet situations.
	Mecomma ambulans, Fieb. .	8	,,	On rushes and grass in dry situations.
HOMOPTERA—				
Cercopidæ . .	†*Philænus spumarius*, L. .	7, 8	abund.	On meadow grasses.
	,, *campestris*, Fall. .	7, 8	occ.	On low herbage in dry situations.
	,, *lineatus*, L. . .	7, 8	v. com.	On all kinds of herbage.
Psyllidæ . .	*Psylla alni*, L. . . .	6	occ.	On alder ; some nymphs were taken.

[1] No attempt was made to review the various species of Aphididæ abundant alike on trees, shrubs, and herbage. Likewise the Coccidæ were not studied. The inter-relationships existing between these families and the various species of lace-wing flies, lady-bird beetles, and ants are, of course, important, as well as the interaction between these same families and the food-plants which their species severally affect.

Table VIII.

Plecoptera, Neuroptera, Mecaptera, Trichoptera recorded in the Association.

* Those starred are invaders from aquatic habits.

Order and Family.	Species	Month.	Remarks on Habits.
PLECOPTERA—			
Perlidæ . .	**Perla* (3 spp.) . . .	8	Larvæ probably in River Dane; adults taken at artificial light in pasture near the river banks.
NEUROPTERA—			
Chrysopidæ .	*Chrysopa vulgaris*, L. .	5, 8	Peculiar stalked eggs laid on stems ; larvæ are aphidivorous and pupate in the ground, forming a densely woven cocoon.
	,, *perla*, L. . .	6, 8	
MECAPTERA—			
Panorpidæ . .	*Panorpa communis*, L. .	8	Very common species at artificial light ; eggs laid in moist earth in margins of ponds, larva in the ground (Shelford, p. 203),[1] adults carnivorous, taken at light.
TRICHOPTERA—			
Phryganeidæ .	**Stenophylax radiatus*, Ramb.	8	Larva in case of small stones fixed or lodged in bed of stream ; River Dane.
	* ,, *alpestris*. .	9	Larva makes case of stones as in the case of the previous species.
	**Halesus digitatus*, Schrk. .	8	Larval case of vegetable fragments arranged longitudinally or obliquely. Often a long piece of wood at one end. Pupal case closed with stones ; River Dane.
Leptoceridæ .	**Odontocerum albicorne*, Scop.	8	Larval case of sand, cylindrical, slightly curved ; blackish membrane with central slit closes tail-end ; mouth closed by single stone before pupation ; River Dane.

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[1] Shelford, W. E., "Annual Communities in Temperate America," *Geog. Soc.*, Chicago, 1912.

Table IX.

Parasitic Hymenoptera recorded in the Association.

Family.	Species.	Month.	Remarks.
Ichneumonidæ	*Amblyteles armatorius*, Forst.	5, 7	Parasitic on *Triphæna pronuba*.
	Phæogenes ophthalmicus, Wesm.	8	Common species among herbage in marshy places.
	Alomyia debellator, Fab.	5, 9	A few specimens among meadow grass.
	Microcryptus nigrocinctus, Grav.	9	This species has been bred from winter moth (Morley, vol. ii, p. 41).[1]
	Glyphicnemis brevis, Grav.	8	Among herbage; has been recorded as a parasite of *Carpocapsa pomonana* (Ratzeburg).
	Phygadeuon fumator, Grav.	8	Adults taken at roots of meadow grasses: reared from *Mamestra* (*Melanchra*) sp.; also has been reared from *Chortophila brassicæ*.
	Hemiteles necator, Grav.	3	Taken at roots of grass, probably hibernating.
	,, *similis*, Gmel.	8, 9	Morley (vol. ii, p. 149)[1] says this species is a common parasite of Microgaster cocoons; also has been reared from garden spider, various moths, and the *Cynips* of the oak-marble gall.
	Stenomacrus laricis, Hal.	8	Taken on *Pteris aquilina* and on grasses.
	Bassus tricinctus, Grav.	8, 9	Reared from pupa of *Platycheirus albimanus*; the adult frequently taken on herbage and flowers.
	Homocidus pectoratorius, Grav.	7, 8	Probably parasitic on Syrphid species.
	,, *tarsatorius*, Panz.	6–9	Parasitic on larvæ of *Platycheirus albimanus*.
	,, *dimidiatus*, Schr.	6–9	
	Promethus sulcator, Grav.	5–9	Very abundant on grass in marshy places.
	,, *cognatus*, Hlgr.	5–9	Very common on grass in marshy places.
	,, *laticarpus*, Thoms.	8	Rare, on low herbage in marshy places.
	,, *pulchellus*, Hlgr.	6, 9	Common on grass. Morley (p. 21),[1] quotes Gravenhorst having reared this species from *Curculio* (*Hypera*) *polygoni*.
	,, *festivus*, Fabr.	8, 9	Swept occasionally from herbage.
	Tryphon vulgaris, Hlgr.	8	Taken on herbage.
	Mesoleptus typhæ, Fourc.	6, 8	Taken on herbage in marshy places.
	Perilissus rufoniger, Grav.	6, 8	Taken on herbage; probably parasite of saw-fly.
	Adelognathus dorsalis, Grav.	8	This species is rare in England (Morley, vol. iv, p. 318),[1] taken on herbage.
	Campoplex pugillator, L.	5, 6	Common on meadow grasses. Brischke (p. 206)[1] reared this species from *Cidaria rubidaria* and *Odontopora dentaria* and *Notodonta dictæoides* (p. 147), *Mamestra dysodea* (p. 149), and *Cucullia* sp. (p. 153).
	Campoplex sp.	8, 9	Taken on herbage.
	Cymodusa cruentata (Grav.)	8	,, ,,
	Omorga difformis, Grav.	8	,, ,,
Braconidæ	*Alysia* sp.	6	Parasitic on *Phytomyza* sp.
	Opius nitidulator, Nees	7, 9	Parasitic on *Pegomyia hyoscyami*.
	Blacus ruficornis	3	Taken at roots of grass in alluvial meadow.
Proctotrypidæ	*Proctotrypa* sp.	6	Taken on grass.

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[1] For literature references in last column, *vide* p. 53.

TABLE X—GLOVER'S MEADOW.

Census of Soil Insects in Measured Samples.

In the column of plant species, (*pre.*) signifies predominant; (*com.*), common; (*f. com.*), fairly common; (*v. com.*), very common; (*occ.*), occasional; (*r.*), rare. Each abbreviation applies to the immediately preceding species or group of species. In the columns of insect species, (*l.*), larva; (*p.*), pupa.

Sample No.	Floristic Composition of Sample.	ANALYSIS OF INSECT SPECIES.							Total No. of Specimens and Species.
		Apterygota.	Neuroptera.	Coleoptera.	Diptera.	Lepidoptera.	Hymenoptera.	Hemiptera.	
1	Ranunculus repens, Holcus lanatus (*com.*); Trifolium repens (*occ.*); Draba verna (2 *specimens*).	2 *Entomobrya nivalis*, 1 *Onychiurus ambulans.*		2 *Anchomenus parumpunctatus*, 1 *Quedius boops*, 2 *Aphodius fimetarius*, 5 *Agriotes lineatus* (l.), 1 *Sitones lineatus* (l.), 1 *Ceuthorhynchus hirtulus* (l.) in gall.	6 *Cecidomyia destructor* (p.), 2 *Tipula oleracea* (l.), 2 *Empis unicolor* (l.), 1 Anthomyiid puparium, 1 *Phytomyza* sp.		2 *Hemiteles necator*; 1 *Blacus ruficornis.*		30, 15 species.
2	Festuca ovina (*pre.*); Cynosurus cristatus, Dactylis glomerata, matting of Brachythecium rutabulum on the surface (*com.*); Ranunculus repens, Plantago lanceolata (*f. com.*); Draba verna (*r.*).			2 *Homalota vicina*, 1 *Tachinus marginellus*, 1 *Quedius tristis*, 9 *Agriotes lineatus* (l.), 2 *Hypera punctata* (l.), 2 *Ceuthorhynchus hirtulus* in galls.	12 *Cecidomyia destructor* (p.), 1 *Scatopse flavicollis.*	1 *Triphæna orbona* (l.), 1 *Agrotis exclamationis* (l.).			32, 10 species.
3	Festuca ovina (*pre.*); Dactylis glomerata (*v. com.*); Holcus lanatus, Ranunculus repens (*com.*); Plantago lanceolata, Brachythecium rutabulum, Poa pratensis, Draba verna (*r.*).			1 *Quedius boops*, 2 *Philonthus laminatus*, 1 *Cryptohypnus riparius* (l.), 2 *Ceuthorhynchus hirtulus* in galls (l.).	2 *Hyctodesia incana* (l.).	1 *Hepialus humuli* (l.).	1 *Selandria* sp. Cocoon parasitised by species of *Pimpla*?		10, 7 species.
4	Lolium perenne (*pre.*); Festuca ovina (*v. com.*); Agrostis vulgaris, Ranunculus repens (*f. com.*); Brachythecium rutabulum (*com.*); Anthoxanthum odoratum, Phleum pratense, Dactylis glomerata, Plantago lanceolata (*occ.*); Trifolium repens, Lotus corniculatus, Prunella vulgaris (*r.*).			2 *Agriotes lineatus* (l.), 1 *Otiorhynchus sulcatus* (l.), 1 *Hypera variabilus.*	1 *Tipula oleracea* (l.), 1 *Rhamphomyia suleata* (l.).		1 Tenthredinid pupa parasitised by Ichneumon sp.		7, 6 species.
5	Lolium perenne (*pre.*); Agrostis vulgaris, A. alba (*com.*); Trifolium repens, Rumex acetosa (*occ.*); Ranunculus repens (*r.*).	2 *Entomobrya albocincta*, 3 *Isotoma grisea.*		1 *Aphodius fimetarius*, 3 *Agriotes lineatus* (l.), 2 *Campylus linearis* (l.).	2 *Rhamphomyia longipes* (l.).				13, 6 species.

TABLE X—*continued.*

Sample No.	Floristic Composition of Sample.	ANALYSIS OF INSECT SPECIES.							Total No. of Specimens and Species.
		Apterygota.	Neuroptera.	Coleoptera.	Diptera.	Lepidoptera.	Hymenoptera.	Hemiptera.	
6	Dactylis glomerata (*pre.*); Ranunculus repens, Trifolium repens, Agrostis vulgaris (*f. com.*); Rumex acetosa (*r.*).			1 *Anchomenus albipes* (l.), 1 *Xantholinus longiventris*, 1 *Aphodius fimetarius.*	6 *Cecidomyia destructor* (p.), 5 *Tipula oleracea* (l.), 1 *Hilara maura* (l.).				15, 6 species.
7	Plantago lanceolata (*pre.*); Brachythecium rutabulum, Holcus lanatus (*occ.*); Ranunculus repens (*r.*).		5 *Chrysopa vulgaris*, cocoons; 2 of them parasitised by a Braconid, *Apanteles* sp.	1 *Leistus ferrugineus*, 1 *Sphæridium scarabæoides*, 2 *Athous hæmorrhoidalis*, 3 *Agriotes lineatus* (l.).	1 *Borborus equinus* (p.), 2 *Leptis lineola.*		1 *Blennocampa* sp. (sawfly (l.).		16, 6 species.
8	Ranunculus repens (*pre.*); Lolium perenne, Brachythecium rutabulum (*f. com.*); Trifolium repens, Rumex acetosella (*occ.*).			2 *Sphæridium scarabæoides*, 1 *Clivina fossor*, 2 *Tachinus rufipes.*	1 *Cecidomyia destructor* (l.), 1 *Leptis scolopacea* (l.), 2 *Empis* sp. (l.), 2 *Hilara maura* (l.), 1 *Dolichopus* sp. (l.).				12, 8 species.
9	Festuca ovina (*pre.*); Brachytecium rutabulum, Trifolium repens (*com.*); Dactylis glomerata, Ranunculus repens (*occ.*).			1 *Pterostichus vulgaris*, 5 *Agriotes lineatus* (l.).	5 *Bibio Marci* (l.), 2 *Rhamphomyia sulcata* (l.), 1 Anthomyiid larva.				14, 5 species.
10	Holcus lanatus (*pre.*); Brachythecium rutabulum (*com.*); Dactylis glomerata, Draba verna (*r.*).			3 galls of Draba verna containing each a larva of *Ceuthorhynchus hirtulus.*	1 *Tipula lateralis* (l.).				4, 2 species.
11	Lolium perenne (*pre.*); Ranunculus repens, Agrostis vulgaris, Dactylis glomerata (*occ.*); Draba verna (1 *specimen*).			5 *Philonthus laminatus*, 5 *Philonthus varius*, 11 eggs, probably of Carabid sp. 4 *Aphodius fimetarius.* 1 *Otiorhynchus sulcatus* (l.). 1 *Ceuthorhynchus hirtulus* (l.) in gall.	24 *Cecidomyia destructor* (p.), 1 *Tipula lateralis* (l.), 2 *Leptis scolopacea* (l.), 2 *Empis* sp. (l.), 1 Anthomyiid (l.).	1 *Agrotis xanthographa* (l.).			58, 12 species.

TABLE XI—ALLUVIAL PASTURE.

Census of Soil Insects in Measured Samples.

Abbreviations as in Table X.

Sample No.	Floristic Composition of Sample.	ANALYSIS OF INSECT SPECIES.							Total No. of Specimens and Species.
		Apterygota.	Neuroptera.	Coleoptera.	Diptera.	Lepidoptera.	Hymenoptera.	Hemiptera.	
1	Trifolium repens (*pre.*); Lolium perenne, Ranunculus repens (*com.*).	2 *Entomobrya nivalis*, 3 *Onychiurus ambulans*.		1 *Nebria brevicollis* (l.), 1 *Pterostichus vulgaris* (l.), 1 *Tachyporus obtusus*, 1 *Xantholinus linearis* (l.), 1 *Agriotes lineatus* (l.), 2 *Sitones lineatus* (l.).	6 *Lasioptera auricincta* (l.), 10 *Tipula oleracea* (l.).				28, 10 species.
2	Agrostis alba (*pre.*); Brachythecium rutabulum (*com.*); Trifolium repens, Ranunculus repens, Luzula campestris, Lolium perenne (*f. com.*); Alopecurus pratensis (*occ.*).	7 *Onychiurus ambulans*, 9 *Isotoma viridis*, 5 *Isotoma grisea*, 6 *Entomobrya nivalis*.		1 *Tachinus rufipes* (l.), 4 *Xantholinus linearis* (l.), 1 *Othius melanocephalus*.	23 *Sciara* sp. (l.), 1 *Empis livida* (l.), 1 *Dolichopus* sp. (p.).				58, 10 species.
3	Lolium perenne (*pre.*); Ranunculus repens (*occ.*).	2 *Onychiurus ambulans*.		2 *Pterostichus vulgaris* (l.), 1 *Oxyporus maxillosus* (l.), 3 *Xantholinus linearis* (l.), 3 *Quedius fulgidus* (l.), 1 *Otiorhynchus sulcatus* (l.).	4 *Cecidomyia destructor* (one l. and 3 p.), 3 *Sciara* sp., 3 *Leptis scolopacea* (l.) (one specimen evidently eating roots of R. repens), 7 *Rhamphomyia sulcata* (l.), 3 *Tipula oleracea* (l.), 2 *Borborus nitidus* (l.), 1 *Pyrellia cadaverina* (p.).				35, 13 species.
4	Lolium perenne (*pre.*); Trifolium repens, Ranunculus repens, Holcus lanatus (*occ.*).				2 *Myiospila meditabunda* (l.), 1 *Hyetodesia incana* (l.).				3, 2 species.
5	Lolium perenne, Trifolium repens (*com.*); Bellis perennis, Festuca ovina (*occ.*).			1 *Homalota vicina*.	2 *Tipula oleracea* (l.), 1 *Hyetodesia signata* (l.), 1 Anthomyiid larva sp. in process of being devoured by a larva of *Tipula oleracea*.				5, 4 species.
6	Lolium perenne (*pre.*); Ranunculus repens, Trifolium repens (*com.*); Brachythecium rutabulum (*occ.*); Agrostis vulgaris (*r.*).			1 *Nebria brevicollis* (l.), 1 *Anchomenus dorsalis* (l.), 3 *Philonthus laminatus*, 1 *Quedius molochinus*, 1 *Sitones puncticollis* (l.).	4 *Empis* sp. (l.).			Remains of seven Aphids, *Schizoneura* sp.	18, 7 species.

TABLE XI—*continued.*

Sample No.	Floristic Composition of Sample.	Analysis of Insect Species.							Total No. of Specimens and Species.
		Apterygota.	Neuroptora.	Coleoptera.	Diptera.	Lepidoptera.	Hymenoptera.	Hemiptera.	
7	Lolium perenne (*pre.*); Ranunculus repens (*com.*); Agrostis vulgaris (*occ.*).	38 *Onychiurus fimetarius*, 1 *Isotoma grisea*, 1 *Lepidocyrtus albus.*		*Anchomenus dorsalis* (l.), 1 *Quedius fulgidus* (l.), 2 *Xantholinus longiventris* (l.).	15 *Cecidomyia destructor* (some as larvæ, others as pupæ), 3 *Sciara præcox* (2 adults and 1 pupa), 4 *Sciara pulicaria*, 9 *Tipula oleracea* (l.), 2 *Orthocladius stercorarius* (l.), 2 *Rhamphomyia* sp. (l.), 1 *Hyetodesia signata* (l.), 40 *Bibio Marci* (l.), 1 *Borborus equinus* (l.).				122, 15 species.
8	Lolium perenne (*pre.*); Ranunculus repens (*com.*); Agrostis alba, Agrostis vulgaris, Avena flavescens (*occ.*); Trifolium repens, Taraxacum dens-leonis, Rumex acetosella (*r.*).	7 *Onychiurus ambulans.*		1 *Pterostichus vernalis*, 1 *Nebria brevicollis* (l.), 1 *Cercyon analis* (l.), 1 *Quedius fulgidus* (l.), 1 *Platysthethus arenarius* (l.), 1 *Agriotes lineatus* (l.).	1 *Cecidomyia destructor* (p.), 20 *Sciara Thomæ* (l.), 1 *Orthocladius stercorarius* (l.), 6 *Tipula oleracea* (l.), 2 *Chloromyia formosa* (l.), 1 *Chorisops tibialis* (l.), 1 *Platypeza* sp. (l.), 1 *Pegomyia nigritarsis* (p.), 1 *Rhamphomyia sulcata* (l.).				47, 16 species.
9	Lolium perenne (*pre.*); Trifolium repens (*com.*); Agrostis vulgaris (*f. com.*); Ranunculus repens (*r.*).			1 *Nebria brevicollis* (l.).	1 *Cecidomyia trifolii*, 1 *Cecidomyia ranunculi*, 1 *Tipula oleracea* (l.), 4 *Platypeza* sp. (l.), 5 *Rhamphomyia sulcata* (l.), 1 *Empis* sp. (l.), 1 *Borborus equinus* (l.).				15, 8 species.
10	Lolium perenne (*pre.*); Trifolium repens (*com.*); Ranunculus acris (*occ.*).			1 *Sphæridium scarabæoides*, 1 *Quedius boops* (l.), 1 *Philonthus ebeninus*, 1 *Philonthus* sp. (p.), 1 *Sitones puncticollis.*	12 *Cecidomyia destructor* (p.), 1 *Cecidomyia* sp. (l.), 6 *Bibio Marci* (l.), 2 *Tipula oleracea* (l.), 1 *Leptis lineola* (l.), 3 *Rhamphomyia longipes* (l.), 2 *Empis* sp. (l.), 2 *Platypeza modesta* (l.), 1 *Pyrellia cadaverina* (p.), 2 *Hyetodesia signata* (l. and p.), 1 *Borborus equinus* (l.), 1 *Phora rufipes.*				39, 17 species.

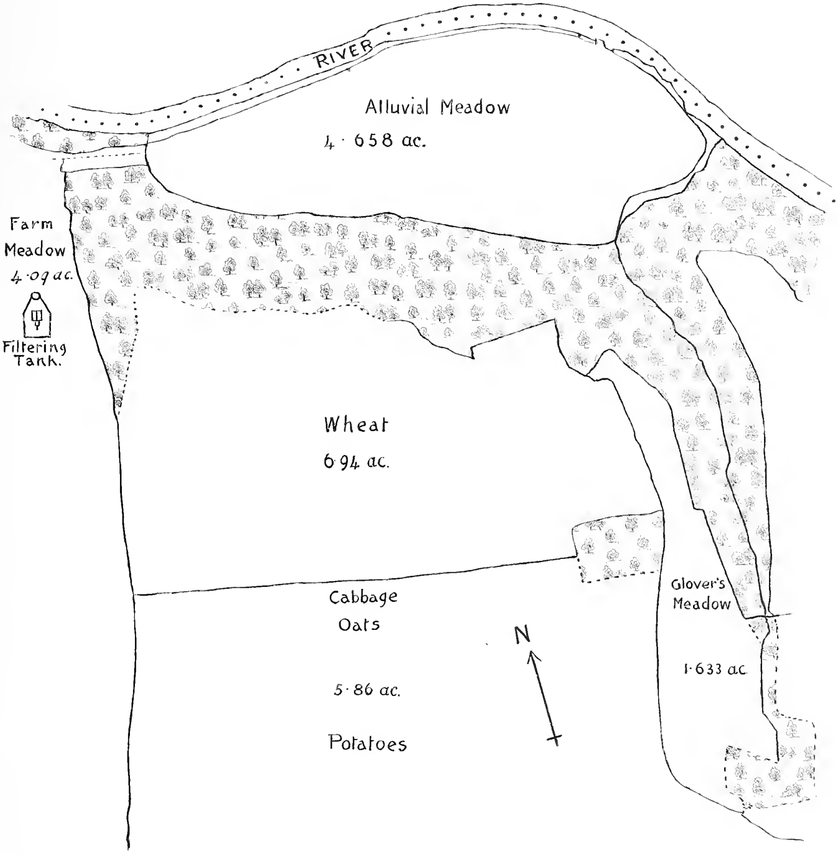
TABLE XI—*continued.*

Sample No.	Floristic Composition of Sample.	Analysis of Insect Species.							Total No. of Specimens and Species.
		Apterygota.	Neuroptera.	Coleoptera.	Diptera.	Lepidoptera.	Hymenoptera.	Hemiptera.	
11	Ranunculus repens, R. acris, Trifolium repens, Lolium perenne (*com.*).			1 *Xantholinus linearis* (l.), 2 *Sitones puncticollis* (l.).	14 *Cecidomyia destructor* (13 p. and one l.), 9 *Bibio Marci* (l.), 3 *Tipula oleracea* (l.), 3 *Rhamphomyia sulcata* (l.), 5 *Hilara maura* (l.), 1 Muscid larva, 1 *Borborus equinus* (l.).	1 *Agrotes* sp.			40, 10 species.
12	Lolium perenne (*pre.*); Trifolium repens (*com.*); Ranunculus repens (*occ.*); Festuca ovina (*r.*).			1 *Nebria brevicollis* (l.), 1 *Tachyporus rufipes*, 1 *Philonthus varius*, 2 *Xantholinus linearis* (l.), 1 *Xantholinus* sp. (l.).	2 *Lasioptera auricincta* (l.), 3 *Leptis scolopacea* (l.), 3 *Empis* sp. (l.), 3 Anthomyiid larvæ 1 *Hyetodesia signata* (l.).				18, 10 species.
13	Lolium perenne (*pre.*); Ranunculus repens, Trifolium repens (*com.*).	5 *Onychiurus ambulans.*		1 *Quedius* sp. (remains), 2 *Sitones lineatus* (l.).	4 *Cecidomyia destructor* (p.), 10 *Tipula oleracea* (l.), 1 *Leptis lineola* (l.), 2 *Rhamphomyia sulcata* (l.), 6 *Empis* sp. (l.), 1 Muscid larva, 1 *Borborus equinus* (l.).				33, 10 species.
14	Brachythecium rutabulum, Agrostis vulgaris, Lolium perenne (*f. com.*); Ranunculus repens, Trifolium repens (*occ.*).			1 *Xantholinus* sp. (l.).	9 *Cecidomyia destructor* (p.), 9 *Tipula oleracea* (l.), 4 *Rhamphomyia sulcata* (l.), 1 *Empis* sp. (l.), 1 *Dolichopus* sp. (l.), 3 *Rhyphus fenestralis* (l.), 2 *Orthocladius stercorarius* (l.), 2 *Borborus equinus* (l.), 1 *Microchrysa polita* (l.).				33, 10 species.

TABLE XII.

PHYSICAL FACTOR.	YEAR 1913.												YEAR 1914.		
	January.	February.	March.	April.	May.	June.	July.	August.	September.	October.	November.	December.	January.	February.	March.
Average barometric pressure	29·51	29·788	29·52	29·58	29·8	29·91	29·89	29·89	29·77	29·66	29·55	29·74	29·90	29·40	29·17
Average maximum air temperature, F.	42·6	47·5	49·6	56·0	60·5	64·76	65·6	68·1	65·7	62·3	59·3	58·0	60·0	56·2	59·4
Average minimum air temperature, F.	34·1	34·5	39·6	44·8	50·9	1·7	50·9	53·4	49·8	53·3	41·9	42·0	35·5	34·6	39·7
Average minimum temperature on grass, F.	31·3	32·5	35·6	39·8	43·1	47·1	46·1	46·5	44·4	44·2	36·6	37·3	37·9	42·2	43·0
Average soil temperature, F., 6 inches deep	38·9	38·9	39·3	45·4	49·8	56·0	58·3	59·1	56·7	50·9	42·9	42·3	44·5	41·0	40·2
Average soil temperature, F., 18 inches deep	40·5	40·5	40·7	45·4	50·3	56·5	58·3	60·0	58	52·9	45·7	43·6	38·6	42·4	41·7
Total rainfall in inches .	2·16	1·01	3·17	3·11	3·59	2·77	1·13	2·83	1·85	7·2	5·00	3·88	2·91	4·75	6·84

Dr. A. E. Cameron: Insect Association.—Plate I.



Diagrammatic Representation of the Area Studied.

FIG. I. ALLUVIAL PASTURE, SOUTH-WEST ASPECT.

Bemrose Collo, Derby

FIG. 2. GLOVER'S MEADOW. NORTH ASPECT.

III.—The Gametophyte of Psilotum. By G. P. Darnell-Smith, B.Sc., F.I.C. *Communicated by* Professor ANSTRUTHER LAWSON, D.Sc. (With Two Plates.)

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1. INTRODUCTION.

Considerable interest attaches to the unravelling of the complete life-history of the Psilotaceæ, since they are apparently the nearest living representatives of the Sphenophyllales.

The recent description of the gametophyte of *Tmesipteris* by Prof. LAWSON, whose figures I had the privilege of seeing before they went to press, and the discovery of the gametophyte of *Psilotum*, which is the subject of the present paper, form a first contribution to the solution of this problem. It is of some interest to note that there remains now no Pteridophyte the gametophyte of which has not been described.

In the early part of this research I was fortunate in finding a locality near at hand in which *Psilotum* flourished, and therefore I had at my disposal abundance of spores and later numerous prothalli.

A general description of the distribution and habitat of *Psilotum* as far as its occurrence in the Hawkesbury sandstone around Sydney is concerned will serve as a fitting introduction to the more detailed consideration of the gametophyte.

Psilotum is most usually found growing in the earth and vegetable debris that collect in deep horizontal fissures which occasionally occur in almost vertical sandstone rocks. These rocks are massive, and the fissures vary in width from a few inches to a fraction of an inch; if they are very wide and contain much earth, *Psilotum* is not generally to be observed in them, and it seldom occurs in vertical or almost vertical fissures. The earth in the horizontal fissures generally contains a very large admixture of coarse sand, a considerable amount of decayed vegetable matter, and abundant remains of *Julus oniscus* and various Coleoptera. As a rule there is very little clay mixed with the earth; and if this earth be shaken up with water, the sand and earth sink almost immediately on standing, and the supernatant liquid is comparatively clear and free from colloidal particles.

Rocks in the fissures of which *Psilotum* is found to be growing are noticed frequently to be somewhat basin-shaped above; in this cavity water collects, and in time a shallow bog with a sandstone bottom is found. From this bog water gradually percolates through the sandstone rocks, keeping the fissures below just moist. In fact, while the aerial parts of *Psilotum* are admirably adapted to withstand extremes of heat and dryness and markedly xerophytic in character, the rhizome appears to require to be constantly surrounded by a damp atmosphere.

While *Psilotum* may be found in abundance upon exposed cliffs, particularly those facing the north, and which are hence exposed to the most prolonged sunshine, it is also to be found in deep gullies if the rocks are massive, and especially in the neighbourhood of small waterfalls. The water in the streams in these gullies frequently contains iron, probably as a sesquicarbonate. Where this water oozes through a rock it deposits a film of the hydrated oxide of iron. In time these films grow into layers of considerable thickness. Occasionally droplets of water become imprisoned in films of oxide of iron before they have had time to evaporate or disperse, and a spongy mass of globules of iron oxide, containing droplets of water in their interior, finally results. As the layers of oxide of iron increase in thickness the direction of the oozing water is slightly altered. In course of time earth and vegetable debris become mingled with the layers of iron oxide, and there results a more or less spongy or shaly mass of flakes of iron oxide, earth, and decayed vegetable matter adjacent to a constant supply of water. In such a porous mass that is always moist the rhizome of *Psilotum* will flourish most vigorously.

If the rhizome of *Psilotum* penetrate to a spot saturated with water, it turns black and decays ; also, if it penetrate to a spot containing much clay, it seems unable to make progress—the rhizoids become clogged and the rhizome decays. The rhizome is never found at the ordinary ground-level, and seems unable to tolerate for any length of time stagnant water, soil that is not porous, or soil from which water cannot drain away very freely. What it appears to require is an atmosphere that is continuously damp rather than a soil that is wet. It flourishes most vigorously where the rhizoids can stand out freely from the rhizome, their tips only touching the surrounding medium, where the superstratum and substratum are continuously moist (though seldom, sometimes never, wetted by rain), and enclose between them a thin layer of decayed vegetable matter.

The rhizome has been found traversing the tortuous tunnels made by white ants, the cavities in sponge-like rock formations, and in fissures in the rocky overarching roof of caverns. In this latter situation, if the lower plates of rock be split off by means of iron wedges, the aerial parts of the *Psilotum* plant are found to arise from a densely coiled and interlaced mass of rhizomes ; the mass may be half an inch in thickness. Where the fissure narrows in the region remote from the opening to the air, strands of rhizome densely covered with rhizoids, which stand out freely from the surface, are found arising from the central mass. Still further in, the rhizome, which possesses little penetrative power, flattens itself out and pursues its way to the remotest and finest parts of the fissure, where the lower slab of rock joins the main roof of the cavern. *Psilotum* also occurs in moist earth held loosely together by the roots of ferns, the felted mass being closely adherent to vertical or almost vertical masses of rock. In such cases the rhizome seeks a position between the rock and the adhering felted mass, and is characterised by the production of an enormous number of bulbils.

While *Psilotum* appears to be usually confined to the situations above described, and *Tmesipteris* is generally to be found upon tree ferns or upon *Todea*, nevertheless I have found *Tmesipteris* growing side by side with *Psilotum* in rock crevices, and I have found *Psilotum* growing upon *Todea*; a fact which suggests that the endophytic fungus found in *Psilotum* and in *Tmesipteris* is the same species, and that, while one plant is mainly xerophytic in character and the other hydrophytic, variations in the aerial structures may occur according to the environment, as is indeed the case.

Psilotum varies very considerably according to the situation in which it occurs. In exposed situations the aerial parts tend to become short and stocky; in sheltered situations they tend to become flaccid and pendulous, while the prominence of the ridges is diminished.

The rhizome will travel several feet in rock fissures, throwing out aerial branches at favourable situations.

Openings in the exposed surface of a rock, apparently quite separate, are frequently united further in as one continuous fissure, and at such openings the aerial parts of *Psilotum* make their appearance.

The sporophylls of *Psilotum* start to produce ripe synangia at the beginning of September, and further sporophylls develop and produce spores till the end of March. At about this time the first shoots of the sporophylls and foliar organs for the ensuing year make their appearance, and have pushed well forward by the end of April. Belated sporophylls that have failed to mature their spores in March may last on through the winter; those whose spores have been shed wither and die.

The sporophylls from very young rhizomes are simple and unbranched, or they consist of a single fork; as the rhizome ages the dichotomous branching becomes more and more extensive.

The synangia are at first covered with a green coat; as they approach maturity the green colour is rapidly changed to a brilliant yellow. A day or two later the yellow colour changes to light brown, the dividing septa split, and the three chambers of the synangia open. The spores are disseminated by the wind. After their discharge the chambers almost close and the synangium turns a dirty brown and frequently drops off.

In this condition it often contains a residue of undischarged spores. These synangia are sometimes collected by ants and carried into clefts in the rocks. In this way some spores of *Psilotum* may be sown in surroundings congenial for their germination; for the rest, it is a fortuitous circumstance if they happen to be blown by the wind into a suitable situation. The following case illustrates how necessary it is to have every condition satisfied. In the Hawkesbury River is a rocky island about eighty acres in extent, distant about half a mile from the mainland. Upon this island I lived for three months: I had, therefore, every opportunity of becoming familiar with the flora. One solitary specimen of *Psilotum* was found which, judging from its size, had produced spores for years, yet no indication of any other *Psilotum* plant was ever found upon the island.

In a plant like *Psilotum*, the sporophyte of which requires an especial environment, it is of the greatest importance that the spores should not germinate until they have reached a suitable locality, otherwise the result of the whole sexual process would be rendered nugatory; and it is probably their refusal to germinate, under any conditions that would be adverse to the sporophyte, that has so long delayed the life-history of the gametophyte being described. They have ceased to show any great amount of adaptability, and it is questionable whether the adaptability of the gametophyte among the Pteridophytes is so general as has been supposed.

Thus Dr Lang * holds the view that "the importance to the species in the vascular cryptogams of satisfactory adaptation of the gametophyte to its environment can hardly be overestimated. For the establishment of the sporophyte in a new situation is entirely dependent on the gametophyte having been able to come to maturity and produce sexual organs, so that the localities of the plants are determined more by their suitability for the gametophyte than for the sporophyte, except in so far as the latter is spread by vegetative propagation."

So frequently did I find *Psilotum* growing in connection with the iron deposits previously described, that I suspected iron might be an element necessary for its development. To test this, a number of *Psilotum* rhizomes were collected, washed thoroughly free from adhering soil, dried, calcined, and the ash tested for iron; this element, however, was not detected.

While *Psilotum* has been found most abundantly near the sea-coast in the neighbourhood of Sydney, I have, nevertheless, found it growing vigorously fifty miles inland.

NOTE ON THE CHEMICAL CONSTITUTION OF HAWKESBURY SANDSTONE.

Appended are the results of six analyses of Hawkesbury sandstones, for which I am indebted to Mr W. G. Card, Curator of the Geological Museum, Sydney.

Analysis of Sydney Sandstone.

	Greens Q, Annandale.	Saunders, Pyrmont.	Purgatory, Pyrmont.	Regans, Waverley.	Phippards, Waverley.	Undercliffe, Tempe.
H_2O-	0·94	0·68	0·33	0·40	0·49	...
H_2O+	2·50	1·80	1·05	0·98	1·41	2·56
SiO_2 (free)	66·35	72·70	83·55	80·50	77·20	81·80
SiO_2 (comb)	12·40	9·35	5·30	6·25	7·55	
Al_2O_3 †	10·93	9·20	6·01	6·12	8·16	9·90
Fe_2O_3	0·10	0·50	0·10	0·30	0·41	0·30
FeO	2·48	1·92	1·37	1·92	1·56	2·07
MnO	0·08	0·05	0·04	0·06	0·04	...
CaO	0·16	0·22	0·08	0·20	0·18	0·11
MgO	0·52	0·39	0·25	0·36	0·36	0·15
K_2O	1·58	1·50	0·81	1·14	1·50	1·45
Na_2O	0·21	0·16	0·01	0·15	0·06	0·18
SO_3	Trace	Trace	Trace	Trace	Trace	None
CO_2	1·61	1·34	0·84	1·29	1·16	1·14
TiO_2	0·51	0·35	0·66	0·69	0·36	0·05
	100·37	100·16	100·40	100·36	100·44	99·80

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* W. H. Lang, "The Prothallus of *Lycopodium clavatum*," *Annals of Botany*, xvii, p. 311.

† Includes P_2O_5.

Such rock does not weather and disintegrate readily, and such soil as is formed is extremely poor in fertility. It is evident that it must have mixed with it a large amount of organic material to enable a saprophyte such as *Psilotum* to develop.

It will be noted that the amount of carbonic anhydride present is greater than the amount required to form carbonate with the magnesium and calcium oxides present; the surplus is probably combined to form ferrous carbonate.

While the solution of the ferrous carbonate as a sesquicarbonate, and its redeposition as hydrated iron oxide in the neighbourhood of streams described above, is a feasible chemical explanation, it is possible that the reactions are brought about or are accompanied by reactions set up by living organisms; and it is noteworthy that where the deposits are being formed an enormous number of diatoms, which are well known to form for themselves siliceous skeletons, are present.

In this connection the suggestion of Sir T. H. HOLLAND * is of interest. After discussing the constitution and formation of laterite, more especially as it occurs in India, he summarises his conclusions as follows:—

(1) Laterite has generally been referred to as a ferruginous clay; but if the term clay is restricted to substances having a basis of hydrous silicate of alumina, this definition is incorrect. The alumina in laterite exists, as it does in bauxite, in the form of hydrous oxides. Kaolin must thus be removed finally from the list of weathering products; it is formed generally, perhaps exclusively, by the action of subterranean vapours on aluminous silicates.

(2) To account for the fact that an aluminous silicate undergoes a more complete disintegration under tropical conditions than under the deep-seated and presumably high temperature conditions of kaolinisation, the writer suggests that laterite is due to the agency of lowly organisms, possibly akin to the so-called nitrifying bacteria. With these there are probably forms akin to the bacteria which oxidise and fix ferrous compounds, and which, precipitating the silica in the colloid form, permit its removal by dilute alkaline solutions, simultaneously formed. This would account for the facts (*a*) that laterite is confined to the tropics, or at least is more conspicuously developed under tropical conditions; (*b*) that although the laterite cover is 100 feet or more in thickness, there is a sharp change from the soft-decomposition product to the absolutely fresh rock below; (*c*) that though laterite can form at temperate altitudes, it is not observed in temperate latitudes, where, with a similar average annual temperature, there is a prolonged winter; and (*d*) that laterite is a superficial product.

2. THE SPORES AND GERMINATION.

The spores of *Psilotum* are bean-shaped bodies measuring on the average 64·8 × 32·4 μ. (Very rarely a spore nearly double this size may be found.) In the natural state they are quite separate from one another at the time of the opening of the ripe synangium, and form a very pale yellow glistening pile which is quickly dispersed as a small cloud by the wind. In the laboratory synangia that are nearly ripe will frequently open on keeping them for a day or two in a covered glass dish, and the spores, instead of being deposited in a small heap, will be all held together in a little yellow ball by a delicate meshwork. Such spores as are not absolutely mature germinate with difficulty.

The mature spore has delicate reticulate epispore structures, and adheres very readily to even a smooth surface, such as glass. The dry spore is a curved bean-shaped body with a narrow ridge joining the two ends of the curve—the regions on either side adjacent to the middle portion of the ridge being depressed.

Along the ridge in the centre a median slit extends for about three-quarters of its

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* "On the Constitution, Origin, and Dehydration of Laterite," Sir T. H. HOLLAND, *Geological Magazine*, 1903, vol. x, p. 59.

length; this slit, from which the prothallium later emerges, is bounded on either side throughout its length by a thick smooth lip (fig. 1).

On placing the spores in water the depressed areas adjacent to the ridge swell somewhat, and the ridge in consequence becomes less marked. Spores thus treated have almost the same specific gravity as water, a point not without significance, as they germinate below the surface of the ground, and, being of about the same specific gravity as water, they are liable to be carried further by it than if they either sank or floated.

Spores placed in water or in any medium unsuitable for their germination usually show in time a vacuole at each end, with the protoplasm collected around the nucleus, which is central, forming an irregular band transverse to the length of the spore (fig. 3). Spores placed in an environment suitable for germination show in a few days a central nucleus surrounded by numerous circular droplets which completely fill the cell (fig. 2). In this condition the spore may remain from four to six months.

Seen in the mass the spores are of a faint yellow colour. When placed in a small heap upon blue litmus paper and moistened, they give a slight acid reaction. In the presence of ammonia vapour they turn a brilliant orange colour. If heated at 70° C. for some time, the cytoplasm turns a greenish brown and the nucleus becomes dark brown.

After repeated failures with a large variety of expedients I succeeded in causing the spores to germinate in the laboratory and in the field. The chief reasons of failure in my earlier attempts may be summarised as follows:—(1) Using sterilised soil in which the endophytic fungus would not be present; (2) using spores that were too old or not absolutely mature; (3) keeping the spores too wet with stagnant water; (4) failure to provide adequate drainage; (5) failure to provide a rigid surface above and below the spores.

I have succeeded in growing spores in the laboratory as follows:—

(*a*) In earth placed between two flat pieces of sandstone. These were placed on pieces of rock in a porous earthenware butter-cooler consisting of two circular chambers. A central one, in which the rocks were placed, had holes in the bottom to provide drainage; it was surrounded by another concentric chamber, the bottom of which was intact. Water was placed in this external chamber, and was replaced frequently as the supply passed away through the porous earthenware. Both chambers were covered with a lid. The air in the central chamber was thus always saturated with moisture. The frequent seepage and renewal of the water seems to be especially valuable in obtaining freedom from moulds, which, where the water is stagnant, are frequently a nuisance, though the spores of *Psilotum* appear to be more or less immune, even when moulds are present.

(*b*) By the removal, from the vertical side of a rock in the open, of a mass of soil and debris felted together by roots, and fixing it by wire to a rock placed vertically in a case in the laboratory.

Psilotum spores were shown between the rock and the felted mass, and the soil was kept moist as follows:—

A vessel containing water was placed above the case containing the rock, and from it a piece of rubber pressure-tubing, $\frac{3}{4}$-inch in diameter with an internal bore of $\frac{1}{8}$-inch diameter, was led in a horizontal direction above the rock and the distal end closed with a pinch-cock. Half a dozen pieces of fine capillary glass tubing 1 inch long were fixed at intervals in holes in the thick wall of the rubber tubing, in such a manner that their ends abutted on the distal side of the internal wall of the rubber tube. The tube was used as in the manner of a siphon, and by adjusting the distance between the internal ends of the capillary glass tubes and the wall of the rubber tube it was possible to obtain a continuous "drip" of water at any desired rate.

I have succeeded in growing spores in the field as follows:—(1) By splitting off with wedges in a suitable locality a large slab of rock, separated from another by a fissure, dusting the spores gently from the flattened end of a platinum wire upon the thin layer of soil exposed, and replacing the slab. (2) By cutting a thin slit in a piece of pumice with a fret-saw, smearing it with earth, dusting spores into the slit, and forcing the piece of pumice so treated into the earth in a rock fissure. (3) By cutting thin sections of dense sponge, dusting spores between two sections, and forcing the pieces of sponge with a scalpel into a damp rock fissure. The value of this method is that the spores can be easily found again for examination. (4) By removing the surface earth from a rock fissure, blowing spores from the end of a flattened platinum wire into it, and then replacing the surface earth removed.

To avoid the very tedious process of hunting with a microscope for germinating spores in the soil treated in the above experiments, the following process was adopted and was found to work well:—

The soil to be examined was agitated gently with water in a 100-c.c. cylinder. On standing, the sand and coarser particles of soil sank quickly and the light particles floated to the surface. Some of the clear water was pipetted off; the germinating and ungerminated spores were found to be suspended in it. This water was placed in two tubes, the heights in the liquid columns were adjusted to the same level, and the tubes were then placed for ten minutes in a centrifuge revolving at a moderate speed. The deposit in the tubes could be quickly and easily examined for spores, and if any special stage was required for mounting it could be picked out by touching the spot of water where it was noticed with a very fine capillary glass tube. The water immediately ascended the tube, owing to capillary attraction, and carried the spore with it.

The first stage noticeable in the germination of the spore, which commences about four months after sowing, is the protrusion of a small lobule covered with a thin membrane through the cleft in the spore. Later the lobule increases in size and the membrane (intine) becomes more attenuated. Near the apex of the lobule, but slightly on one side, a number of small yellowish-brown patches (probably chromoplasts) often slightly raised from the surface become noticeable (fig. 4). At this period the nucleus of the spore has divided into two; of the daughter nuclei one remains within the spore and one travels towards the brownish area at the top of the protuberance. The droplets in the spore become more transparent, and many of them pass out into the growing portion. The area containing the chromoplasts is somewhat bulged, and, the cell membrane being delicate, it is very liable to become slightly invaginated at this point, a false fold thus apparently cutting off the yellowish cap that is destined later to become the apical cell (figs. 6 and 7).

3. Developmental Stages.

Later a transverse wall appears, cutting the cell in two in a plane at right angles to the axis of emergence. There is thus formed a basilar cell and an upper cell. The extine of the spore clings as a mere shell to the basilar cell, which is large and globular; in this position it may remain some time. In the upper cell two series of segments arise by inclined walls formed alternately right and left. Growth at first is slow; from the first emergence from the spore to the three-celled stage takes three weeks. By the time the third cell wall has formed, the colouring matter of the chromoplasts of the now constituted apical cell becomes more diffuse and the chromoplasts begin to lose their distinctness. Little papillæ may be found here and there upon the large apical cell (figs. 5 and 8). A further division of cells gives rise to a small cell-mass, which is early penetrated by an endophytic fungus. The first fungus threads I have seen have been at the three-celled stage. The cells of the first cell-mass are very light brown in colour, and become heavily infected with fungus. Usually there is a fairly well-marked point at which the interrelationship of fungus and host seems to be well established; from this point onwards nearly all the cells of the prothallium except the external layer are almost full of dense skeins of fungal hyphæ, and are darker in colour than the earlier-formed cells. The prothallium widens rapidly till it attains the diameter that it will approximately retain throughout its growth (fig. 19).

Note.

Before passing to a consideration of the mature prothallus, which bears both male and female organs, it will be convenient to refer here to a communication made by Mr T. Whitelegge to the Linnean Society of New South Wales on April 26, which I give in full, and with which I find myself in entire disagreement:—

"Mr T. Whitelegge exhibited a series of mounted slides illustrating the sexual generation of *Psilotum triquetrum*. The spores were grown on the living rhizomes of *Davallia pyxidata*, in a small Wardian case. The spores of *Psilotum*, although isosporous, are strictly diœcious. The male gametophyte consists of about eight cells. These are unequal in size, with clear, thin walls, enclosing very many extremely minute antherozoids. The cells are distinct, being only slightly adherent to each other, easily detached, and often float free when placed in water. The larger cells are equal to the diameter of the spore, the smaller to that of the nucleus. Spores destined to produce the female gametophyte contain an indefinite number of small cells. A single dome-shaped body emerges from the centre of the spore, and is about equal to its diameter. The structure consists of many irregular cells, apparently held together by gum; some project on the sides either near the summit or base; the latter, at its junction with the spore, exhibits a well-defined ring of brown cells, encircling an opening, leading from the interior of the spore into the hollow part of the dome. The projecting cells may represent the tips of archegonia. Sections will be required to settle the question. Failing to secure ripe spores of *Tmesipteris*, old synangia were dissected. Traces of both male and female gametophytes were found, proving that the spores often germinate in capsules. After this discovery, further examinations of the old synangia of *Psilotum* were made. Many contained self-germinated spores, and afforded a better supply of material for study than by cultivation."

4. The Mature Prothallus.

The mature prothallus is a cylindrical, single or branched, saprophytic body, subterranean, light brown in colour, radially symmetrical, and densely covered with long brown rhizoids. It is monœcious. It is best obtained by taking a quantity of earth from fissures in rocks where *Psilotum* is growing, teasing up the earth finely and spreading it as a thin layer over the surface of a sheet of white paper, and examining the earth with a hand lens magnifying 15 diameters. I first discovered it in this way.

Moist earth from deep in the rock fissures, scraped out with a steel wire with the end flattened and bent at right angles, must be examined. If fissures can be found below a spot where a clump of *Psilotum* plants have long ago established themselves so that the neighbourhood has become well dusted with spores, the locality is a hopeful one. Searching on the surface or on the ground-level is useless, and even in a favourable locality some bucketfuls of soil may be examined without success.

The prothallia may be found in various stages of development from November till February. The branching of the prothallium is quite irregular, the most usual form being a short growth from the spore and then the formation of two branches of unequal length. The average diameter of a branch is from 468 μ to 655 μ, and the average length about 2457 μ.

The growing point is light yellow or white in colour, very obtuse, and differentiation behind it is very rapid. If a prothallium has received a check there may be a slight constriction behind the growing point. Normally the prothallium is turgid and brittle; it soon becomes flaccid in the absence of moisture, but quickly regains its turgidity in water. Occasionally a prothallium may be found the distal end of which is dead, while the end near the growing point is alive and produces normal antheridia and archegonia.

As the prothallus pushes its way through the rock crevices or gritty earth, some of the cells near the growing point are very liable to be injured, there being no root-cap. Such injured cells turn a dark brown colour, they frequently lose their nuclei, and later stand out in little groups of from three to eight cells as characteristic brown patches upon the surface of the prothallus.

The general external cells are elongated, thin-walled, light brown in colour, and have conspicuous nuclei.

Frequently ramifying over the surface of the prothallus, fine brown non-septate fungal hyphæ are to be observed. In all cases in which I have grown *Psilotum* spores these brown thick-walled fungal hyphæ have been present in the soil.

The prothallus frequently has upon it small bulbils. Each is carried upon a short stalk with a transverse wall, and is very easily detached. In the young stage they are white and consist of four to six cells, with distinct nuclei surrounded by highly refringent granules. Later the cells of the bulbil become more numerous and darker in colour (figs. 29, 30, and 31).

NOTE.

The prothallus described by Dr LANG * and provisionally referred to *Psilotum* would appear to have been that of some Lycopod.

5. DETAILS OF VEGETATIVE CHARACTERS OF THE PROTHALLUS.

The details of the structure of the mature prothallus have been determined by the examination of a number of sections.

In transverse section the prothallus is found to be nearly circular, and to consist of a number of thin-walled roughly pentagonal cells, bounded on the outside by oblong cells, slightly cuticularised externally. Many of these latter give rise upon slightly raised cushions to long brown tubular rhizoids.

The whole of the cells of the prothallus may contain an endophytic fungus, but where it occurs there is no difference in the conformation or structure of the cells. Nearly all of the older cells except those of the external layer are usually filled with dense skeins of this endophytic fungus (fig. 15). It passes quite easily through the cell walls, and a pentagonal cell may frequently be observed with a dense fungal skein, obliterating the nucleus, from which fungal hypha pass out through each of the five walls of the cell (fig. 17). In longitudinal section fungal skeins may be found in cells a short distance behind the growing point, and from these fungal hyphæ extend as fine infection threads to the young cells. Fungal hyphæ pass down the centres of many of the tubular rhizoids, their ends being in contact with the extreme tip of the rhizoid. Sometimes two hyphæ occur in one rhizoid. The cell from which the rhizoid arises may have a fungal skein within it; more usually the fungal hypha arises from a fungal skein contained in the cell immediately internal to that giving rise to the rhizoid (figs. 16 and 18).

The thickness of the hyphæ, which are non-septate and colourless, varies greatly.

Fungal hyphæ have been observed in the antheridia and in the canal cells of the archegonium, but not in the egg cell or in the chamber in which the egg cell lies.

6. THE ANTHERIDIUM.

The antheridia project freely from the surface of the prothallus. The antheridium encloses a large spherical mass of sperm-mother-cells which form spermatozoids

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* W. H. LANG, "On a Prothallus provisionally referred to *Psilotum*," *Annals of Botany*, vol. xviii, p. 571.

which are set free when mature by the swelling of the contents and the breaking down of one or more of the central cells of the wall. The wall in section is seen to consist of from six to eight cells, the base of the antheridium being supported upon two or four large cells. The spermatozoids can be seen within a mature antheridium to be spirally wound. When set free they uncoil somewhat, and are propelled by numerous cilia. One portion of the spermatozoid, placed externally along the greater portion of the spire, stains much more readily than the rest. The antheridia are found at a very early stage in the development of the prothallus. They may develop upon any part of the cylindrical body. When young they arise immediately behind the growing point, and appear as small, white, glistening knobs; when older they turn brown (see figs. 26, 27, and 28).

7. The Archegonium.

In the archegonium the oosphere lies in a sunken hexagonal venter, the walls of which are brown and much thickened. The median cell-wall immediately below the venter is much thickened also. The projecting neck of the archegonium consists of four tiers of four cells enclosing a ventral canal cell and apparently two canal cells. The three upper tiers of canal cells break off very easily when cleaning a prothallus (see figs. 22 and 23).

The breaking off of the three upper tiers of canal cells is rendered the more liable to occur in older archegonia because the product of the breaking down of the canal cells becomes hard and brittle, and in many preparations will be found projecting as a small spike between the four canal cells that are left.

The four basal canal cells are slightly sunk in the prothallus, and their walls, except those adjoining the prothallium, are somewhat thickened. The ragged edge left where the superimposed tier of cells has been broken off may be frequently observed.

On account of the lowest tier of four canal cells only remaining attached to the mounted prothallus, and the dark brown colour of the venter walls, the archegonia appear in surface view as dark brown spots surrounded by four raised cells arranged symmetrically in the form of a rosette, the outer wall of each cell being sharply curved (fig. 25).

The oosphere, which completely fills the venter, contains a large nucleus which itself often contains from two to three bodies, which stain deeply. Similar deeply staining bodies are sometimes found in the cytoplasm. These deeply staining bodies may be sections of spermatozoids; but as no longitudinal section of a spermatozoid that would place the matter beyond doubt has been obtained, the suggestion must be regarded as purely tentative (fig. 24).

The archegonia usually occur upon the older parts of the prothallium, and may arise upon any part of its circumference. They are interspersed among the antheridia, and often occur more or less in groups.

The young archegonia are almost white and somewhat translucent; the necks may be seen projecting from the broad, obtuse growing point of the prothallus.

There are indications that the plant resulting from fertilisation leads a subterranean existence for some time. The formation and development of the embryo and the possible relationships of *Psilotum* will be, however, the subjects of a future communication by Prof. LAWSON, who has this investigation now well in hand.

8. SUMMARY.

The spores of *Psilotum* require a special environment to induce them to germinate.

They produce a cylindrical, radially symmetrical prothallus.

The prothallus is a brown, subterranean saprophytic tuberous body without chlorophyll, and contains an endophytic fungus. Antheridia and archegonia are borne upon the same prothallus.

The antheridia produce spermatozoids having spirally wound bodies and numerous cilia.

The archegonia are very simple. They consist of a venter containing the oosphere sunk in the prothallus, a ventral canal cell, and probably two canal cells. These latter are bounded by four tiers of four neck-cells that project at right angles to the surface.

I am indebted to my assistant, Mr. W. A. BIRMINGHAM, for much careful work in the preparation of material and sections.

I have to thank Prof. LAWSON, in whose laboratory much of the work was carried on, for much kindly advice and criticism during the progress of the investigation.

EXPLANATION OF FIGURES.

Fig. 1. A mature spore of *Psilotum*, showing the cleft from which the first cell of the prothallium emerges upon germination. The cleft has a lip on either side throughout its length.

Fig. 2. A *Psilotum* spore, seen in optical section, that has lain in a suitable medium for four months, showing the condition just prior to germination. The nucleus is distinct and the spore is filled with globules.

Fig. 3. A *Psilotum* spore, seen in optical section, that has lain in an unsuitable medium. The protoplasm has shrunk around the nucleus; such a spore will not germinate.

Fig. 4. First stage in the germination of a *Psilotum* spore. Several chromatophores are seen near the apex of the emerging cell, which contains numerous droplets.

Fig. 5. Another stage in the germination of the *Psilotum* spore. At the apex are the chromatophores, and a small papilla is visible. The droplets show a tendency to congregate into two groups. A slight fold is seen near the apex. The exospore is seen as a shell at the base of the figure.

Figs. 6 and 7. Surface view and side view of a germinating spore, showing a fold in the cell membrane produced by the partial invagination of the thin cell-wall.

Fig. 8. Germinating spore of *Psilotum*, showing the formation of the first cells of the prothallium by

dividing walls (*a*), (*b*), (*c*). The apical cell (*d*) contains a few chromatophores from which the colour has, for the most part, diffused.

Figs. 9–14. Prothallia of *Psilotum* in different stages of development, all drawn to the same scale. Figs. 9–13 are perfect prothallia. The ends of the prothallium in fig. 14 have been broken off. Most of the rhizoids have been removed from all the prothallia. In fig. 14 the antheridia are shown as small protuberances, and patches of brown, dead superficial cells give the prothallium a speckled appearance.

Fig. 15. Transverse section of a prothallium, showing the disposition of the endophytic fungus in dense skeins in the interior cells.

Fig. 16. A rhizoid, showing two fungal hyphæ entering it. One of them traverses the rhizoid to the extreme tip.

Fig. 17. An internal cell of the prothallium, showing the passage of fungal hyphæ through its walls.

Fig. 18. A rhizoid, the end of which is broken off, leaving the fungal hypha within the rhizoid exposed.

Fig. 19. The youngest part of a prothallium, showing the cells first formed after germination. They produce a cell-mass slightly different in character from the remainder of the prothallium. The dark line indicates the position at which the character of the cells becomes uniform, and beyond which the prothallium rapidly attains its maximum diameter.

Fig. 20. Surface view of a prothallium near the growing point, showing an archegonium as four rosette-shaped cells, and near to it wandering fungal hyphæ are visible.

Fig. 21. Surface view of a prothallium, showing several antheridia and three archegonia. Two of these are mature; they show the dark-coloured venter lying within the prothallium, bounded by four canal cells symmetrically arranged around the canal. The points at which numerous rhizoids have been broken off are seen as small circles in the centre of the cells.

Fig. 22. A young archegonium from near the growing point. The four tiers of four canal cells are visible.

Fig. 23. Section of an archegonium, showing the venter and the canal bounded by the four canal cells upon either side.

Fig. 24. Section of an archegonium from which the upper three tiers of canal cells have broken off, the edges of the basal ones only being attached to those that remain. The oosphere, with a nucleus and nucleolus, is seen within the venter. Two deeply staining bodies, one in the nucleus and one in the cytoplasm, are present; these are not always found. The venter has much-thickened walls; so also have the basal canal cells.

Fig. 25. The basal canal cells surrounding the canal seen obliquely upon the surface of the prothallium.

Fig. 26. Section of a young antheridium, showing the spermatozoid mother-cells.

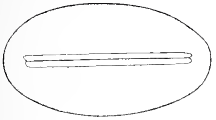
Fig. 27. View of a mature antheridium.

Fig. 28. Four spermatozoids; two show the spirally wound body. Upon one the numerous cilia are visible.

Fig. 29. Surface view of a portion of the prothallium, showing three antheridia and a bulbil upon its stalk. Near the bulbil the neck of an archegonium is visible.

Figs. 30 and 31. Stages in the development of a bulbil.

G. C. Darnell-Smith : Gametophyte of Psilotum.



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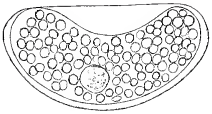

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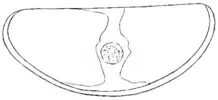

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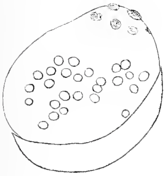

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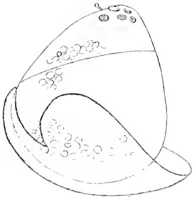

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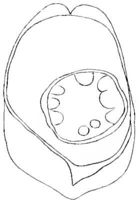

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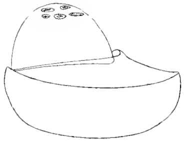

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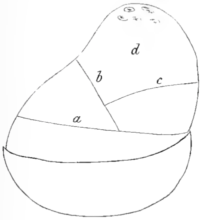

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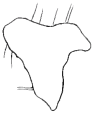

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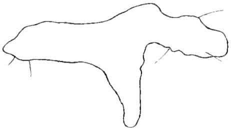

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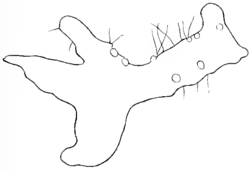

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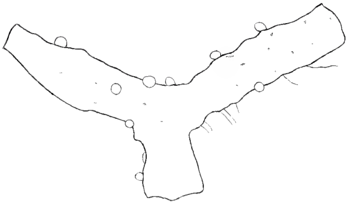

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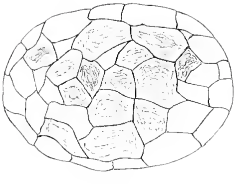

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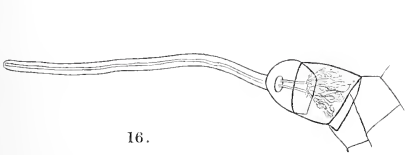

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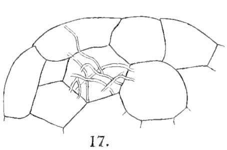

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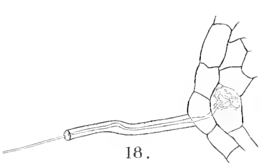
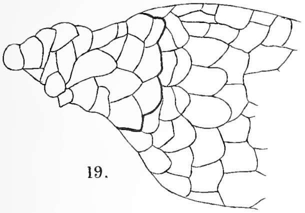


18.

G. C. Darnell-Smith, *del.*

M'Farlane & Erskine, Lith., Edin.

G. C. DARNELL-SMITH: GAMETOPHYTE OF PSILOTUM.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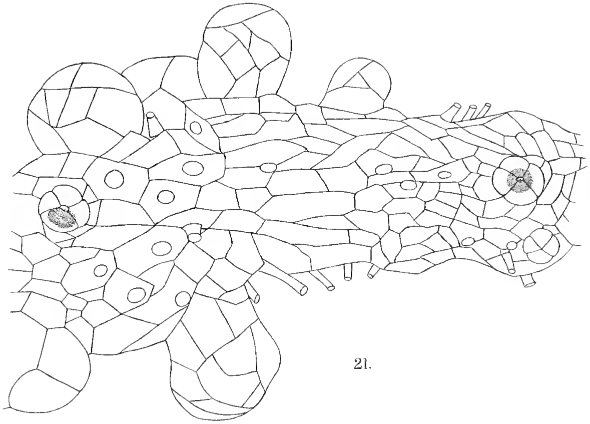
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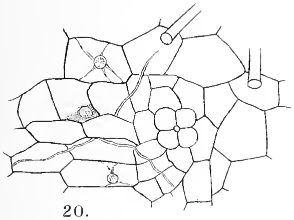
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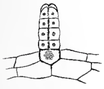
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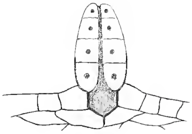
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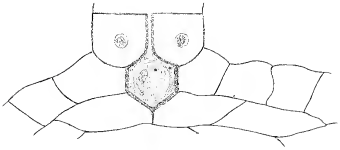
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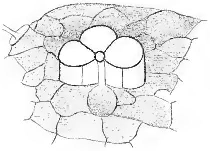
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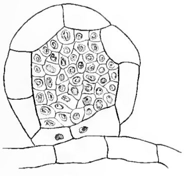
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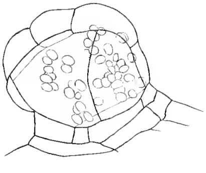
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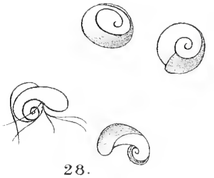
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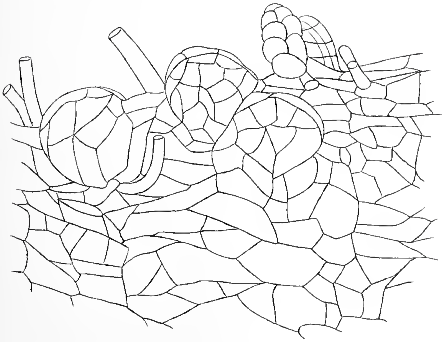
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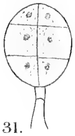
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G. C. Darnell-Smith, *del.*

M'Farlane & Erskine, Lith., Edin.

IV.—The Gametophyte Generation of the Psilotaceæ.

By A. Anstruther Lawson, D.Sc., Professor of Botany, University of Sydney. (With Five Plates.)

(MS. received December 16, 1916. Read February 5, 1917. Issued separately June 13, 1917.)

INTRODUCTION.

Since the preliminary announcement of the discovery of the prothalli of *Tmesipteris* and *Psilotum* communicated to the Royal Society of Edinburgh in June 1916,* a considerable amount of additional material has been found, and it seems therefore desirable to place on record a more detailed account of these interesting structures. The preliminary description, as published, was based upon but a few specimens, and these were not sufficient to reveal all of the vegetative and reproductive features, nor enough to justify any broad general conclusions as to the phylogenetic position of the Psilotaceæ. The discovery, however, has filled in an important and interesting gap in our knowledge; for the Psilotaceæ are the very last of the known Pteridophytes to surrender their gametophytes to the light of science.

While the present paper gives a fairly complete account of the vegetative character of the prothallus and the development of the antheridium and archegonium, it does not include the embryo. I have advisedly left this for a future contribution, realising that the embryology is the most important phase in the life-history of these plants. The additions to my stock of material have added to the embryo stages already reported, but these are not yet sufficient to show a complete unbroken series. I have therefore considered it advisable to defer the account of the embryo, feeling confident that I will be able to fill in the missing gaps. I have learned how and where to obtain material, and it is therefore only a matter of patient searching until the series is complete.

TMESIPTERIS TANNENSIS, BERNH.

The Vegetative Features of the Prothallus.

It is a generally accepted belief that *Tmesipteris tannensis* always grows upon the trunks of tree ferns. This idea, however, is not in accordance with the facts and not in harmony with my own observations. The plant certainly grows more luxuriantly upon the trunks of *Dicksonia*, and frequently on *Alsophila* and *Todea barbara*; but in certain localities and under certain conditions I have found it in nature growing plentifully in soil and in the crevices of rocks. It was the discovery of it growing freely in soil which rendered it possible to find the prothalli in quantity. I had searched laboriously through many tree-fern trunks, and after patiently working

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* LAWSON, A. A., 1916.

through the countless wire-like roots of the fern was rewarded by finding two or three prothalli. But this source of material became so laborious, and occupied so much time with such uncertain results, that I abandoned it upon discovering the soil material. Having found certain localities where very young sporophytes were growing in abundance in soil, it became an easy matter to find the prothalli in considerable numbers. But the experience of searching in the tree-fern material was by no means lost, for during those months of almost fruitless searching I finally learned what to look for, and also how to use the searching lenses to the best advantage. My final and successful method for locating the prothalli was as follows:—I would, in the first place, go to a locality where I knew the young sporophytes grew in quantity. Certain patches of soil where young plants were just emerging from the soil were then selected. At first it was very difficult to distinguish these young plants from suckers growing up from old rhizomes, but after some considerable experience I soon learned to identify the sporelings at a glance. I would then proceed to lift a patch of soil containing the sporelings to a depth of three or four inches. Several such patches of soil were taken and carefully placed in pasteboard boxes. These were brought home to the laboratory, and practically every particle of soil was closely examined with a lens or a binocular microscope. My theory was that where the very young sporelings were growing there should also be other prothalli which had not yet produced embryos; for it seemed improbable that the spores, which are produced in great numbers, would germinate as isolated individuals. It seemed more probable that they would fall to the ground in scattered masses, and the washings of the rains would carry them into the interstices of the soil, where they would germinate below the surface. This proved to be true, for in almost every patch of soil taken as described above, more than one prothallus was found. Three or four were frequently found growing close together, and in one case twelve prothalli were found in one small pocket of soil. In several instances the prothallus was found still attached to the young sporophyte.

From the numerous examples observed it seems clear that the prothallus of *Tmesipteris* is subterranean. I found none exposed to the light. Some were about half an inch deep, but the majority were at least an inch below the surface of the ground. They were more frequently found in wet, sandy soil; and in many instances it was difficult to detect their presence, so closely were they covered with particles of sand and the like. The presence of the long rhizoids, and the extension of these beyond the immediately surrounding soil, gave the clue to the existence of the prothallus. Such small masses of soil were carefully removed and placed in fresh water, where they were gently stroked with the fine camel-hair brush until most of the soil particles were removed. The destruction and removal of many rhizoids during this process was unavoidable. In some cases, however, the particles of soil came away more easily, and the natural appearance of the prothallus could be studied.

In examining the soil with a lens or binocular microscope one frequently meets with small fragments of rhizomes, and these at first, mainly on account of their colour, were mistaken for prothalli. The latter structures have the same characteristic light-brown colour of the rhizomes, but the vascular tissues give the rhizomes a rigidity which one soon learns to detect, and which is not a feature of the prothallus. In none of the specimens examined was there any trace of the pigment chlorophyll. One is justified, therefore, in the conclusion that, like *Botrychium*,* *Lycopodium*, and other subterranean pteridophyte prothalli, the gametophyte generation of *Tmesipteris* is saprophytic in its method of nutrition.

From the numerous additional specimens discovered since the preliminary account was published, I have been enabled to obtain a more accurate knowledge of the shape and size of the prothalli. Of the first lot found all were quite small, the largest specimen measuring but one-eighth of an inch in length. In the material found later much larger specimens were obtained, several of them nearly half an inch, and one or two three-quarters of an inch long. So that in size alone there seems to be a wide range—this of course being in mature plants bearing both antheridia and archegonia. All of these specimens examined were cylindrical in form, but not necessarily straight. They became bent, curved, and sometimes twisted in curious forms, as if their general configuration were determined by the surrounding particles of rock and other obstructions met with in the soil in the course of their development. In one or two examples the prothallus consisted of a short attenuating unbranched cylindrical structure, but in the majority of the specimens examined there was undoubted branching, each branch terminating in a merismatic organic apex.

In the preliminary paper † I have already figured the method of branching. In fig. 1 of the present paper is shown an entire prothallus. As it still shows a distinct and active meristem at the apex, it is evidently not fully grown. The irregular configuration of the cylindrical body is quite characteristic. In preparing this specimen most of the rhizoids were removed with the clinging particles of soil; but sufficient remain to show how very numerous and how long these structures are, and what an immense absorbing surface they afford. The development of these rhizoids may be followed from such a specimen as this. At the merismatic apex one may observe all stages in their differentiation from superficial cells (fig. 1). This specimen also shows developing archegonia and antheridia near the apex.

The appearance of the apex of an older branch is shown in fig. 2. Here it will be noted that the merismatic nature of the cells at the apex is not so evident. The great length of the mature rhizoids is very characteristic. One antheridium and eleven archegonia are to be observed in a small surface area. The majority of the archegonia shown in the figure are drawn from the view looking down into the neck cells. One of them, however, is seen from the side view, and shows how the necks of the young archegonia project like tubes for a short distance beyond the surface of the

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* Jeffrey, E. C., 1898; Bruchmann, 1898–1904; Lang, W. H., 1901.

† Lawson, A. A. (1916), *l.c.*

prothallus. Another feature to be observed in this figure is the presence of an endophytic fungus in the prothallial cells. Many cells, even from the surface view, show the presence of this fungus.

The internal tissue of the prothallus shows very little differentiation. The cells appear to be all very much alike. The external or "epidermal" layer is slightly different from the other cells, by reason of more sharply defined and slightly thicker outer walls. Apart from this slight difference, one may see that the prothallial tissue is practically uniform throughout. Each cell contains a finely granular colourless cytoplasm and a small but deeply staining nucleus. There is clearly no differentiation of the body of the prothallus into vegetative and reproductive regions which is so characteristic of the prothallus of *Lycopodium*. The antheridia and archegonia were found upon all surfaces, and, like the rhizoids, apparently developed quite indiscriminately. They were not confined to any particular region or surface. In fig. 3 is represented a fair sample of a transverse section of the prothallus. It will be seen that the prothallus is approximately cylindrical, with a definite layer of superficial cells. Many of these superficial cells develop into rhizoids. Nuclei and protoplasm are present in the majority of the cells. But, as shown in the section, many of the cells are infected with an endophytic fungus. The section here represented was taken from near the apex, and the tissue is therefore not very old. It will be noticed in this young tissue the endophytic fungus has not spread to any great extent, and the superficial cells seem not to be infected at all. In fig. 4, however, which was taken from an older region of the same prothallus, the infection of the fungus has spread to practically all of the internal cells. Only the superficial cells are free, and even these in older conditions become infected.

A careful examination of the fungus with the higher power of the microscope shows it to be of a non-septate nature. The hyphæ are therefore very probably of a phycomycetous fungus somewhat resembling *Pythium*. A more highly magnified representation of the effect of the fungus in the prothallial cells is shown in fig. 6. This figure was drawn from cells very near the centre of the prothallus. It will be seen that in many cases the nucleus disintegrates and eventually disappears. All stages in these changes may be observed from any section from an old prothallus. Eventually the cell cavities become almost filled with the fungal hyphæ and the cell walls become a dark-brown colour. From these studies there is little doubt in my mind that, while there may be an advantage, in the matter of nutrition, to the prothallus as a result of the association with the fungus, the parasitic nature of the hyphæ eventually results in the destruction of the cells infected. In the older regions of certain specimens the cells showed no signs of being alive, but their cavities were filled with hyphæ, which in their turn showed signs of disintegration.

It seems quite probable that the prothallial cells become infected from the external substratum by way of the rhizoids. In many specimens examined the hyphæ of the fungus were observed extending through the entire length of rhizoids, and then penetrating the cell walls and entering the cell below. This was especially noticeable in older rhizoids whose apices had become injured. Fig. 5 is a representation of a few superficial cells of the prothallus bearing such rhizoids. Here it will be seen that the fungus traverses the entire length of the rhizoids and enters the internal cells of the prothallus. It seems highly improbable that the direction of growth of these hyphæ is away from the food supply in the living prothallial cells. It seems more probable that it is directed towards the host cells, and that they have entered the apex of the rhizoid from the surrounding soil. These infected rhizoids, showing the great length of the fungal hyphæ, offered excellent conditions for observing the latter and their non-septate nature. The infection of the fungus is not limited in its distribution to certain definite zones, as in *Lycopodium*.* The infection is fairly uniform throughout. In its saprophytic habit and its subterranean habitat the prothallus of *Tmesipteris* does recall that of *Lycopodium*, but structurally there is no real resemblance.

The Antheridia.

The number and distribution of the antheridia seemed to vary considerably in the numerous prothalli examined. There was no evidence to show that they were confined to any particular region; on the contrary, they were found on every region of the surface. They were, however, almost invariably accompanied by archegonia. The distance between these two reproductive bodies was never very great. In some specimens there were only two or three antheridia present, but in others they were quite numerous, as many as forty having been counted on a single prothallus. In the latter cases they were very closely set together and projected out as minute spherical beads from the surface. The antheridium is much larger than the archegonium, as indicated in figs. 1 and 2. They are nearly spherical in form and extend out quite conspicuously from the surface. In this respect the antheridia of *Tmesipteris* are in great contrast to those of *Lycopodium*,† *Equisetum*,† *Ophioglossum*,† and *Botrychium*,† in which the antheridium invariably develops below the surface of the prothallus.

In regard to the development of the antheridium in *Tmesipteris* an interesting and fairly complete series of stages was obtained. From the early stages it would seem that the antheridium begins as a superficial cell. A very young stage is shown in fig. 7. This is from a median section, showing three wall cells which envelop a large inner cell, whose nucleus has just undergone division. The two nuclei thus formed are very large, and their chromatin stains deeply. They stand out very conspicuously as compared with the nuclei of the wall cells and other vegetative prothallial cells. The cytoplasm surrounding them is also very dense and granular. In fig. 8 we have represented a median section of a young antheridium slightly older

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* Bruchmann, H., *l.c.*

† Bruchmann, H., *l.c.*; Campbell, D. H., 1913; Jeffrey, E. C., 1898.

than that shown in fig. 7. The wall cells have increased in number, and the inner cells have undergone mitosis, their delicate cell walls separating the nuclei. There are eight inner cells shown in the section. As this is a median section, it represents the sixteen-cell stage of the inner antheridium. The dense granular cytoplasm and the large deeply staining nuclei render these cells sharply differentiated from the vegetative cells. The young antheridia in section appear at this time as conspicuous semicircular protuberances projecting from the surface of the prothallus.

A still older stage in the development of the antheridium is represented in fig. 9. Here it will be seen that the inner cells have undergone repeated mitosis. There is now a large central mass of sperm-mother cells, or spermatocytes. The wall cells have also enlarged, and the young antheridium as a whole has increased to more than twice the size of that shown in fig. 8.

A more mature stage is represented in fig. 10. At this time the antheridium has become almost spherical in form and increased greatly in size. The number of spermatocytes is apparently the same as that in stage shown in fig. 9, but the internal space has increased greatly, and the spermatocytes are less crowded. These latter seem now to be separating from one another by intercellular spaces. In fig. 11 we have represented a tangential section of a nearly mature antheridium. The nuclei of the spermatocytes have undergone a change. They appear now as very dense crescent-shaped or coiled bodies, that stain deeply. These are the immature spermatozoids. In one or two instances these spermatozoids seemed to be ciliated, but the nature of the cilia was not made out with certainty. They seemed to be of the same nature as those of *Psilotum*, which will be described in detail in the following pages. An external view of a mature antheridium showing only the wall cells, is represented in fig. 12.

THE ARCHEGONIA.

As stated above, there is clearly no differentiation of a vegetative and reproductive region of the prothallus. It would seem that any part of the surface of the prothallus may give rise to archegonia as well as antheridia. In all cases examined the archegonia were much more numerous than the antheridia. In the young prothalli one will probably find very few archegonia; but as the development proceeds they become very numerous and widely distributed over the surface. I have counted as many as fifty archegonia in one field of the microscope. A fair sample of the manner of their occurrence is indicated in fig. 2, which represents the end of a branch of the prothallus. From the view there shown one may look down into the necks of ten archegonia. If this specimen were turned over there would be quite as many archegonia found on the opposite side. This figure also shows the small size of the archegonia as compared with the antheridia. Looking down from the surface view it is quite clear that the neck of the archegonium consists of four rows of cells; and these project beyond the surface—the venter remaining below the surface. In several instances the young archegonium was observed; and in such cases the neck cells, consisting of four rows of four tiers each, formed a short tube with a rounded apex, as shown in fig. 2. A sectional view more highly magnified is shown in fig. 13. The position of the venter below the surface is indicated, and also the curious form of the lower tier of neck cells. It will be noticed that they spread slightly out and terminate in pointed margins.

The surface view of the archegonia more highly magnified is shown in fig. 14. The four cells represented in each case are the lowest tier of neck cells mentioned above. The neck canal is a narrow channel surrounded by these four cells. The narrowness of the channel is due to the construction shown in fig. 13. The maturing of the archegonium and its preparation for fertilisation are very curious. In other Pteridophytes such as *Equisetum*, *Lycopodium*, or *Botrychium* the archegonium matures by the separation of the apical tier of cells and then spreading out to form a gaping channel down the neck of the archegonium. In *Tmesipteris* I was unable to find any evidence of this. In fig. 15, for instance, we have a representation of a mature archegonium ready for fertilisation. It will be observed that the main portion of the neck, consisting of the three upper tiers of cells, has been torn away, leaving behind only the lower tier with the egg cell in the venter. In fig. 16 we have represented a somewhat similar condition. The upper tiers of neck cells have broken away, but traces of the cell walls of the second tier are to be seen. A similar condition is shown in fig. 17. These three figures are fair samples of the appearance of the mature archegonia. There were scores of others observed. I was first inclined to think that these archegonia were injured in the handling of them, and that in removing the particles of soil from the surface of the prothallus the necks were broken off with the camel's-hair brush. Having examined scores of prothalli—and many of these were handled with the greatest care—I am inclined to the belief that this breaking away of the upper part of the archegonium is a natural one, and not due to artificial causes. As shown in fig. 13, the lower tier of cells is sharply defined. As I have already pointed out, these cells extend slightly beyond the surface, and in section their margins seem to spread, giving the appearance of a constriction at this region of the archegonium. These four cells that are left form a flat disc, slightly concave in the middle, but otherwise parallel with the surface of the prothallus. This of course results in a great shortening of the neck of the archegonium at the time of fertilisation, and it seems not unreasonable to interpret it as a special adaptation to meet the unusual conditions of subterranean fertilisation.

PSILOTUM.

The Vegetative Features of the Prothallus.

The method adopted for securing specimens of the prothallus of *Psilotum* was practically the same as that used in the case of *Tmesipteris*, with slight modifications due to the difference in habitat. Localities were found where the plants grew in abundance. It should be pointed out that while one may occasionally find *Tmesipteris* and *Psilotum* growing together, that is the exception, not the rule. The rule is that the *Tmesipteris* is found deep in the gullies, or in wet, sheltered, shady places, protected from the winds by cliffs or overhanging rocks, and by vegetation where *Dicksonia* or *Alsophila* or *Todea* are to be found. In New South Wales it seems to reach its maximum development on the trunks of *Dicksonia*. *Psilotum*, on the other hand, flourishes best in just the opposite kind of habitat. One may find it in great abundance in the immediate environs of Sydney growing out of the crevices in the sandstone cliffs exposed to the sun and winds. It would be difficult to imagine two habitats so utterly different. Although the dry xerophilous conditions are characteristic for *Psilotum*, I have found it often growing luxuriantly in a saturated atmosphere within the spray of waterfalls. It is under these latter conditions that one is more likely to find the prothalli. I have occasionally found prothalli in the soil contained in the deep crevices of the sandstone rocks, by chiselling away the rocks and gathering the soil in which young plants were growing. It is easier, however, to obtain the prothalli from soil near water, where the older plants have been established for years, and have been continually shedding their spores in the wet sandy soil. The moisture is not only necessary for the germinating of the spore, but it seems also to bring about a condition suitable to the endophytic fungus which infects the cells of the young prothalli. From such wet sandy soil patches were selected containing young sporophytes, and this material was later carefully worked through with a lens, by the same method as that used in finding the prothalli of *Tmesipteris*. It proved to be a much easier and more certain method than that first tried of chiselling the rock away and examining the soil in the crevices. In the free wet soil I was successful in finding several small pockets of prothalli, and these were enough to show all the essential features, vegetative and reproductive.

As in *Tmesipteris*, *Psilotum* has a subterranean prothallus. None of the specimens obtained were less than half an inch below the surface. The habitat of the *Psilotum* prothallus is essentially the same as that of *Tmesipteris*—in wet soil about one inch below the surface. As we shall see from the following description, the prothalli of these two plants are remarkably alike.

A description of the spore and its germination has already been given by Mr DARNELL-SMITH,[*] and a repetition of these stages is not necessary. I will only add that I have carefully examined Mr DARNELL-SMITH'S specimens, and fully accept his interpretation. There are, however, other points of detail which need amplification, especially in regard to the development of the antheridia and archegonia.

The general form of the prothallus is very like that of *Tmesipteris*. In nearly all the specimens found, however, the prothallus was larger and thicker than those

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[*] See preceding Paper, *The Gametophyte of Psilotum*, by G. P. DARNELL-SMITH.

of the latter. Some specimens appeared to be lighter coloured, more of a light yellow-brown than the darker colour of *Tmesipteris*. As in the latter, there is no trace of chlorophyll in any of the prothallial cells. It branches irregularly, and each branch terminates in a merismatic apex. It is clothed with numerous long rhizoids, which extend out from all sides and become intimately associated with particles of soil. A fair sample is that shown in fig. 18. This represents an entire prothallus. It shows the more or less cylindrical form, and the irregular manner of branching. Numerous rhizoids are to be seen growing out in all directions from the superficial cells. It should be noted that many rhizoids were broken away in freeing the prothallus from the particles of soil; so that in nature they are much more numerous than indicated in this figure. It will be observed that there is a merismatic region at the apex of each branch, and in this particular specimen a branch has apparently just bifurcated, and consequently there are two terminal meristems close together. On the surface of this specimen we may see numerous archegonia and antheridia in various stages of development. The endophytic fungus inhabiting the cells of the prothallus is quite observable from the surface view.

The size of the prothalli obtained varied considerably. For instance, in fig. 19 we have a superficial view of an exceptionally large prothallus. The portion here represented is only half the length of the specimen. The entire prothallus from which this figure was drawn measured just under three-quarters of an inch in length, and it was greater in diameter than any other specimen found. The immense number of antheridia and archegonia projecting from its surface was very striking. From this view alone there are forty antheridia and twenty archegonia visible, and quite as many on the opposite side. Several such specimens[*] as this were found, and they afforded excellent material for microtome sectioning, and following out the various stages in the development of the reproductive organs. The average size and form of the prothallus found is that represented in fig. 24. This is probably a younger state, but sufficiently mature to bear numerous antheridia and archegonia. The curious and rather indefinite sort of branching is indicated, as well as the merismatic apices of the branches. In such specimens as those represented in figs. 19 and 24 one may very easily observe the spherical form of the antheridia, and the straight tube-like neck of the archegonia.

An examination of the prothalli shown in figs. 18 and 24 will reveal a meristem at the apex of each branch, just exactly as it is in *Tmesipteris*. A longitudinal section through such a merismatic apex is represented in fig. 21. A study of these sections taken in series shows quite clearly that the apex consists of a mass of small cells, with dense finely granular cytoplasm and deeply staining nuclei. One of these cells (marked *Ap.*) I interpret to be the apical cell. An apical cell has been

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[*] Comparing such specimens as these with the figures and descriptions given by Lang (1904) of the prothallus which he provisionally referred to *Psilotum*, it will be seen that there is not the slightest resemblance.

described for the sporophyte,* and it seems highly probable that each growing branch has a single apical cell.

It is a matter of interest to note that none of the meristem cells or other cells at the growing point show any trace of the endophytic fungus (fig. 21). The region that is free from this fungus is, however, not great. Fig. 20, for instance, represents a transverse section taken not far from the apex, and here we see many of the cells filled with fungal hyphæ. As in *Tmesipteris*, the infection spreads uniformly throughout the prothallus. There is no zone or region differentiated as an infected area. Fig. 20 represents a fairly typical section through any region of the prothallus except that at the growing point. Here we see the majority of cells harbouring the fungus. Fig. 22 represents a longitudinal section to show the distribution of the fungus from this view. In both transverse and longitudinal sections it was clear that the superficial cells are not frequently infected. A more highly magnified view of a few infected cells from the interior of the prothallus is shown in fig. 25. This illustrates the effect of the endophytic fungus on the cytoplasm and nuclei of the host cells. The fungus is clearly a parasite living on the protoplasm of the prothallus. It will be seen from this figure that in the more advanced stages the nuclei have completely disintegrated. Eventually the hyphæ become coiled in dense masses, and fill the main space of the cell-cavities. When one compares this figure with fig. 6, which represents a corresponding condition in *Tmesipteris*, one is inclined to believe that it is the same species of fungus, or at any rate the same genus. Here it will be seen that the hyphæ are non-septate, just as it is shown in figs. 5 and 6 described above. Here also the infection seems to be by way of the rhizoids. Numerous examples were found showing the long hyphal threads extending the length of the rhizoids.

From the description of the vegetative characters of the prothalli of *Psilotum* † and *Tmesipteris*, it would be difficult to find two types more closely resembling one another. They have the same general form: they are subterranean, and devoid of chlorophyll; they are both saprophytic and infected with an endophytic mycorrhizal fungus of the same type; the distribution of the fungus in the tissues is the same in each case. They have all these vegetative features in common, yet they do not bear a very close resemblance to other subterranean pteridophytic prothalli.

THE ANTHERIDIA.

Abundance of material has been found for the study of the antheridia. Every prothallus procured bore these sexual organs. On some specimens these organs were

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* SOLMS-LAUBACH, 1884; FORD, S. O., 1904.

† In his general account of the prothallus of *Psilotum* (see preceding paper, pp. 87–89), I quite agree with Mr DARNELL-SMITH.

Reference should also be made to a note published in the *Proceedings of the Linnean Society of New South Wales.* This is a note by Mr T. WHITELEGGE giving an account of an object which he believed to be the gametophyte of *Psilotum triquetrum.* This description has been referred to and fully quoted by Mr DARNELL-SMITH (p. 86). I will only add that I can fully endorse Mr DARNELL-SMITH's observations, but have found nothing that in any way agrees with Mr WHITELEGGE's account.

comparatively few in number, but on the majority of the older prothalli, as seen in fig. 19, the antheridia could be counted by the score. In such old prothalli the antheridia were so numerous that an almost complete series of developmental stages could be obtained from a single specimen.

From a superficial study it becomes evident that the antheridia are not confined to any particular region. They may be observed on all sides, and apparently develop from any surface. They originate and develop with the young tissue at the growing point. It was only in such apical regions that the developmental stages were found. Only mature antheridia were observed on the older-established prothallial tissues. Serial sections beginning at the apex showed all the essential stages of development. Some of these sections are represented in figs. 23, 26, and 27. From these figures the evidence is quite conclusive that the antheridia are borne upon all sides, and not limited to any one surface. Fig. 23 represents a transverse section through the prothallus some considerable distance behind the apex. Four mature antheridia are shown. One of the latter is empty, and has evidently discharged its contents. The other three clearly show numerous coiled spermatozoids. In fig. 26 we have another section from the same prothallus. In the one plane we may see three antheridia alternating with four archegonia. Two of these antheridia contain coiled spermatozoids, and the archegonia are evidently ready for fertilisation. Fig. 27 represents another section similar to that shown in fig. 26. Two antheridia are to be seen, one of which has discharged its gametes.

From these figures it became quite evident that the antheridia are almost spherical in form and extend out quite conspicuously from the surface of the prothallus (figs. 23, 26, and 27). In this regard they stand in sharp contrast to the type of antheridium described for *Equisetum*, *Lycopodium*, *Ophioglossum*, *Botrychium*, etc.

In all these types the antheridium develops below the surface of the prothallus. The antheridium of *Psilotum* is in this regard exactly like that of *Tmesipteris*, as described above. I know of no other subterranean types that have this superficial antheridium. It is a point of some significance that *Psilotum* and *Tmesipteris* should have this feature in common.

In regard to the development of the antheridium, a complete series of stages was obtained with the exception of the first initial cell. It would be difficult to identify such a stage as this from other cells near the merismatic region. As development proceeds, however, one may very easily identify the young stages. Fig. 28, for instance, represents a median section through a young antheridium. It extends out very slightly from the surface of the prothallus. There are four external wall cells and two inner cells as seen in the section. The inner cells stand out very conspicuously by their dense granular cytoplasm and very large deeply staining nuclei. An examination of the sections preceding and following this one showed that the inner portion of the antheridium consists of two cells at this stage. A slightly older condition is represented in fig. 29. The outer wall has the same arrangement as that shown in the previous figure, but the inner part has divided further, and three nuclei are visible in this median section. The next stage found is that shown in fig. 30. It will be seen that the outer wall cells have increased in number, and that the young antheridium bulges out as a rounded protuberance from the surface. The section is quite median, and shows six cells, indicating a more advanced division of the inner antheridium. Fig. 31 represents a median section showing ten cells of the inner region. A still more advanced stage of the same is represented in fig. 32. These developmental stages shown in figs. 28 to 32 were quite frequently found from sections taken near the growing apex, and they are fair samples of the regular development of the antheridium.

Throughout its entire development the antheridium of *Psilotum* * bears a very close resemblance to *Tmesipteris*. This is quite evident by comparing the series in figs. 28 to 32 with that of figs. 7 to 10. There is, however, one curious difference to be noted. In all these stages here represented, and in many others that were observed and measured, the antheridium of *Tmesipteris* is just about twice the size of that of *Psilotum*.

This difference was not merely in regard to the entire structure of the antheridium, but was quite noticeable in the individual cells. If, for instance, we compare fig. 7 with fig. 28, or fig. 8 with fig. 31, or fig. 9 with fig. 32, it will be seen that this difference is cytological as well as structural. These figures were all drawn with the same microscope and camera-lucida, and are of the same magnification. It is quite clear that the cells and nuclei of *Tmesipteris* are larger than those of *Psilotum*. It is difficult to understand the reason for this difference. The difference in size of the mature antheridia of the two plants is indicated in figs. 12 and 34.

In regard to the cytological details associated with spermatogenesis, not sufficient microtome sections were made for the purpose. I am therefore, as yet, unable to say whether blepharoplasts are a feature of spermatogenesis in either *Tmesipteris* or *Psilotum*. I hope to investigate this detail when material at hand is more plentiful. In fig. 33 we have a representation of a median section of a nearly mature antheridium. The nuclei of the spermatocytes have undergone a marked change. They have become crescent-shaped, or even coiled. They stain very deeply with nuclear stains, and are really spermatozoids not quite mature. A surface view of the antheridium at this time is represented in fig. 34. Only the wall cells are shown, and the arrangement of these into a large spherical envelope is very characteristic. A somewhat oblique section of a mature antheridium is represented in fig. 35. The coiled, deeply staining, mature spermatozoids are clearly visible.

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* LANG'S (1904) description of the antheridium (on a prothallus provisionally referred to *Psilotum*) is as follows:—"From the few developmental stages observed it was clear that the antheridium originates in the same way as that of *Lycopodium*, the first division separating an outer cell, which forms the wall, from an inner one giving rise to the mass of spermatocytes. The outer wall of the mature antheridium is one layer of cells thick, and is nearly level with the surface of the prothallus."

In such mature antheridia—and they were frequently found—it is comparatively easy to follow the general transformation of the spermatocytes into coiled spermatozoids when one uses a high-power, oil-immersion lens. In fig. 36 several of the spermatocytes are represented. The nuclear substance has become a very dense coiled, or slightly spiral tapering filament, occupying the periphery of the cell. The cytoplasm appears as a vesicle within the coils of the nucleus. The vesicle, like the cytoplasm, is not a feature of the mature gametes. As indicated in fig. 37, these bodies are multiciliate, and their characteristic appearance at maturity is here shown. I unfortunately was unable to find this corresponding stage for *Tmesipteris*. A comparison of the size of the two spermatozoids should prove interesting in view of the difference in size of the cells in the earlier stages.

The Archegonia.

In the case of *Tmesipteris*, as I have stated above, the archegonia were of more frequent occurrence than the antheridia. Just the reverse is the rule with *Psilotum*. At least, that is true if the prothalli studied may be taken as fair samples. In every prothallus of *Psilotum* observed, the antheridia appeared in much greater numbers than the archegonia. But, as in *Tmesipteris*, these latter organs develop from all sides. They appear on every surface quite indiscriminately among the rhizoids and antheridia. Compared further with *Tmesipteris*, there is one other point of difference, which, although perhaps of no great importance, is quite obvious. In *Tmesipteris* I pointed out that the archegonia nearly always appear in crowded masses (fig. 2). I have never observed this in *Psilotum*. These organs as a rule are more scattered, and more widely separated from one another. In fig. 24 we have represented the surface view of a young prothallus, and the manner of the distribution of the archegonia is shown. Seven archegonia may here be seen widely separated from one another. In fig. 18, twelve of these organs may be seen widely distributed over the prothallus. This may be observed even to better advantage in the older prothalli. From the view shown in fig. 19 no less than twenty archegonia may be counted. In none of these cases is there any tendency to the crowding of these organs which appears to be characteristic of *Tmesipteris*.

From these figures one may also see quite clearly that the venter of the archegonium is below the surface of the prothallial tissue, and the neck projects out at right angles as a short straight tube. There is no curvature to the neck. In the younger stages, as one may see in fig. 24 (*Ar*), the apex of the neck is round or dome-shaped; but in the older conditions one or more tiers of cells break away, and the neck as a consequence is shortened and abruptly squared off.

In the transverse views of the prothalli represented in figs. 26 and 27 the archegonia may be studied in longitudinal section. In fig. 26 one may see four such sections of archegonia alternating with three antheridia. In fig. 27 there are two archegonia represented. In all of these the short straight neck may be seen, and also the breaking away of one or more tiers of neck cells. The venter, with its conspicuous egg-nucleus below the surface, is quite evident in all these cases where the section is a median one. These archegonia are apparently mature, and ready for fertilisation.

Compared with the *Tmesipteris* archegonium there are one or two minor points of difference to note. In the first place, the archegonia of *Psilotum* are smaller. They are a little more than half the size of those of *Tmesipteris*. This difference in size is quite noticeable in both the longitudinal view and the surface view. The surface view represented in fig. 14, compared with fig. 40, shows quite clearly that the archegonium of *Tmesipteris* is just about twice as large as that of *Psilotum* ; for both these figures are drawn at the same magnification. Comparing figs. 15, 16, and 17 with figs. 41, 42, and 43, the same difference in size is noticeable. Even the egg-nucleus of one plant in each case is larger than the other. It should be noted that a corresponding difference has been mentioned above in connection with the size of the antheridia.

In *Psilotum* there are four rows of neck cells to the archegonium, surrounding a neck canal. A typical example of this, as seen from the surface view, is represented in fig. 40. As shown in figs. 38 and 39, there are evidently six tiers of cells in the neck. In fig. 38 is shown a longitudinal section of the archegonium, not quite in the median plane. It clearly shows six tiers of neck cells, and the egg cell with its nucleus in the venter. Fig. 39 is a similar view, but in a median plane. The neck canal is represented ; but I was unable to determine the number of cells it contained.

The manner of the breaking away of the distal tier of neck cells seems to be different from that which I have described for *Tmesipteris*. It was the rule in the latter plant that all but the basal tier of neck cells broke away (figs. 15, 16, 17). I have observed very few such cases in *Psilotum*. Fair samples of the mature archegonia in the latter are represented in figs. 41, 42, and 43. In the first of these, two tiers of neck cells are left ; in fig. 42 one may see four tiers ; and in fig. 43 there is but one. From the numerous examples studied it seems evident that the number of tiers of neck cells broken away is not as constant as in *Tmesipteris*. In more than one case, coiled bodies, in every essential resembling spermatozoids, were observed associated with the opening of the neck canal. Such a fertilisation stage is represented in fig. 43.

It is evident from this account that the archegonium in *Tmesipteris* and *Psilotum* is of the same type. The only essential difference is that of size, and this was also noted as a conspicuous difference in the antheridium of these two plants.

THEORETICAL CONSIDERATIONS.

In organisms such as the Pteridophyta, where there are two distinct phases in the life-history—the gametophyte and the sporophyte,—it becomes a matter of great interest and importance to have as complete a knowledge as possible of both these generations. Such a knowledge is necessary in assisting us to arrive at conclusions in regard to the problems of their ecology, their geographical distribution, and, above all, their phylogenetic relationship.

Our knowledge of both generations of existing Pteridophyta is fairly complete. The gametophyte generation of extinct types, however, will probably never be known. If the prothalli of these latter types were of the same nature as the Lycopodiales or the Equisetales—races that are practically extinct—it is not likely that they could ever be preserved. Their structure is too delicate and perishable to leave hope of their being found as fossils, or even impressions. Our knowledge of such extinct races is therefore dependent entirely upon the fossil remains of the sporophyte structures, and at most such remains are fragmentary.

From the study of the geological history of plants, it seems quite certain that the Lycopodiales, Equisetales, Sphenophyllales, and Ophioglossiales are types representing merely the vestiges of races of plants of great antiquity, which in early geological times constituted vast and important features of the earth's vegetation. In the survival or extinction of such races it is obvious that the adaptations of the gametophyte, as well as the sporophyte, become a determining factor. It would seem that the production of gametes and fertilisation is essential to all Pteridophytes, and consequently the nutrition of the gametophyte generation is a matter of vital importance to such races.

In this connection it is of prime importance to note that in all of the abovementioned types of Pteridophyta, with the exception of the single genus *Equisetum*, the nutrition of the gametophyte is of a highly specialised nature. It is saprophytic, and dependent upon the co-operation of a mycorrhizal endophytic fungus. It is therefore not surprising to find this same highly specialised form of nutrition in the isolated, practically extinct race represented by *Tmesipteris* and *Psilotum*.

To what extent this highly specialised form of nutrition in the most critical phase of the life-history has affected the powers of adaptation of the sporophyte it is difficult to say. But if one may judge from a comparison of these types with the Filicales, which have free-living, chlorophyll-bearing prothalli, the effect appears to be great. From this general comparison it would seem that where we find a saprophytic nutrition in the gametophyte there is a reduction in the structures of the sporophyte, and where the gametophyte is free and with the power of photosynthesis, as in the Filicales, the sporophyte shows a high state of organisation and reaches its maximum development. The most striking exception to this rule is *Equisetum*, but even here the sporophyte is a much more highly organised structure than in any of the existing types of the Lycopodiales, Sphenophyllales, or Ophioglossales. In regard to the Psilotaceæ themselves, in this connection, we might quote from Professor Bower in *The Origin of a Land Flora*: "So far as expressed, current opinion seems to favour the probability of reduction in accordance with habit, and especially so in the case of *Psilotum*, where the leaves lend themselves readily to an interpretation as reduced structures."

The main point of interest of the Psilotaceæ, however, is the question of their affinity to one or other of the known groups of the Pteridophyta. Attempts have been made to classify them with the Lycopodiales, with the Equisetales, and finally with the Spenophyllales. Professor SEWARD,[*] on the other hand, believes that the position of *Tmesipteris* and *Psilotum* in the plant kingdom will be probably best expressed by adopting the group-name Psilotales, rather than by transferring the recent genera to the Sphenophyllales. This view is also held by Miss SYKES.[†]

Dr SCOTT[‡] was one of the first to emphasise the importance of recognising the possible affinity of the recent Psilotaceæ with the extinct fossil Sphenophylls. Since his views were published other investigators have confirmed his results. These more recent inquiries, especially those of BOODLE[§] (1904), BOWER[||] (1908), FORD[¶] (1904), and THOMAS[**] (1902), based upon anatomical, soral, and fossil evidence, have done much to direct current opinion to the view that the Psilotaceæ are more nearly related to the fossil Sphenophylls than to any other known groups of the Pteridophyta.

It is obvious, of course, that the gametophyte generation of *Tmesipteris* and *Psilotum* can offer no positive evidence in support of this view, because the corresponding phase of the Sphenophylls is entirely unknown. The prothalli of these two recent types, however, prove quite conclusively that the Psilotaceæ are related to neither the Lycopodiales nor the Equisetales. This inquiry reveals no features that would conflict with the view that the Psilotaceæ should be classed with the Sphenophyllales.

SUMMARY.

The results of this investigation may be briefly summarised as follows:—

The gametophyte of the Psilotaceæ is a subterranean prothallus of a light-brown colour.

It has a cylindrical branching form of body, each branch terminating in an apical meristem.

The prothallial tissue is uniform, there being no differentiation into vegetative and reproductive regions.

The gametophyte is devoid of chlorophyll. It is completely saprophytic, and for its nutrition is dependent upon the co-operation of a mycorrhizal fungus.

This fungus is endophytic and not localised in its distribution in the body of the host. It may infect any cells of the prothallus except those at the merismatic apex.

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[*] SEWARD, A. C., 1910.

[†] SKYES, M. G., 1908.

[‡] SCOTT, D. H., 1897–1900.

[§] BOODLE, L. A., 1904.

[||] BOWER, F. O., 1908.

[¶] FORD, S. O., 1904

[**] THOMAS, A. W. P., 1902.

The surface of the prothallus bears numerous long rhizoids which grow out from all sides.

The antheridia and archegonia are always borne upon the same prothallus, and are not localised in their distribution. The male gametes are coiled multiciliate bodies.

The antheridia develop from superficial cells, and in their mature state appear as spherical-shaped bodies that extend out beyond the surface of the prothallus. They are very numerous, and develop from all surfaces.

The archegonium consists of a venter which lies below the surface, and a straight neck which projects as a short tube beyond the surface. The neck consists of four rows of cells arranged in several tiers surrounding a neck canal.

Like the antheridia, the archegonia develop from all surfaces.

Both in their vegetative and reproductive characters the gametophytes of *Tmesipteris* and *Psilotum* bear a remarkable resemblance to one another. They differ from one another in the following features :—

In *Tmesipteris* the archegonia are much more numerous than the antheridia. In *Psilotum* the antheridia are much more numerous than the archegonia.

In *Tmesipteris* the archegonia appear in dense crowded groups. In *Psilotum* these organs are widely separated and more scattered over the surface of the prothallus.

There is a marked difference in the size of the sexual organs of the two plants. The antheridia and archegonia of *Tmesipteris* are just about twice the size of those of *Psilotum*.

From this inquiry it seems quite clear that the gametophyte generation of the Psilotaceæ bears no structural resemblance to the prothallus of either *Lycopodium* or *Equisetum*.

While the evidence shows quite conclusively that *Tmesipteris* and *Psilotum* are very closely related, it also proves that the Psilotaceæ are very remote indeed, in their phylogenetic relationship, from either the Lycopodiales or the Equisetales.

There were no new facts revealed that would tend to discount the view, now generally held, that the Psilotaceæ are more nearly related to the extinct Sphenophyllales than to any other known group of the Pteridophyta.

EXPLANATION OF FIGURES.

Figs. 1–17 are of *Tmesipteris tannensis*.

Fig. 1. A representation of an entire prothallus of *Tmesipteris*. The curious irregular form suggests that its configuration is determined by the particles of sand and other obstructions met with in the soil in the course of its development. The figure shows a distinct organic apex ; at least two antheridia and several archegonia. The numerous long rhizoids are also indicated. × 55.

Fig. 2. A portion of a prothallus drawn from the surface view. Eleven archegonia are to be observed in a small area, and one antheridium. The majority of the archegonia are drawn from the view looking down into the neck cells. One of them, however, is seen from the side view, and shows how the necks of

the young archegonia project like short tubes for a considerable distance beyond the surface of the prothallus. Many cells—even from the surface view—show the presence of the endophytic fungus. × 55.

Fig. 3. This figure represents a transverse section of the prothallus. It will be seen that the prothallus is more or less cylindrical, with a definite layer of superficial or epidermal cells from which the rhizoids are given off. Nuclei and protoplasm are present in the majority of the cells, but many of them are infected with an endophytic fungus. × 75.

Fig. 4. This represents a section of an older region of the prothallus. It will be observed that the superficial cells are the only ones not infected by the fungus. Many of the cells have lost their nuclei and cytoplasm, the entire contents being replaced by the fungus. × 75.

Fig. 5. A representation of a few superficial cells of the prothallus with rhizoids. A study of these rhizoids suggests a possible source of infection. It would seem from a study of these older rhizoids that the fungus enters the prothallus by way of the rhizoids. In the figure the fungus is shown traversing the entire length of the rhizoid and entering the cells of the prothallus. These infected rhizoids, showing the great length of the fungal hyphæ, make it easy to prove the non-septate nature of the latter. × 290.

Fig. 6. Here we have a representation to show the effect of the fungus on the infected cells. The figure was drawn from cells near the very centre of the prothallus. It will be seen that in many cases the nucleus disintegrates and eventually disappears. The cell cavities become almost filled with the fungal hyphæ, and the various stages in the degeneration of the nuclei are indicated. × 290.

Fig. 7. This figure represents a section of a very young antheridium. The wall consists of a few superficial cells covering a large inner cell whose nucleus has just undergone a division. The two nuclei thus formed are very large, and are very conspicuous as compared with the nuclei in the wall cells. The cytoplasm of the inner antheridial cell is dense and granular. × 290.

Fig. 8. We have here represented a section of an antheridium slightly older than that shown in fig. 7. The wall cells have increased in number, and the inner cells have undergone mitosis, and cell walls have been formed between them. There are eight inner cells shown in the section. The dense granular cytoplasm and large deeply staining nuclei make these cells stand out in sharp contrast to the ordinary vegetative cells of the prothallus. The young antheridium projects as a spherical protuberance from the prothallus. × 290.

Fig. 9. A representation of an antheridium at an older stage in its development than that shown in fig. 8. It will be observed that the inner cells have undergone repeated mitoses, and there is now a large central mass of sperm mother-cells or spermatocytes. The wall cells have also enlarged, and the young antheridium has increased considerably in size. × 290.

Fig. 10. This represents a section of an antheridium further developed than that shown in fig. 9. The size has still further increased, and the spermatocytes, by reason of the increased space in the interior, are less crowded. They even appear to be separating from one another. × 290.

Fig. 11. This figure represents a tangential section of a nearly mature antheridium. It will be seen that the nuclei of the spermatocytes have undergone a change. They appear now as dense crescent-shaped or slightly coiled bodies that stain very deeply with nuclear stains. These are the immature spermatozoids. × 290.

Fig. 12. We have represented here a mature antheridium, as seen from the surface. Only the wall cells are represented, and their arrangement in the form of an almost spherical body is very characteristic. × 290.

Fig. 13. This figure represents a longitudinal median section of a mature archegonium. It will be seen that the egg cell lies below the surface of the prothallus, and the neck forms a short straight tube projecting at right angles to the surface. The neck consists of at least four tiers of cells. × 290.

Fig. 14. This figure represents a surface view of three archegonia. It shows quite clearly that the neck of the archegonium which projects above the surface of the prothallus consists of four cell rows, and that the latter enclosed a comparatively narrow channel occupied by the neck canal cell. This is a very characteristic appearance of the archegonia when viewed from above. × 290.

Fig. 15. A representation of a longitudinal section of a mature archegonium. It will be observed that the main portion of the neck, consisting of the three upper tiers, has been torn away, leaving behind only the lower tier with the egg cell in the venter. × 290.

Fig. 16. This figure likewise represents a longitudinal section of a mature archegonium about the same stage as that shown in fig. 15. The upper tiers of the neck cells have broken away, but traces of the cell walls of the second tier are to be seen. A dense cytoplasm and a large egg nucleus are conspicuous features of the venter. × 290.

Fig. 17. The stage represented here is about the same as that in fig. 16. Only the lower tier of neck cells is present, but this tier (as shown in figs. 15 and 16 also) projects slightly over the surface of the prothallus in a very characteristic fashion, with thin curiously pointed margins. This archegonium is ready for fertilisation. × 290.

Figs. 18–43 are of *Psilotum triquetrum.*

Fig. 18. This is a representation of an entire prothallus of *Psilotum.* It is more or less cylindrical in form, branches irregularly, and with numerous long rhizoids growing out in all directions from the superficial cells. There is a merismatic organic apex at the end of each branch, and over the surface of the prothallus there are numerous antheridia and archegonia. The endophytic fungus inhabiting the cells of the prothallus is quite observable from the surface view. × 55.

Fig. 19. This is a superficial view of an exceptionally large prothallus of *Psilotum.* The portion here represented is only half the length of the specimen, which was over half an inch long. The immense number of antheridia and archegonia projecting from its surface was very striking. These reproductive organs were just as numerous on the one side as on the other, and the prothallus itself was nearly perfectly cylindrical. The rhizoids and endophytic fungus are also very obvious. × 55.

Fig. 20. This figure represents a transverse section of the prothallus of *Psilotum.* The main characters of the prothallial cells with their cytoplasm and nuclei are indicated. The distribution of the endophytic fungus is also shown. The hyphæ of the latter are seen in only a few of the superficial cells, but quite conspicuous in the interior cells of the prothallus. × 75.

Fig. 21. This is a representation of a longitudinal section through the merismatic apex of the prothallus. The apex consists of a mass of small cells with dense cytoplasm and deeply staining nuclei. One of these cells (marked *Ap*) I interpret to be the apical cell. It will be observed that none of the cells in this merismatic region are infected with the fungus. × 75.

Fig. 22. We have here represented a longitudinal section of the prothallus taken some distance behind the apex. It shows the fairly even distribution of the endophytic fungus throughout the prothallial tissue, but the superficial cells are practically free from infection, only a few of the cells containing hyphæ. × 75.

Fig. 23. A transverse section through the prothallus. The presence of endophytic fungus is clearly indicated, and four mature antheridia are shown. One of the latter is empty, and the other three clearly show numerous coiled spermatozoids. × 75.

Fig. 24. This figure represents an entire prothallus of *Psilotum.* It is comparatively of small size, but sufficiently old to bear several antheridia and archegonia. The curious indefinite sort of branching is indicated, as well as the merismatic apices of the branches. The spherical form of the antheridia and the straight tube-like nature of the necks of the archegonia are clearly shown (*Ar.*, *An.*). × 55.

Fig. 25. This figure represents a few cells from the interior of the prothallus, as seen in transverse section. It shows the effect of the endophytic fungus in the cytoplasm and nuclei of the prothallial cells. In the more advanced stages the nuclei have completely disintegrated, and the hyphæ become coiled in dense masses, and fill the main space of the cell cavity. The phycomycetous nature of the fungus is also indicated in its non-septate hyphæ. × 290.

Fig. 26. We have here a representation of a transverse section of the prothallus. In the one plane three antheridia and four archegonia are shown. Two of the antheridia contain mature coiled spermatozoids, and the archegonia appear to be ready for fertilisation. The terminal tiers of the neck cells of the archegonia have broken away, and the egg cell is clearly visible in the venter. × 75.

Fig. 27. This figure represents another section similar to that shown in fig. 26. There are two antheridia to be seen, one of which has discharged its spermatozoids. Two archegonia are to be seen, and these show the conspicuous egg cell in the venter and end cells of the neck broken away. The archegonia are ready for fertilisation. This and the preceding figure show the presence of the fungus in the interior of the prothallus. × 75.

Fig. 28. This represents a median section through a very young antheridium. There are three or four wall cells and two inner cells. This is the youngest stage of the antheridium found. The inner cells are conspicuous by the dense granular cytoplasm and the large deeply staining nuclei. × 290.

Fig. 29. This figure also represents a median section through a young antheridium, but a stage in the development slightly in advance of that shown in the preceding figure. The inner cells have divided, and we thus have the four-celled stage. × 290.

Fig. 30. This is a representation of a slightly older stage in the development of the antheridium as seen in median section. The wall cells have evidently increased in number, as also have the inner cells. This is no doubt the eight-celled stage. × 290.

Fig. 31. This figure represents a median section through a young antheridium. It is a stage in the development slightly in advance of that shown in fig. 30. It is the sixteen-celled stage of the inner cells. × 290.

Fig. 32. This figure also represents a young antheridium in median section. It is a stage in development following immediately on that shown in the preceding figure. It is the thirty-two-cell stage of the antheridium. × 290.

Fig. 33. A representation of a median section of a nearly mature antheridium. The nuclei of the spermatocytes have undergone a change. They have become crescent-shaped or slightly coiled deeply staining bodies. They are the immature spermatozoids. × 290.

Fig. 34. This represents a mature antheridium as seen from the surface. Only the wall cells are represented, and the arrangement of these into a large almost spherical structure is very characteristic. × 290.

Fig. 35. This figure shows a tangential section through a mature antheridium. The mature coiled deeply staining spermatozoids are clearly visible. × 290.

Fig. 36. This figure represents a few immature spermatozoids taken from the antheridium shown in fig. 33, but more highly magnified. It will be seen that the nucleus becomes crescent-shaped and then coiled, and stains very deeply with saffranin. × 900.

Fig. 37. This represents several mature spermatozoids taken from the antheridium represented in fig. 35, but much more highly magnified. The coiled and multiciliate nature of these gametes is clearly indicated. × 900.

Fig. 38. This figure represents an archegonium from a section that was not quite median. There are shown six tiers of cells in the neck and the venter containing the egg cell below the surface. × 290.

Fig. 39. This represents a median section through the archegonium. It shows a distinct egg cell in the venter, a straight neck of six tiers of cells, and two nuclei in the neck canal. × 290.

Fig. 40. This figure represents an archegonium as seen from above. There are four cell rows which enclose a channel occupied by the neck canal cell. × 290.

Fig. 41. This represents a median section through a mature archegonium. The large deeply staining egg nucleus is a conspicuous feature of the venter. The distal tiers of the neck cells are broken away, leaving only two tiers. This archegonium is ready for fertilisation. × 290.

Fig. 42. This figure represents a stage similar to that shown in fig. 41, but it also shows a variation in the number of tiers of neck cells that are left after the breaking away of the distal tiers. Here it is clearly shown that there are three left. In fig. 41 there were two, and in fig. 43 there is but one. × 290.

Fig. 43. A median section through a mature archegonium at the time of fertilisation. The venter with its conspicuous egg nucleus and cytoplasm and the remaining tier of neck cells are represented. There are also to be seen deeply staining coiled structures that I interpret to be spermatozoids at the entry of the neck canal. × 290.

LITERATURE CITED.

BERTRAND, C. EG., "Recherches sur les Tmesipteridées," *Archives botaniques du Nord de la France*, Lille, 1881–3.

BERTRAND, C. EG., "Le type Tmesipteridée," *Bull. de la Soc. Bot. de France*, Lille, t. xxx, Paris, 1883.

BERTRAND, C. EG., "Note sur la nature morphologique des rameaux aeriens des Psilotums adultes," *Bull. de la Soc. Bot. de France*, 1883.

Boodle, L. A., "Secondary Tracheids in *Psilotum*," *New Phytologist*, Feb. 1904.

Boodle, L. A., "On the Occurrence of Secondary Xylems in *Psilotum*," *Ann. Bot.*, No. 71, p. 505, 1904.

Bower, F. O., "Studies in the Morphology of Spore-producing Members, Equisetineæ and Lycopodineæ," *Phil. Trans.*, 1894.

Bower, F. O., "General Comparisons and Conclusions," *Phil. Trans.*, 1903.

Bower, F. O., *The Origin of a Land Flora*, Macmillan & Co., London, 1908.

Bruchmann, H., *Ueber die Prothallien und die Keimpflanze mehrerer europaischer Lycopodien*, Gotha, 1898.

Bruchmann, H., "Ueber das Prothallium und die Keimpflanze von *Ophioglossum vulgatum*," *Bot. Zeit.*, lxii, p. 227, 1904.

Campbell, D. H., *Mosses and Ferns*, London, 1913.

Darnell-Smith, G. P., "The Prothallus of *Psilotum*," *Trans. Roy. Soc. Edin.*, 1916.

Ford, S. O., "The Anatomy of *Psilotum triquetrum*," *Ann. Bot.*, vol. xviii, No. 72, p. 589, 1904.

Jeffrey, E. C., "The Structure and Development of the Stem in Pteridophyta and Gymnosperms," *Phil. Trans. Roy. Soc.*, 1902.

Jeffrey, E. C., "The Gametophyte of *Botrychium virginianum*," *Proc. Can. Inst.*, v. 1898.

Lang, W. H., "On the Prothalli of *Ophioglossum pendulum*, *Helminthostachys zeylanica*, and *Psilotum*," *Proc. Roy. Soc.*, 1901.

Lang, W. H., "On the Prothallus provisionally referred to *Psilotum*," *Ann. Bot.*, vol. xviii, 1904.

Lawson, A. A., "The Prothallus of *Tmesipteris*," *Trans. Roy. Soc. Edin.*, 1916.

Lignier, O., "Equisétales et Sphenophyllales: leur origine Filicinéenne commune," *Bull. de la Soc. Linn. de Normandie*, sér. 5, vol. vii, Caen, 1903.

Scott, D. H., *Studies in Fossil Botany*, London, 1900.

Scott, D. H., "On *Cheirostrobus*, a new type of Fossil Cone from the Lower Carboniferous Strata," *Phil. Trans.*, 1897.

Seward, A. C., *Fossil Plants*, Cambridge University Press, 1910.

Sykes, M. G., "The Anatomy and Morphology of *Tmesipteris*," *Ann. Bot.*, vol. xxii, No. 85, p. 63, 1908.

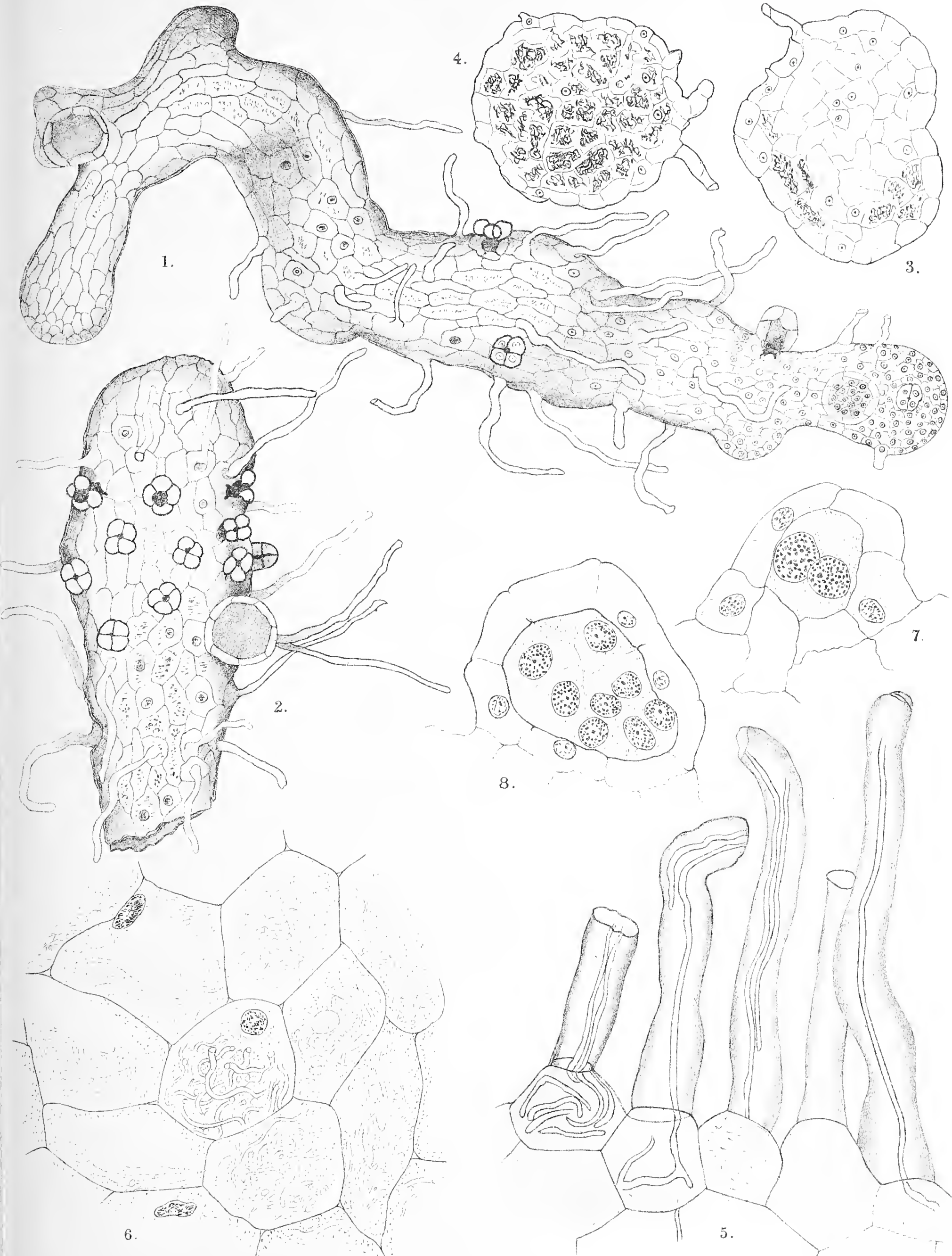
Thomas, A. W. P., "The Affinities of *Tmesipteris* with the Sphenophyllales," *Proc. Roy. Soc.*, vol. lxix, 1902.

Treub, M., "Études sur les Lycopodiacées," *Ann. du Jard. Bot. de Buitenzorg*, 1886.

Vaughan Jennings, A., and Hall, K. M., "Notes on the Structure of *Tmesipteris*," *Proc. Roy. Irish Acad.*, 1891.

Whitelegge, T., "Notes and Exhibits," *Proc. Linn. Soc. New South Wales*, April 26, 1916.

LAWSON: PSILOTACEÆ.



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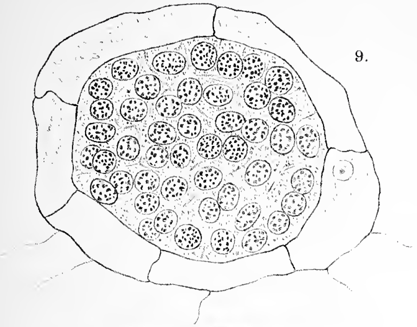
TMESIPTERIS.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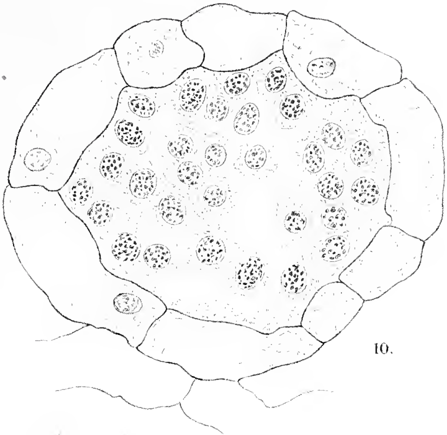
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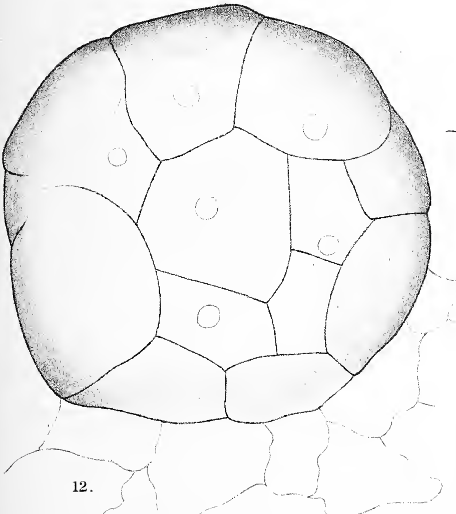
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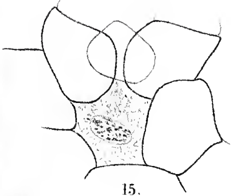
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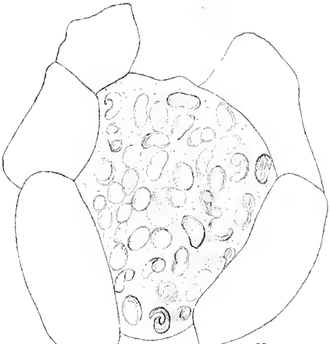
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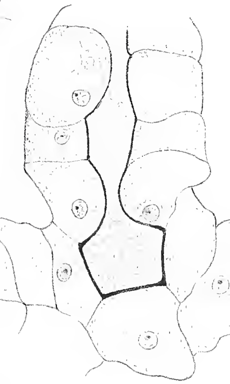
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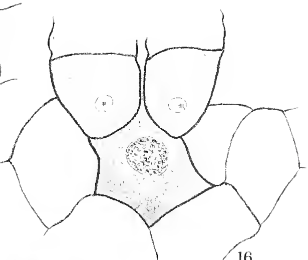
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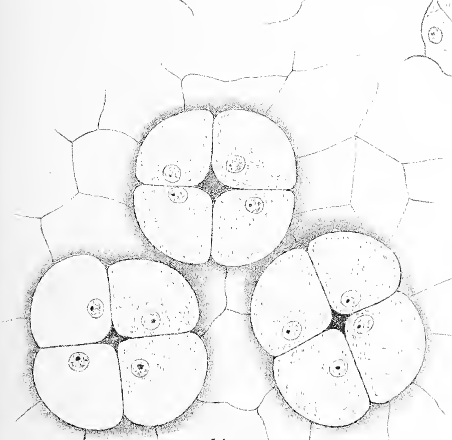
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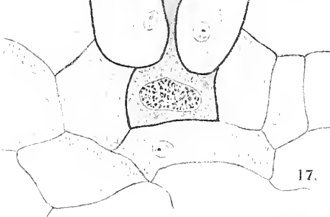
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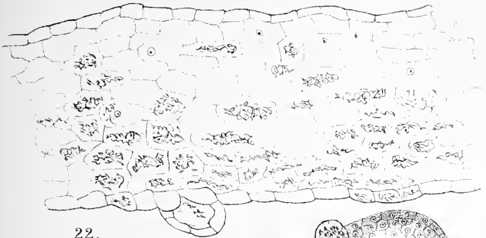
Tmesipteris.

Lawson: Psilotaceæ.



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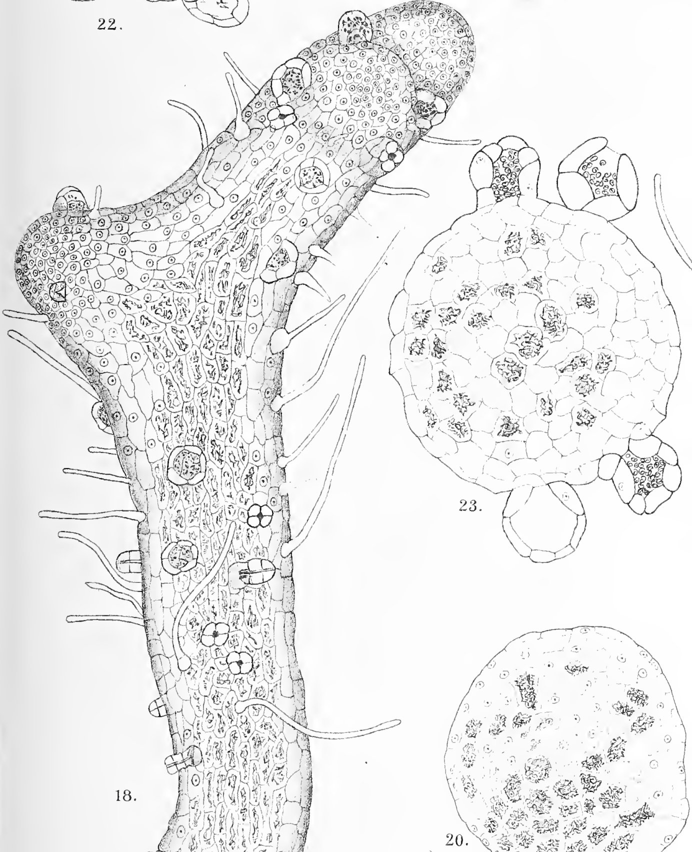

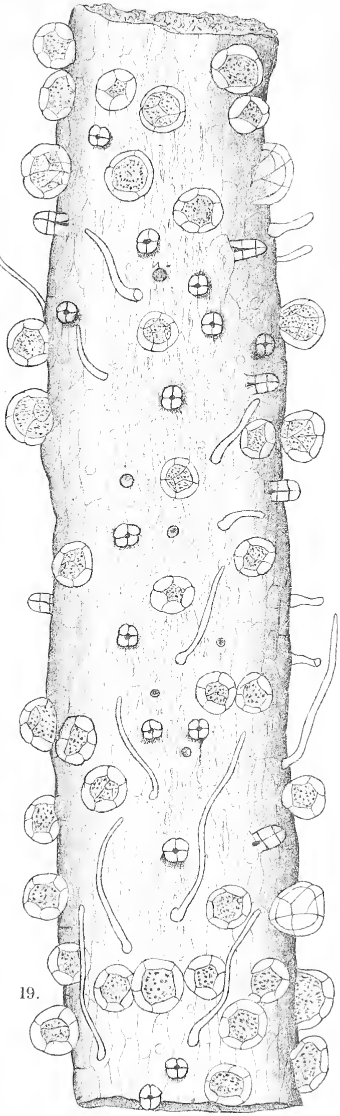

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Psilotum.

LAWSON : PSILOTACEÆ.

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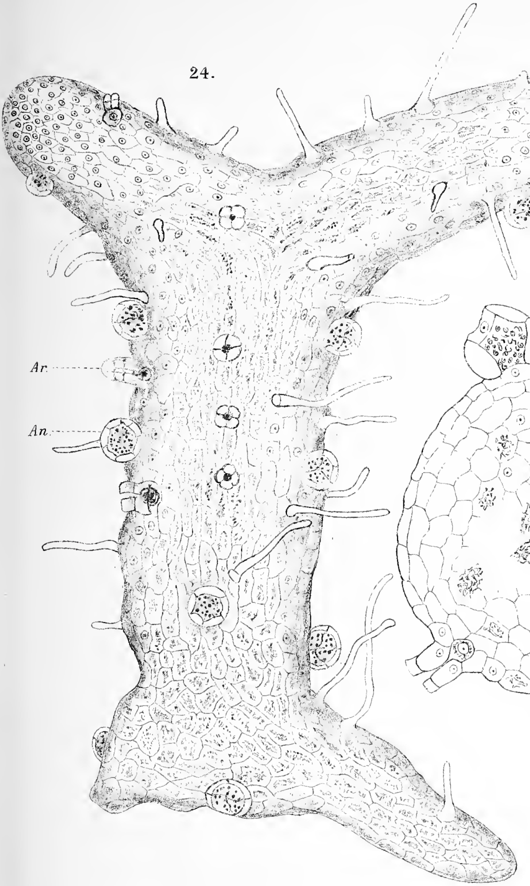

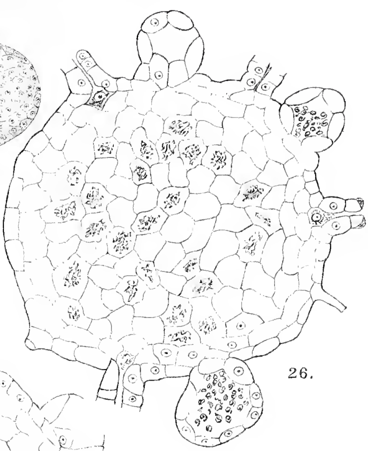

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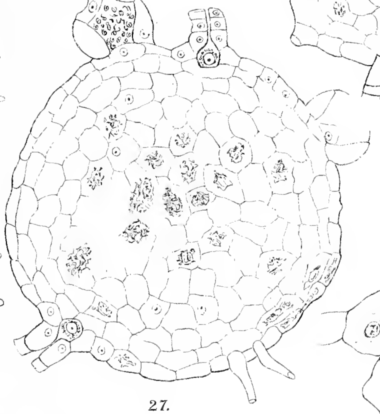

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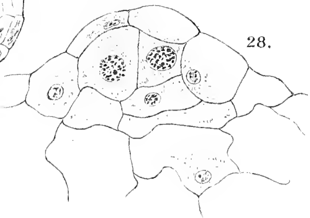

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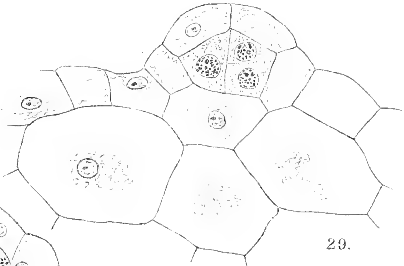

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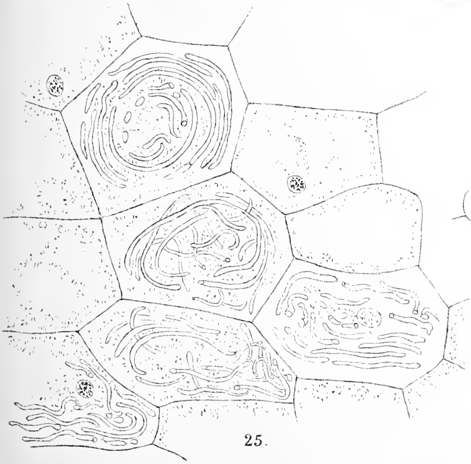

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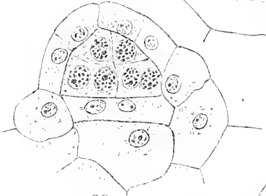

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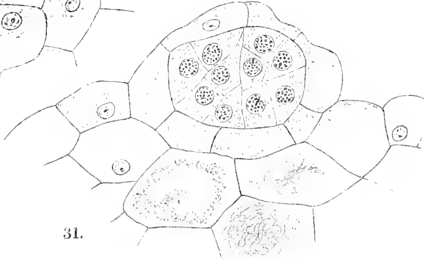

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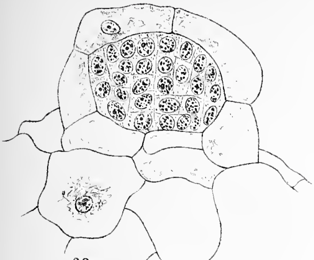
A. A. Lawson, *del.*

M'Farlane & Erskine, Lith., Edin.

PSILOTUM.

Lawson: Psilotaceæ.



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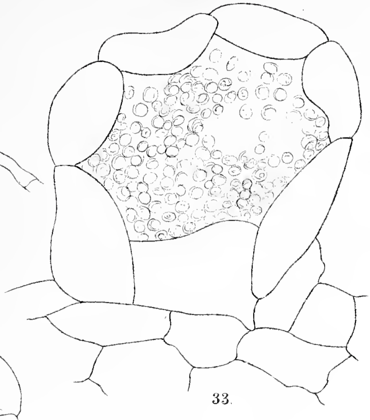

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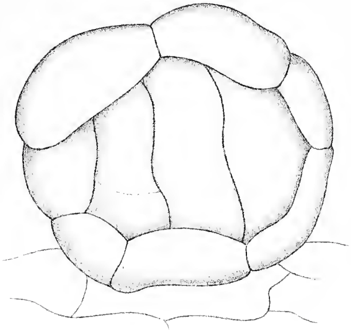

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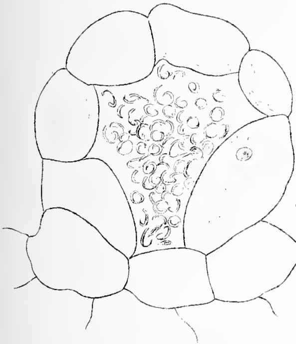

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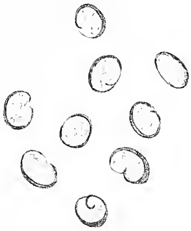

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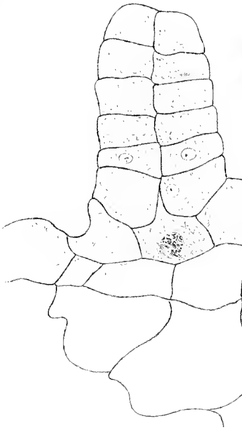

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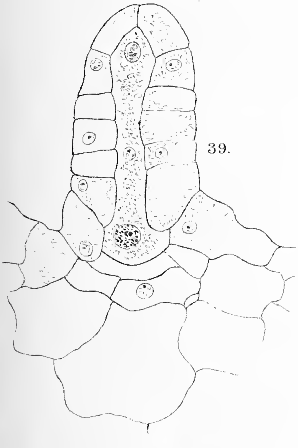

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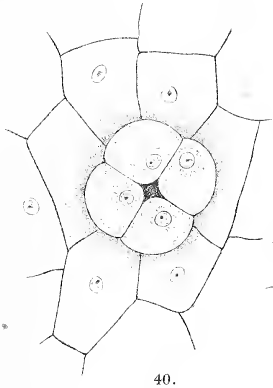

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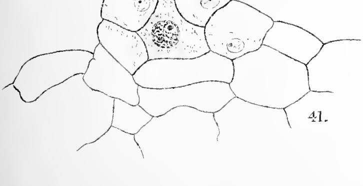

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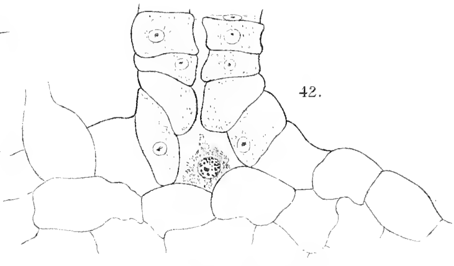

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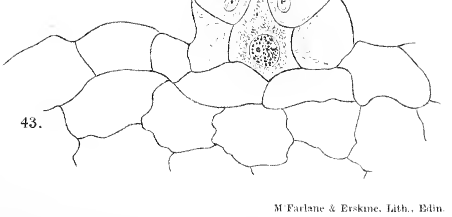

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A. A. Lawson, *del.*

M'Farlane & Erskine, Lith., Edin.

Psilotum.

V.—The Moulting of the King Penguin (Aptenodytes patagonica). By Professor J. Cossar Ewart, F.R.S., and Dorothy Mackenzie, F.S.Z.S. (With Two Plates.)

(Read November 15, 1915. MS. received January 23, 1917. Issued separately June 14, 1917.)

CONTENTS.

THE MOULTING OF THE SECOND OR JUVENILE DOWN.

As the King Penguin chick grows, the down tassels forming the prepennæ increase in length until they measure from 50 to 75 mm. (2 to 3 inches) over the greater part of the body. Some of the barbs of the juvenile down carry for some time natal down barbs on their tips, and the inner ends of all the barbs forming the tassels are eventually found to be continuous with barbs of either the main shaft or the after-shaft of the developing true feathers. How long the down coat is worn by any given King Penguin is not definitely known—it is said that King Penguins may not moult the prepennæ until they are nearly a year old; neither is it known at what time of the year the majority of the King Penguins living under natural conditions in South Georgia shed their prepennæ, or how long the moulting process usually lasts.

From the information collected by Mr Murphy* and others, it is evident that the breeding season lasts as long as the Antarctic summer, and that throughout the summer there are moulting as well as breeding birds on the rookeries. If some birds are hatched in January and others in March, and if the prepennæ are worn as a rule for about ten months, and got rid of in from ten to twenty days, one would expect to find many birds in the act of shedding their down during the Antarctic midsummer. The view that a coat of true feathers is acquired, and that the young are ready to take to the water before the Antarctic summer comes to an end, is confirmed by Murphy, who came across a number of King Penguins in the act of shedding their down coats on December 16, 1913—these birds were full-grown, but still had tell-tale ragged patches of long down attached to their newly acquired true feathers.

From young penguins living in captivity nothing very definite has yet been

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[*] Murphy, *Science Bulletin*, The Museum of the Brooklyn Institute of Arts and Sciences, vol. ii, No. 5, p. 109.

learned, either as to the moulting period or as to the time occupied in substituting true feathers for prepennæ. In the case of the two young King Penguins in down presented to the Scottish Zoological Society* in January 1914, the moulting was, obviously, abnormal. One bird began to moult on May 22nd, 1914, but only completed the process about the middle of August; the second bird started to moult about the middle of May, but the process was arrested for some weeks, with the result that the last of the long down tassels (prepennæ) were only finally got rid of in September.

In referring to the moulting of King Penguins in South Georgia, MURPHY states that the down, shortest on the head and hair-like and matted on the body, gradually fades and finally assumes a golden-brown or yellowish colour. He further points out that the down on the flippers is the first to go, that next it is lost from the lower breast, then from the back, and lastly from the upper breast, throat, and head. Fragments remained longest on the nape of the neck. About the immature plumage, it is stated that the new feathers of the upper breast reveal a pale yellow tinge; that the auricular patches, though brighter than the throat, fail to suggest the brilliant orange hue of the mature plumage; and that the subtle greenish-yellow gloss or bloom seen on the crown of the head of many King Penguins makes its appearance soon after the down has entirely disappeared. According to MURPHY, the young King Penguin of South Georgia, soon after the down is shed, may be regarded as a less glorified replica of the adult.†

Dr WILSON, in his monograph on penguins in the *Report of the National Antarctic Expedition*,‡ points out that the plumage of the immature King Penguin differs in several respects from that of the adult. The nature of some of these differences is made abundantly clear by means of coloured drawings. One of these drawings represents the head of a young bird upon the completion of the moult from the down; one the head of an ordinary adult in full plumage; and one the head of an extraordinary adult, in which the characteristic greenish-yellow sheen on the top of the head has been developed to an unusual extent. The difference between the head of the young immature bird just moulted from the down, and the heads of the adults is very striking: in the immature bird the colour of the throat and the auricular patches is pale yellow, in the adults it is brilliant orange. In the richly coloured old bird the greenish-yellow sheen on the top of the head is specially marked, whereas in the immature bird the top of the head is of a bluish-grey colour.

A similar blue-grey patch is present on the head of the young Emperor Penguin (*Aptenodytes forsteri*). Because of the presence of a blue-grey patch on the head of young King and Emperor Penguins, it has been suggested that both these species

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* Two adult and two young King Penguins from South Georgia were presented to the Scottish Zoological Society in 1914 by Messrs Salvesen & Co., Leith. One of the old birds died soon after its arrival.

† MURPHY, *loc. cit.*, p. 110.

‡ *National Antarctic Expedition*, vol. ii, *Zoology*, 1907.

are descended from a common ancestor. Seeing that the head of WILSON's immature King Penguin is relatively small, it may perhaps be assumed that immature penguins with pale yellow patches have moulted prematurely—moulted when they had only reached the phase in the ancestral history characterised by a blue-grey patch on the crown of the head.

When the young King Penguins in the Scottish Zoological Park had completely shed their down they very closely resembled in their plumage one of the newly moulted old birds which accompanied them from South Georgia. Instead of developing a patch of blue-green on the top of the head, one of them soon acquired the peculiar bloom usually associated with mature birds. More remarkable still, as the greenish-yellow sheen developed on the head, the sheath of the mandible gradually changed from the dark tint characteristic of immature birds to a lighter tint, and some weeks later it assumed the orange-pink colour usually associated with mature birds. In the second young bird there was no hint of a greenish sheen on the top of the head in 1914, neither is there any suggestion of this subtle greenish gloss in 1915.* In all probability the differences noticed amongst birds which have just lost their down are due to late-hatched birds moulting at or about the same time as birds hatched during the early part of the breeding season.

THE MOULTING OF THE IMMATURE AND ADULT PLUMAGE.

(1) *Time of Moulting.*

From the observations made by Dr WILSON during the *Discovery* expedition, we know that the Emperor Penguin breeds during the winter; that the eggs are laid *on sea ice* early in July—the darkest and coldest month of the Antarctic winter,—and that the young are hatched about the end of August, and moult at the end of December when about four months old; and that the adult birds, having finished all their duties to the young, leave them to themselves and retire southwards in January and February to take up their retreat and moult in safety on fast ice. The Emperor Penguin, even when moulting, never sets foot on land. The immature Emperors when on the point of moulting also "wander south to find fast ice, on which they remain while the process lasts, knowing that in the disintegrating ice-pack they might be forced to take to the water when it would be highly inconvenient for them to do so." † A young Emperor brought on board the *Discovery* in Lady Newnes Bay shed its immature coat and donned the adult plumage and all the distinctive characters of the fully adult bird when seventeen months old—this bird probably began to moult in the middle of January.

The rookeries of the King, unlike those of the Emperor Penguins, are on land,

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* In the surviving old bird from the Antarctic, a greenish sheen has never made its appearance on the top of the head.

† WILSON, *loc. cit.*, p. 19.

and are used for moulting as well as for the hatching and rearing of young. The hatching of young and the moulting of immature and adult King Penguins seem to go on during the greater part of the Antarctic summer. According to MURPHY, the King Penguins assume the adult plumage when about two years old. Though some old birds may only begin to moult about the middle of March, young birds, as a rule, begin to shed the immature coat early in February. A King Penguin which reached the Gardens of the Zoological Society of London in February 1911 underwent a complete moult in March, and six months later again moulted.* The majority of our British birds moult in the late summer or early autumn after they have recovered from the hatching and rearing of their young. Hence the captive King Penguin which moulted first in March and then in September, first observed the time devoted to moulting by penguins living under natural conditions in South Georgia, and then the time usually followed by birds in England. The explanation of this unusual procedure is probably that the captive penguin became so completely adapted to its new environment during the summer of 1911, that it readily responded in September to the stimuli which induce the post-nuptial moult in so many of our British birds.

That the conditions which prevail in Britain tend to induce imported penguins to moult in the autumn is further suggested by a second penguin in the London Gardens, and by one of the penguins brought to Scotland in January 1914. The former, two years running, moulted in August–September; the latter moulted in October 1914, but in 1915, when better adapted to its new surroundings, it moulted early in September.

Two King Penguins in the Scottish Zoological Park, which moulted in 1914 out of the down into the immature plumage, also support the view that acclimatised captive birds from the Far South may be expected to moult about the same time as our native birds. One of these birds in 1915 began to shed its immature coat towards the end of July, the other in the middle of August.†

(2) *Duration of the Moulting Period.*

It was a surprise to ornithologists to learn that the King Penguin, under natural conditions, wears its down coat for ten months; it will be a still greater surprise if it is demonstrated that a complete new coat is, as a rule, substituted for the old one in ten days. In the case of amphibians and many reptiles the horny layer of the skin is completely shed several times a year. If moulting in birds is an inheritance from remote reptilian ancestors, it is extremely probable that even in the Cretaceous period birds moulted several times a year. At the present day the ptarmigan undergoes one complete and two nearly complete moults annually, and in grouse and pigeons exchange of feathers takes place during the greater part of the year. The

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* SETH-SMITH, *Proc. Zool. Soc.*, 1912.

† These two young Kings were probably nine or ten months old when they reached Scotland in January 1914, and two and a half years old when they assumed the adult plumage in August 1915.

ptarmigan moults several times annually, not because its reptilian ancestors frequently moulted, but rather that it may in summer and autumn as well as in winter have the advantage of being protectively coloured. Probably the changes in the plumage of grouse are also adaptive; but why, in pigeons, new feathers are being substituted for old during the greater part of the year is not so obvious.

It is extremely difficult (even if one adopts the doctrine of sexual selection and admits that much is gained by being protectively coloured) to account for the many peculiarities met with in the plumage of birds. It would not cause much surprise should an ornithologist with a bias in favour of Lamarckism arrive at the conclusion that birds have a keen appreciation of both form and colour, and have in fact long been striving to acquire as fine a plumage as the circumstances under which they live and move and have their being permitted. A Neo-Lamarckian might even assert that, notwithstanding the necessity to moult, birds have long been endeavouring not only to obtain as brilliant a nuptial plumage as possible, but to wear fine feathers all the year round. As a matter of fact, many birds, without incurring undue risks, acquire at a very early period, and perpetually wear, fine feathers, while others wear a fine coat during a considerable part of each year. The chief difficulty encountered was the renewal of the flight feathers without the loss of the power of flight. Kingfishers and many other birds which early assume the nuptial coat and wear it throughout the year have overcome this difficulty by only moulting a few of the wing quills at a time—the use of the wings being assured all the year round, there was probably little difficulty in reducing or suppressing the nestling down stage and in exchanging the old for new feathers so gradually that the brilliancy of the plumage was maintained almost unimpaired all the year round.

In the case of the Great Northern Diver an ideal plumage has only been partially realised, apparently because all the flight feathers are lost at or about the same time. Hence, although in both sexes a fine nuptial dress has been acquired, it cannot be safely worn when the wings are out of action. If our more familiar birds—*e.g.* thrushes, starlings, and pigeons—were annually to lose for some weeks the use of their wings they would run the risk of being rapidly exterminated. In aquatic birds the power of flight is not, as a rule, as imperative as in land birds. Nevertheless, in the Great Northern Diver—a bird so highly specialised for an aquatic life that walking on land is no longer possible—the loss of the power of flight is probably so serious that, in order to diminish the risk when the wings are out of action, the brilliant nuptial coat is for a time exchanged for a sober inconspicuous coat. This implies that the Great Northern Diver (the female as well as the male) moults twice a year. The nuptial plumage gives place at the end of the breeding season to a sober post-nuptial or winter plumage, and this in turn gives place to the brilliant nuptial plumage. Though the wing quills are not shed until about the end of December, the moulting of the inconspicuous winter coat begins about the beginning of December, but the progress is so slow that the new nuptial coat—characterised by black feathers, with purple and green reflections on the head and neck, glossy black feathers with large, distinct, white spots on the back, and pearly white on the under surface—is not finally established in all its splendour until about the end of May.* The result is that in the Great Northern Diver moulting is going on during the greater part of the year.

The common duck (*Anas boschas*), though doubtless aiming as high, has not yet reached the stage gained by the Great Northern Diver, for the female still wears an inconspicuous coat all the year round.† In the male duck, as in the Great Northern Diver, many months are occupied by the double moult; in the ptarmigan and grouse more or less obvious changes are taking place in the plumage all the year round, and, though not so obvious, this is also true of pigeons, kingfishers, parrots, and many other birds. In the penguins, on the other hand, the actual moulting period is short, and there is no difficulty in ascertaining exactly when it begins and when it ends. In the immature Emperor Penguin taken on board the *Discovery* in Lady Newnes Bay the moulting "took twenty days from start to finish." In this case "the feathers clinging close to one another came off in spurious sheets or handfuls, first from the breast and thighs and then from the face and tail and flippers, but most irregularly, until at length there was nothing left but a ruffle of old feathers round the neck."‡ It is conceivable that under natural conditions the duration of the moult in this bird would have been under twenty days.

In the King Penguin which moulted in 1897 in the London Gardens the feathers began to fall out about the end of August, but the moult was only completed in the third week of September. In 1898 this bird again moulted in August–September, and the duration was again about a month.§ In the case of the King Penguin which moulted twice in six months in the London Gardens, the "process was completed on both occasions in just four weeks."‖ Though in the King Penguins in the London Gardens the duration of the moulting process was decidedly longer than in the immature Emperor on the *Discovery*, an immature Humboldt's Penguin (*Spheniscus humboldti*) which reached the London Gardens in 1878 moulted in ten days. This bird, though out of condition on arrival, rapidly improved. By feeding freely and passing much time in the water, it was extremely vigorous when the feathers began to fall off on February 26. BARTLETT points out, the process of moulting proceeded so rapidly "that by the 7th of March the bird had entirely renewed its plumage and appeared in the adult dress." Though this immature *Spheniscus*, about February 22, appeared dull, was spiteful and ill tempered, and

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* An account of the moulting of the Great Northern Diver, by SMALLEY, will be found in the *Annals of Scot. Nat. Hist.*, 1909, p. 139.

† Both the duck and the diver, in having an immature down coat, are decidedly less specialised than kingfishers and parrots.

‡ WILSON, *loc. cit.*, p. 19.

§ W. E. DE WINTON, *Proc. Zool. Soc.*, 1898.

‖ SETH-SMITH, *loc. cit.*, *Proc. Zool. Soc.*, 1912.

avoided going into the water, its appetite continued good, and it apparently fed as freely as usual until the feathers began to fall out.[*] It is extremely probable that, both in the time and in the duration of the moult, this bird conformed to the practice followed by immature birds living under natural conditions on the Pacific Coast of South America.

If the two young King Penguins which reached Scotland in January 1914 after a six weeks' voyage were hatched in January 1913, they would, had they remained in South Georgia, in all probability have donned the immature coat in February 1914, and assumed the adult plumage in February or March 1915. Upset by the voyage, they made no attempt to moult either in February or March 1914; and when in May a beginning was made to shed their down, the response to the stimuli was so feeble that little progress was made, with the result that the assumption of the immature coat was delayed until the autumn—the moult being completed in August by one bird, and in September by the other. There was, however, compensation for the five or six months' delay in as far as the down coat, instead of being succeeded by an ordinary immature coat, gave place, as already indicated, to a coat having nearly all the characteristics of the mature or adult plumage.

By the time the immature coat was completed in the autumn of 1914, the two young King Penguins had evidently become thoroughly acclimatised. One result of the adaptation to the new environment was the absence of any attempt to moult in the spring of 1915. In May 1915 the two immature birds, and the surviving old King Penguin brought along with them from South Georgia, were transferred to a specially constructed enclosure provided with a pool large enough and deep enough to admit of their taking ample exercise. Up to about the middle of July they fed freely, and were probably as healthy and vigorous and provided with as fine a coat as their relatives of a like age in South Georgia. But towards the end of July, in their every movement and attitude they gave onlookers the impression that life was no longer worth living. They took little exercise, ate little, and rarely made any attempt to smooth down their ruffled and somewhat faded feathers. But when, on August 17, moulting actually started, their drooping spirits revived, and, instead of brooding over their troubles, they set to work to scrape off the dead, but still adhering, feathers. The moulting, once begun, proceeded at so rapid a pace that, in one of the immature birds, the whole of the old feathers were completely displaced by full-grown, brilliant new feathers in the short period of ten days; in the other two birds the moulting from start to finish was completed in eleven days.

Had the adult bird which reached the Scottish Zoological Park in January 1914 remained in South Georgia, it would probably have moulted in February or March; but owing to the different climate, and the unusual conditions it encountered before and after its arrival in Scotland, moulting was postponed until October. But by the summer of 1915 the old bird was so completely acclimatised that, like the acclimat-

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[*] Bartlett, *Proc. Zool. Soc.*, 1879

ised King Penguins in the London Gardens, it moulted in the autumn. On August 9 there were indications that moulting was imminent, and on September 4 the old feathers began to fall off. By September 15 the whole of the feathers were shed and a complete new coat of full-grown feathers had taken their place. We can only account for the King Penguins in the Scottish Zoological Park completing their moult in about one-third of the time taken by the Kings in the London Gardens by assuming that the Scottish specimens were more completely acclimatised, or that (like Humboldt's Penguin in the London Gardens in 1878) they were healthier and more vigorous.

From what has been said, it is evident that the King Penguin differs in the following respects from the kingfisher and other birds which wear or appear to wear the same plumage all the year round.

(1) The true feathers of the penguin are preceded by two coats of down; in the kingfisher the down coats are practically suppressed.

(2) In the penguin an immature coat is assumed about the end of the first year, and the adult coat about the end of the second year; in the kingfisher the adult coat is practically assumed before the young leave the nest.

(3) In the penguin the new coat is substituted for the old during a distinct moulting period (which may only last ten or eleven days), and is preceded by marked constitutional disturbance; in the kingfisher new feathers are being substituted for old throughout the greater part of the year, but there is no obvious moulting period, nor yet any indication of constitutional disturbance.

(4) During the moulting period the penguins living under natural conditions *never* enter the water, and hence never have a chance of obtaining any food; the kingfisher takes to the water, and feeds all the year round.

The Great Northern Diver mainly differs from the King Penguin in moulting twice a year; first into a sober or "eclipse" coat at the end of the breeding season, and then back into the brilliant adult or nuptial coat, the substitution of the nuptial for the post-nuptial plumage occupying a period of nearly six months.

In the case of the common duck there is the further difference that the female, throughout life, wears an inconspicuous coat, which is, in a sense, comparable to the immature coat of the penguins.

Seeing that penguins fast during the moulting period, it is obviously an advantage that the exchange of the old for a new coat should be effected as expeditiously as possible.

ORDINARY BEHAVIOUR OF KING PENGUINS IN CAPTIVITY.

As already stated, a consignment of penguins (two adult and two young Kings, one Gentoo, and one Rockhopper) reached the Scottish Zoological Park from South Georgia on January 24, 1914.

One of the first things noted about these penguins was their great exclusiveness

—at feeding times only would the three varieties associate together; at all other times each kind kept itself very much to itself. MURPHY noticed this in regard to King and Gentoo Penguins in South Georgia; but in the case of the Penguins in the Scottish Zoological Park, the Rockhopper was equally exclusive.

One of the adult Kings died three weeks after arriving in this country, and the Gentoo succumbed two months later. The Rockhopper survived until November 1914; but beyond observing that it kept up its aloofness to the end, no special notes were taken of its habits during its brief sojourn in Scotland. The three remaining Kings did not seem to miss their relatives in the smallest degree.

The adult bird ("A") during the spring of 1914 occasionally took a swim, but spent most of its time sitting about with the young ones. The two immature birds ("B" and "C") *never* went into the water in the down stage, but fed freely all the time—ten to twelve fresh whitings being greedily consumed by each of them daily.

About the 17th of May 1914 one of the young birds ("C") began to show signs of losing the brown down and acquiring its new feathers. This was most noticeable on the legs just above the feet, but the process was very soon arrested, and only resumed and completed in September. In the other young bird ("B") the moulting began on the 22nd of May, but proceeded very slowly until the 9th of July, when the new tail quills began to show. On the 6th of August, however, a real start was made, the brilliant colouring of the auricular patches and the throat became very noticeable, and by the 14th of the same month the bird had lost all its down and acquired a coat almost as brilliant as that of the adult.

The young penguins, soon after the moult was completed, began to assume the orange-pink tint which distinguishes the lower mandible of the adult; up to this time the mandible was of a nearly black colour. It is interesting to note that of the three King Penguins, only one of them ("B") has assumed the green gloss or bloom on the top of the head.

The voice of the young penguin is a kind of clear whistle, very gentle and quite musical. With the change of coat, however, this note was gradually altered till it became a fair imitation of the trumpet-like voice of the adult. About a month after the moult was completed the whistle was never used except occasionally at feeding time, and later the trumpet-call only was used, so that by December 1914 the voices of the young birds could not be distinguished from that of the old one. Up till this time the young birds had made very little use of their pond, but gradually they took more and more to the water, and spent several hours in it daily. The adult and two young birds were very friendly with each other and always went about together—if one started for a walk, the others solemnly followed in single file, and if the leader elected to go into the water the others did the same.*

Curiosity appears to be one of the chief characteristics of penguins. Anything

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* In May 1915 the penguins were transferred to new quarters, including a pool in which they could swim and dive when the spirit moved them.

unusual interests them enormously, and they are not satisfied till they have investigated new objects very thoroughly. A looking-glass kept them occupied quite a long time; they gazed at their image as if fascinated, occasionally pecking at it as if to test its reality, but the peck was very gentle and quite different from the savage dart of an angry bird. When defending themselves from attack they use their beaks and flippers simultaneously—a blow from either may be extremely painful.

When pebbles of various sizes, shapes, and colours were placed in their enclosure, they selected the bright ones, turning them over with their beaks to make a more thorough examination. They very quickly, however, tired of any one object, and soon moved on to the next one.

They do not appear to have stated times for sleeping or swimming, but spend a very considerable portion of the day in the water, both summer and winter. Their swimming powers are wonderful, and they seem to fly under the water with nearly as great ease and grace as an ordinary bird cleaves the air. Whatever one of them does, the others almost invariably do the same, so that when one settles down to sleep, or starts for a walk, or makes for the water, the others follow suit. They walk in single file as a rule, and when they reach the water's edge the leader invariably pauses.* A peck from the next one is a reminder that it must not dally too long, so in it plunges, instantly followed by the others. Their movements in the water are very rapid, and they propel themselves solely by means of their flippers. They seem to prefer to swim at a good depth, and may often be seen chasing each other and thoroughly enjoying themselves. They set to work to wash themselves with much energy, using the beak, legs, and flippers in the operation. After the bath they spend a short time apparently resting on the surface of the water, with the head and tail submerged, and only the back showing. In this position they are extremely difficult to see, as they lie so still. Another favourite way of resting on the surface of the water is with the head slightly raised, the back and tail almost submerged, the legs stretched out alongside the tail, and the flippers hanging straight down. They do not, however, rest very long when in the water; they prefer to play and enjoy themselves in the water and do their resting on land.

On emerging from the water—in single file, as they entered it—they set to work at once to preen themselves and smooth their feathers, and so compact is their coat and so impervious to water, that in about ten minutes they are quite dry. Very frequently they may be seen standing on one leg, and scratching the top of the head with the other—a marvellous feat of balancing, and only successfully accomplished by making use of the tail as a prop! After the bath they very often have a

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* In his book on Antarctic penguins, Dr MURRAY LEVICK makes mention of this pause before diving into the water, and explains that the probable reason is owing to the presence of sea-leopards—the chief enemies the penguins have to fear in the Antarctic seas. Though the penguins he refers to are the Adelie Penguins, probably the same reason holds good in the case of the King Penguins.

rest, and go to sleep. Penguins sleep either upright or else lying down. In the upright position they flex their flipper-like wings, under one of which the beak is frequently tucked away both when standing and when lying down; the legs are stretched out to their utmost, and the beak also; they thus assume very much the same attitude as when resting on the water's surface.

The trumpet-call of the King Penguin has been very well described by MURPHY, who says: "The voice of the adult King Penguin is a martial sound, a long-drawn bugle-call, highly musical, and almost worthy of being called a tune. When delivering the call, the bird stretches grandly to its full height, points its bill skywards, and the long volley rings forth from an expanded chest. At the close of the effort the head is tilted forward with a jerk and the bird stands at attention—a rigid, constrained pose, always held for several moments."

When and why the penguins utter this sound has never been accurately determined. The zoologist of the *Pourquoi Pas* Expedition termed it the "chant de satisfaction," and Dr MURRAY LEVICK says it may be "likened to the crowing of a cock, or the braying of an ass."

The penguins at the Scottish Zoological Park very frequently utter this call, but never at stated times, and very often not for many days, or even weeks. During May and June 1915 they would "bugle" with great regularity about half an hour after feeding time, but they have been heard at all hours of the day, so that "chant de satisfaction" scarcely applies in their case. Penguins have also another call; a single loud alarm or warning note, which is used on various occasions.

Though they usually enter and leave the water together, it sometimes happens that one of them leaves the pool before the others, and looks anxiously to see if its mates are following, and then moves on a step or two. If the others show no signs of following, it gives this loud call, which may or may not be answered from the pool. If no answer is forthcoming, the solitary penguin returns to the water. This has been done as often as four times in succession, and the bird is not satisfied till the two remaining penguins answer the call and leave the water. This alarm call is also uttered when a penguin gets separated from its mates; its agitation on being parted from the others is very great, and when it once sights its friends it literally runs to meet them.

The penguin's gait is very ungainly. The legs are so short, and set so far back, that in the King Penguin the stride only amounts to 3½ or 4 inches. In walking it uses its flippers to balance itself, and in climbing out of the pool it uses both beak and flippers. Penguins have also another mode of progression, which has been termed "tobogganing." MURRAY LEVICK describes it thus: "When wearied by walking or when the surface is particularly suitable, they fall forward on to their white breasts, smooth and shimmering with a beautiful metallic lustre in the sunlight, and push themselves along by alternate powerful little strokes of their legs behind them. . . . In this way they relieved the monotony of their march, and gave periodical rest to different groups of muscles and nerve-centres." Tobogganing has never been observed at the Scottish Zoological Park.

They do not appear to care about diving into the water from a height, but prefer to go in from the water's edge, and they have never been seen to jump out of their pool after the manner of the Adelie Penguin as described by MURRAY LEVICK.

When being driven from one end of their enclosure to the other, the penguins, as they walk backwards, hold themselves very erect, compress their feathers tightly to their bodies, hold their flippers well in front of them, bravely facing the foe all the time.

BEHAVIOUR OF KING PENGUINS BEFORE AND DURING THE MOULTING PERIOD.

A penguin, in ordinary circumstances, is very vain and most particular about its personal appearance—any speck of dirt on its shimmering white breast, or any sign of untidiness of the feathers, being looked on askance by its fellows.

Towards the end of July 1915, about three weeks before the moult actually commenced, there were indications that something unusual was pending, and that things were not going as placidly and smoothly as is usual in penguin life. The feathers of the back began to lose their lustre and colour, and gradually assumed a sort of rusty-fawn tint; the white feathers of the breast and abdomen also lost their sheen and gradually turned to a kind of pale fawn (fig. 1). The yellow feathers of the throat and auricular patches faded away to a dirty cream colour, and the whole appearance of the bird suggested great untidiness and dejection—its only desire was to be left alone in its abject misery. In addition, the feathers, instead of lying closely and compactly against the body, stood almost on end, thus giving the bird the appearance of being nearly twice its usual size (fig. 2). Its untidy appearance led its companions, ordinarily so friendly, to exhibit marked disapproval, with the result that the unfortunate bird was sent to Coventry. This seeming aversion was apparently quite mutual! for the moulting penguin pecked furiously at either of the others if they had the temerity to disturb its solitude. The appetite also began to fail, and on some days the sickening bird would eat nothing at all, in spite of much coaxing on the part of its keeper. During the few days immediately preceding the actual shedding of the body feathers, the tail quills, very worn and bedraggled, dropped out, giving the bird a curiously dumpy appearance and depriving it of a most valuable support—the loss of the tail no doubt tended to increase the penguin's misery, discomfort, and unhappiness. During these changes the trumpet-call was never used, nor did the bird spend any time in the water, though it would occasionally sit at the edge of the pool considering whether or not a swim should be indulged in—invariably the latter idea prevailed! For some time before moulting the breathing was very laboured and quite distressing to watch, the inspirations numbering as many as 26 to the minute, whereas the usual number appears to be about 16.

Once, however, the actual shedding of the feathers started, the bird's health and temper appreciably improved; and though it only ate one fish (on the sixth day) during the whole moulting period, its condition and fatness did not seem to be affected by the fast, as may be gathered from the photographs. The day before the moult finished the general appearance, health, and temper of the bird had so much improved that its companions began to be more friendly, and on the day after the moult was completed no one could have imagined that anything like a disturbance in the family camp had taken place.

Daily Notes made by Miss Mackenzie during the Moulting Period of one of the King Penguins in the Scottish Zoological Park.

First Day, Aug. 17, 1915. (Fig. 3.)

General health and temper very bad. Gasped painfully a good part of the day. Sat huddled up all day, entirely deserted by its companions.

Feathers on lower abdomen began to fall off. Back very ruffled, but not actually shedding. Yellow feathers fading rapidly to a dirty cream.

Ate nothing, and did not enter the water.

Second Day, Aug. 18. (Figs. 4 and 5.)

General health better, breathing less laboured, but temper worse.

Feathers on abdomen falling off in sheets. Underside of flippers began to moult. The three remaining tail quills dropped out and the new quills began to show. Back more ruffled than yesterday, but not yet shedding. Yellow feathers even paler.

Ate nothing, and did not enter the water.

Third Day, Aug. 19. (Figs. 6 and 7.)

General health and temper better, breathing almost normal.

Breast feathers about half moulted. Back more and more ruffled, and a few feathers shed. Yellow patches pale cream. Underside of flippers finished moulting.

Ate nothing, and did not enter the water.

Fourth Day, Aug. 20. (Figs. 8 and 9.)

Health and temper both vastly improved.

Breast moulted almost up to the yellow throat feathers, which by this time had lost all their colour. Back very ruffled, but still only a few feathers shedding. Feathers on the top of the head beginning to fall off, also from the outer side of the flippers (fig. 8).

Ate nothing, and did not enter the water.

Fifth Day, Aug. 21. (Figs. 10 and 11.)

Health and temper both quite good.

Yellow throat feathers beginning to shed, also the back and side of head (not auricular patches) (fig. 10). Outer side of flippers more than half moulted.

Ate nothing, and did not enter the water, though it sat by the edge of the pool for most of the afternoon.

Sixth Day, Aug. 22. (Fig. 12.)

Health good, but temper rather doubtful.

New yellow feathers of the throat showing very distinctly, but rather pale. Flippers almost finished moulting; head shedding all over. Back now moulting rapidly.

Ate one fish, but did not enter the water.

Seventh Day, Aug. 23. (Figs. 13 and 14.)

Health and temper both excellent.

New yellow feathers of the throat getting brighter. Head moulting rapidly all over. Auricular patches shedding and now showing new yellow feathers, still rather pale. Green bloom on top of head now clearly noticeable. Back moulting rapidly, but in patches—not as symmetrically as the breast. Flippers quite finished. Right mandibular sheath shed, leaving the mandible a very pale pink colour.

Ate nothing, and did not enter the water.

Eighth Day, Aug. 24. (Fig. 15.)

Health and temper normal.

A few old yellow throat feathers still left. Back and auricular patches about half moulted. Left mandibular sheath shed.

Ate nothing, and did not enter the water.

Ninth Day, Aug. 25. (Fig. 16.)

Health and temper both excellent.

Yellow throat feathers almost all gone—new ones much brighter. Auricular patches nearly finished, but new feathers still very pale. Back almost finished, still a very decided "ruff" on the back of the neck and a few odd feathers at the base of the beak. Mandible very pale—a sort of delicate shell-pink colour.*

Ate nothing, and, though it watched the others swimming, did not join them.

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* The mandible had resumed its normal colour by Sept. 7, and this bird gave its first trumpet-call on the same day, viz. twenty-one days from beginning of moult. The voice was very squeaky and high-pitched and occasionally threatened to break down, but in a week's time, by dint of much practice, it had quite recovered.

Tenth Day, Aug. 26. (Figs. 17 and 18.)

Health excellent, except for a short and slight return of the gasping. Temper good.

Moult practically complete, except for the remains of the "ruff" and a few stray feathers above the nostrils.

Ate nothing. Stood in a few inches of water for a short time. The other penguins beginning to show signs of friendliness.

Eleventh Day, Aug. 27.

Moult complete, except for a few feathers on the head and at the base of the nostrils.

Ate four fish, and spent many hours in the water with its companions.

While the young penguin ("B") (described above) was moulting, the adult bird ("A") was preparing to moult. Though the time occupied by the adult bird in moulting was very much the same as in the young bird, there were various points of difference in the behaviour of the respective birds which are noted below.

On 9th August "A's" feathers began to lose some of their gloss and brightness. The bird continued to feed and to go into the water both before and during the moult, and, though the other two did their best to shun it, they were not successful, for the old bird followed them about everywhere, even going into the water after them. Though the young birds could not by any stretch of imagination be said to be cordial, still, like true philosophers, they made the best of a bad job, and allowed their shabby relation to spend all its time in their company.

On the 25th of August the left mandibular sheath peeled off, and the right sheath was shed the following day.

On the 30th of August the bird looked very ruffled, and was extremely irritable. Its breathing was very laboured—24 inspirations to the minute. It ate nothing, and felt too ill to go into the water, though it sat and watched the others all the time they were swimming.

On the 31st of August its general health and temper were pretty much the same. Inspirations were 18 per minute, but the gasping was very painful to watch. Again it ate nothing, and did not go into the water. The tail quills began to drop out.

On the 1st of September the inspirations were only 16 per minute; but though the general health was better, the temper was much worse. It ate nothing, and did not go into the water.

On the 2nd of September the inspirations were 24 to the minute, but, strange to relate, the bird seemed to be much better both in health and temper. It ate a good-sized whiting, but, though it sat for a long time on the edge of the pool, did not enter the water.

On the 3rd of September the inspirations were again down to 16; the bird ate one fish and spent a long time in the water, both morning and afternoon.

On the 4th of September the actual shedding of the feathers commenced, and the moult was completed on the 15th. By the following day the bird was once more quite normal, ate five large whitings, and spent a long time in the pool. It gave its first trumpet-call on the 26th September—22 days from the beginning of the moult,—but its lower mandible did not resume its normal orange-pink colour until the end of October.

Note on the Moulting of the three King Penguins in 1916.

In 1914 the order of moulting was "C," "B," "A," and in 1915 the same order was observed; but in 1916 it was exactly reversed, "A," the adult bird, moulting first (duration of moult 17 days, as against 11 in 1915); "B" second (duration of moult 10 days, as in 1915); and "C" third (duration of moult 12 days, being about the same time as in 1915). In 1916 "A" began to moult on the 14th of July—in 1915 a start was only made on the 4th of September. In 1916 "B" began to moult on the 26th of July—three weeks earlier than in 1915. "C" kept to more or less the same time as in the previous year.

There were considerable differences in the behaviour of the birds in 1916.

The desire for solitude, *e.g.*—so very pronounced at the beginning of last year's moult—was conspicuous by its absence in 1916. During the whole of the moulting period, which extended from the 14th of July to the 8th of August, the three birds might be seen together on quite friendly terms with each other. This may possibly be explained by the fact that in 1916 the birds, instead of moulting in succession, moulted almost simultaneously, so that they had not such opportunities of adversely criticising each other's personal appearance as in the previous year.

Another point of interest was the very great improvement in their general health. There was at times difficulty with their breathing, but not nearly so pronounced as before, and, though they looked very untidy and ragged, they did not have the very miserable and dejected appearance as in the previous year.

"A" and "C" shed their mandibular sheaths before the moult, but "B" shed them on the 7th day of the moult.

"A" ate nine fish during the 17 days occupied in moulting, which was the same number consumed by "B" in the ten days of moult.

"B" is again the only one of the three penguins to show the green "gloss" on the top of the head. It was first observed the day after the moult was completed.

In all three cases the penguins entered the water on the last day of the moult.

"A" gave its first trumpet-call on the day after the moult was ended, but its voice was very feeble and squeaky. "B" made its first attempt on the day before the moult was completed, but it also was not a great success, and, as the others did not approve, it was not allowed to "bugle" to a finish.

In "B's" case this year the tail feathers only finished shedding on the 5th day of the moult.

To celebrate the end of this most trying period of the year, "A" consumed twenty-one whitings on the day after its new coat was acquired, sixteen on the following day, and again twenty-one the day after. Since then, however, its appetite has resumed a normal size, and it now contents itself with from ten to twelve fish daily. It may be mentioned that the adult penguin ("A") on 12th April 1916 weighed 31·5 lbs.

The authors are indebted to the Zoological Society of Scotland for the opportunities given them for observing and photographing the King Penguins.

LIST OF PAPERS AND BOOKS REFERRED TO.

Bartlett, A. D., "Remarks upon the Habits and Change of Plumage of Humboldt's Penguin," *Proc. Zool. Soc.*, 1879.

De Winton, W. E., F.Z.S., "On the Moulting of the King Penguin (*Aptenodytes pennanti*)," *Proc. Zool. Soc.*, 1898.

Seth-Smith, David, F.Z.S., "On the Moulting of the King Penguin," *Proc. Zool. Soc.*, 1912.

Wilson, *National Antarctic Expedition*, vol. ii, *Zoology*, 1907.

Pycraft, *National Antarctic Expedition*, vol. ii, *Zoology*, 1907.

Levick, Murray, *Antarctic Penguins.*

Smalley, *Annals of Scot. Nat. Hist.*, 1909.

Murphy, R. C., "The Penguins of South Georgia," *Science Bulletin*, vol. ii, No. 5, The Mus. of Brooklyn Inst. of Arts and Sciences, 1915.

EXPLANATION OF PLATES.*

Fig. 1. A King Penguin 2½ weeks before moulting actually began. The feathers had lost their lustre, were of a rusty brown colour on the back and a pale fawn on the breast; the throat and auricular patches were no longer of an orange or bright yellow tint.

Fig. 2 A King Penguin the day before moulting started. Compare with fig. 18, a bird in nearly normal plumage. Observe that the bird represented in fig. 2 appears to be very much stouter than a normal bird. The increase in size is partly due to the feathers about to be shed projecting at nearly right angles from the tips of the new feathers about to displace them.

Fig. 3. First day of moult. In this bird the feathers are in the act of falling off from the lower abdomen; those on the back, though faded, untidy, and somewhat raised, are still intact. The majority of the tail feathers are already shed. The feathers of the throat and auricular patches are now of a dirty cream colour.

Figs. 4 and 5. A King Penguin, showing the stage reached on the second day of moulting. The feathers are now falling off in sheets from the whole of the abdomen, the last of the tail feathers have dropped out, and the small scale-like feathers are beginning to be shed from the under surface of the wings. The back is still more faded and ruffled, and the throat and auricular patches are still paler.

Figs. 6 and 7. A King Penguin, showing the stage reached on the third day of moult. Nearly the

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* With the exception of fig. 12, all the figures are from photographs by Miss Dorothy Mackenzie. Fig. 12 is from a photograph by Mr J. C. M'Kechnie.

whole of the feathers have been shed from the abdomen, about half of the breast feathers are moulted, and feathers are beginning to fall from the greatly ruffled back. The under sides of the flippers have got rid of all the old feathers.

Figs. 8 and 9. Two figures of a penguin to show that on the fourth day the breast is more than half moulted, that the back is slowly shedding its feathers, and that the top of the head and the outer side of the flippers are beginning to lose their old feathers.

Fig. 10 and 11. Two figures of a penguin at the fifth day of moulting. By the end of the fifth day nearly the whole of the breast feathers are shed, the yellow throat feathers are beginning to fall off, and the back and head are slowly getting rid of their feathers. The lower half of the outer surface of the wing is nearly moulted.

Fig. 12. On the sixth day the new yellow throat feathers are beginning to appear, and the old feathers are rapidly falling from the back; the flippers are nearly completely moulted, and the head feathers are being freely shed.

Figs. 13 and 14. The stage reached in a King Penguin on the seventh day of moulting. By the end of the seventh day the majority of the old throat feathers are shed, and the moulting of the auricular patches has begun. Considerable progress has been made by the head and back, and the flippers are almost free of dead feathers. Further, on the seventh day there is an indication of the green sheen on the top of the head, the right half of the mandibular sheath has been cast off, and the new tail feathers are making their appearance.

Fig. 15. A view of a King Penguin on the eighth day of moulting. On the eighth day there are still a few old throat feathers; the new feathers of the auricular patches are making their appearance, but are still very pale; the head and greater part of the back are now clear of their faded dead feathers. The left half of the mandibular sheath was shed on the eighth day. Note flexion at elbow and wrist.

Fig 16. This figure indicates the stage reached on the ninth day of moulting. Note the "ruff" of old feathers on the back of the neck, the small groups of dead feathers on the shoulders, the upper part of the back, and the base of the beak. The throat and auricular patches are almost clear of old feathers, but the new auricular feathers have not yet acquired their rich colour, and the mandibular sheath is still very pale. The tail feathers have reached a considerable length.

Figs. 17 and 18. Two figures of a King Penguin on the tenth day of moulting. With the exception of a remnant of the neck "ruff" and a few feathers above the nostrils, the moulting of a King Penguin may be complete on the tenth day. By the eleventh day the only indication of the old coat in the penguin figured consisted of a few dead feathers on the head and at the base of the beak.

J. C. Ewart and Dorothy Mackenzie: — Moulting of King Penguin.


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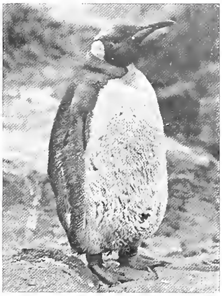
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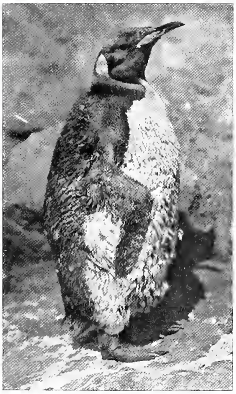
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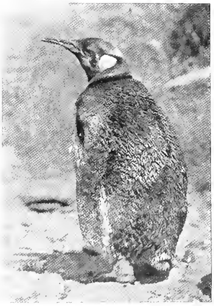
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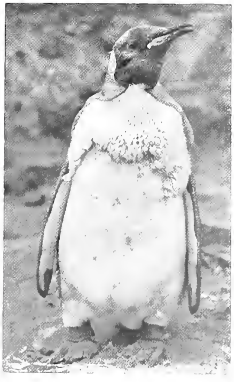
6 (3rd Day)


7 (3rd Day)


8 (4th Day)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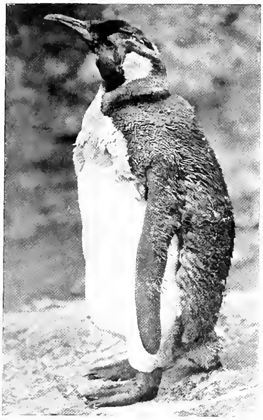
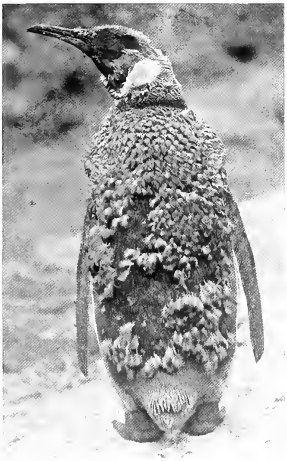
J. C. EWART AND DOROTHY MACKENZIE :— MOULTING OF KING PENGUIN.



10 (5th Day)

11 (5th Day)

12 (6th Day)



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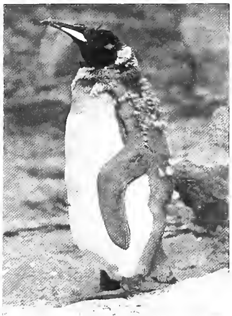
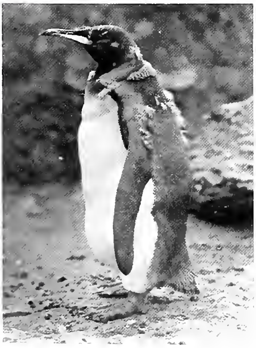
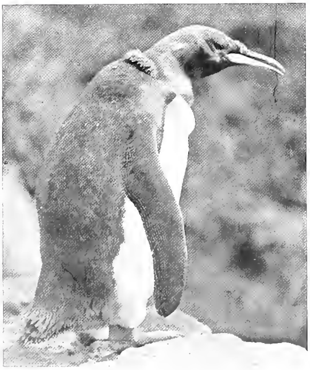


15 (8th Day



16 (9th Day



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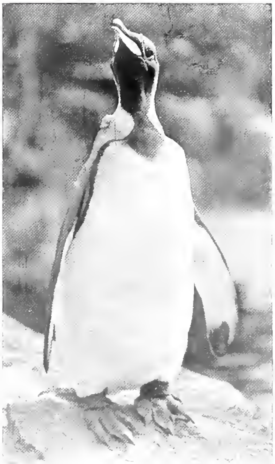


18 (10th Day)

VI.—The Anatomy and Affinity of Stromatopteris moniliformis, Mett.

By **John M'Lean Thompson**, M.A., D.Sc., Senior Assistant to the Professor of Botany, and late Robert Donaldson Research Scholar, Glasgow University. *Communicated by* Professor F. O. Bower, Sc.D., F.R.S. (With Four Plates, and Figures in the text.)

(Read February 5, 1917. MS. received February 6, 1917. Issued separately June 15, 1917.)

HISTORICAL SURVEY.

In the year 1861 the ferns collected by VIEILLARD in the island of New Caledonia were described by METTENIUS in a paper entitled "Filices Novæ Caledoniæ" (*Ann. Sc. Nat.*, iv, 15). Among the organisms described was a new and remarkable fern for the reception of which a new Gleicheniaceous genus *Stromatopteris* was founded. Having noted in particular the absence of roots, and the hairy and sclerotic character of the axis, METTENIUS figured the latter as obliquely ascending at its base, but as upright and closely and repeatedly branched more distally. The simply pinnate unbranched leaf was described as a direct continuation of a branch of the axis, with nodular base, slender rachis, and many small leathery pinnæ with sympodial dichotomous venation. With regard to the sori, attention was directed in particular to their development singly on the pinnæ and towards the base of the upper margins, and to the mound-like hairy receptacle which lodged the forking of the basal acroscopic vein. The sporangia, numbering from two to six, were stated to be distributed on the back and towards the periphery of the receptacle; their stalks were short and massive, the annulus complete and transverse, and dehiscence longitudinal and extrorse.

At the present day, when such criteria as the anatomical features of stem and leaf and the exact details of sporangial-form and spore-output are more fully appreciated by the systematist, generic rank might not be assigned to any organism on the evidence given above; but it was on these characters of pinna-form, soral position, venation, sporangial-form, and dehiscence alone that METTENIUS relied in founding this new genus, and in recognition of the peculiar arrangement of the leaves he named its first and only species *Stromatopteris moniliformis*, Mett.

But MOORE, on the other hand, was not inclined to consider the features noted by METTENIUS sufficiently individualistic to allow of a new foundation, and in his *Index Filicum*, ii, p. 379, 1862, *Stromatopteris* was sunk in *Gleichenia*, and appeared in the enumeration of the species as *Gleichenia moniliformis*, Moore; and later, in Lyell's *Geographical Handbook* it was similarly named.

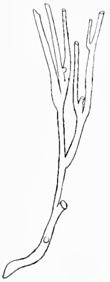
In 1873 further reference to this plant was made by FOURNIER in his "Filices Novæ Caledoniæ: Enumeratio monographia" (*Ann. Sc. Nat.*, v, 18); but, in reasserting that *Stromatopteris* was a genus distinct from *Gleichenia*, the author judged entirely by a character which METTENIUS had not considered of paramount importance. Relying on leaf-form alone, FOURNIER divided the Gleicheniaceæ of ROBERT BROWN into two genera, the first being *Stromatopteris*, Mett., *with simply pinnate leaves*, and the second *Gleichenia*, Smith, *with dichotomously branched leaves.* The true value of this distinction in systematic grouping may be more easily assessed when it is recalled that as early as 1810 ROBERT BROWN had employed it in separating *Platyzoma* as a genus distinct from *Gleichenia* (*Prodromus Floræ Novæ Hollandiæ et Insulæ Van Diemen*, p. 160), but that in 1814 he had already discounted it as a generic distinction (*General Remarks, Geographical and Systematic, on the Botany of Terra Australiensis: Misc. Bot. Works of Rt. Brown*, vol. i, p. 59, Roy. Soc. Publications, 1866). The existence of a Gleicheniaceous plant bearing both simply pinnate and branched leaves is sufficient to discount the distinction set up by FOURNIER between *Stromatopteris* and *Gleichenia*, and, as was pointed out by BOWER in 1899 ("Studies in the Morphology of Spore-producing Members," *Phil. Trans. Roy. Soc. London*, vol. 192, p. 32), both *Platyzoma* and *Gleichenia circinata* supply the demonstration. *Gleichenia simplex* itself is typically simply-pinnate, although its leaves are occasionally branched, and leaf-branching is common in such forms as *Polypodium vulgare*, *Scolopendrium*, *Nephrodium molle*, and *Osmunda regalis*. It is, in fact, recognised that the character on which FOURNIER relied in separating *Stromatopteris* from *Gleichenia* is not sufficiently distinctive to act as a generic criterion, and, as will be shown below, it is in this case really valueless, for the leaves of *Stromatopteris* may occasionally be branched. It is, then, evident that FOURNIER's observations neither strengthened nor weakened the conclusion arrived at by METTENIUS.

Regarding the discovery and habitat of *Stromatopteris*, FOURNIER merely stated that it had been collected by VIEILLARD and others in the folds of the ferruginous hills on the way to Canala; and in 1874 ("Dispersion géographique des Fougères de la Nouvelle Caledonie," *Ann. Sc. Nat.*, v, 19) he further stated that *Stromatopteris* was a genus peculiar to New Caledonia.

In the *Synopsis Filicum* (Hk. and Bk.), 1874, 1883, this fern appeared as a *Gleichenia*, and as the first species of the sub-genus *Eugleichenia*, under the name of *G. Eugleichenia moniliformis*, Moore. The distinguishing features of the *Eugleichenias* here noted were, that the sori are solitary upon the apex of a veinlet, on the superior base of a lobe, and that the lobes of the pinnæ are small and suborbicular. In the accompanying description of the species it was stated that the slender sub-stipiform axis was *erect* and branched, the unbranched leaves were some 12 inches long, with tufted leaf-stalks and leathery fronds, deeply pinnatifid, and with numerous concave pinnæ. The sori were described as solitary, and mixed with ferruginous hairs. A note was appended in recognition of the remarkable appearance of this species, but maintaining that the latter did not merit by itself generic rank. In emphasising this, and in merging *Stromatopteris* in *Eugleichenia*, HOOKER and

BAKER were merely indicating a wider possession of the above-mentioned characters of pinna and sorus than METTENIUS had recognised in 1861.

In 1893 attention was redirected by POIRAULT to the absence of roots in *Stromatopteris* ("Recherches anatomiques sur les Cryptogames vasculaires," *Ann. Sc. Nat.*, vii, 18, p. 114), and in this connection he stated that, "with the exception of certain *Trichomanes*, all belonging to the section *Hemiphlebium*, and one of the Gleicheniaceæ, *Stromatopteris*, and *Salvinia*, all the plants which come within the scope of our study are provided with roots." In a footnote it was added that, "as to *Stromatopteris*, that curious fern of New Caledonia, for which METTENIUS has founded a special genus, I have examined a large number of specimens in the herbarium of the Museum (presumably in Paris), and on none of them have I found roots." It seems improbable that both METTENIUS and POIRAULT should have been misled on this point, for neither records incompleteness of axis in the specimens examined. The axis figured by METTENIUS is apparently complete (text-fig. 1), and shows an obliquely ascending and basally tapered portion, on which, if on any part, roots would most probably have been found. The conclusion seems justifiable that the oblique and tapered portion was in reality the axis of the young emancipated sporophyte. It has been noted that in 1874 the axis was described in the *Synopsis Filicum* as *erect*, but BOODLE has informed me that the specimens in Kew Herbarium all appear incomplete below and devoid of roots, and it was on these that HOOKER and BAKER based their statement. And further, a specimen kindly lent for examination by Professor BALFOUR, F.R.S., is likewise basally incomplete and bears no roots. The date of collection of this specimen is 1893. The statement of the anatomy of *Stromatopteris* set forth in this memoir is based on two specimens collected by LE BOUCHER at Baie de Sud, New Caledonia, in 1903, and for which we are indebted to the Director of the National Herbarium of New South Wales. The axis in both of these is *erect* but *incomplete*. It bears no roots, and shows no sign of the basal tapering delineated by METTENIUS. It follows, then, that the description of the



TEXT-FIG. 1.

axis as *erect* is not wholly justifiable, for it seems based on the examination of incomplete specimens; but the general absence of roots from the erect portion of the stem is supported by observations ranging in time from 1861 to the present day. The materials available for examination can neither support nor refute METTENIUS's statement that *Stromatopteris* is rootless. It seems probable that his remark on this point was fully justified by his specimens, but, should later examination reveal the presence of roots in *Stromatopteris*, they will probably be found confined to the short, basal, horizontal or oblique portion which formed the axis of the young sporophyte.

In *Die Farnkrauter der Erde*, p. 339, 1897, CHRIST referred to *Stromatopteris* as *Gleichenia moniliformis* (Mett.), Moore. He further noted its unique form and xerophytic characters, its reniform elevated receptacle, and its distribution among the ferruginous clay hillocks of the New Caledonian coast.

In 1901 BOODLE ("On the Anatomy of the Gleicheniaceæ," *Ann. Bot.*, xv) expressed the opinion that the simple pinnatipartite leaves of *Gl. moniliformis* and *Gl. simplex* marked these plants as reduced forms, and with regard to its protostelic axis further stated that *Stromatopteris* is the most aberrant of the Gleicheniaceæ, "in that no protoxylem elements are present in the mature stem, and the tracheides all appear to be scalariform. The absence of spiral protoxylems is interesting, because this species is the only one of its genus with an upright stem. It was noted among the Hymenophyllaceæ, where spiral protoxylems are general, that their absence in certain species of *Trichomanes* appeared to be correlated with an upright habit (*T. spicatum* and *T. Bancroftii*). Both *Gl. moniliformis* and the species of *Trichomanes* just mentioned have probably been derived from forms with a creeping rhizome, and the change to the upright stem has been accompanied with diminished length of the internodes and slower growth of the rhizome. This makes it easy to understand the disappearance of the spiral elements." Support for BOODLE's belief in an originally creeping rhizome in *Stromatopteris* seems ready to hand in METTENIUS's original figure, and the absence of spiral protoxylems seems undoubtedly due to slow growth of axis in this xerophilous plant.

In 1900 and 1902 *Stromatopteris* was well figured by DIELS (ENGLER and PRANTL, *Natürliche Pflanzen-Familien*, i, 4), and in reaffirming its generic rank he laid emphasis on its unusual form and isolated position in the arid commons of New Caledonia. In the *Index Filicum* of 1908, CHRISTENSEN maintained that *Stromatopteris* is a distinct genus; BOWER (*The Origin of a Land Flora*) commented on the simple pinnate form of leaf in *Stromatopteris* as an occasional condition among the Gleicheniaceæ; and TANSLEY (*Lectures on the Evolution of the Filicinean Vascular System*) referred to *Stromatopteris* as an aberrant, xerophilous, and distinctly reduced species, comparable in this respect with *Platyzoma*. And finally, in 1910 (*Die Geographie der Farne*), CHRIST figured two plants of *Stromatopteris*, in one of which a branched leaf is shown (fig. 59), and in discussing external form he compared *Stromatopteris* with *Platyzoma* as extremely xerophilous and with the aspect of extreme reduction.

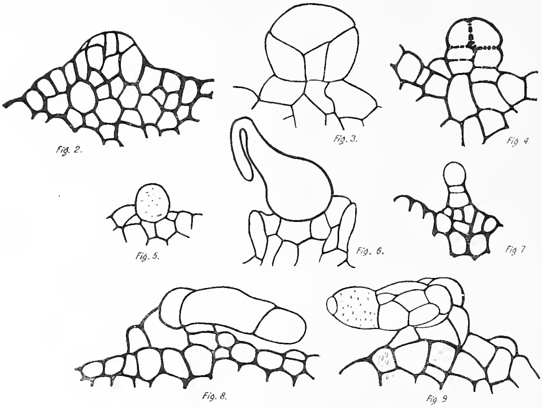
The foregoing survey will suffice to show how little has been added by later authorities to METTENIUS's original statement. The kinship of *Stromatopteris* and *Gleichenia* has indeed remained unchallenged, and the demonstration of a protostelic axis in the former is valuable; but apart from this, nothing has been advanced to finally establish its affinity, or further define its position within the group. The anatomical states of a plant undoubtedly provide valuable systematic data, but in themselves they are seldom determinative, for conservatism in these may be linked with advance in other characters, and the converse is equally true. It is, in fact, on the summation of characters that a reasonable conclusion regarding any organism may be founded, and it cannot be said that the summation for *Stromatopteris* has been completed. It is the object of the present memoir to provide details regarding the external form, the dermal appendages, the anatomy of stem and leaf, soral constructions, sporangial form, and spore-output of *Stromatopteris*, and thus to render possible a clearer view of its near affinities.

DESCRIPTION OF MATERIALS.

The materials available for study were two incomplete herbarium specimens and a fertile leaf, courteously supplied by Dr MAIDEN, F.R.S., of the Sydney Herbarium; and although it has been impossible to obtain from these the valuable information which a study of sporangial development would have provided, it is believed that the facts of mature anatomy are in themselves sufficient justification for the present statement, and will go far towards establishing the nearer affinity of *Stromatopteris*. For purposes of description and comparison it is convenient to deal with the plants separately, and withhold the general consideration of form until the fuller facts of anatomy have been discussed.

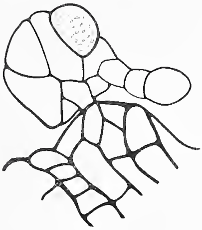
In the first specimen (figs. 20, 58) the slender, erect, and cylindrical axis is incomplete below. Towards its base it is branched, but the right-hand limb of the branching has been broken off. A slight displacement from the vertical occurs in the left branch immediately above the point of forking, but the erect position is resumed in it, and maintained for about $\frac{1}{2}$ inch. Above this a second forking occurs, resulting in the formation of two diverging limbs. Close to its base the right limb is divided into two unequal branches, the left-hand member of which is short, conical, and complete. It is almost horizontal in position, and is little more than $\frac{1}{8}$ inch in length. It appears, indeed, to be merely a short lateral appendage of the right-hand member. The latter continues vertically upwards for over 10 inches, and, without further branching, ends abruptly in a fractured surface. There are two marked differences of appearance between this latter branch and the lower portions of the plant so far considered. The latter are rugged and cylindrical; the former—except at its base—is a smooth and dorsiventral structure, channelled on one side (its left), and curved on another (its right) like the free rachial portion of a leaf. The left-hand limb of the second branching mentioned above is cylindrical and rugged like the lower part of the plant. For about $\frac{3}{4}$ inch it remains slender, but above this it widens considerably and divides into three parts. The middle part is a short columnar structure with a slight central depression on its broad apex. The two lateral members show the same rachial characters as were noted above; for though they are perfectly cylindrical for about 2 inches from their bases, they finally assume a dorsiventral form. Their channelled surfaces face each other, and no branching occurs. They end distally in fractured surfaces.

The three distal branches may be tentatively held to be of petiolar character, while the remaining portions of the plant may be considered axis. This division is in keeping with the figures and descriptions given of *Stromatopteris*. In the plant under discussion the petiole is exceedingly long, and greatly exceeds the 4-inch measurement given elsewhere; but it should be remembered that during development the petiole is open to intercalary growth, and is accordingly liable to vary considerably in length. At no point in this specimen are roots apparent, and, as will be shown immediately, they are entirely absent.



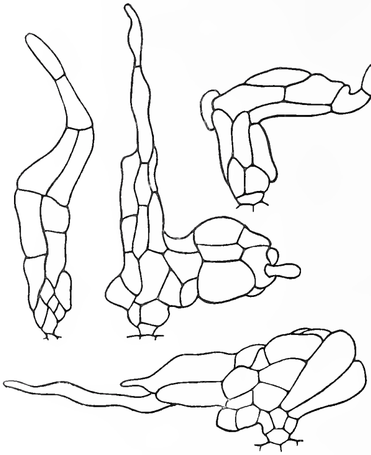
TEXT-FIGS. 2–9.

The rugged appearance of the branched axis is due to a very varied assemblage of emergences and dermal appendages. In some cases the emergences are mounds of thick-walled cells, irregularly disposed, and devoid of intercellular spaces. One of these mounds is represented in sectional view in text-fig. 2. On the other hand, many are large conical structures, composed of thick-walled elongated cells, which converge on a small-celled apical group. From the centre of this group springs a straight and massive brown scale which projects freely from the surface of the stem (text-fig. 13). On the other hand, there are small, simple, unicellular and multicellular hairs which clothe the greater part of the stem surface but are not raised on emergences. Typical examples of these are given in text-fig. 12. Besides these are curious structures which appear to be modifications or combinations of the smaller emergences and the simple hairs. In text-fig. 3 is represented the external aspect of a dome-shaped emergence, while a sectional view of a similar, though somewhat smaller, dome is shown in text-fig. 4. As will be seen from the latter figure, the outer walls of these domes are thick, and the inner walls are both thick and pitted. Combinations of the emergence and the hair are not uncommon, though in these, as a rule, the emergence is low and the hair short (text-fig. 7). But apart from these types other and more aberrant forms are frequently encountered. In some cases the latter are low mounds bearing single spherical cells with conspicuously pitted outer walls (text-fig. 5). In other cases the emergence is more massive, and springing from a depression on its broad upper surface is a large, irregular, flask-shaped cell devoid of pits (text-fig. 6). Of still more elaborate and irregular form are such types as are shown in text-figs. 8, 9, and 10. In the first of these the emergence is low, and the linear series of cells forming the hair is laterally inserted. In the second a similar arrangement of parts is seen, but, instead of a simple hair, there is a more massive columnar structure with a curious and pitted terminal cell. The most elaborate appendage of this type found is shown in text-fig. 10. The emergence which bears it is fairly prominent, and the body of the appendage is dome-shaped and raised upon a one-celled stalk. A conspicuously pitted cell is borne upon its side, while from the basal margin of the dome springs a hair which lies close to the surface of the emergence. Many of these elaborate appendages were examined, and, although a remarkable variety of details was observed in them, they resembled each other in being pressed close to the surface of the stem, and, as a rule, in possessing cells with pitted outer walls.


TEXT-FIG. 10.

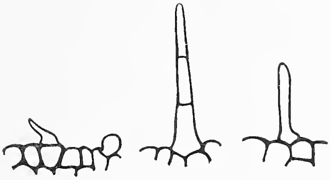
But irregularity of form is not confined to the smaller appendages. It is extended to the scales also, and in our specimens the straight lanceolate scale is not the dominant type. In the majority of cases the scales are tortuous or branched, and instead of being raised upon conical emergences, or projecting freely from the surface of the stem, they frequently arise from single epidermal cells, are closely pressed to the stem surface, and generally point *downwards*. A few of these irregular forms are illustrated in text-fig. 11. They may be considered transitional between the more elaborate of the small appendages and the freely projecting lanceolate scales.

It is impossible to determine from dead materials the functions fulfilled by these various dermal appendages, but it is generally assumed that hairs and scales act chiefly as protections for the growing stem, by providing a mechanical safeguard, a zone of dead air, or an excretion of mucilage in which the growing parts are bathed. It seems reasonable to assume that some or all of these protections are necessary to so xerophilous a plant as *Stromatopteris*.

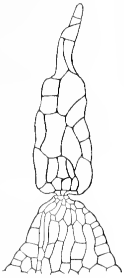


Text-fig. 11.

But while the possession of both simple hairs and scales of an advanced type is interesting, attention is chiefly centred on the intermediate types of dermal appendages. From a developmental standpoint these may be regarded as forms transitional between the simple hairs and the erect lanceolate scales, and as showing a combination of characters. But it is noteworthy that neither the simple hairs nor the irregular and straight scales possess cells with pitted outer walls, whereas the columnar and dome-shaped appendages are almost invariably provided with superficially pitted cells, and similar cells are common upon the general surface of the stem. These latter appendages are common on the lower parts of the axes, and, while they may be structures of a glandular excretory nature, they are also open to interpretation as organs of absorption. If it could be finally established that the mature sporophyte is almost or entirely rootless, the latter view of these organs would be greatly strengthened. But in the absence of certainty regarding roots, the cortex of the stem is deserving of special comment. It is sclerotic and composed entirely of brown-walled fibrous elements, bearing many large oval pits on all their thickened walls (text-figs. 14, 15). In the mature cortex there are no intercellular spaces, and even in the cortex of the immature stem intercellular spaces are few and very small. But further, while the still thin-walled cells of the immature cortex possess delicate protoplasts, the thick-walled pitted cells of the mature cortex seem entirely devoid of protoplasts. The presence of pitted thick-walled fibrous elements and the absence from these of intercellular spaces are common features of the cortical tissues of ferns; but if *Stromatopteris* is rootless, and absorption is conducted by the general stem-surface, or by dermal appendages, the empty cortical cells may be regarded as a supplementary conductive system, rather than as a storage or mechanically effective zone.



Text-fig. 12.



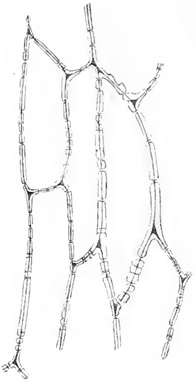
Text-fig. 13.

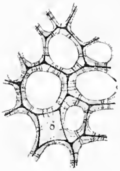
The dermal appendages of ferns can seldom be relied upon in systematic determinations; for while in a general sense the simple hair is usually considered a primitive structure, and the massive scale derivative or advanced, it is recognised that the peculiar life conditions of any organism may determine to a greater or less extent the types of appendages developed. Within the genus *Gleichenia* itself variations in this respect are found; for while *Gl. pectinata* and *Gl. lineata* have hairs alone, *Gl. simplex* has scales, while *Gl. circinata* has both hairs and scales.

The simple hairs and massive scales of *Stromatopteris* may then be matched from the genus *Gleichenia*, and the transitional types may be regarded as expressive of peculiar physiological conditions; but the absence of hairs or scales would not of necessity alter the general relationships of these organisms.

With the conical emergences, however, the case seems different. Such emergences are uncommon, but they are characteristic of certain *Gleichenias*. They are well developed in *Gl. circinata*, and in this species bear tufts of stiff hairs instead of scales, as in *Stromatopteris*. In themselves these emergences may be regarded as indicative of a relationship between *Stromatopteris* and *Gleichenia*.

The axis of *Stromatopteris* is protostelic, the stele consisting of a broad pericycle, a narrow zone of phloëm, and a relatively bulky parenchymatous xylem (fig. 21). At some points the xylem-parenchyma is fairly evenly distributed between the tracheides, while at other points the bulk of the latter is peripherally disposed and the parenchyma is centrally aggregated (compare figs. 21 and 28). The former condition is typical of those portions of the stele which lie between the points of branching of the stem; the latter is usually seen at or near these points. The relative proportion of parenchyma to tracheides is liable to vary considerably, and, while at some levels—and particularly beneath the points of branching—the parenchyma may be considerable, at other points, particularly the bases of the branches, the stele has an almost solid core of tracheides. These variations will be readily understood when it is recognised that it is chiefly by parenchymatous increase that the stele is widened preparatory to a branching, and that at such points of preparation the bulk of the tracheides is not really diminished, but is, as a rule, augmented. On the other hand, the condensation of tracheides and reduction of parenchyma, shown in the stele at the base of a branch, may be interpreted on mechanical grounds as necessary to ensure rigidity in the branch.


TEXT-FIG. 14.


TEXT-FIG. 15.

The tracheides themselves may vary considerably in size, but no general statement can be made on this point beyond that where the bulk of the parenchyma is centrally aggregated, groups of small narrow tracheides are usually lodged within the parenchymatous mass, and that at other points conspicuously narrow elements may be absent, or, if developed at all, they may be peripherally disposed. These narrow elements bear multiseriate pits, and are not to be confounded with spiral protoxylems, and indeed, as has already been stated, spiral protoxylems are absent from the upright portion of the stem. Their absence is undoubtedly due to slow differentiation or only slight extension during the development of the stele. But although the absence of spiral protoxylems in the erect branch of *Stromatopteris* prevents comparison with the mesarch protoxylems of *Gleichenia*, it in no way militates against a Gleicheniaceous affinity for *Stromatopteris*. In fact, in possessing a protostelic axis, *Stromatopteris* is well in line with the majority of the Gleicheniaceæ, and differs in this respect only with *Platyzoma* and *Gl. pectinata*. The former possesses a medullated protostele with internal phloëm, the latter a solenostele.

In the plant which has been under discussion the basal sections of the stem show the stele in process of division. The xylem is divided into two similar though somewhat unequal masses separated by a zone of parenchyma. The phloëm is divided into two arcs, the margins of which are passing into the separating zone of parenchyma, and are about to extend so as to completely invest the xylem-groups (fig. 1). When division is completed the stele is divided into two similar parts (fig. 2). Of these the right-hand member passes directly into the broken branch, while the left is continued into the deflected stem.

A comparison of the form of our plant with the specimen in Edinburgh Herbarium, and the figures and descriptions referred to, strengthens the opinion that the broken branch which was thus supplied with a protostele was of axial nature.

As the left branch is ascended its stele widens and prepares to divide (fig. 3). The division of the stele which now follows and which precedes the wide forking of the axis is an unequal one (fig. 4). The xylem of the left stele is wide and parenchymatous, while that of the right is condensed and slender. The condensed form of the latter is not, however, long maintained, and within $\frac{1}{8}$ inch from the point of branching the right-hand stele has become elliptical in section and parenchymatous, and is already preparing for a new and final division (fig. 5). This latter division is noteworthy. It results in the formation of two steles of about equal diameter (fig. 6); but while the xylem of the left-hand stele thus formed is an almost solid mass of tracheides, and is surrounded by phloëm of uniform thickness, the xylem of the right-hand stele is crescentric in section, and the phloëm is then opposite the parenchymatous bay. The solid protostele supplies the short conical branch, while the stele with the crescentric xylem passes on into the base of the apparently petiolar branch. Throughout the length of this short, conical, and almost horizontal branch, the protostelic state is maintained, the xylem becomes more parenchymatous (fig. 7), and, towards the very tip of the stele, becomes very reduced in bulk (fig. 8) before ending abruptly in an apical mass of undifferentiated cells.

As to the meristele entering the branch which may be held as petiolar, it will suffice to state that within the cylindrical basal portion of the branch the stele first widens considerably, and the xylem assumes a more or less horse-shoe appearance in section (fig. 9). The phloëm still completely invests the xylem, but the thinness of the former opposite the parenchymatous bay in the latter is maintained. At a slightly higher level an open horse-shoe form is established in both xylem and phloëm, and the parenchymatous bay enclosed by the xylem is placed in open contact with the pericycle (fig. 10). This condition is likewise maintained throughout the dorsiventral portion of the branch. The petiolar nature of this branch is then structurally established, and the small conical protostelic branch is regarded as a displaced and arrested axis. Had the arrestment of this axis been more complete, merely a nodular swelling would have been developed at the base of the petiole, and METTENIUS's description of the external aspect of the leaf as nodular at its base, and a direct continuation of a branch of the axis, would have found its demonstration.

It will be remembered that when the wide forking of the stem occurred, giving rise on the one hand to the branch bearing the arrested axis and the petiole, which have just been described, and on the other hand to the left branch, the stele which entered the latter was wide and parenchymatous (fig. 4). As this branch is ascended these characters of the stele are maintained, and as the distal swelling is approached the stele becomes very elliptical in section (fig. 11). This is immediately followed by a massing of the tracheides on the right of the ellipse, and a tendency on the part of this mass to draw off from the remainder of the xylem, leaving the latter in the form of a horse-shoe on the left of the stele (fig. 12). The division of the stele into two dissimilar parts thus prefigured is soon completed (fig. 13), forming on the right hand a small protostele, and on the left a large trace, with open horse-shoe xylem and phloëm. The trace thus formed is continued directly into the left-hand member of the three branches into which the stem divides, and the petiolar structure of this branch is finally established.

But while this foliar trace is passing upwards into its petiole, the small protostele on the right widens considerably, and quickly divides, giving rise to two steles (figs. 14, 15, and 16). The steps of this division are interesting, for the xylem and phloëm first divide into two dissimilar portions, that on the left being protostelic, while that on the right is a crescentic mass of xylem with phloëm on its convex face alone. It is, in fact, like a foliar trace. When the division of the stele is completed the protostelic condition is maintained in the left-hand portion, and assumed in the right. In the latter, in fact, is shown a state similar to that seen in the base of the first petiole considered. It only remains to state that this trace enters the remaining branch of petiolar appearance, and that, as the branch becomes free, the protostele is transformed into a typical leaf-trace, with an open horse-shoe of xylem and phloëm (fig. 17).

There still remains for discussion the small columnar structure standing between the two petioles. It is supplied by the protostele which was the left-hand product of the last division (fig. 16). As the column is entered, the xylem becomes parenchymatous (fig. 18), and as the broad apex is approached the stele is found to be immature, and apparently arrested in development. As will be seen from fig. 19, a preparation for a further division of the stele has been initiated, and it is to this that the terminal depression and the broadening of the apex of the column are due.

The view which is taken of this short columnar branch is similar to that held regarding the small conical branch, associated with the right-hand petiole of this plant. It is believed to be an arrested axial branch, which initially bore the right-hand petiole but has now been displaced so that the latter appears to form the direct upward continuation of the main axial branch. The middle petiole shown on the specimen is likewise considered to have been initiated on the small columnar branch. But while on the right of the plant the formation of a single leaf is followed by arrest of the axis, on the left the formation of two leaves has ensued before the arrest occurred. Even then the formation of a third leaf upon the small columnar axis is indicated structurally.

The following conclusions may, then, be drawn from the examination of the first specimen of *Stromatopteris.* The leaves are borne upon the distal branches, but during development these leaf-bearing branches are more or less arrested, while the leaves become increasingly dominant. Complete arrest of axis-formation is not shown at any point, but its accomplishment would lead to a truly terminal position for the leaf, and the transition from the protostele of the axis to the typical leaf-trace would then probably be gradual. As the matter stands, however, the leaf-trace has been shown to have been quickly and clearly defined when the formation of any one leaf has not hindered the subsequent successful development of another. But when leaf-formation is followed by arrest of the axis, the typical leaf-trace is not immediately established, but fluctuations occur, suggesting a partial imposition of the characters of the stele of the arrested axis upon the trace of the dominating leaf. The clearly defined leaf-trace with horse-shoe xylem and phloëm, separating directly as such from the stele of the axis, may be considered the typical trace in *Stromatopteris*, while the trace which shows fluctuations in its structure, or passes by gradual transitions from a protostele to a foliar meristele, is held to be secondary and derivative. I do not think that the latter is to be interpreted as a primitive form, resembling in general the trace described by Gwynne-Vaughan and Kidston for *Thamnopteris* (*Proc. Roy. Soc. Edin.*, 1908). It is rather a consequence in a xerophytically reduced plant of the arrest of the axis, the dominance of the leaf at an early stage in development, and the consequent assumption by the leaf of a directly vertical position. Among flowering plants its condition finds a parallel in the aerial fertile branch of *Juncus conglomeratus*, in which the flowering spike emerges obliquely from the massive leaf-sheath, and the cylindrical leaf is continued vertically upwards above the displaced axis. In this case the same general anatomical characters are shown by the leaf in its free cylindrical and erect distal portion as is shown in the stem beneath the point of separation of leaf-sheath and axis. In this case, as in *Stromatopteris*, the assumption of an erect position by the leaf, and the accompanying lateral displacement of the flower-bearing axis, are linked with a continuation of the structural features of the axis into the leaf itself.

The second specimen of *Stromatopteris* may now be briefly described (fig. 41). Its slender axis is incomplete below, and near its base it is branched. The right branch has been broken off, but the left is continued obliquely upwards for a short distance. It is then sharply diverted from the oblique position to the vertical, and is finally branched. The right member of this branching has also been broken off, and the left limb is continued vertically upwards for a considerable distance before finally dividing. The basal portion of the right branch thus formed is little more than a nodular swelling, while the remainder is a slender tapering column, ending above in a small rounded tip. The left-hand limb is slender, and, while its linear form is maintained throughout, it bears at about one inch from its base a small incomplete horizontal branch. The general position and the smoothness of surface of the two distal branches suggest that they are of petiolar nature, while the rugged appearance of the remainder of the specimen confirms the latter as axial.

The anatomy of this specimen is of special interest as confirming the opinions expressed regarding the first specimen, and supplying a demonstration of the complete local abortion of axis which the first plant prefigured. The basal sections of the stem show a simple protostele (fig. 21), and, as the point of first branching is approached, a widening and equal division of the stele occur (figs. 22 and 23). The broken branch is supplied by the right protostele, while the obliquely ascending limb receives the left (fig. 24). The latter stele quickly widens (fig. 25), and divides into two unequal protosteles, the smaller of which is directed towards the left or convex surface of the oblique axis (fig. 26). These two protosteles become widely separated, though still completely enclosed by the cortex of the stem, and as the widening increases the left-hand stele dwindles rapidly (fig. 27). Beneath the point where the left surface of the stem is sharply changed from a convexity to a concavity, this smaller stele suddenly dies out, while the remaining protostele passes on into the erect continuation of the axis (fig. 28). The sudden change from the obliquely ascending to the erect position of the axis has accordingly found its explanation. The stele has been branched preparatory to a forking of the axis, but one limb of this forking has been suppressed, and the point of change from convexity to concavity marks the position of the arrested branch. It has been noted that in the first specimen of *Stromatopteris* arrest of axis was confined to the distal leaf-bearing branches, but in the second specimen abortion has been continued downwards into the lower branches. There will then be little cause for surprise when it is found that reduction and abortion are even more prominent in the distal portions of this specimen than they were in the corresponding parts of the first plant.

The steps of stelar division which precede the next branching are represented in figs. 29, 30, and 31. From them it will be seen that the division is initially unequal, but that the two steles finally formed are of almost equal dimensions. The somewhat smaller stele supplies the erect left-hand branch. Throughout the greater part of this branch it remains relatively small (fig. 32), but distally it widens and divides into two similar portions (figs. 33, 34, and 35). Of these, the right portion will be followed first. As the branch which it supplies becomes free, the stele, at first slender and condensed, becomes wide and parenchymatous (figs. 36 and 37). Within the nodular swelling it expands and divides unequally (figs. 38, 39, and 40). Of the two steles thus formed, the smaller left-hand member is rapidly reduced, and dies out without even the accompaniment of a protuberance on the surface of the nodule. It is believed that this aborted stele should have supplied a laterally displaced axis, and it would not be surprising if an anatomical study of the nodular swellings which METTENIUS observed at the leaf-bases of *Stromatopteris* revealed a branching of stele and abortion of axis similar to that just described.

The tapered columnar structure which is the direct upward continuation of the nodule is supplied by the surviving protostele (figs. 40 and 42), but it will be noted that the phloëm of the latter has become ill defined. A sudden transition to a V-shaped arrangement of the xylem follows almost immediately the entry of the stele into the branch (fig. 43), but this condition is in turn quickly replaced by a return to protostely (fig. 44). In these fluctuations is seen the same uncertainty as to stelar structure as characterised the base of the dominating right petiole of the first plant, and the petiolar nature of the branch under discussion seems obvious. The final establishment of the horse-shoe leaf-trace is gradually accomplished as the petiole is ascended (figs. 45 and 46); but as the distal portion is approached, reduction of the trace, both as regards dimensions and internal specialisation, takes place. This reduction fundamentally affects the phloëm and xylem. The former can no longer be clearly recognised, while the latter becomes gradually disintegrated, and when the tip of the column is reached there survive only three small groups of tracheides. The steps in this reduction are illustrated in figs. 47 to 52. The tissues of this branch are fully matured, and it is regarded as a petiole which should have been continued by a pinnate portion. But the abortion which stunted the stem, and led to the formation of the nodule, has extended to the leaf also. Pinna formation was entirely suppressed, and the leaf expanded as a relatively short filiform structure consisting entirely of rachis. It cannot be argued here whether or not filiform leaves are common in *Stromatopteris*, but an arrestment of the leaf, similar to the one just described, is figured by DIELS (*loc. cit.*), and on the specimen in Edinburgh Herbarium there is one leaf showing the condition depicted in text-fig. 16. It is of a slender and reduced type, and bears distally a few incomplete pinnæ.

As regards the left-hand branch of the specimen which has been under discussion, it will suffice to state that at its base the stele at first shows signs of adopting the structure of a leaf-trace (fig. 53), but as the point of branching is approached the stele widens and divides into two dissimilar portions (figs. 54, 55, and 56). The one is a small protostele, the other a typical leaf-trace. The protostele enters the small incomplete horizontal branch, which might or might not prove to be axis, but the leaf-trace passes on into the free rachial portion, and its typical structure is maintained until the upper fractured surface is reached (fig. 57).

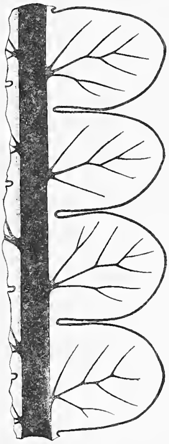
The foregoing survey of the axis and rachis of this second specimen brings the latter well into line with the conditions shown by the first specimen. But reduction and abortion, which have modified the first plant's structure, have more fundamentally affected the second specimen. Malnutrition may have been a potent factor, which had been superposed upon xerophytic life conditions; and the form and structure of this second specimen bear eloquent evidence to the dictatorial nature of the environment. The anatomical study of the materials available has disclosed stelar and leaf-trace characters which lend strong support to a relationship between *Stromatopteris* and *Gleichenia*. It has been shown that drastic reductions in the branch-sytem occur, and that these affect in particular the leaf-bearing branches and the leaves themselves. *Stromatopteris* may indeed be considered a very xerophilous and reduced type.


TEXT-FIG. 16.

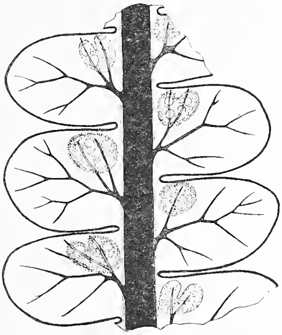
It seems probable that the leaves of *Stromatopteris* are typically simply pinnate and unbranched, and the specimen available for study is of this unbranched type (fig. 58). The leaves of the plants in Kew Herbarium are all unbranched, and the Edinburgh specimen shows a similar condition. But branching of the leaf may occur, and an example of this is shown in the right-hand plant in fig. 59. No surprise need be felt at an occasional branching in this xerophilous type, if, as comparison indicates, it arose from a stock where the leaves are typically branched. Indeed, branched pinnate leaves occur in *Platyzoma*, in which reduction of the leaf has become a dominant process, and, as I have shown elsewhere (*Trans. Roy. Soc. Edin.*, vol. li, 1916), has led to the production of characteristic filiform leaves.

Both fertile and sterile leaves are present in the Kew and Edinburgh specimens, and no difference in form is recognisable between them. The pinnæ are universally small and leathery, with slightly revolute margins, and with stomata restricted to the lower surface. As will be seen from text-figs. 17 and 18, there is an alternation of the pinnæ of the rows on either side of the rachis. The traces draw off from the rachis towards the basiscopic margins of the pinnæ, and are universally of extra-marginal origin (figs. 60 and 61). The venation is liable to vary as to details from pinna to pinna, but is universally a sympodial dichotomy, in which the basiscopic member of the first dichotomy is usually dominant, and by its further branching supplies the greater part of the pinna. The acroscopic member remains unbranched or divides but once, and supplies only the basal acroscopic portion of the pinna. A thick-walled hypoderma is developed towards the upper surface and around the revolute margins of the pinna, and tannin-mucilage cells are numerous in the general mesophyll and along the margins of the bundles (fig. 66). The latter do not reach the margins of the pinnæ, and their endings are weak and poor in storage tracheides. In form of leaf and leaf-trace, and in pinna-trace origin and venation, *Stromatopteris* is typically Gleicheniaceous, and the anatomical characters of the pinnæ are further proofs of the xerophytic life conditions of this plant.

The sorus remains to be considered. It may be stated at once that its position is constant towards the base of the upper margin of the pinna (text-fig. 18). The massive receptacle varies in form and size. It is typically disc-shaped or reniform, and is supplied by the basal acroscopic vein or by its branches, and only occasionally are other veins involved in it. The veins either terminate within the receptacle or pass beyond it towards the upper margins of the pinna. Many of the pinnæ on our specimen bear sterile receptacles, but neither size nor form seems a sure guide as to sterility and fertility. In only a few cases were sporangia found still attached to the receptacle, but it was evident from the points of sporangial insertion that the number of sporangia per receptacle is open to considerable variation. The smallest number of insertions observed was two, the highest six. Where the number of sporangia had been relatively high, the arrangement upon the receptacle was more or less rosette; but where the number had been small, there had been a tendency for the sporangia to have developed above a vein. The surface of the receptacle is densely covered by a very varied assemblage of irregularly branched hairs and small



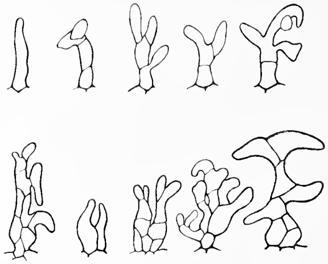
TEXT-FIG. 17.



TEXT-FIG. 18.

irregular scales, typical examples of which are shown in text-fig. 19. These closely invest the short massive stalks of the sporangia, and clothe the steep margins of the elevated receptacle (fig. 66). The position and vascular supply of the sorus, and the variation in arrangement and number of sporangia, are features typical of *Gleichenia*, and the possession of them greatly strengthens the Gleicheniaceous affinity of *Stromatopteris*.

Seven sporangia were available for study. They were borne on separate sori, and it was impossible to judge by them as to what credence is due to METTENIUS's remark that in the sporangia of *Stromatopteris* dehiscence is *extrorse*. Extrorse dehiscence, as a defined character, is unknown in the Gleicheniaceæ, although variations in sporangial orientation occur, but it may be said that in at least two of the sporangia available dehiscence appeared to be *introrse*. The sporangia varied in form and size, and the degree of variation in these respects may be judged by the illustrations given (figs. 62, 63, 64, 65, and 71–74). These sporangia have all been drawn to the same scale, and are represented in various positions. The sporangial stalks are short and massive (fig. 66) and the heads are more or less globular. The largest sporangium found is depicted in figs. 62 and 63. From these views it will be seen that the annulus is transverse, irregular, and massive. The region of dehiscence is well defined, and dehiscence is vertical. This sporangium was open, and accordingly its spore output could not be estimated. The sporangium represented in figs. 67 and 68 is of the same general form as the one just described, but its annulus is oblique and uniseriate. The zone of dehiscence is ill defined and narrow, but dehiscence is clearly vertical. There is here seen the kettle-drum-shaped sporangium typical of *Gleichenia*. This sporangium had been entirely emptied of its spores. A much smaller sporangium, but similar in form to the one just described, though possessed of a wider region of dehiscence, is shown in figs. 64 and 65. It merely illustrates that variation in sporangial size common in *Gleichenia* itself, and which may be due to faulty nutrition and arrest. One large sporangium of the type just described was found to be unopened. Its spores



TEXT-FIG. 19.

were counted and were found to number about 480, all of which appeared to be fully developed. In itself the sporangial form bore strong evidence of the Gleicheniaceous affinity of *Stromatopteris*, and the spore-count greatly strengthens this relationship. But while the bond of kinship of these plants is thus further tightened and strengthened by the evidence of the spore-output in *Stromatopteris*, the gulf between *Platyzoma* and both *Stromatopteris* and *Gleichenia* remains wide. Both *Platyzoma* and *Stromatopteris* are clearly seen to be xerophytically reduced and specialised types, but the latter has been conservative of the stock character of spore-output, whereas the former has drifted further in this respect than in any other from the Gleicheniaceous type, for the highest spore-count which has been made in *Platyzoma* is 32.

Two sporangia of a more aberrant type remain to be mentioned. The first is represented in figs. 71 and 74. On its upper slanting surface is a rosette of eight indurated cells, displayed around a single central cell. There is no defined zone of dehiscence, but dehiscence is probably accomplished vertically on the convex unindurated side. This sporangium was unopened, and accordingly supplied a second spore-count. It contained at least 416 mature spores. The second anomalous sporangium is represented in figs. 72 and 73 as seen from above and below. It has an apical cap of four unthickened cells, bordered by a perfectly transverse uniseriate annulus. There are thirteen indurated cells, a clearly defined zone of dehiscence, and vertical dehiscence. Its stalk is short and massive. This sporangium was empty. The form of the first of these anomalous sporangia is suggestive of that of certain of the *Schizæas*, but the consensus of the other features, and in particular the characters of the majority of the sporangia and the spore-output of *Stromatopteris*, are distinctly against a *Schizæa* affinity. The spore-output is much higher than that of any known member of the Schizæaceæ, and harmonises well with the Gleicheniaceous types. The form of these two sporangia is considered an anomaly of which other examples probably occur, but it is not considered hostile to a Gleicheniaceous affinity for *Stromatopteris*. It rather serves as a proof of a certain aloofness on the part of *Stromatopteris*, than as a suggestion of a possible link with *Schizæa*.

The spores are all of one type (figs. 69 and 70). They are remarkably thin-walled and smooth, and suggest structures designed for quick germination.

General Conclusions.

When the details given above are surveyed, it is found that structurally *Stromatopteris* comes well in line with most *Gleichenias*, but is possessed of an individuality of form which is not matched by any known *Gleichenia*. It may be held that many of its peculiarities are consequent on the assumption of an erect position by the branched portions of the axis, and are accentuated by the poverty in roots, or the extremely xerophytic life conditions. The transitional types of dermal appendages, however, supply a peculiarly distinctive character, and, while they may be expressive of special adaptation in a physiological xerophyte, they serve, at the same time, to justify the recognition of *Stromatopteris* as generally distinct from *Gleichenia*. With *Platyzoma* it has no close kinship, and indeed they have little in common beyond the hallmarks of a xerophytic existence; for *Platyzoma* shows sporangial advance with a relatively primitive, though somewhat anomalous, vegetative condition, but *Stromatopteris* is conservative of the structural and sporangial characters which are considered typical of the Gleicheniaceous stock. It is, then, believed that *Stromatopteris* is worthy of recognition as a distinct monotypic genus, closely allied to *Gleichenia*, but clearly distinguished from it by well-marked peculiarities of form and construction.

Summary.

The chief facts obtained from the herbarium specimens available of *Stromatopteris* have now been described. At some points the account has been less complete than would have been the case if undamaged plants had been available. The absence of perfect specimens has rendered impossible a definite conclusion regarding the form and position of the main axis in the growing plant, and it has likewise been impossible to determine whether or not the mature sporophyte of *Stromatopteris* is rootless. Development has been necessarily omitted. But the fuller facts relating to mature form and structure which have been acquired may help towards establishing the position which this plant should hold in relation to other ferns.

The habit of the plant is chiefly notable in relation to the vertical position of the branched portions of the axis, and the apparently terminal position which is, at times, assumed by the leaves as an accompaniment of displacement and abortion of the leaf-bearing branches. The plant is, in fact, of a xerophytically reduced type. The lower portions of the axis show dichotomous branching, but suppressions may occur leading towards complete abortion of a branch. The leaves are developed distally on the branch-system, and are produced singly on a branch or in small numbers. The development of the leaf is accompanied by the arrest and displacement of the supporting axis, and the dominating leaf may thus appear to be a direct upward continuation of the axis. The arrest of the axis which accompanies leaf-formation may be complete or incomplete, and when complete leads to the formation of a nodular swelling at the base of the dominating leaf. It is in the distal portions of the branch-system that abortion is most evident, but it may also appear in the lower branch-system. It may similarly appear in the leaves themselves, and lead to the formation of leaves of a reduced type. Branchings of the leaf may occur. It is probable that such branchings are of the same nature as those seen in the *forma furcata* of many ferns. The erect position of the branched portion of the axis, and the dominance of the leaves over the supporting branches, are features in strong antithesis to the typically horizontal position of the axis and the continued axial growth shown by the *Gleichenias*, with which *Stromatopteris* has been habitually and closely grouped.

The anatomical evidence shows that the branching in *Stromatopteris* is fundamentally dichotomous, but the branches of the dichotomy may not develop equally, and indeed one branch may be partially or almost completely suppressed, and may survive only as an apparent nodule at the base of the petiole of the leaf which it has produced. Professor BOWER has drawn my attention to the fact that this condition is of interest in connection with a question raised by Dr SCOTT (*Studies in Fossil Botany*, pt. i, p. 318), and discussed also by SCHOUTE (*Über verästelte Baumfarne und die Verästelung der Pteropsida in allgemeinen*, 1914, pp. 94, 95). It will be well to quote the passage from Dr SCOTT's book. In discussing the morphology of *Zygopteris*, and the interpretation to be put upon it by the comparative morphologist, he makes the following statements :—

"The great peculiarity of *Zygopteris corrugata* as compared with the other three species in which the stem is known, consists in its mode of branching, which is not axillary, but rather of the nature of a dichotomy, the stem forking into two nearly equal branches without obvious relation to the leaf-insertion. This fact raises the question whether, as has been suggested, the apparent axillary branching of other species and of recent Hymenophyllaceæ may not be a modified dichotomy, in which case the 'undivided leaf-trace' would really be the stele of the smaller branch, and the 'subtending' leaf would belong to this branch and not to the main axis. The data are insufficient to settle the question, but for the present it seems better to keep up the distinction between the two kinds of branching."

From a wide study of branching SCHOUTE has concluded that the evidence is strongly in favour of the belief that dichotomous branching is primitive, and that axillary branching is secondary and has commonly arisen by the modification of a dichotomy. This process is indeed held to have had a wide application in the higher plants. Now it is apparent that if, in the specimens of *Stromatopteris* described in this memoir, the suppressed apex had been arrested slightly earlier, it would actually have a position axillary to the leaf. In ferns generally this is an uncommon condition, but it exists, in point of fact, in *Zygopteris* and the Hymenophyllaceæ. It is not suggested that there is any near affinity between *Stromatopteris* and either *Zygopteris* or the Hymenophyllaceæ, but the similarity of the disposition of axis and leaf in all of these is sufficiently striking to justify the comparison, and the case of *Stromatopteris* may help to elucidate what in these other plants has been regarded as an exceptional state for relatively primitive ferns.

The presence of both hairs and scales accords with what is seen in certain *Gleichenias*. But apart from these extreme types of appendages, *Stromatopteris* possesses a curious assemblage of irregular transitional forms, which have not been matched from any other known Gleicheniaceous plant. These transitional forms range from irregularly inserted hairs to massive domes and tortuous and branched scales. They are open to interpretation either as excretory structures or organs of absorption. Support for this latter view of these appendages is found in the fact that no roots have been observed in *Stromatopteris*, and METTENIUS has clearly affirmed that they are entirely absent. A belief in the specialisation of these appendages as organs of absorption is further strengthened by the structure of the cortex of the stem, which is composed of thick-walled and elaborately pitted elements, devoid of protoplasts and intercellular spaces. These cortical cells may possibly form a supplementary conductive system. In external form *Stromatopteris* holds a unique position among the Gleicheniaceæ, and its aloofness is further accentuated by its apparently rootless condition, and by its possession of dermal appendages of anomalous type. But, on the other hand, it resembles certain of the *Gleichenias* in possessing conical sclerotic emergences which act as supports for certain of the dermal appendages. Such emergences are uncommon among ferns, and their possession by *Stromatopteris* tends to strengthen its affinity with *Gleichenia*.

The protostelic axis of *Stromatopteris* is in accord with that of most Gleicheniaceous plants, and any peculiarities which are associated with the branching of the stele are believed to be the result of abortion. The leaf-trace is of an advanced Gleicheniaceous type, but when arrest and abortion of the leaf-bearing axis have been accompanied by dominance of the leaf, and when the latter appears as a distinct upward continuation of the axis, the passage from the protostele of the axis to the typical foliar trace is gradual. Abortion within the leaf itself leads to abnormal structure, which cannot be safely cited in a phyletic discussion.

The characters of the pinnate portion of the leaf are such as to strengthen the relationship between *Stromatopteris* and *Gleichenia*. The small orbicular pinnæ have sympodial dichotomous venation, and the pinna-trace supply is extra-marginal. The pinnæ are of a leathery character, and their construction is indicative of specialisation for a xerophytic existence.

The sori are developed singly upon the forking of a basal acroscopic vein. The receptacle is massive, and either disc-shaped or reniform. Its surface is clothed by a curious assemblage of branched hairs and small scales, and it bears a variable number of short and massive-stalked sporangia. The position of the sorus, the form of the receptacle, and the variation in sporangial number are in keeping with the characters of certain *Gleichenias*, especially of the section *Eugleichenia*.

The apparently typical sporangium has a short and massive stalk, a globular head, a transverse or oblique annulus, and vertical dehiscence. In form and dehiscence the sporangia of *Stromatopteris* are typically Gleicheniaceous, but anomalies of form occur. These affect in particular the size of the sporangium and the form of the annulus, but do not appear greatly to disturb the spore-output. Their presence is held to indicate a certain aloofness on the part of *Stromatopteris* from *Gleichenia*, rather than to indicate for the former some other affinity. The spore-output is high and is typical of the Gleicheniaceæ; and as such numbers as have been observed are uncommon outside Eusporangiate ferns, they form the strongest argument which can be advanced in support of an affinity with *Gleichenia*. The spores are peculiar in possessing exceedingly delicate and smooth walls, and may be adapted to conditions of quick germination.

It is believed that the general characters revealed in this study of *Stromatopteris* justify its recognition as a distinct monotypic genus, allied to *Gleichenia*, but clearly distinguished from it by well-marked peculiarities of form and construction. The erect position of the branched portion of the axis of *Stromatopteris* may be a secondary feature, but the recorded facts are wholly insufficient to allow of a confident opinion. It has still to be shown whether the horizontal or the vertical position was primitive for the axis of *Gleichenia* itself. The stele of *Stromatopteris* is at points strongly reminiscent of that of *Rachiopteris cylindrica*, Will. ("A Contribution to our Knowledge of *Rachiopteris cylindrica*, Will.," N. BANCROFT, *Ann. Bot.*, vol. xxix, 1915), and may prove to be of as primitive a type. The stelar structure is not, then, considered a reduction form related to the xerophytic conditions which appear to have modified *Stromatopteris* in other respects; it is rather to be considered primitively protostelic.

DESCRIPTION OF FIGURES IN THE TEXT.

Text-fig. 1. Axis of *Stromatopteris* as figured by METTENIUS. × $\frac{2}{3}$.

Text-figs. 2–13. Illustrations of the dermal appendages and emergences of *Stromatopteris*. These range from simple hairs to irregular and branched scales, and lanceolate scales on massive conical emergences. All × 18.

Text-figs. 14 and 15. Longitudinal and transverse sections of the cortical tissues of *Stromatopteris*. × 45.

Text-fig. 16. An arrested leaf of *Stromatopteris* on the specimen in Edinburgh Herbarium. × $\frac{2}{3}$.

Text-fig. 17. Plan of pinnation and venation in sterile leaf of *Stromatopteris*. × 8.

Text-fig. 18. Plan of pinnation, venation, and soral form and position in *Stromatopteris*. × 8.

Text-fig. 19. Types of hairs and scales on the receptacle of *Stromatopteris*. × 35.

DESCRIPTION OF FIGURES IN THE PLATES.

PLATE I.

The sections depicted in this plate all belong to specimen represented in fig. 20.

Figs. 1 and 2. Transverse sections of stele of plant of *Stromatopteris*, showing steps of first branching. × 30.

Figs. 3 and 4. Sections showing steps of second branching. × 30.

Figs. 5 and 6. Sections showing steps of branching in right-hand branch during formation of short aborted axis and erect petiole. × 30.

Figs. 7 and 8. Steps of stelar reduction in the arrested axis which is displaced by the above-mentioned petiole. × 30.

Figs. 9 and 10. Steps in formation of typical "open" foliar trace within the base of the above-mentioned petiole. × 30.

Figs. 11–13. Steps of first branching in base of distal swelling in left-hand branch, and leading to the liberation of the foliar trace of the right petiole. × 30.

Figs. 14–16. Steps of second branching within the above-mentioned swelling, resulting in the formation of the stele which enters the short columnar branch and the trace for the middle petioles. × 30.

Fig. 17. Section of leaf-trace of middle petiole when the latter is free from the axis. × 30.

Figs. 18 and 19. Successive sections in the columnar arrested axis standing between the left-hand and middle petioles. × 30.

Fig. 20. Incomplete specimen of *Stromatopteris* from which the above-mentioned sections are taken. × $\frac{2}{3}$.

Plate II.

The sections depicted in this plate all belong to specimen depicted in fig. 41.

Figs. 21–23. Steps of stelar division preparatory to basal branching. × 30.

Figs. 24–27. Steps of division leading to total abortion of a left-hand branch. × 30.

Figs. 28–31. Steps of second branching. × 30.

Figs. 32–35. Steps of third branching. × 30.

Figs. 36–40. Steps of stelar division within the nodular swelling of right member of this latter branching, and showing the reduction of the axial stele. × 30.

Fig. 41. Incomplete specimen of *Stromatopteris* from which the above-mentioned sections are taken. × $\frac{2}{3}$.

Plate III.

Figs. 42–52. Steps in formation of typical foliar trace in right-hand aborted leaf of the specimen figured on Plate II, and the stelar reductions which characterise the terminal portion of this leaf. × 30.

Figs. 53–56. Steps in the single branching of the left limb of the above-mentioned specimen. × 30.

Fig. 57. Section of the foliar trace which enters the left petiole of the above-mentioned specimen. × 30.

Fig. 58. Photographic reproductions of the fertile leaf and the first specimen of *Stromatopteris* on which this paper is founded. × $\frac{1}{2}$.

Fig. 59. Photographic reproductions of specimens of *Stromatopteris* figured by Christ, and showing branching of a single leaf. × $\frac{1}{2}$.

Figs. 60 and 61. Sections of a basal and a terminal portion of the rachis of *Stromatopteris* showing the stele with extra-marginal pinna-trace supply. × 30.

Plate IV.

Figs. 62 and 63. Back and front views of the same. Sporangium of *Stromatopteris*, with massive transverse annulus and vertical dehiscence. × 60.

Figs. 64 and 65. Back and front views of a small sporangium with oblique uniseriate annulus. × 60.

Fig. 66. Section of sorus bearing leaf of *Stromatopteris*. × 45.

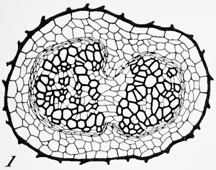
Figs. 67 and 68. Back and front views of a large sporangium with uniseriate oblique annulus. × 60.

Figs. 68 and 69. Two views of the thin-walled spores of *Stromatopteris* × 280.

Figs. 71 and 74. Back and front views of a large anomalous sporangium of *Stromatopteris*. × 60.

Figs. 72 and 73. Top and bottom views of a small anomalous sporangium of *Stromatopteris*. × 60

J. M. Thompson: Stromatopteris moniliformis.



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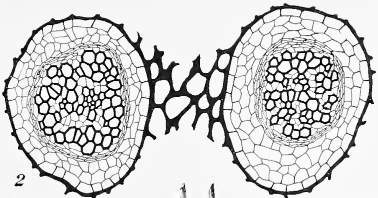

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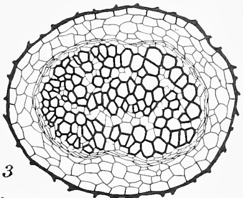

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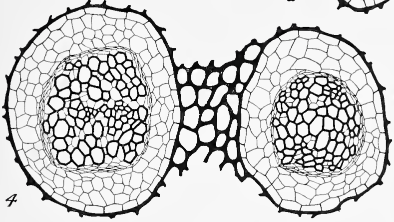

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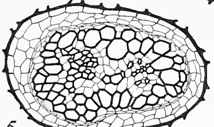

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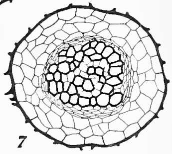

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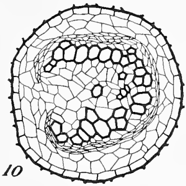

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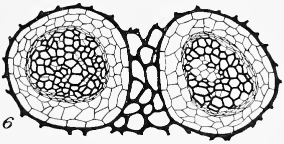

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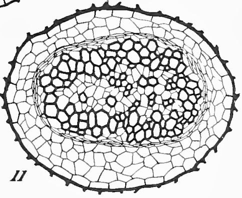

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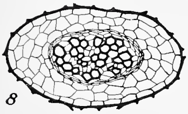

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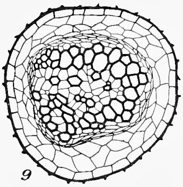

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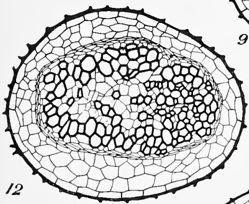

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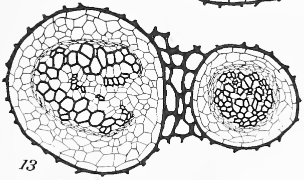

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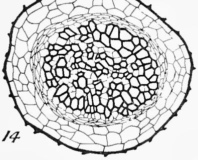

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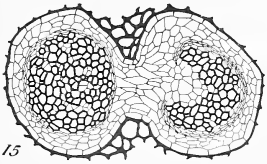

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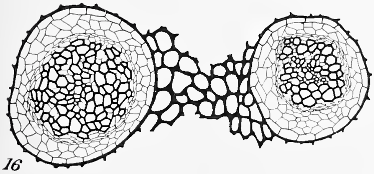

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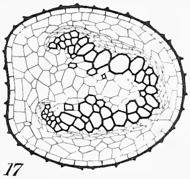

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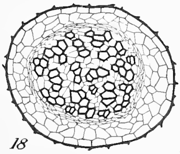

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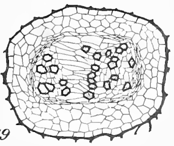

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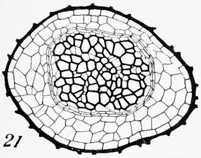
J. M. THOMPSON: STROMATOPTERIS MONILIFORMIS.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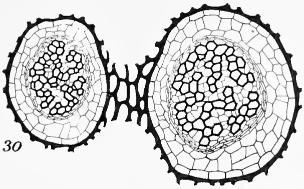
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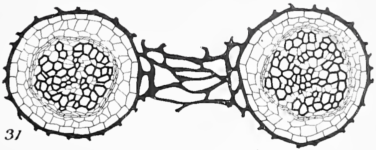
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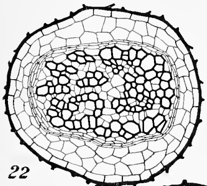
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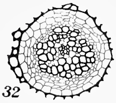
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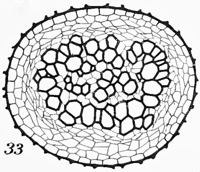
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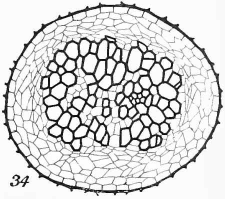
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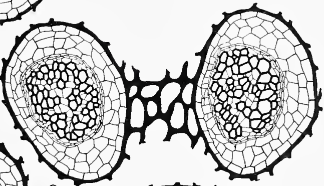
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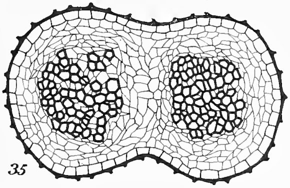
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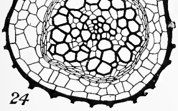
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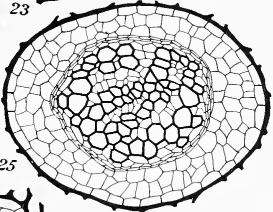
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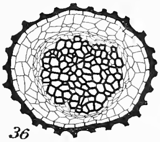
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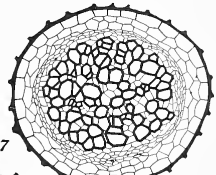
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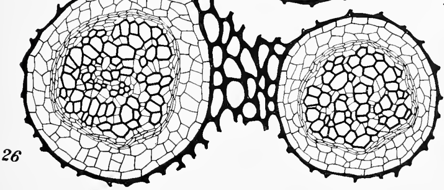
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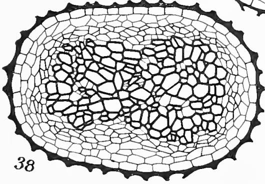
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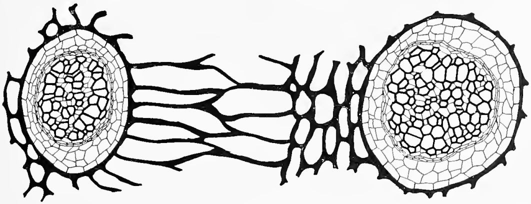
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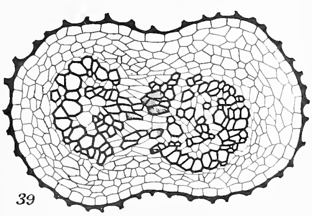
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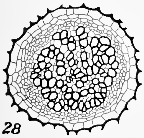
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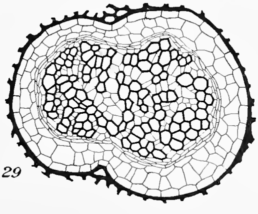
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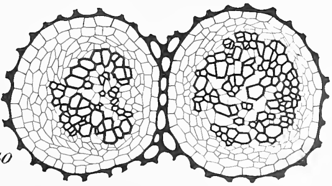
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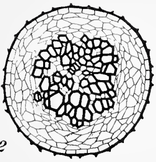
J. M. Thompson: Stromatopteris moniliformis.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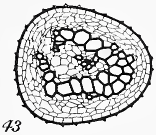
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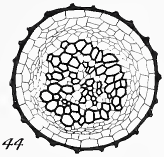
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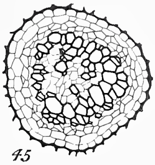
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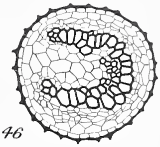
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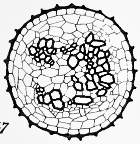
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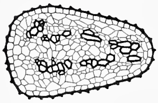
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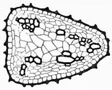
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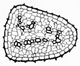
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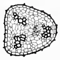
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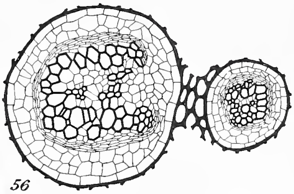
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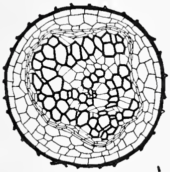
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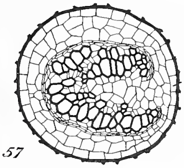
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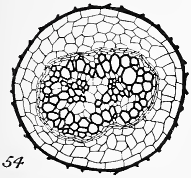
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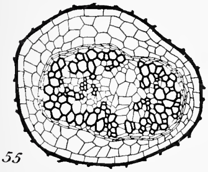
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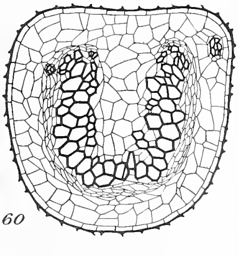
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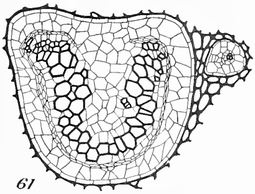
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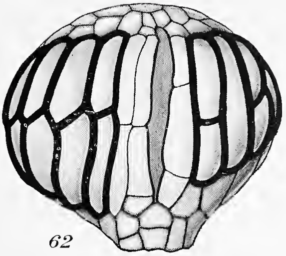
J. M. Thompson: Stromatopteris moniliformis.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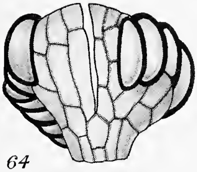
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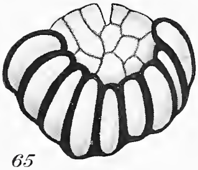
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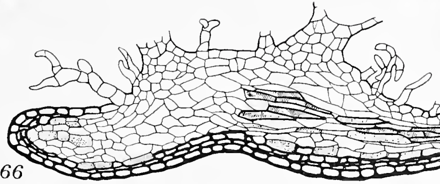
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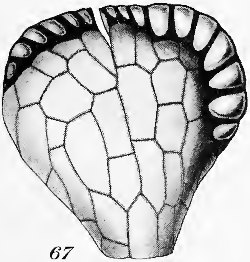
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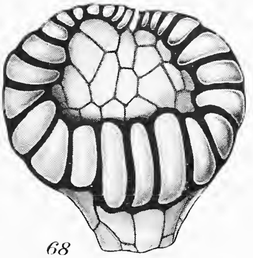
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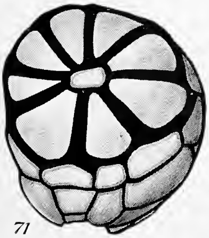
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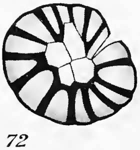
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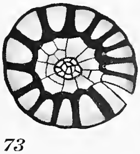
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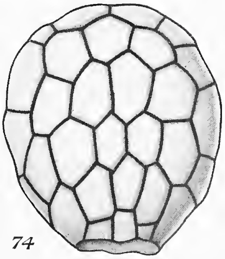
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VII.—A Further Contribution to the Knowledge of Platyzoma microphyllum R. Br.

By **John M'Lean Thompson**, M.A., D.Sc., Glasgow University.

(With Seventeen Figures in the Text.)

(MS. received July 9, 1917. Read July 9, 1917. Issued separately October 5, 1917.)

In a previous paper on the anatomy and affinity of *Platyzoma microphyllum* R. Br. (*Trans. Roy. Soc. Edin.*, vol. li, No. 20, 1916), the structure of a single herbarium specimen of this rare Australian fern, collected by Professor Baldwin Spencer in 1902, at Boorroololoo, N.T., was described. Attention was directed in particular to the remarkable heterophylly, the anomalous stelar structure, and the unique sporangia and spores. The facts detailed made it difficult to indicate any known fern with which *Platyzoma* could be reasonably compared. They might be considered to suggest a probable derivative position for *Platyzoma* from some Gleicheniaceous source; but their divergence from the *Gleichenia* characters was so pronounced that it seemed impossible to retain a view of close affinity between *Gleichenia* and *Platyzoma*.

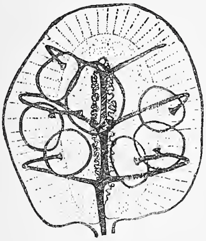
It was deemed advisable to delay the further consideration of the systematic position of *Platyzoma* until fuller facts were secured. In particular, it was desirable to determine the origin of the anomalous stelar structure, and to throw light upon the nature of the sporangia and spores. By the courtesy of Dr Bailey of the Brisbane Botanic Gardens I have now been supplied with a number of herbarium specimens of *Platyzoma*, and with materials preserved in spirit. These have provided important evidence as to the stelar state, and the structure of the mature sporangia and spores of this fern. A full account of the stelar structure will be given later, but in the present paper the mature sporangia and spores will be considered.

It may be well to recapitulate the facts which emerged from the examination of the very limited materials dealt with in the first memoir. The fertile pinnæ were ovate-orbicular in outline, and their margins were so revolute that the stomata—which were restricted to the lower surface—were in an almost closed chamber. The margins of the pinnæ bore minute irregular hairs which helped to reduce the entrance to the chamber. The venation was a short sympodium. The sporangia were disposed either terminally upon the main lateral branches of the sympodium; or if more than one sporangium were developed upon a branch of the sympodium, the distal portion of the branch was forked, and the sporangia were again terminal (text-fig. 1). The mature sporangia were almost sessile, and were hidden beneath the revolute margins of the pinnæ: They were of irregular form, and their dehiscence was variable. The sporangia in any one pinna varied in size, but, although the larger sporangia were commonly upon the distal branches of the sympodium, no very definite arrangement according to size was recognised. The capsule was globular, ovoid, or pear-shaped, and was frequently lopsided. The annulus was variable in position and form; it was seldom, if ever, perfectly regular, and was typically very irregular. In a few cases it was almost horizontal, passing round the capsule as an irregular broken ring, and having no clearly organised stomium. In the large majority of the sporangia the annulus was almost vertical, though typically irregular, and a definite stomium was present. The annulus usually began at the back of the stalk. It passed obliquely and with irregularities upwards, and, having surmounted the capsule, descended to the stalk once more as a well-defined stomium. It was evident that in the majority of the sporangia the annulus was interrupted by the stalk. The stalk was of variable construction. In the small sporangia it usually consisted of three rows of cells, but a four-rowed stalk was not uncommon. The stalks of the large sporangia showed the same variation. The large sporangia contained small numbers of large spores, the small sporangia larger numbers of small spores. The largest number of spores observed in a large sporangium was 16; 14 was a common count, and 12 was a rare spore-number. The largest spore-number in a small sporangium was 32, and such numbers as 30, 29, 28, and 26 were frequently counted. There were also spores intermediate in size between the large and small forms. These were not restricted to either type of sporangium. They were present in both large and small sporangia. Thus in one large sporangium 14 large spores and 2 of intermediate size were found; a small sporangium contained 3 intermediate and 28 small spores. Both large and small spores were found in the same sporangium.

Such remarkable differences in the size of sporangia and spores are unknown outside heterosporous plants, and it is accordingly desirable to know if *Platyzoma* is truly heterosporous.

It would appear that in homosporous Leptosporangiate ferns marked differences in sporangial size in any one species are rare. When such variations do occur the spore-output per sporangium may be affected, but uniformity of spore-size and form remains. This condition is seen in *Stromatopteris* (*Trans. Roy. Soc. Edin.*, 1917). In modern heterosporous Pteridophytes sporangial size is in general a guide to the nature of the spores. The size of the sporangium is indicative of the size, number, and *sex* of the spores. The large sporangia contain small numbers of large *female* spores, the small sporangia a larger number of small *male* spores. In possessing both large sporangia with few large spores, and small sporangia with more numerous small spores, *Platyzoma* is in line with most heterosporous Pteridophytes.

But heterospory may occur without recognised distinctions of either sporangial or spore size. Thus in *Equisetum*, which produces male and and female prothalli, spore-sex is not indicated by differences in the size or form of either sporangia or spores. The nature of the spores is not manifested until germination, and the well-marked sexual distinctions are seen only in the established gametophytes. There is no *a priori* reason why differences in the size of sporangia and spores should not accompany true homospory, for the nutrition of the individual sporangium might conceivably lead to these differences, without involving sexual distinctions in the gametophytes. The balance of evidence is, however, clearly in favour of heterospory when marked differences in the size of sporangia and spores occur; but the homosporous or heterosporous condition of any fern is demonstrable only after germination. In certain instances, as in *Ceratopteris*, which are considered homosporous, poorly nourished prothalli are small, and bear only antheridia. The more robust prothalli are bisexual or female. It may be that, as with the gametophytes of *Ceratopteris*, so also with the sporangia and spores of *Platyzoma*, the sex of the individual is a concomitant of its nutrition.



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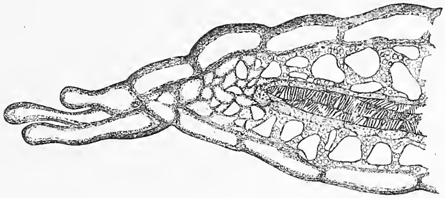

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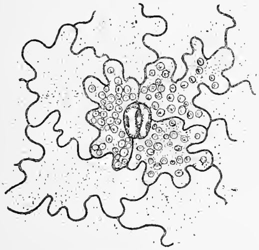

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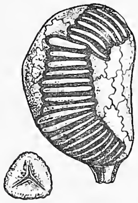

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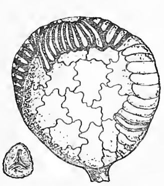
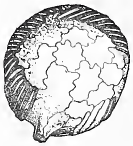


Text-fig. 5.

The materials of *Platyzoma* available were unsuitable for the study of sporangial development. The number and fate of the spore-mother cells in the two sporangial types is, then, unknown. The spores have not been germinated, and the nature of the gametophytes remains uncertain. In the absence of information on these important points the facts now to be detailed regarding the mature sporangia and spores may indicate the importance of the mixed sporangial characters, and will link, at a later date, the facts of sporangial development with those of gametophyte construction.

As in the first materials examined, so also in the second, the margins of the fertile pinnæ are so revolute that the sporangia are in an almost closed chamber (text-fig. 1). The entrance to this chamber is much reduced by short thick-walled hairs borne on the margins of the pinna (text-fig. 2). The outer walls of the upper epidermal cells are particularly thickened. The mesophyll is well supplied with intercellular spaces, and the bundle-sheaths have mucilaginous contents. The stomata are numerous, and are restricted to the lower surface of the pinna. A curious feature is shown in some cases by the epidermal cells surrounding the stomata. They include starch grains similar to those present in the mesophyll (text-fig. 3). The disposition of the sporangia upon the sympodial vein-system has already been described, and the careful protection of the sporangia against xerophytic conditions is manifest.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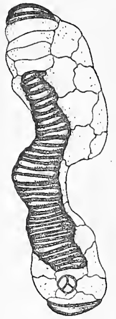
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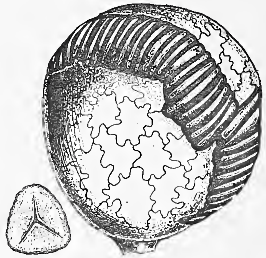
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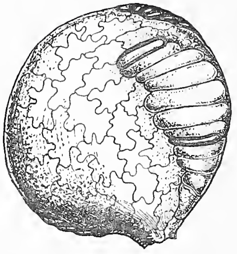
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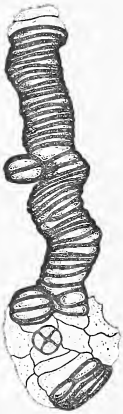
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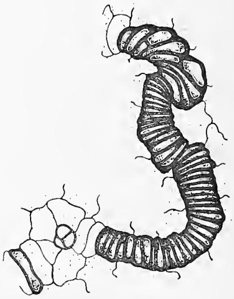
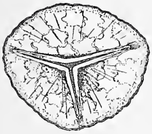

Text-fig. 11.

All the sporangia on several plants have been examined, and the size and form of the sporangia, and the spore size and output per sporangium, have been determined in 1000 cases. Of these sporangia 890 or 89 per cent. were small, 110 or 11 per cent. were large. The largest number of sporangia observed on a pinna was 11, the smallest 5. When the number of sporangia per pinna was large the majority of the sporangia were small. Thus of the 11 sporangia in one pinna 10 were small, 1 was large. When the number of sporangia per pinna was small the large sporangia were usually more numerous. The largest number of large sporangia observed in any pinna was 3, and there was an accompanying reduction in the number of the small sporangia out of all proportion to the increase in number of the larger forms. Thus one pinna contained 2 large and 3 small sporangia. The majority of the pinnæ bore both small and large sporangia. In some cases only small sporangia were present, but in no pinna were large sporangia alone developed.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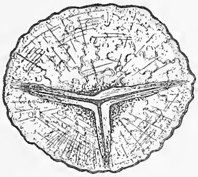
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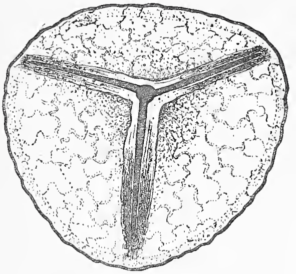
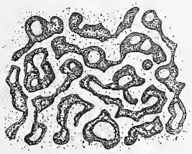
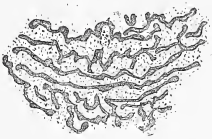
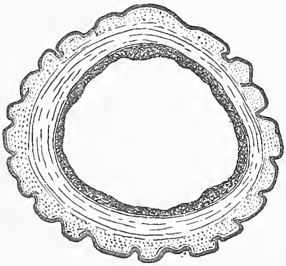

Text-fig. 14.


Text-fig. 15.


Text-fig. 16.


Text-fig. 17.

Typical views of small sporangia are shown in text-figs. 4, 5, and 6. The stalk is short and the globular capsule is commonly lopsided. The annulus is variable in position and is typically irregular. It usually begins at the back of the stalk, and passes obliquely over the top of the capsule. There is a well-defined stomium.

The most regular annulus observed is depicted in text-fig. 7. The sporangium has been ruptured, and shows the entire course of the annulus. In the majority of the small sporangia the stalk consists of three rows of cells, but four-rowed stalks have been encountered.

Typical views of large sporangia are given in text-figs. 8 and 9. These show the same general features as are seen in the small sporangia. Size is the only point of discrepancy between the two types. The stalk of the large sporangium is occasionally four-rowed, and the annulus is commonly very irregular (text-figs. 10 and 11). The sporangial characters which were previously described have accordingly been confirmed.

The three types of tetrahedral spore already recorded were easily recognisable in the new materials (text-figs. 12, 13, 14). The spore-markings were invariably moats and irregular channels. Those on the convex sides of the spores were deep and broad (text-fig. 15), while those on the remaining triangular surfaces were narrow and shallow (text-fig. 16). Many mature spores of each type were seen in section. The spore-wall was invariably remarkably thick, and was differentiated into two zones of approximately equal breadth (text-fig. 17). A protoplasmic lining was the only recognisable content of any spore. It follows that while the spores are still within the sporangia, the only recognisable distinction between the three spore-types is one of size.

The majority of the spores in any small sporangium were of the smallest type, but an admixture of intermediate or large spores was also shown. This may be illustrated by a table in which are set down the spore-output per sporangium, and the number of small, intermediate, and large spores actually present in certain of the small sporangia :—

Total Number of Spores present in the Sporangium.	Number of Small Spores present.	Number of Intermediate Spores present.	Number of Large Spores present.
32	32	0	0
32	31	0	1
31	31	0	0
31	28	3	0
30	30	0	0
29	29	0	0
29	27	0	2
29	27	2	0
28	28	0	0
28	13	15	0
27	27	0	0
19	12	6	1
17	17	0	0
17	12	4	1
16	6	10	0
16	0	16	0
9	7	0	2

Out of 890 small sporangia examined, 739 had each more than 29 spores. In these sporangia spores of intermediate size were rare, and the largest number of large spores in any one sporangium was 3. 124 sporangia had each from 27 to 29 spores; 23 had not less than 19 spores, and in only four instances did the spore-count fall below 16. In the small sporangia the number of intermediate spores was increased when the spore-output was small. The number of large spores in the small sporangia was invariably low.

A similar analysis of the spore-numbers may be made for the large sporangia. As is shown in the following table, the large majority of the spores in the large sporangia were of the large type:—

Total Number of Spores present in the Sporangium.	Number of Small Spores present.	Number of Intermediate Spores present.	Number of Large Spores present.
16	0	0	16
16	0	1	15
16	1	0	15
15	0	0	15
15	1	0	14
14	0	0	14
14	1	0	13
13	0	0	13
12	0	0	12
12	0	2	10
12	1	5	6

Out of 110 large sporangia examined, 73 had each more than 14 spores. In these sporangia spores of either intermediate or small size were uncommon. In the remaining 37 sporangia the number of small spores did not increase in proportion to the fall in the number of large spores. The number of intermediate spores was, however, increased.

The examples given in the above tables are representative of the entire number of sporangia examined. The conclusion seems justifiable that the small and large sporangia are not chance developments in *Platyzoma*, but constitute well-defined generic features. The small spore is characteristic of the small sporangium; the large spore is typical of the large sporangium. The intermediate spore is an accompaniment of reduced spore-output in both sporangial types. The small and large spores are the dominant types. The spore-output in the small sporangia is typically high, over 80 per cent. of the small sporangia examined having spore-numbers between 29 and 32. The spore-output in the large sporangia is typically low. It has never been seen to exceed 16, but in 70 per cent. of the large sporangia examined it did not fall below 14. These figures suggest that the spore-output per small sporangium is theoretically 32, while that of the large sporangium is 16. It will not be surprising if, when the sporangial development in this fern is known, it is found that the distinctions between large and small sporangia are indicated when the spore-mother cells are formed. The evidence is still insufficient for the determination of the nature of the spores, but the facts now advanced seem to strengthen a belief in the heterosporous nature of *Platyzoma.* As is commonly the case in heterosporous Pteridophytes, the small sporangia are most numerous. But if *Platyzoma* is heterosporous it is probably an upgrade fern type in which segregation of the microsporangia and megasporangia is not yet completed, and in which the megaspores do not declare their female character until they are shed. A point of contrast with the modern heterosporous Lycopods may thus be provided. On the other hand, should sporangial development and spore-germination prove this plant to be homosporous, its anomalous structure and unique position among living Pteridophytes will be accentuated, and a warning provided against the employment of spore-size alone in the determination of the sporangial conditions of fossil forms.

SUMMARY.

In this paper are set down additional facts relating to the mature sporangia and spores of *Platyzoma.* Confirmation is given of the disposition of the sporangia upon the pinnæ, and of the well-marked differences in sporangial and spore size and spore-output already recorded for this fern.

In the absence of knowledge of the sporangial development and spore-germination it has been impossible to determine if *Platyzoma* is truly heterosporous.

The large majority of the sporangia are small, and the spore-output per sporangium in these is approximately 32.

The remaining sporangia are large, and have an approximate spore-output of 16 per sporangium.

The sporangial stalk is typically three-rowed, but four-rowed stalks occur. The annulus is usually irregular, but is interrupted by the stalk.

The small and large spores are the dominant types, and the spores of intermediate size are developed when the spore-output in any sporangium is greatly decreased.

The three types of spore have similar spore-markings. Their walls are thick, and no sign of germination is found in any spore-type while still contained within the sporangium.

The balance of the evidence seems in favour of a heterosporous condition for *Platyzoma.* Should a homosporous condition be demonstrated at a later date, the anomalous condition of this remarkable fern will be further accentuated.

DESCRIPTION OF FIGURES IN THE TEXT.

Fig. 1. Diagram of a fertile pinna of *Platyzoma* seen from below. The margins are very revolute. The sporangia are of variable size, but are *invariably* inserted *terminally* upon the main lateral veins or upon branches of these. × 10.

Fig. 2. Transverse section of the revolute margin of a fertile pinna of *Platyzoma*. × 36.

Fig. 3. Stoma from the under surface of a fertile pinna of *Platyzoma*, and with starch grains in the surrounding epidermal cells. × 36.

Figs. 4, 5, 6. Various views of a small sporangium of *Platyzoma*. × 36. Figs. 4 and 5 show the sizes of the small and intermediate spores relative to the sporangia.

Fig. 7. A small sporangium opened. It shows the three-rowed stalk, and the least irregular annulus observed. × 36.

Figs. 8, 9. A back and a front view of a large sporangium of *Platyzoma*. Fig. 8 shows the size of a large spore relative to the sporangium. × 36.

Figs. 10, 11. Two large sporangia opened. These show the variation in the construction of the stalk, and the conspicuous irregularities in the annulus. × 36.

Fig. 12. A spore of the *smallest* size. × 60.

Fig. 13. A spore of the *intermediate* size. × 60.

Fig. 14. A spore of the *largest* size. × 60.

Fig. 15. Spore-markings on the convex surface of each spore-type. × 90.

Fig. 16. Spore-markings on the flat triangular faces of each spore-type. × 90.

Fig. 17. Transverse section of a large spore of *Platyzoma*. × 60.

The author is indebted to the Carnegie Trust for their assistance in the illustration of this paper.

VIII.—Factorials and Allied Products with their Logarithms. By Frank Robbins, F.R.A.S. *Communicated by* Professor Whittaker.

(MS. received October 10, 1916. Read November 20, 1916. Issued separately October 20, 1917.)

When any one of the following tables has been given in the past to an extent useful at the present time, it will be found by the computer that the necessary volume is only with difficulty accessible and hardly ever to be purchased. That these tables are obviously useful is perhaps all that need be said in justification of their more extended computation.

The first table contains the logarithm (with eighteen decimal places) of factorial n. The limits of n are 1 and 120.

If $\lambda = 2 . 4 . 6 \ldots (2n-2)(2n)$, then in the second table will be found log λ also with eighteen decimal places.

The limits of the argument ($2n$) are 2 and 120.

Similarly, if $\mu = 1 . 3 . 5 \ldots (2n-1)(2n+1)$, the third table gives log μ for values of $(2n+1)$ from 3 to 119.

The connection between these three functions is

$$x\,! = \lambda_x \times \mu_{x-1}$$

when x is even, or

$$x\,! = \lambda_{x-1} \times \mu_x$$

when x is odd.

These relationships were used to test the accuracy of $n!$, which had been obtained in the usual way by continual addition of logs. The agreement obtained step by step was complete, and it may be taken as proving both the accuracy of λ and μ as well as that of the factorial in the unabridged tables.

For example, the last respondent from Table II, when added to the last from Table III, gives

198·82539 38472 19721 542,

in exact agreement with log 120 !, found independently and given in Table I.

These three functions were in the first instance based on logs to fifteen decimal places taken from Houel (1) for the integers from 2 to 100, and from Leonelli (2) for those between 100 and 110. As a check upon these, comparison was made with a table giving eighteen decimal places specially prepared by the aid of Gray (3). When cut down to fifteen places complete agreement was observed between Houel and Leonelli on the one part and Gray on the other, and it was felt that the logs in hand were fit for the purpose in view, and that the only faults of which these three completed tables could be suspected were those unavoidably occurring in the end figures and due to the missing sixteenth place. Towards a forecast of this effect, the not unreasonable assumption was made that on the average the error in one of the fundamental logs would be 2×10^{-16}, but no guess could be made as to the sign of the error, whether plus or minus. Although some compensation might conceivably arise from the balancing of excess and deficit, it seemed clear that towards the end of Tables II and III, where the respondent is the sum of, say, 60 logarithms, some cumulative error must occur. Still more strongly it was felt this would be the case in regard to the closing values in Table I, where log 120 ! is the sum of 119 logarithms. But the result was not as expected. The tables having been completed, Dr CARGILL G. KNOTT was so good as to make a comparison with the treasured MS. tables given to the nation by the daughters of the gifted Dr EDWARD SANG (7). Between expectation and realisation there is always a gap, but here the differences, although on the whole arithmetically smaller than expected, were puzzling. In the case of Table I, for the first forty values of the argument no difference worth mention occurred. From this point differences of two units in the fifteenth place appeared (always + in the sense Sang – Robbins), and growing steadily the difference reached a maximum of 5 for argument 79. Thereafter they decreased more rapidly, becoming 2 at argument 97 and then tailing off to zero at the end of the table.

Another comparison made by myself with the British Museum copy of the very rare Degen (6) fully confirmed Dr KNOTT's report. There was the same exact agreement at both ends of the table, and a maximum of the same magnitude occurred at the same point. Under these circumstances the tables prepared with so much care were abandoned, new foundation stones were dug out of Dr SANG's quarry, and the Tables I, II, and III were rebuilt with twenty-eight decimal places, but cut down on completion to eighteen. Not often perhaps has such a severe pruning been given—it should put the final results above suspicion.

Lastly, sixty values of log 2^n from $n=1$ to $n=60$ were prepared and applied by addition to $n!$, so as to find checks on the sixty values of log λ.

The fourth table contains factorial n as far as $n=50$, and in each case to its full extent. Every care was taken to secure accuracy, and each value was obtained twice, in the first place by pencil and then on an arithmometer.

Further, at short intervals other checks were applied such as—

$$35! = 1190 \times 33! = 1256640 \times 31!$$
$$36! = 2 \times 7 \times 90 \times 34!$$
$$43! = 1806 \times 41!$$
$$45! = 146611080 \times 40!$$
$$48! = 8 \times 6 \times 47! = 3 \times 4 \times 4 \times 47!$$
$$50! = 254251200 \times 40!$$

The table of factorial n was submitted to the following final test.

It is easy to see

$$50! = 2^{47} \,.\, 3^{22} \,.\, 5^{12} \,.\, 7^{8} \,.\, 11^{4} \,.\, 13^{3} \,.\, 17^{2} \,.\, 19^{2} \,.\, 23^{2} \,.\, 29 \,.\, 31 \,.\, 37 \,.\, 41 \,.\, 43 \,.\, 47.$$

These elements were re-grouped so as to produce factors of easy application—

$$
\begin{aligned}
50! &= (23 \,.\, 29 \,.\, 31 \,.\, 37 \,.\, 41 \,.\, 43 \,.\, 47\,) \times 11\,(7^3 \,.\, 11^3 \,.\, 13^3) \\
&\qquad (7^2 \,.\, 17^2)\,(7^3 \,.\, 19^2)\,(2^9 \,.\, 3^5)^2\,(2^6 \,.\, 3^{13})\,2^{11} \,.\, 23 \,.\, 10^{12} \,.\, 1/3 \\
&= 63392725189\,(11033033011)\,(14161)\,(123823)\,(124416)^2\,(102036672)\,(2048)\,23 \,.\, 10^{12} \,.\, 1/3,
\end{aligned}
$$

and the multiplications being done, the extended value of this factorial exactly reproduced the result obtained step by step and so confirmed the whole table—except for compensating errors.

Comparison was made with ZIMMERMANN (4), who stops at 20!.

The last table—the reciprocals to eighty-five decimal places of the factorials—gave me most trouble. Each result, as soon as obtained by division, was checked either by multiplication or by repetition on the arithmometer. Apart from this, the reciprocal of 14! was again produced as the quotient of one by $1001 \times 3^3 \times 4^3 \times 7 \times 8 \times 9 \times 10^2$, and the reciprocal of 20! was found therefrom by a further division by $2^5 \times 3^3 \times 17 \times 19 \times 10^2$. The results agreed to the eighty-seventh decimal.

Other tests applied were such as $25! \times 1/25!$, which would give unity if we could find the reciprocal completely. Assuming my value of $1/25!$ to be too large by 5 in the eighty-seventh place, then multiplication by 25! would give $1 + 775 \times 10^{-64}$. By actual multiplication I obtained $1 + 2 \times 10^{-62}$.

So too by actual multiplication of my values for 40! and $1/40!$ I obtained $1 + 36 \times 10^{-40}$, which indicates an error of no more than 5×10^{-87} in my value of $1/40!$. But I relied most of all on the value of $(e-1)$ given by the casting of these reciprocals. By proceeding to $1/64!$ and including eighty-six decimal places I found

$$
\begin{aligned}
e = 2{\cdot}7182818284590452353602874713526624977572470936999595 \\
74966967627724076630353547594571 3,
\end{aligned}
$$

which is too small by a unit in the eighty-fifth place, as I find by comparison with the value to 137 places given by Dr GLAISHER (5). Lastly, these reciprocals were read with the table to twenty-eight significant places given in the same paper. To save space in the printed page, (m) indicates m cyphers between the decimal point and the first significant figure.

The second and third tables are extensions of some made many years ago to evaluate WALLIS's formula,

$$
\frac{\pi}{2} = \frac{2 \,.\, 2 \,.\, 4 \,.\, 4 \,.\, 6 \,.\, 6 \,.\, 8 \,.\,.\,.}{1 \,.\, 3 \,.\, 3 \,.\, 5 \,.\, 5 \,.\, 7 \,.\, 7 \,.\,.\,.},
$$

a formula of engaging simplicity but of a tediousness quite wearisome if more than a moderate number of decimal places are required. But these tables help here; they also give the coefficients in EULER's formula for $\tan^{-1} t$ and those which occur in $F_1\kappa$ and $E_1\kappa$.

Factorial n and its reciprocal have been included at the suggestion of Professor E. T. WHITTAKER for the benefit of those who, in yearly increasing numbers, realise that an arithmometer—in suitable work—is more speedy than a table of logarithms, and, what is even more important, is less fatiguing to eye and to brain.

Mr J. Abner Sprigge, of H.M. *Nautical Almanac* Office, examined and checked the whole work as at first arranged, and found one wrong figure in log λ and a small error in e at the eighty-fifth decimal. But it is to Dr Cargill G. Knott that special thanks are due, seeing that he gave me access to Dr Sang's standard MS. tables, and by his advice enabled me to finish the work in a satisfactory manner.

REFERENCES.

(1) Houel, J., *Recueil de formules et de tables numeriques*, troisième édition, nouveau tirage, Paris, 1901.

(2) *Supplément logarithmique par Leonelli, à Bordeaux.* An onze. Extrait des Publications de la Société des Bibliophiles de Guyenne, Paris, 1875.

(3) Gray, Peter, *Tables for the formation of Logs and Anti-logs to twenty-four or any less number of places*, London, 1876.

(4) Zimmermann, Dr H., *Rechentafel nebst Sammlung häufig Gebrauchter Zahlenwerthe*, Berlin, 1899.

(5) Glaisher, J. W. L., *Trans. of the Cambridge Philosophical Society*, vol. xiii, 1883, pp. 246, 247, and 252.

(6) Degen, C. F., *Tabularum Enneas*, Copenhagen, 1824.

(7) Sang, Dr Edward, *MS. Tables of Logs of Nat. Nos. to Twenty-eight Decimal Places.*

TABLE I.

LOGARITHMS OF FACTORIAL n TO $n = 120$.

n	Log n !	n	Log n !	n	Log n !
1	0·00000 00000 00000 000	41	49·52442 89248 75606 033	81	120·76321 27413 78242 407
2	0·30102 99956 63981 195	42	51·14767 82152 73506 496	82	122·67702 65937 61959 097
3	0·77815 12503 83643 633	43	52·78114 66708 53093 023	83	124·59610 46861 38033 001
4	1·38021 12417 11606 023	44	54·42459 93473 39280 454	84	126·52038 39721 99914 659
5	2·07918 12460 47624 828	45	56·07781 18611 14624 133	85	128·44980 28979 14207 393
6	2·85733 24964 31268 460	46	57·74056 96927 96198 208	86	130·38430 13491 57775 114
7	3·70243 05364 45525 291	47	59·41266 75507 31915 672	87	132·32382 06017 76393 639
8	4·60552 05234 37468 877	48	61·09390 87881 07502 890	88	134·26830 32739 26562 265
9	5·55976 30328 76793 751	49	62·78410 48681 36016 552	89	136·21769 32805 71475 050
10	6·55976 30328 76793 751	50	64·48307 48724 72035 356	90	138·17193 57900 10799 925
11	7·60115 57180 35018 792	51	66·19064 50485 69971 722	91	140·13097 71823 31893 525
12	8·68033 69640 82643 620	52	67·90664 83922 04770 882	92	142·09476 50096 77448 794
13	9·79428 03163 89480 389	53	69·63092 42618 05559 927	93	144·06324 79582 31383 911
14	10·94040 83520 67718 415	54	71·36331 80216 28528 435	94	146·03637 58118 31082 570
15	12·11649 96111 23399 657	55	73·10368 07111 22772 280	95	148·01409 94171 19930 337
16	13·32061 95937 79324 438	56	74·85186 87381 28972 696	96	149·99637 06501 59498 750
17	14·55106 85151 57598 366	57	76·60774 35938 01464 095	97	151·98314 23844 25743 602
18	15·80634 10202 60904 436	58	78·37117 15873 64401 378	98	153·97436 84601 18238 459
19	17·08509 46212 13733 398	59	80·14202 35990 06545 568	99	155·97000 36547 15788 374
20	18·38612 46168 77714 593	60	81·92017 48493 90189 201	100	157·97000 36547 15788 374
21	19·70834 39116 11633 861	61	83·70550 46844 00956 234	101	159·97432 50284 98430 948
22	21·05076 65924 33840 097	62	85·49789 63738 99210 109	102	161·98292 52002 60348 509
23	22·41249 44284 51432 976	63	87·29723 69233 52791 815	103	163·99576 24249 65520 714
24	23·79270 56701 63038 999	64	89·10341 68973 36678 986	104	166·01279 57642 64301 069
25	25·19064 56788 35076 608	65	90·91633 02539 79534 560	105	168·03398 50633 34239 142
26	26·60561 90268 05894 573	66	92·73587 41895 21403 233	106	170·05929 09285 99009 383
27	28·03698 27909 64881 884	67	94·56194 89922 22229 667	107	172·08867 47062 84219 024
28	29·48414 08223 07101 106	68	96·39445 79049 28465 986	108	174·12209 84617 71168 726
29	30·94653 88202 06057 193	69	98·23330 69956 65721 302	109	176·15952 49597 11792 361
30	32·42366 00749 25719 630	70	100·07840 50356 79978 133	110	178·20091 76448 70017 402
31	33·91502 17687 59992 310	71	101·92966 33843 99053 419	111	180·24624 06236 56674 836
32	35·42017 17470 79898 286	72	103·78699 58808 30321 879	112	182·29545 86463 26856 448
33	36·93868 56869 57785 764	73	105·65031 87409 50777 781	113	184·34853 70898 10276 170
34	38·47016 46040 00040 888	74	107·51955 04606 81753 973	114	186·40544 19411 46748 765
35	40·01423 26483 50316 523	75	109·39461 17240 73454 019	115	188·46613 97815 00360 448
36	41·57053 51491 17603 788	76	111·27542 53163 54245 371	116	190·53059 77707 27278 926
37	43·13873 68731 84598 785	77	113·16191 60415 26727 243	117	192·59878 36324 73440 570
38	44·71852 04698 01408 942	78	115·05401 06442 17207 645	118	194·67066 56397 79565 955
39	46·30958 50768 27908 148	79	116·95163 77355 07649 073	119	196·74621 26011 72096 714
40	47·91164 50681 55870 539	80	118·85472 77224 99592 658	120	198·82539 38472 19721 542

TABLE II.

LOGARITHMS OF λ WHERE $\lambda = 2 . 4 . 6 . . . (2n)$.

$2n$	Log λ	$2n$	Log λ	$2n$	Log λ
2	0·30102 99956 63981 195	42	26·02997 38205 55238 960	82	61·86665 87470 98835 037
4	0·90308 99869 91943 586	44	27·67342 64970 41426 391	84	63·79093 80331 60716 695
6	1·68124 12373 75587 218	46	29·33618 43287 23000 466	86	65·72543 64844 04284 417
8	2·58433 12243 67530 804	48	31·01742 55660 98587 684	88	67·66991 91565 54453 043
10	3·58433 12243 67530 804	50	32 71639 55704 34606 489	90	69·62416 16659 93777 918
12	4·66351 24704 15155 632	52	34·43239 89140 69405 648	92	71·58794 94933 39333 187
14	5·80964 05060 93393 657	54	36·16479 26738 92374 155	94	73·56107 73469 39031 847
16	7·01376 04887 49318 438	56	37·91298 07008 98574 572	96	75·54334 85799 78600 260
18	8·26903 29938 52624 508	58	39·67640 86944 61511 854	98	77·53457 46556 71095 117
20	9·57006 29895 16605 703	60	41·45455 99448 45155 487	100	79·53457 46556 71095 117
22	10·91248 56703 38811 939	62	43·24695 16343 43409 362	102	81·54317 48274 33012 678
24	12·29269 69120 50417 962	64	45·05313 16083 27296 533	104	83·56020 81667 31793 033
26	13·70767 02600 21235 927	66	46·87267 55438 69165 206	106	85·58551 40319 96563 274
28	15·15482 82913 63455 148	68	48·70518 44565 75401 525	108	87·61893 77874 83512 976
30	16·63194 95460 83117 585	70	50·55028 24965 89658 356	110	89·66033 04726 41738 017
32	18·13709 95244 03023 561	72	52·40761 49930 20926 816	112	91·70954 84953 11919 628
34	19·66857 84414 45278 685	74	54·27684 67127 51903 008	114	93·76645 33466 48392 222
36	21·22488 09422 12565 950	76	56·15766 03050 32694 360	116	95·83091 13358 75310 700
38	22·80466 45388 29376 107	78	58·04975 49077 23174 762	118	97·90279 33431 81436 086
40	24·40672 45301 57338 497	80	59·95284 48947 15118 347	120	99·98197 45892 29060 913

TABLE III.

LOGARITHMS OF μ WHERE $\mu = 1 . 3 . 5 . . . (2n + 1)$.

$2n+1$	Log μ	$2n+1$	Log μ	$2n+1$	Log μ
3	0·47712 12547 19662 437	41	25·11770 43947 18267 536	81	60·81036 78466 63124 060
5	1·17609 12590 55681 242	43	26·75117 28502 97854 063	83	62·72944 59390 39197 964
7	2·02118 92990 69938 073	45	28·40438 53640 73197 742	85	64·65886 48647 53490 697
9	2·97543 18085 09262 947	47	30·07648 32220 08915 206	87	66·59838 41173 72109 222
		49	31·76667 93020 37428 868	89	68·54777 41240 17022 007
11	4·01682 44936 67487 988	51	33·47424 94781 35365 234	91	70·50681 55163 38115 607
13	5·13076 78459 74324 757	53	35·19852 53477 36154 279	93	72·47529 84648 92050 723
15	6·30685 91050 30005 999	55	36·93888 80372 30398 125	95	74·45302 20701 80898 490
17	7·53730 80264 08279 928	57	38·69476 28929 02889 524	97	76·43979 38044 47143 342
19	8·81606 16273 61108 889	59	40·46561 49045 45033 714	99	78·43542 89990 44693 257
21	10·13828 09220 95028 158	61	42·25094 47395 55800 748	101	80·43975 03728 27335 831
23	11·50000 87581 12621 036	63	44·05028 52890 09382 453	103	82·45258 75975 32508 036
25	12·89794 87667 84658 646	65	45·86319 86456 52238 027	105	84·47377 68966 02446 109
27	14·32931 25309 43645 958	67	47·68927 34483 53064 461	107	86·50316 06742 87655 750
29	15·79171 05288 42602 045	69	49·52812 25390 90319 777	109	88·54058 71722 28279 385
31	17·28307 22226 76874 725	71	51·37938 08878 09395 063	111	90·58591 01510 14936 819
33	18·80158 61625 54762 203	73	53·24270 37479 29850 965	113	92·63898 85944 98356 542
35	20·34565 42069 05037 838	75	55·11776 50113 21551 011	115	94·69968 64348 51968 226
37	21·91385 59309 72032 835	77	57·00425 57364 94032 883	117	96·76787 22965 98129 870
39	23·50492 05379 98532 042	79	58·90188 28277 84474 311	119	98·84341 92579 90660 629

Table IV.

n	Factorials $n\,!$ to $n = 50$.
1	1
2	2
3	6
4	24
5	120
6	720
7	5040
8	40320
9	36288 0
10	36288 00
11	39916 800
12	47900 1600
13	62270 20800
14	87178 29120 0
15	13076 74368 000
16	20922 78988 8000
17	35568 74280 96000
18	64023 73705 72800 0
19	12164 51004 08832 000
20	24329 02008 17664 0000
21	51090 94217 17094 40000
22	11240 00727 77760 76800 00
23	25852 01673 88849 76640 000
24	62044 84017 33239 43936 0000
25	15511 21004 33309 85984 00000 0
26	40329 14611 26605 63558 40000 00
27	10888 86945 04183 52160 76800 0000
28	30488 83446 11713 86050 15040 00000
29	88417 61993 73970 19545 43616 00000 0
30	26525 28598 12191 05863 63084 80000 000
31	82228 38654 17792 28177 25562 88000 0000
32	26313 08369 33693 53016 72180 12160 00000 0
33	86833 17618 81188 64955 18194 40128 00000 00
34	29523 27990 39604 14084 76186 09643 52000 0000
35	10333 14796 63861 44929 66665 13375 23200 00000 0
36	37199 33267 89901 21746 79994 48150 83520 00000 00
37	13763 75309 12263 45046 31597 95815 80902 40000 0000
38	52302 26174 66601 11176 00072 24100 07429 12000 00000
39	20397 88208 11974 43358 64028 17399 02897 35680 00000 00
40	81591 52832 47897 73434 56112 69596 11589 42720 00000 000
41	33452 52661 31638 07108 17006 20534 40751 66515 20000 00000
42	14050 06117 75287 98985 43142 60624 45115 69936 38400 00000 00
43	60415 26306 33738 35637 35513 20685 13997 50726 45120 00000 000
44	26582 71574 78844 87680 43625 81101 46158 90319 63852 80000 00000
45	11962 22208 65480 19456 19631 61495 65771 50643 83733 76000 00000 00
46	55026 22159 81208 89498 50305 42880 02548 92961 65175 29600 00000 000
47	25862 32415 11168 18064 29643 55153 61197 99691 97632 38912 00000 00000
48	12413 91559 25360 72670 86228 90473 73375 03852 14863 54677 76000 00000 00
49	60828 18640 34267 56087 22521 63321 29537 68875 52831 37921 02400 00000 000
50	30414 09320 17133 78043 61260 81660 64768 84437 76415 68960 51200 00000 00000

TABLE V.

n	RECIPROCALS OF FACTORIALS, $1/(n!)$ TO $n=61$.
1	1
2	0·5
3	0·1$\dot{6}$
4	0·041$\dot{6}$
5	0·008$\dot{3}$
6	0·0013$\dot{8}$
7	0·0 001$\dot{9}$8 412$\dot{6}$
8	0·0 00024 8$\dot{0}$158 7$\dot{3}$
9	0·0 00002 7$\dot{5}$573 19223 98589 065$\dot{2}$
10	0·0 00000 27$\dot{5}$57 31922 39858 9065$\dot{2}$
11	0·00 00000 2$\dot{5}$052 10838 54417 187$\dot{7}$
12	0· (8) 20 $\dot{8}$7675 69878 68098 97921 00903 21201 43231 25434 23654 53476 564$\dot{5}$
13	0· (9) 1$\dot{6}$ 05904 38368 21614 59939 23771 70154 94793 27257 10503 48828 12$\dot{6}$
14	0·(10) 11 47074 55977 29724 71385 16979 78682 10566 62326 50359 63448 66186 13602 74058 68675 710
15	0·(12) 76 47163 73181 98164 75901 13198 57880 70444 15510 02397 56324 41240 90684 93724 57838 1
16	0·(13) 47 79477 33238 73852 97438 20749 11175 44027 59693 76498 47702 75775 56678 08577 86149
17	0·(14) 28 11457 25434 55207 63198 94558 30103 20016 23349 27352 04531 03397 39222 40339 9185
18	0·(15) 15 61920 69685 86226 46221 63643 50057 33342 35194 04084 46961 68554 10679 11299 955
19	0·(17) 82 20635 24662 43297 16955 98123 68722 80749 22073 89918 26114 13442 66732 17368 2
20	0·(18) 41 10317 62331 21648 58477 99061 84361 40374 61036 94959 13057 06721 33366 08684
21	0·(19) 19 57294 10633 91261 23084 75743 73505 43035 52874 73790 06217 65105 39698 1366
22	0·(21) 88 96791 39245 05732 86748 89744 25024 68343 31248 80863 91898 41388 16809 71
23	0·(22) 38 68170 17063 06840 37716 91193 15228 12323 17934 26462 57347 13647 02960 7
24	0·(23) 16 11737 57109 61183 49048 71330 48011 71801 32472 61026 07227 97352 92900
25	0·(25) 64 46950 28438 44733 96194 85321 92046 87205 29890 44104 28911 89411 716
26	0·(26) 24 79596 26322 47974 60074 94354 58479 56617 42265 55424 72658 42081 43
27	0·(28) 91 83689 86379 55461 48425 71683 64739 13397 86168 71943 43179 33635
28	0·(29) 32 79889 23706 98379 10152 04172 73121 11927 80774 54265 51135 4773
29	0·(30) 11 30996 28864 47716 93155 87645 76938 31699 24405 01470 86598 440
30	0·(32) 37 69987 62881 59056 43852 92152 56461 05664 14683 38236 21994 8
31	0·(33) 12 16125 04155 35179 49629 97468 56922 92149 72478 51043 94192
32	0·(35) 38 00390 75485 47435 92593 67089 27884 12967 88995 34512 319
33	0·(36) 11 51633 56207 71950 28058 68814 93298 22111 48180 40761 31
34	0·(38) 33 87157 53552 11618 47231 43573 33230 06210 24060 02239
35	0·(40) 96 77592 95863 18909 92089 81638 09228 74886 40171 493
36	0·(41) 26 88220 26628 66363 86691 61566 13674 65246 22269 86
37	0·(43) 72 65460 17915 30713 15382 74503 07228 79043 84513
38	0·(44) 19 11963 20504 02819 25100 72237 65060 20801 0119
39	0·(46) 49 02469 75651 35433 97694 15993 97590 27694 90
40	0·(47) 12 25617 43912 83858 49423 53998 49397 56923 7
41	0·(49) 29 89310 82714 24045 10789 12191 44872 1201
42	0·(51) 71 17406 73129 14393 11402 67122 49695 52
43	0·(52) 16 55210 86774 21951 88698 29563 37138 5
44	0·(54) 37 61842 88123 22617 92496 12644 0259
45	0·(56) 83 59650 84718 28039 83324 72542 28
46	0·(57) 18 17315 40156 14791 26809 72291 8
47	0·(59) 38 66628 51396 05938 86829 1977
48	0·(61) 80 55476 07075 12372 64227 50
49	0·(62) 16 43974 70831 65790 33515 8
50	0·(64) 32 87949 41663 31580 6703
51	0·(66) 64 46959 64045 71726 80
52	0·(67) 12 39799 93085 71485 9
53	0·(69) 23 39245 15256 0658
54	0·(71) 43 31935 46770 49
55	0·(73) 78 76246 30492
56	0·(74) 14 06472 5544
57	0·(76) 24 67495 71
58	0·(78) 42 54303
59	0·(80) 72 107
60	0·(81) 12 02
61	0·(83) 20

IX.—The Highland Border Rocks of the Aberfoyle District. By Professor T. J. Jehu and Dr Robert Campbell. (With Six Plates and Ten Text-figures.)

(Read June 4, 1917. MS. received September 10, 1917. Issued separately December 4, 1917.)

CONTENTS.

I. INTRODUCTION.

The South-Eastern Highlands are made up of metamorphic rocks chiefly of sedimentary but partly also of igneous origin, all of which have been included by Sir ARCHIBALD GEIKIE under the term "Dalradian." These rocks have been divided into bands, which can be traced more or less continuously across Scotland from north-east to south-west. There is an apparent order of superposition, and in Perthshire the groups or bands are arranged in what looks like an ascending order from the Highland Boundary Fault northwards.

The age of the Dalradian sediments is still an unsolved problem, and great uncertainty prevails regarding the true original sequence and the tectonics of the various rock groups. It is possible and even probable that in the Dalradian Series we have rock groups belonging to different geological periods, though all have been affected by a common system of folding.

Along the southern margin of the Dalradian area, immediately adjoining the Highland Boundary Fault, a group of rocks can be traced as an interrupted belt from Stonehaven to Arran, and this belt reappears in the same geological position, but on a more extensive scale, in Ireland. It consists of grits, shales, limestone, cherts or jaspers and cherty shales, graphitic shales, and various igneous rocks sometimes highly altered. This group of rocks is usually designated "The Highland Border Rocks."

II. REVIEW OF PREVIOUS WORK.

The literature on the Highland rocks is so extensive that it is impossible within the limits of this paper to enumerate all the references to the series with which we are immediately concerned. It will suffice to state that in the earlier communications and maps the Highland Border Rocks are taken as forming a part of the metamorphic complex of the Southern Highlands, though it is often recognised that for the most part they are not so much altered as those occurring to the north. We shall note only some of the more important publications which have a direct bearing on the series under consideration.

Professor JAMES NICOL in his *Guide to the Geology of Scotland* (1844) noted the close resemblance of some of the Highland Rocks to the Silurian strata in the south of Scotland, and in a subsequent paper communicated to the Geological Society of London in 1849, referring to the band of clay-slate extending from Stonehaven to Arran, he says, "this band of slate may form the continuation of the Silurian beds on the south, rising up on the other side of the synclinal valley in which the Carboniferous strata of Scotland have been deposited."*

In 1863 NICOL in a paper "On the Geological Structure of the Southern Grampians"† described a series of sections traversing the southern margin of the Highlands at various places from Bute north-eastwards to Forfarshire. In the south-west of Scotland the grits and shales on the southern margin of the Highlands are shown to be dipping towards the south-east and to overlie the rocks to the north; immediately to the east of Loch Lomond these beds dip at angles approaching the vertical, and from the Pass of Leny and Callander north-eastwards the dip is to the north-west, and so the beds appear to pass under the rocks of the Highlands to the north. He expressed the belief that the normal sequence is that seen in Bute, and that as the marginal belt is followed north-eastwards a reversion of the strata takes place. Though he does not refer specifically to the rocks in the Aberfoyle district, it is obvious that he regards the apparent dip of these rocks under the more metamorphosed rocks to the north as abnormal.

In this paper NICOL concludes that the rocks of the Southern Highlands are in the main more ancient than those in the South of Scotland, but he expressly notes the unaltered character of some of the rocks of the marginal belt, for, in referring to the section at Leny Old Lime Quarry, Callander, he remarks that "both the texture and colour of the limestone, and the black carbonaceous-looking shales associated with it, remind us rather of the Carboniferous formations than of a primary deposit."‡

In 1891 Sir ARCHIBALD GEIKIE in his Presidential Address to the Geological Society of London§ gives a table showing in the apparent descending order the various subdivisions of the rocks in the Highlands of Perthshire recognised by members of the Geological Survey. The group which we now term the Highland Border Rocks is placed as the base of the column underlying, and so presumably older than, all the other formations.

In the *Annual Reports of the Geological Survey* from 1893 onwards we find valuable summaries of the work carried on along this marginal belt of rocks. The

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* *Quart. Journ. Geol. Soc.*, vol. vi, p. 60, 1850.

† *Ibid.*, vol. xix, p. 180, 1863.

‡ *Ibid.*, p. 187.

§ *Ibid.*, vol. xlvii, p. 74, 1891.

Report for 1893 states that though these rocks had been mapped for many miles, no clue as to their age had yet been obtained. During that year Mr J. R. DAKYNS in the Aberfoyle district and Mr GEORGE BARROW in Forfarshire and Kincardineshire had noted the occurrence of graphitic schists associated with cherts and green igneous rocks. Mr PEACH detected *Radiolaria* in some of the cherts. Messrs PEACH and HORNE were struck with the close resemblance in lithological characters and general sequence of these Border Rocks with the Lower Silurian Series in the Southern Uplands of Scotland. "The association of a zone of green basic eruptive rock with the graphitic schist and red and black radiolaria-bearing cherts, so exactly a counterpart of the Arenig succession in the South of Scotland, affords a strong presumption that Lower Silurian rocks are included along the Highland Border." *

In the Aberfoyle area Mr DAKYNS noted that the zone of black shales and cherts was associated with bands of greywacke, sandstones, and hornblende schists. It is further stated that "these strata along their northern margin are apparently (but perhaps deceptively) overlain by a group of massive greywackes, sometimes pebbly, with occasional bands of purple slate." †

The exposures in Forfarshire and Kincardineshire were described more fully by Mr BARROW in a paper contributed to the Geological Society of London in 1903,‡ and again in the *Proceedings of the Geologists Association* for the year 1912. He arranges the rocks in two divisions: 1. The Jasper and Green Rock Series; 2. The Margie Series, resting unconformably upon the former. He holds that everywhere these Highland Border Rocks are separated from the rocks to the north by a plane of overthrust, and that while in the Highland Rocks all traces of clastic micas have disappeared, in the Border Rocks the original sedimentary micas can still be detected under the microscope.

It is understood that Mr BARROW now regards these Highland Border Rocks as pre-Cambrian in age though younger than the Highland Schists. §

The *Annual Report of the Geological Survey* for 1895 || gives a brief account of Mr CLOUGH's work along the belt between Aberfoyle and Loch Lomond. It states that "notwithstanding his detailed mapping we are still unable to form a definite conclusion as to the structure of this difficult piece of ground." With some hesitation Mr CLOUGH inclined to the belief that there are indications of a stratigraphical break between the black shales and cherts and what are termed "the Aberfoyle Grits," which apparently include grits associated with the Border Rocks as well as what are now called Leny Grits. It is even suggested in the Report that "the Aberfoyle Grits" might be grouped with the shales and cherts as probably of Lower Silurian age, though it is admitted that this would only shift the difficulty

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* *Annual Report Geol. Survey* for 1893, p. 266.

† *Ibid.*

‡ BARROW, "On the Occurrence of Silurian (?) Rocks in Forfarshire and Kincardineshire along the Eastern Border of the Highlands," *Quart. Journ. Geol. Soc.*, vol. lvii, p. 328, 1901.

§ GREGORY, "Problems of the South-western Highlands," *Trans. Geol. Soc. Glasgow*, vol. xiv, pt. 1, p. 15, 1910.

|| *Ann. Rep. Geol. Survey* for 1895, p. 26.

further north, "for we should still have to find somewhere a southern line of demarcation for the schistose rocks of the Highlands."

The same difficulty in separating the presumably Lower Silurian belt from the grits and slates of the Highland Series was found by Mr CLOUGH in the mapping of the exposures in the Callander district.*

The results of the survey of the Highland Border Rocks from Loch Lomond to Callander by Messrs DAKYNS and CLOUGH are shown on the Geological Survey map (scale one-inch to a mile), Sheet 38. The provisional correlation of these rocks with the Lower Silurian rocks of the Southern Uplands by Messrs PEACH and HORNE led to their being marked on the Survey maps as doubtfully Silurian. The doubt arose from the fact that the evidence then obtained was not regarded as sufficient to prove the correlation. The junction between the Border Rocks and the Leny Grits to the north is marked by a discontinuous line indicating an uncertain boundary.† Similar discontinuous lines are shown on the map separating various members of the Highland Border Group and running in the direction of the strike of the rocks.

A strip of rocks in North Glen Sannox, Arran, has been mapped and described by Mr W. GUNN as "Arenig" (?). This strip is shown on the Geological Survey map (scale one-inch to a mile), Sheet 21, and the description is given in the Survey Memoir on "The Geology of North Arran, South Bute, and the Cumbraes" (1903). The group consists of igneous rocks, both volcanic and intrusive, associated with black shales and thin bands of chert. In the neighbourhood of Scalpsie Bay in Bute exposures of epidiorite passing into hornblende schist and of serpentine are recorded as representing intrusions probably of Arenig age.

In a paper, entitled "The Lower Old Red Sandstone Rocks of the Balmaha-Aberfoyle Region," communicated to the Edinburgh Geological Society in 1902,‡ Mr ALEX. DU TOIT discusses the origin of the gabbro-serpentine-dolomite complex which occurs along the line of the Highland Boundary Fault and the jaspery zone which can be traced along a branch of that fault further north-west. The gabbro-serpentine-dolomite belt is regarded as being made up of crystalline igneous, pyroclastic, and sedimentary material, much altered by dolomitisation and silicification. The serpentine and gabbro originally formed part of a plutonic mass earlier than the Lower Old Red Sandstone. The jasper belt has undergone a similar series of changes, the original serpentine having been changed into a sheared rock, in which carbonates and silicates of lime and magnesia predominated, and subsequently the calcareous matter was replaced by silica stained with ferric oxide.

Mr PETER MACNAIR in his volumes on *The Geology and Scenery of the Grampians* (1908) maintains that the Highland Border Rocks form an integral part of the Highland Schist Series, and he places the group at the base of that series.§

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* *Ann. Rep. Geol. Survey* for 1896, p. 28.

† For Dr CLOUGH'S views on this boundary line see p. 209.

‡ *Trans. Edin. Geol. Soc.*, vol. viii, pt. 3, p. 315, 1905.

§ *The Geology and Scenery of the Grampians*, vol. i, pp. 41 and 194, 1908.

Professor J. W. GREGORY in a Presidential Address to the Geological Society of Glasgow, 1910, on "The Problems of the South-Western Highlands," discusses the age, origin, and relations of the Border Rocks. While admitting the uncertainty that prevails, he puts forward the view that "they are either the uppermost part of the series which includes the Aberfoyle slates and grits, or a younger series, separated from the Aberfoyle Series by a still doubtful unconformity and by the absence of cherts from the Aberfoyle Series." *

Some of the bedded rocks of this marginal belt are so little altered that it was expected that a careful search would eventually result in the discovery of fossils, and so shed fresh light on the question of their age. This expectation was fulfilled, and in 1911 Dr CAMPBELL recorded the presence of brachiopods, phyllocarid crustaceans, and worm-like tubes in cherty shales and jaspers which he found associated with spilitic lavas at Stonehaven immediately south of the Highland Boundary Fault. †

In the following year a somewhat similar suite of fossils was found by Dr JEHU in cherty beds belonging to the Border Rocks near Aberfoyle, but here the belt lies on the north-west side of the Highland Boundary Fault. ‡ Subsequently a graptolitic form was recognised amongst the collection of fossils obtained at Aberfoyle, and a description of that form by Miss GERTRUDE ELLES is given in a paper by Dr JEHU on "The Highland Border Series, near Aberfoyle," which appeared in the *Geological Magazine* in 1914. These discoveries at Stonehaven and Aberfoyle afforded strong evidence for the Upper Cambrian or Lower Ordovician age of the Black Shale and Chert Series.

III. GENERAL ACCOUNT OF THE STRATIGRAPHY OF THE HIGHLAND BORDER ROCKS.

The Highland Border Rocks in the Aberfoyle district emerge from under a covering of Upper Old Red Sandstone due north of Gualann, and extend in a north-easterly direction for seven miles to a distance of a mile north-east of the village of Aberfoyle. They form a belt of narrow but varying width between the Lower Old Red Sandstone on the south-east and the Leny Grits on the north-west. The belt is widest near Gualann, where the width exposed is about half a mile; as traced north-eastwards it narrows, until between Arndrum and Dungarrow it is reduced to little over 100 yards, after which it swells out to from 300 to 400 yards, narrowing a little again as we approach the village, where it is lost under alluvium. North-east of Aberfoyle the belt is extremely narrow (under 100 yards), and it disappears just beyond the old limestone quarry above Upper Dounans.

The junction with the Leny Grits appears to be everywhere a line of dislocation; that with the main area of the Lower Old Red Sandstone is again a fault—the Highland Boundary Fault—but in the western part of the belt, beds belonging to that formation have been faulted down to the north-west of the main boundary.

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* *Trans Geol. Soc. Glasgow*, vol. xiv, pt. 1, p. 16, 1910.

† *Geol. Mag.*, dec. v, vol. viii, p. 63, 1911; *Trans. Roy. Soc. Edin.*, vol. xlviii, pt. 4, No. 34, p. 927, 1913.

‡ *Nature*, vol. lxxxix, p. 347, 1912; *Rep. Brit. Assoc.*, p. 463, 1912.

The Highland Border Rocks include (*a*) a series of black and grey shales, cherts and cherty mudstones, with which are associated both volcanic and intrusive igneous rocks, and which are overlaid unconformably by (*b*) a series of grits and shales with calcareous bands. The general strike of the beds is north-east and south-west, the general dip to the north-west at high angles. The beds are often seen to be isoclinally folded along nearly vertical axial planes (Plate V, fig. 3). The whole belt is affected by crush lines, extending usually in the direction of the general strike of the beds.

The Lower or Black Shale and Chert Series is made up of cherts, cherty shales, black and grey shales, and mudstones passing downwards into and interbedded with volcanic rocks of the spilitic type. The associated intrusive rocks include albite diabase, albite gabbro, and serpentine. Here may be included also a belt of highly metamorphosed rocks—hornblende schists, chlorite schists, and quartz schists, representing respectively the intrusive igneous rocks, the lavas, and the siliceous sediments.

The Upper Series, which may be termed the Margie Series,* consists of grits, shales, and limestone, and has a remarkable breccia at its base. The breccia is often richly charged with fragments of vesicular volcanic rock, a fact which points to a recrudescence of volcanic activity in the district at the time when the basement beds of the Upper Series were being deposited.

For convenience of description detailed accounts of the above succession will be given in the following order:—

(*a*) The Rocks of the Lower or Black Shale and Chert Series.
(*b*) The Rocks of the Upper or Margie Series.
(*c*) Palæontology of the Beds.
(*d*) The Age of the Highland Border Rocks.
(*e*) The Intrusive Igneous Rocks.
(*f*) The Hornblende-Schist Complex and Associated Sediments.

IV. The Rocks of the Lower or Black Shale and Chert Series.

The Spilitic Lavas.—The spilitic lavas, which are the lowest visible members of the series, are exposed at the surface only in that part of the area which lies to the south-west of the Kelty Water. The best exposures occur in the upper course of the Corrie Burn, and in and near the most westerly of the two small tributary streams flowing down the eastern slope of Gualann. Other exposures are seen in the two small tributaries which join the Corrie Burn from the north-west. The spilites appear again at the surface in several rather poor exposures on the slopes of the hill north-west of a small tarn which is a noteworthy feature in the landscape just west of the new Loch Katrine aqueduct.

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* The term "Margie" has been applied to the Upper Series in Kincardineshire and Forfarshire by Mr Barrow, See *Quart. Journ. Geol. Soc.*, vol. lvii, p. 328, 1901.

The spilites are green, compact, non-porphyritic rocks, occasionally vesicular, and sometimes veined with yellow epidote. Pillow structure has not been observed, owing perhaps to the unsatisfactory character of the exposures, but the usual association with chert has been noted. The rocks are sometimes shattered and broken, and the specimens from Gualann exhibit frequently a well-marked flaser structure.

In thin section all the spilites are seen to be highly altered, and in the majority of the specimens examined the characters of the original minerals are quite undeterminable. The outlines, however, of some of the constituents (notably the felspars) are still discernible, and the igneous texture is clear. The felspar of the freshest specimens is albite; the ferro-magnesian minerals are completely decomposed, and are represented by secondary chlorite and carbonates. Many of the rocks consist entirely of secondary minerals—chlorite, quartz, carbonates, colourless micas, epidote, and iron oxides. An exceptionally fresh spilite from Gualann exhibits good variolitic structure (Plate III, fig. 1); other examples show good fluidal arrangement of felspar laths; only rarely are the rocks micro-porphyritic, with small phenocrysts of felspar. Amygdales of the vesicular varieties consist of quartz and chlorite; they are small, and usually almost circular in section.

In their mineral composition and texture and in their association with siliceous sediments the spilites resemble the green basic lavas associated with the Cambrian and Ordovician formations elsewhere in Britain. Spilites have already been described from Arran * in the west and from the Forfarshire-Kincardineshire † area in the extreme east, and their recognition in the Aberfoyle district adds another link to the chain of lithological evidence which has been used to correlate the various separated areas that make up the belt of Highland Border Rocks.

The Cherts and Shales.—The spilites are overlaid by a group of compact, fine-grained, fossiliferous sediments consisting of grey cherts and black carbonaceous shales, usually intimately associated, grey cherty shales, and mudstones. Every gradation is found between hard almost pure cherts on the one hand, and soft mudstones and shales on the other. The cherts are often finely banded, with alternating darker and lighter coloured laminæ, the thickness of which frequently shows a rapid variation even within the limits of a hand specimen, but is usually $\frac{1}{4}$ inch or less. Breccias of angular chert fragments set in a matrix of black shale are of common occurrence along crush lines. The cherty shales often show an imperfect cleavage rudely parallel with the bedding planes, and this feature is particularly well marked in the belt of cherty shales adjoining the Leny Grits. The sediments of this series are often traversed by minute veinlets of quartz, chalcedony, pyrites, and carbonates.

In thin section the cherts are seen to consist almost entirely of chalcedonic silica in a finely granular condition, throughout which is irregularly distributed opaque

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* *Mem. Geol. Survey: The Geology of North Arran*, etc., pp. 18–21, 1903.

† *Trans. Roy. Soc. Edin.*, vol. xlviii, p. 926, 1913.

black and greyish amorphous material, probably carbonaceous and ferruginous. Conspicuous also are circular and oval areas of chalcedony, representing doubtless casts of radiolaria. The "lattice-structure" of the radiolaria is not seen in thin section, but may often be detected in hand specimens (Plate I, fig. 13). Pyrites in nodular form may sometimes be observed, and with high powers minute flakes of authigenous mica and thin needles of rutile are seen to occur sporadically. Clastic terrigenous material is absent. The typical cherty mudstones and shales have as their chief constituents small, colourless, authigenous micas, and granular, finely crystalline or crypto-crystalline chalcedony. They are invariably crowded with tiny, brownish, hair-like needles of rutile. Pyrites in small cubes and nodules and irregular patches of carbonates also occur. Radiolaria are less conspicuous than in the cherts. Mudstones and shales with little or no free silica are of infrequent occurrence. Like the cherty mudstones, they are crowded with rutile needles. Their distinctive character lies in the presence of a fairly large proportion of recognisable clastic material in the shape of grains of quartz, muscovite, and zircon. The dominant sediments are the black shales and the cherty shales and mudstones. The cherts are characterised by their richness in radiolaria, and by the absence of terrigenous material; the more muddy types by the comparative scarcity of radiolaria, by the abundance of rutile needles, by the occasional presence of clastic grains, and in the case of the black shales by the abundance of carbonaceous matter. Most of the mica, the rutile, and the chlorite are doubtless in every case authigenous. The pure cherts evidently represent radiolarian oozes which accumulated under clear-water conditions; the interbedded spilites are the product of contemporaneous submarine volcanic eruptions, and the cherty shales and mudstones bespeak deposition at or near the margin of an area of terrigenous sedimentation.

V. The Rocks of the Upper or Margie Series.

The rocks of the Margie Series are sharply contrasted with those of the underlying Black Shale and Chert Series. Grits form the dominant type of sediment, and the shales which, in the Aberfoyle area, are relatively unimportant, are accompanied by limestone, never by cherts or cherty shales and mudstones.

The Basement Breccia.—At the base of the series occurs a remarkable breccia, best seen in the neighbourhood of Clashbeg Wood, but exposed also to the west of the Bofrishlie Burn fossil locality, again near a small stream about 300 yards north-east of the ruins of Bofrishlie Farm, and also about one-third of a mile further east midway between Kirkton Hill and the Pow. In the western part of the area it appears along the southern margin of the first spilite outcrop to the west of the Kelty Water. It is found as the basement member of the series on both sides of the ridge formed by the underlying black shales and cherts (see Map, Plate VI).

The most striking feature in the breccia at Clashbeg Wood is the presence of numerous large angular fragments of cherty shales, identical in character with certain shales of the underlying series. Blocks as large as 3 feet by 1½ feet have been noted (see Plate V, fig. 4). Apart from the above exceptionally large fragments, the chief constituents of the breccia are vesicular palagonite, quartz, and smaller pieces of cherty mudstones and shales.

The dominant material in nearly all the specimens is the palagonite, which occurs in fragments, the irregular shape of which has been determined by the fracturing of numerous vesicles and the consequent production of concave embayments on the margin of the grains (Plate III, fig. 2). The largest pieces are several millimetres in diameter, and all gradations are found down to minute particles showing characteristic "ashen structur." The palagonite is pale brown to greenish-grey in transmitted light, greyish-white in reflected light. The vesicles are infilled most frequently with green chlorite, less often with quartz and chalcedony, alone or in association with scaly chlorite. The glass has undergone complete alteration, and the only indication of the former presence of crystals is the occurrence of "shapes" of felspar microlites.

The fragments of sedimentary rocks show little variation in character. For the most part they are grey, greyish-black, and black shales and mudstones richly charged with rutile needles, and recalling at once the sediments of the Black Shale and Chert Series. Large blocks with thick white weathered crust are of the same type as the muddy radiolarian chert of the underlying series; they resemble also the Glenkiln Flints * of the Southern Uplands. In thin section they show the characteristic "shapes," indicative of the presence of radiolarian tests as well as rhombs of ferrous carbonate.

Quartz grains are always numerous, and in some specimens bulk quite as largely as the palagonite and sediments. They are often black in colour, and usually contain the inclusions characteristic of the quartz of granite rocks. A considerable proportion exhibit a unique type of recrystallisation, the origin of which is uncertain. Small separated portions, more or less circular, polarise differently from the quartz grain as a whole in such a way as to suggest that the quartz has undergone recrystallisation at isolated centres. There is sometimes a tendency for these areas to be arranged along a line or lines, and in one case they occur in such a way as to suggest that they have been developed along lines of conchoidal fracture; more often, however, their distribution is quite irregular. A point of some interest is that these unique quartzes appear to be confined to the basement breccias of the Margie Series; they have not been found in the associated grits or in the Leny Grits immediately to the north.

Felspar pebbles occur sparingly, and are absent in many specimens. In most cases they are orthoclase, less often perthite and acid plagioclase.

Another type of pebble of not infrequent occurrence consists essentially of a fine-

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* *Mem. Geol. Survey: The Silurian Rocks of Britain*, vol. i, p. 41, 1899.

grained mosaic of quartz often associated with chlorite. The source of these is uncertain, but they resemble closely the material which infills many of the vesicles of the palagonite fragments. In one section there was noted a broken crystal of zircon.

The matrix in which the above pebbles are embedded consists of small clastic quartzes, colourless micas, felspars (both orthoclase and acid plagioclase), along with what must have been originally a fine mud, and which now consists for the most part of minute flakes of mica, scales of chlorite, and needles of rutile, all probably authigenous in character. Locally there is evidence of rather intense silicification, resulting in the formation of crystalline quartz round the margin of the original quartz pebbles and as authigenous granules in the matrix. To some extent also there is local calcification, later than the silicification.

The Clashbeg breccias may be taken as typical of all the occurrences, but there are points of difference in the character of the minor constituents and in the relative abundance of the dominant palagonite, quartz, and sedimentary fragments. The breccias north-east of Bofrishlie Farm, for example, yield occasional pieces of characteristic spilites with the felspars in good preservation; they contain, too, the dark green tourmaline and the pleochroic zircons which are constant accessories of the overlying grits.

The Grits.—The grits belonging to this series are for the most part rather fine-grained, with the grains less than 1 mm. in mean diameter; occasionally they are somewhat coarser, containing pebbles of quartz and shale up to 5 mm. or more in diameter. Pieces of the black shales can often be recognised, and occasionally cherty fragments derived from the underlying series; many specimens are seen to be rich in pink felspar: the dominating quartzes are very often black in colour but white and blue opalescent varieties are also common; not infrequently the grits are distinctly micaceous. The prevalent colour of the rocks is green or greyish-green, changing to rusty brown tints on weathered surfaces.

In thin section the larger grains (from ·2 mm. to 2 mm. in diameter) are seen to consist mainly of quartz, felspar, and micas; zircon and tourmaline are found in almost every slide, and composite rock fragments occur occasionally. The grains are sometimes well rounded, sometimes subangular. The quartz is for the most part typical granitic quartz, with inclusions of fluid cavities, rutile needles, and less often tourmaline, biotite, etc. It is invariably the dominant constituent, but in some of the arkose-like grits felspar is nearly as abundant. The felspars include microcline, orthoclase, perthite, and plagioclase, the last ranging from albite to andesine, but being mainly a variety near oligoclase in composition. The larger grains are nearly all of alkali felspar, chiefly microcline; most of the plagioclase grains are less than ·1 mm. in diameter, and belong to the finer sand of the matrix, where they are often in excess of the orthoclase and microcline, and in the more highly felspathic types form no inconsiderable proportion of the rock. On the whole the felspars are remarkably fresh, but occasionally the orthoclases show advanced sericitisation. Clastic muscovite appears in every specimen examined. In a few cases it is accompanied by biotite (usually partially or completely chloritised), either in parallel intergrowth or in separate fragments. Zircons, sometimes highly coloured and pleochroic, and often zoned, are constant accessory constituents, and are often very abundant. Dark green tourmaline is rarely absent.

The composite grains include quartz-orthoclase, quartz-biotite, quartz-muscovite, orthoclase-biotite, orthoclase-zircon, etc., all derived doubtless from the disintegration of granites, fragments of black shales and sandy mudstones, and in several instances pieces of decomposed volcanic rocks, in most cases spilites.

The matrix is very uniform in character, consisting of small detrital fragments of the same minerals as the larger grains, together with what must have been a fine argillaceous paste or mud. The latter, as in the basement breccias, is now represented by authigenous minerals in the form of flakes of colourless micas, green scaly chlorite, rutile needles, and pyrites. Locally the matrix has undergone silicification, and subsequent partial calcification is sometimes met with. The Margie Grits of the Aberfoyle district, however, do not show the rich development of carbonates, which is given by Mr Barrow as a distinctive character of the grits of the Forfar-Kincardine area.*

Shales.—The fine-grained greyish-green shales and mudstones of the Margie Series consist of authigenous scaly chlorite, colourless micas, iron oxides, and occasional rutile needles, along with small clastic grains of quartz, muscovite, and biotite. They are well exposed in the Corrie Burn section.

Limestone.—The limestone occurs in the old lime quarry north of Upper Dounans, where it is faulted down between the local serpentine and the Lower Old Red Sandstone (see text-fig. 10). It is a bluish crystalline limestone, appearing yellow or brown on weathered surfaces. It is usually much brecciated and veined with white calcite. Its chief interest centres round the fact that it has been proved to be in places highly fossiliferous.

The fragments of sedimentary rocks included in the Margie Grits recall at once the sediments of the underlying series. The larger inclusions in the basement breccia must either have fallen from cliffs adjoining the Margie sea, or be due to volcanic explosions on the sea floor; the abundant palagonite fragments point to a recrudescence of volcanic activity at the beginning of Margie times. The fact that pieces of the spilite lavas and the underlying black shales are of common occurrence both in the basement breccias and the grits indicates a noteworthy amount of denudation of the Lower Series. The main constituents of the grits, however, show clearly that they were derived in large measure from the denudation of an area of granitic rocks.†

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* *Quart. Journ. Geol. Soc.*, vol. lvii, p. 329, 1901.

† This point is discussed more fully in the comparison of the Margie Grits with the Leny Grits on page 200.

VI. Palæontology of the Beds.

The great majority of the fossils noted are in Professor Jehu's collection. A few are in the collection of the Geological Survey and these were found by Mr D. Tait, kindly sent by Dr Flett, Assistant Director of the Survey, at Professor Jehu's request, to search for specimens. The interest of the fossils lies not so much in their nature as organisms, but rather in the light they throw on the age of the rocks; that is to say, their importance is stratigraphical rather than palæontological. The localities at which fossils have been found are indicated on the map (Plate VI).

I. *The Lower or Black Shale and Chert Series.*

No undoubted organic remains have been recorded from the black shales. This is probably due to the intense movement they have undergone, resulting in the production of well-marked flaser structure.

"Ghosts" of graptolites have been noted in the less altered bands of black shale, but these are too shadowy to be regarded with confidence as fossils. It is probable, however, that the carbonaceous material which gives the shales their black colour, and causes them to stain the fingers, is an indication of the presence of life in the waters under which the sediments accumulated.

The fossils which have been obtained occur in beds of pale grey, somewhat muddy cherts and cherty shales, 1 to 4 inches in thickness. The principal fossiliferous locality is on the south-east side of the Bofrishlie Burn, about 400 yards north-west of Arndrum. Here the belt of Highland Border Rocks is very narrow, the width being only a little over 100 yards. The cherty beds and associated black shales are sharply folded along nearly vertical axial planes, and frequently the folds have snapped, resulting in small overthrusts (Plate V, fig. 2). Sometimes the chert beds and black shales are so crushed together as to be intermixed or to form a breccia of angular fragments. The cherty beds are traversed frequently to such an extent by joints, small faults, and minute veins of quartz as to render it extremely difficult to split the rock along the planes of lamination.

Another exposure of cherty beds yielding fossils occurs on the same horizon 580 yards further north-east, measuring along the strike of the belt. This spot is situated on the top of the ridge of black shales and cherts, north-west of a sharp bend in the course of the Bofrishlie Burn.

Again a few fossils were obtained from nearly pure chert beds on the hill-top just above and north-west of the road where the old aqueduct of the Glasgow Waterworks crosses the valley opposite the Drum of Clashmore.

LIST OF FOSSILS FROM THE CHERTY BEDS.

I. *Radiolaria.*
II. *Graptolitoidea.*
  Forms belonging to the family of *Diplograptidæ*—*Trigonograptus* or *Cryptograptus.*
  A form of the family *Retiolitidæ.*
III. *Brachiopoda.*
  Obolus, Eichwald—species indeterminate.
  Lingulella aff. *ferruginea*, Salter.
  ,, aff. *nicholsoni*, Calloway.
  Acrothele (*Obolella*) *maculata*, Salter.
  ,, (*Redlichella*) *granulata*, Linn.
  Acrothele aff. *coriaceæ*, Linn.
  Acrotreta nicholsoni, Dav.
  ,, *socialis*, von Seebach.
  ,, aff. *sabrinæ*, Calloway.
  Siphonotreta aff. *micula*, M'Coy.
  ,, aff. *scotica*, Dav.
  ? *Schizambon*, Walcott.
IV. *Phyllocarida* (*Leptostraca*).
  Modiolocaris dakynsi, Peach, *nov.*
  Other forms allied to *Lingulocaris*, Salter, and to *Peltocaris*, Salter.
V. *Incertæ sedis.*
  Various remains of Arthropods, etc.

I. RADIOLARIA.

Remains of *Radiolaria* occur in profusion in the purer cherts and to a less extent in the cherty shales, not only at the fossil localities indicated on the map, but also elsewhere. They are seen to be abundant on a microscopic examination of thin sections of the rock, and can be detected even in hand specimens by means of a strong lens. Usually they appear as mere casts, round or oval in form; frequently they show a lattice-like pattern, or look like small circles with spines radiating from the centre like the spokes of a wheel (Plate I, figs. 5, 7, and 11).

II. GRAPTOLITOIDEA.

Graptolites are extremely scarce. A few specimens have been obtained from the cherty shales at the Bofrishlie Burn locality, between Arndrum and Dungarrow. The first specimen identified as a graptolite was detected by Dr Ami of Canada in the collection of fossils from the Aberfoyle district exhibited by Dr Jehu at the Dundee Meeting of the British Association in 1912. In a letter to Dr Horne, Dr Ami stated that he had recognised an obscurely preserved graptolite resembling *Retiolites ensiformis* Hall, a type characteristic of the Sillery Sandstones of the Quebec Group (Upper Cambrian). This specimen was examined subsequently by Miss Gertrude Elles, Cambridge, who kindly supplied the following figure and description:—

"The specimen appears to me to show traces of thecæ, with a fairly well-developed reticula and clathria. It would appear to belong to the *Retiolitidæ.* The strands belonging to the clathria are the median longitudinal strand and several lateral fragments seen on its left side; those on the right are more obscure. The reticula is of much the same nature as that of *Plegmatograptus nebula*, but this graptolite has no well-developed clathria. Four thecal apertures are discernible, three close together on the extreme left, and one some little distance below them. The fact that none are seen on the right is probably due to the fact that the left side of the polypary is turned towards the observer, the right being turned away."*

Other specimens of graptolites were obtained later from the same exposure. These also were examined by Miss ELLES, who reported that they belong to the family *Diplograptidæ*, the genus being either *Trigonograptus* or *Cryptograptus*. Photographs of these specimens (magnified) are shown on Plate II, figs. 1 and 2. In the specimen represented by figs. 2A and 2B the outlines of the thecæ can be distinctly seen, and the position of the septum or axis is evident. A photograph of the counterpart of this specimen is also given (fig. 2). Owing to the oblique way in which the rock split the aspect of the polypary appears somewhat different. In the description of *Cryptograptus* given by ELLES and WOOD,† it is stated that the polypary varies much in appearance, according to the aspect from which it is seen.

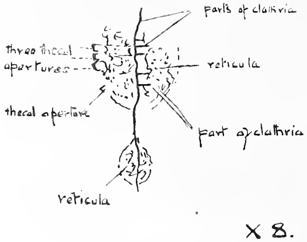

FIG. 1.

The specimens shown in figs. 1 and 1A are again counterparts. In these Miss ELLES detected definite cells, which appear to show that the form is a *Diplograptid*—probably *Cryptograptus*.

The genus *Trigonograptus* is recorded from the Upper Skiddaw Slates (Arenig) of the Lake District, and *Cryptograptus* ranges from the Middle Skiddaw Slates through the Ordovician System.

III. BRACHIOPODA (see Plate I).

The most numerous of the fossils which can be seen with the unaided eye are horny, hingeless brachiopods, often minute in size. The genera comprise *Obolus*,

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[*] *Geol. Mag.*, dec. vi, vol. i, p. 404, 1914.

[†] *Monog. Brit. Grap.* (Pal. Soc.), vol. i, p. 295.

Lingulella, *Acrotreta*, *Acrothele*, *Siphonotreta*, and possibly *Schizambon*. *Acrotreta* is by far the commonest genus, and several species are represented, the most abundant being *Acrotreta nicholsoni*, Dav. Next in relative abundance are the genera *Lingulella and Acrothele.*

The identification of the specific forms belonging to each genus is often difficult, owing to the minute size of the fossils or to their imperfect state of preservation. The list gives the names of forms that can be determined with some approach to accuracy.

Genus OBOLUS, Eichwald.

More or less rounded Obolids have been found which appear to be referable to this genus, but it has not been possible to determine the species. WALCOTT* gives the range of this genus as Lower Cambrian to Lower Ordovician.

Genus LINGULELLA, Salter.

Lingulella aff. *ferruginea*, Salter.—The majority of the specimens of *Lingulella* found approach *L. ferruginea* in form and character. The shell is small, somewhat convex, and ovate in form. The front is rounded, the sides sub-parallel, tapering towards the beak. The median septum is seen in many specimens, and occasionally traces of muscle scars can be detected (figs. 20, 21, and 22).

L. ferruginea has been recorded from the Middle and Upper Cambrian of Wales and the Upper Cambrian of Shropshire.†

Lingulella aff. *nicholsoni*, Calloway.—A larger form of *Lingulella* is less common. That shown in fig. 23 is somewhat distorted and broken. It is the interior of the dorsal valve showing the median septum, from the end of which two lines appear to bifurcate. Traces of muscle scars can be detected in the specimen. This form approaches in shape and characters to *L. nicholsoni*, as described by CALLOWAY.‡ The front and sides are rounded, and the margins of the shell are marked by fine concentric lines of growth. CALLOWAY'S specimen is from the Shineton Shales of Shropshire. A similar form has been obtained from the Upper Cambrian of the Malvern Hills.§

Genus ACROTHELE, Linnarsson.

Acrothele (*Obolella*) *maculata*, Salter.—Several specimens of this form have been obtained (figs. 1, 2, 3). DAVIDSON‖ has remarked on the very transverse shape of the shell, and on the fact that it is often found much flattened. This is the largest brachiopod yet found in the Aberfoyle district. The best specimen (fig. 2) shows

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* *Camb. Brach.* (U.S. Geol. Survey Monog., vol. li, pt. 1), p. 378, 1912.

† DAVIDSON, *Brit. Fossil Brach.* (Pal. Soc.), vol. iii, pt. 7, p. 337; MATLEY, *Quart. Journ. Geol. Soc.*, vol. lxvii, p. 301, 1911.

‡ *Quart. Journ. Geol. Soc.*, vol. xxxiii, p. 668, 1877.

§ *Ibid.*, vol. lviii, p. 141, 1902; DAVIDSON, *Sil. Brach.* (Pal. Soc.), Suppl., p. 208, pl. xvii, figs. 31 and 32.

‖ *Monog. Brit. Fossil Brach.* (Pal. Soc.), vol. iii, p. 341.

the exterior of the dorsal valve, with the ventral valve appearing from underneath due to displacement, and with the pedicle foramen appearing above. Apparently this species hitherto has been recorded in Britain only from the Middle Cambrian of Wales.

Acrothele (*Redlichella*) *granulata*, Linn.—The exterior of the ventral valve is shown in fig. 5, and with a strong lens the granulation on the surface, which is typical of this species, can be seen. A drawing of this surface ornamentation is given as an inset to fig. 5. This form has been recorded from the Middle Cambrian of Shropshire,* Warwickshire,† and from the Lower Ordovician of the South of Scotland.‡

Acrothele aff. *coriacea*, Linn.—In the specimen figured (fig. 4) we see the rough external surface of the ventral valve, and a strong lens makes it clear that the roughness is due to minute granulation and fine, slightly elevated striæ, as described by WALCOTT.§ It has been found in the Cambrian Rocks of Scandinavia, and WALCOTT gives the range of this species as Middle Cambrian to the Passage Beds between the Cambrian and Ordovician Systems.

Genus ACROTRETA, Kutorga.

Acrotreta nicholsoni, Dav. (figs. 7–12).—Specimens of this species are the most numerous by far of all the forms obtained in the cherty beds of the Aberfoyle district. The ventral valve has a conical or pyramidal form, with the circular pedicle opening at the apex. The posterior margin is triangular in shape and grooved, forming a pseudo-deltidium. The dorsal valve is relatively more depressed in form. Fine concentric striations are seen by the aid of a lens on the external surface of the shell. This species has been recorded from the Shineton Shales of South Shropshire and the Bonsil Shales of the Malvern Hills.‖ It is common in the Arenig and Llandeilo Beds of the South of Scotland, and extends also into the Caradoc Formation.¶

Acrotreta socialis, von Seebach (figs. 13–15).—Fig. 14 shows an exceptionally well-preserved example. It is the interior of the dorsal valve, and the position of the median septum, the central muscle scars and the cardinal scars can be discerned. In another specimen the interior of the ventral valve is shown with a well-marked apical callosity (fig. 15). This species occurs in the Middle Cambrian of Sweden and Denmark,** and very similar forms have been recorded from the Middle Cambrian of Comley (Shropshire) †† and the Upper Cambrian of the Malvern Hills.‡‡

Acrotreta (*Obolella*) aff. *sabrinæ*, CALLOWAY.—The specimen, of which a photograph is given (fig. 16), is the interior of the dorsal valve. The photograph is not good; the characters are better displayed in the actual specimen. The shell is somewhat

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[*] MATLEY, *Quart. Journ. Geol. Soc.*, vol. lxvii, p. 302, 1911.

[†] LAPWORTH, *Proc. Geol. Soc.*, vol. xv, p. 346, 1888–89.

[‡] *The Silurian Rocks of Britain* (Mem. Geol. Sur.), vol. i, p. 675, 1899.

[§] WALCOTT, *Camb. Brach.* (U.S. Geol. Survey Monog., vol. li, pt. 1), p. 642, 1912.

[‖] *Ibid.*, p. 696.

[¶] *The Silurian Rocks of Britain* (Mem. Geol. Survey), vol. i, p. 675.

[**] WALCOTT, *Camb. Brach.* (U.S. Geol. Survey Monog., vol. li, pt. 1), p. 713, 1912.

[††] MATLEY, *Quart. Jour. Geol. Soc.*, vol. lxvii, p. 303, 1911.

[‡‡] *Ibid.*, vol. lviii, p. 144, 1902.

crushed from side to side; a pair of cardinal scars can be discerned near the apex, and a median septum is faintly seen. Fine concentric lines of growth are shown towards the anterior margin of the shell. This species occurs in the Upper Cambrian of Shropshire [*] and the Malvern Hills.[†]

Genus SIPHONOTRETA, de Verneuil.

Siphonotreta aff. *micula*, M'Coy.—A photograph and a drawing of a specimen are shown in figs. 17 and 17A. It is the exterior of the ventral valve broken across. The characteristic punctations are seen on the surface and concentric lines of growth. *S. micula* has been recorded from the Ordovician of Wales and the South of Scotland.[‡]

Siphonotreta aff. *scotica*, Dav.—The specimen shown in figs. 18 and 18A resembles very closely *S. scotica* as figured and described by DAVIDSON.[§] The fossil is a cast of the interior of the ventral valve with a part of the rim of the exterior of the valve. Concentric lines of growth are faintly seen, and small pits or dots at places. Around the rim, fringes of spines are seen to take their rise from the shell. *S. scotica* has been obtained from the Llandeilo Beds of the Girvan district, South of Scotland.[||]

Genus ? SCHIZAMBON, Walcott.

Another form appears to belong to the family *Siphonotretidæ*, but it differs from *Siphonotreta*, and seems to bear a closer resemblance to *Schizambon* as figured by WALCOTT.[¶] Figs. 19 and 19A show the interior of the dorsal valve, in which the septum and muscle scars can be discerned. Faint traces of spines can be detected. It has not been found possible to determine the species. Hitherto this genus has been recorded only from the Upper Cambrian and Ordovician of Russia and North America.[**]

IV. PHYLLOCARIDA (LEPTOSTRACA).

Remains of bivalved phyllocarid crustaceans are found which appear to be allied to the genera *Lingulocaris*, Salter, *Ceratiocaris*, M'Coy, and *Peltocaris*, Salter. These are all Upper Cambrian and Ordovician genera.

The best preserved specimen is shown on Plate II, fig. 3. Dr PEACH has supplied a drawing (Plate II, fig. 3A) of this specimen and a description from an examination of the specimen figured and of its counterpart (not figured). He says:—

"This is a bivalved phyllocarid allied to the Ordovician *Ceratiocaris*. It shows the exterior of the left valve of the carapace, and also traces of five thoracic and six

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[*] CALLOWAY, *Quart. Jour. Geol. Soc.*, vol. xxxiii, p. 669, 1877.

[†] MATLEY, *Quart. Jour. Geol. Soc.*, vol. lviii, p. 143, 1902.

[‡] DAVIDSON, *Brit. Fossil Brach.* (Pal. Soc.), vol. iii, pt. 7, p. 77.

[§] *Brit. Silurian Brach.*, Suppl., p. 217, pl. xvi, figs. 31–33.

[||] *Ibid.*, p. 217.

[¶] *Camb. Brach.* (U.S. Geol. Survey Monog., vol. li, pt. 2), pl. lxxxiv, 1912.

[**] *Ibid.*, pt. 1, p. 104.

abdominal segments ending in a styliform telson. It appears to differ from its Palæozoic congeners as yet described in having some of the tergites of the abdominal segments produced into pleuræ or lappets. From the resemblance of the valves in shape to the lamellibranch shell *Modiola* it is proposed to institute a new genus *Modiolocaris*, and to name the species *Modiolocaris dakynsi* after the late J. R. Dakyns, who was the first to map the Aberfoyle district for the Geological Survey. A common habit of these organisms in dying has been to throw out the body from beneath the protective carapace."

V. INCERTÆ SEDIS.

Amongst the fossils found there are many which are either so fragmentary or so obscurely preserved that we cannot be certain of their true systematic position. Some of these have been photographed, and are shown in Plate II, figs. 4–9. They include (1) the jaw of an Annelid or one of the cheliceræ of some Arthropod; (2) the cercopods of a Phyllocarid Crustacean; (3) fragments of some Arthropods—possibly of Trilobites or of Phyllocarids; (4) pieces of the punctate skin of some Arthropod; (5) a curious pitted triangular plate.

II. *The Upper or Margie Series.*

The Aberfoyle Limestone is regarded as a member of the Upper Series, and it probably corresponds with the Kilmahog Limestone, Callander, and the Margie Limestone of Forfarshire. It is exposed in an old limestone quarry about a mile north-east of the village of Aberfoyle, just at the limit of our district. This limestone is now involved in the crushed rocks along the Highland Boundary Fault, and at places is much brecciated. Though crystalline in texture, a close examination has proved this rock to be fossiliferous. Remains of Crinoids have been detected, and one of them is shown on Plate II, fig. 10. The determination of these remains as plates of Crinoids has been confirmed by Dr Bather of the British Museum. When examined in thin sections under the microscope the limestone is seen to contain also the remains of other organisms. Specimens of the limestone, together with sections for microscopic examination, were sent to Dr G. Jennings Hinde. He has kindly supplied the following report:—

"NOTES ON FRAGMENTS OF LIMESTONE FROM A QUARRY NEAR ABERFOYLE IN THE HIGHLAND BORDER. By Dr G. J. Hinde.

"Dr Jehu has forwarded to me some small fragments of limestone rock and a series of thin sections, five in number, taken from them, and asked for notes as to their microscopic characters. There is not much to be said about the general characters of the limestone as shown in these small fragments; it is a compact, bluish-grey rock, crystalline, with occasional veins of calcite. The sections prove that the rock is organic in character, but the organisms have been considerably altered in fossilisation, and minute structural details are rarely recognisable.

"The sections are noted in the order in which they are marked.

"1. About one-third of this section is a coarsely crystalline rock, mostly without organisms; the larger part consists of small fragments of organisms, some of rounded or oval forms, with walls either entire or perforated by small canals; the interiors are either of crystallised rock or of fragmental organic débris. These bodies may be Foraminiferal in origin. Intermingled with them are numerous elongated fragments, dark in appearance, probably hollow originally, which seem to be organic, but I cannot say to what organisms they belong. (Plate II, fig. 11.)

"2. The rock section is like the preceding—in large part of coarse-grained crystallised limestone, in which are embedded fragments, irregular in outline, of fossils of very minute calcite grains. Some of these are very probably calcareous *Algæ*. The marked difference between the coarsely crystalline limestone matrix and the extremely minute grains composing the fragments of calcareous *Algæ* can be well seen in this slide. (Plate II, fig. 13.)

"3. Here again the difference between the very fine character of the grains of the portions which were probably calcareous *Algæ* and that of the calcite matrix can be clearly seen.

"4. This rock section is of comparatively similar grains of limestone, and no fossil fragments appear therein.

"5. A large part of the rock consists of rounded organisms with walls perforate, also of elongate bodies, and these fossils are of limestone in extremely fine grains. The rounded bodies are apparently *Foraminifera*." (Plate II, fig. 12.)

VII. The Age of the Highland Border Rocks.

The striking resemblance of the members of this marginal strip of rocks to the Arenig succession in the South of Scotland has already been remarked upon. This similarity is evident not only in the black shales and cherts, but also in the associated igneous rocks, both lava-form and intrusive, and in the highly metamorphosed bands.* This lithological resemblance led Messrs Peach and Horne to correlate the rocks of the two regions, and consequently the Highland Border Rocks are marked as doubtfully Lower Silurian on the Geological Survey Maps.

The assemblage of fossils obtained from the cherts is strongly suggestive of an Upper Cambrian or Lower Ordovician horizon. The brachiopods and phyllocarid crustaceans are represented by genera and species which are characteristic of Upper Cambrian and Lower Ordovician rocks elsewhere. A few of the brachiopods have been noted hitherto only from the Middle Cambrian. The graptolites, on the other hand, point to an Ordovician horizon. Taking the evidence from the fossils as a

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* *The Silurian Rocks of Britain*, vol. i, Scotland (Mem. Geol. Survey), p. 46, 1899; Sir A. Geikie, *Ancient Volcanoes of Great Britain*, vol. i, p. 201, 1897.

whole, we are justified in fixing the horizon of the Lower or Black Shale and Chert Series as Upper Cambrian or the Passage Beds between the Cambrian and the Ordovician.

In this connection it may be noted that Dr PEACH, in his Presidential Address to the Geological Section of the British Association at the Dundee meeting in 1912, expressed the opinion that Upper Cambrian strata will yet be found in the Girvan area—a view, he adds, which had been previously suggested by Professor LAPWORTH.*

It follows that the Upper or Margic Series, which is unconformable to the Lower Series, must belong at any rate to later Ordovician times. Here again the resemblance to the succession in some parts of the Southern Uplands still holds, for, in the Girvan area, on the north side of the Stinchar Valley, grits, shales, and conglomerates overlie unconformably the cherts, black shales, and volcanic rocks of the Lower Series, and the conglomerates include fragments of the underlying rocks.†

The presence of the remains of Crinoids and of other organisms in the Aberfoyle Limestone of the Upper Series affords additional and conclusive evidence of the later Ordovician age of the series. The occurrence of calcareous *Algæ* and *Foraminifera* with the remains of Crinoids suggests a correlation of this Limestone with the Stinchar and Craighead Limestones, which likewise contain calcareous *Algæ*, *Foraminifera*, and occasional crinoidal remains.‡ A further search may result in the discovery of other organisms in the Aberfoyle Limestone.

VIII. INTRUSIVE ROCKS OLDER THAN THE LOWER OLD RED SANDSTONE.

These rocks include albite diabase, albite hornblende gabbro, and serpentines. An albite diabase intrusion occurs on the watershed to the north-west of Gualann, and others outcrop at intervals along the ridge of black shales and cherts as far east as a point south-east of Garbeg Hill. An intrusive rock, shown on the accompanying map as albite diabase, but which is so highly decomposed that its affinities are somewhat uncertain, is seen on the left bank of the Bofrishlie Burn east of Dungarrow. Diabases, in all probability intrusive in character, are associated with the spilites where they first make their appearance west of the Kelty Water, but they have not been mapped separately, and they are so highly altered that it has not been found possible to determine their systematic position.

The serpentines and gabbros form part of a complex of igneous, sedimentary, and vein rocks which can be traced almost continuously from the old limestone quarry north of Upper Dounans to Gualann. The most interesting exposures occur in and to the south-west of the above-mentioned quarry and in the neighbourhood of Maol Ruadh and Lime Hill.

Petrography of the Albite Diabase.—The freshest specimens were obtained from the large intrusion opposite Gualann. They consist chiefly of the three minerals

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* PEACH, *Rep. Brit. Assoc.*, p. 453, 1912.

† *The Silurian Rocks of Britain*, vol. i, Scotland (Mem. Geol. Survey), pp. 45–47, 1899.

‡ *Ibid.*, p. 46.

which are characteristic of albite diabases elsewhere,* namely, augite, albite, and ilmenite (see Plate III, fig. 3). Occasionally biotite occurs in considerable amount, and the rocks are rich also in accessory apatite. Olivine appears to be absent. The pyroxene has the purple tint usual in titanaugites; it is sometimes perfectly fresh, sometimes partially or completely altered to chlorite and carbonates—in one instance only, in the fine-grained margin of the largest intrusion, it is entirely replaced by fibrous green hornblende; in the coarser parts of the rock it is anhedral, in the finer parts it tends to show crystal outlines. The albite which occurs in narrow laths penetrating the augite in subophitic fashion is more often in broad rectangular crystals, and is the most abundant constituent of the rock. The crystals have the "spongy" centre, with the associated chlorite, epidote, and prehnite usually found where lime-rich plagioclase has undergone albitisation; the marginal portions are compact, and grade sometimes into interstitial water-clear albite. In the weathered rocks, which are rich in chlorite and carbonates, the albite is usually unaltered. The ilmenite is in large skeletal growths, occasionally in graphic intergrowth with augite, and always more or less altered to leucoxene and sphene. Biotite, which is for the most part chloritised, occurs in association with the ilmenite in the same fashion as in the Carboniferous teschenites,† and also as isolated crystals enclosed in the felspars; it contains sometimes minute inclusions with pleochroic halos.

Highly felspathic acid veins and segregations, the pink colour of which is in striking contrast with the dark bluish-grey of the mass of the rock, are conspicuous features of the largest intrusion. Included fragments of black cherty shale have been converted into spotted adinoles.

As regards the age of these intrusions, they are of course younger than the black shale and chert into which they are intruded; how much younger the field evidence does not enable us to say. But their petrographical characters show clearly their affinities with the spilites, an association which, as FLETT and DEWEY ‡ have pointed out, is invariable both in Europe and America.

Petrography of the Serpentine-Gabbro Complex.—The igneous rocks of this complex present many puzzling features. They are for the most part in a highly altered condition, and their study is further complicated by a great development of vein rocks associated with the faults which bound the complex on either side. It is clear, however, that the original intrusion included both serpentine and gabbro.

At Maol Ruadh and at the Upper Dounans Limestone Quarry occur good examples of dunite serpentine rich in chrome spinels (Plate III, fig. 4). In the latter the olivine is replaced partly by serpentine, partly by tremolite. Sections of the Maol Ruadh rock are of especial interest, because along narrow lines of shearing the serpentinised olivine is traversed by anthophyllite in lamellar crystals and tufted fibrous aggregates. The mesh structure in both of these rocks is well seen,

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* H. DEWEY and J. S. FLETT, *Geol. Mag.*, dec. v, vol. viii, p. 206, 1911.

† *Trans. Edin. Geol. Soc.*, vol. ix, p. 126, 1910.

‡ *Loc. cit.*, p. 206.

and there can be no doubt that they were originally of the nature of dunites. Du Toit[*] has noted the occurrence of diallage and enstatite. The fine-grained compact serpentines at Maol Ruadh often show no trace either of the original minerals or textures. Sometimes, however, they contain corroded crystals of albite. The interpretation of these rocks presents considerable difficulty, but we have arrived at the conclusion that they represent serpentinised albite gabbros.

The albite gabbros at Maol Ruadh consist essentially of a coarsely crystalline granitic aggregate of albite and compact green hornblende. The albite is of the same type as that of the albite diabases, and represents doubtless albitised lime-rich plagioclase. In one instance we found the felspar of the gabbro to be saussuritised. Locally both the felspars and the hornblende are replaced in whole or in part by a green serpentinous substance similar in its optical properties to the material of the compact serpentines. Whether the final product is compact serpentine, a serpentine with corroded albites, or an albite gabbro depends on how far the process of serpentinisation has progressed. The available evidence shows that albitisation has preceded the serpentinisation. It is of importance to note, however, that veinlets of water-clear albite, similar to those found in the hornblende schists (see p. 198), traverse not only the fractured fresh hornblende of the albite gabbro, but also the partially serpentinised constituents. Hence there was also an introduction of albite at a later phase in the history of the rock.

The serpentines usually contain in greater or less abundance secondary carbonates after olivine. When this process of replacement is complete the resulting rock (see Plate IV, fig. 5) is a ferruginous dolomite, in which the original mesh structure of the dunite serpentine may still be seen, but in which the only original minerals remaining are the chrome spinels. This development of a ferruginous dolomite at the expense of the serpentine was recognised by Du Toit.[†] Dolomites, commonly creamy-white in colour, but sometimes tinted with delicate shades of green and rose-red, and weathering with a reddish-brown crust, now form perhaps the major portion of the complex, and there can be no doubt that they are in large measure "pseudomorphs" after serpentine. Some of the dolomite of course, notably the veins which intersect the adjacent conglomerates of the Lower Old Red Sandstone, is vein-rock of the ordinary type. The dolomite is sometimes veined with jasper and chalcedony, deposited at a later period from solutions charged with silica.

Like the rocks of the similar complex at Toward and Inellan,[‡] the serpentines sometimes, for example near the ruins of Bofrishlie Farm, show evidence of intense shearing, and have apparently shared in the movements which induced the foliation of the rocks to the north.

Gabbros and serpentines occur in association with spilitic lavas in Ayrshire, in Cornwall, and elsewhere. In discussing the spilitic sequence Flett and Dewey[§]

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[*] *Trans. Edin. Geol. Soc.*, vol. viii, p. 323, 1905.

[†] *Ibid.*

[‡] *Mem. Geol. Survey: Geology of Cowal*, p. 73, 1897.

[§] *Loc. cit.*, p. 243.

confess that, while it is difficult to explain that association as a mere accident, they have not been able to establish definitely that the one series is the plutonic representation of the other, and they regard the question as an open one. The occurrence of albite gabbros in the above complex seems to us to go far towards proving that in the Aberfoyle area at least the coarsely crystalline rocks are comagmatic with the albite diabase and spilites.

IX. The Hornblende-Schist Complex and Associated Sediments.

A belt of metamorphic rocks has been traced from Gualann north-eastwards to a point opposite the south-west end of the Drum of Clashmore, a distance of about 2½ miles. It is bounded on the south by a fault which is probably a branch of the Highland Fault, and a line of dislocation separates it from the unaltered igneous and sedimentary rocks to the north. The belt consists mainly of metamorphosed igneous rocks, chiefly hornblende and chlorite schists, but schists of sedimentary origin are found along the northern margin and also intercalated with those of igneous types. Their highly foliated character distinguishes the metamorphic rocks clearly from the unaltered rocks to north and south. The direction of the general strike of the foliation is north-east and south-west, and the foliation planes dip at high angles towards the north-west.

Schists of Igneous Origin.

Eastwards from the most easterly tributary of the Corrie Burn the schists are very uniform in character. The dominant type is a well-foliated crystalline hornblende schist, usually flaggy in character, dark green in colour, with a beautiful silky lustre, and sometimes veined with yellow epidote. The minerals entering into the composition of these rocks are mainly hornblende, albite, and epidote. Accessory minerals include zoisite, sphene, and apatite; secondary chlorite, quartz, and carbonates occasionally make their appearance.

The typical hornblende schists over most of that area are medium to fine-grained in texture, and show a well-marked linear foliation. The dominating constituent is hornblende in elongated crystals, euhedral in the prism zone but with irregular terminations, and showing pleochroism in pale greenish-yellow (X), olive-green (Y), and blue-green (Z) tints. It is accompanied by albite in more or less equidimensional grains along with a varying amount of epidote and accessory constituents. The felspar is rarely distributed uniformly. More usually it occurs alone or in association with epidote in rather persistent bands parallel to the foliation planes. In the medium-grained varieties, for example opposite Maol Ruadh, those bands swell out to form lenticles conspicuous in hand specimens. The latter represent perhaps large crystals or groups of crystals of the felspar of an original gabbro or coarse diabase, and their occurrence suggests that the rock had been consolidated prior to its conversion into a schist. The elongated hornblende crystals (see Plate III, fig. 6, and Plate IV, fig. 1) curve round the mosaics of albite or albite and epidote which constitute the "eyes," showing that the movements which induced the molecular change from augite to hornblende and from labradorite to albite and epidote were the movements which produced the foliation. Veinlets of water-clear albite, or less often chlorite, traverse the schist structures; those were formed after the movements of compression had ceased.

Locally the hornblende schists pass into massive epidiorite, in which the relations of the felspar to the hornblende are sometimes suggestive of the preservation of ophitic structure. None of the original minerals remains, however, and, as in the foliated types, the rocks have undergone complete reconstruction.

The rocks of the western part of the belt are less uniform in character. They may be studied best in the main branch of the Corrie Burn. There they are seen to include two main groups: (*a*) hornblende schists, (*b*) chlorite schists, occupying respectively the eastern and western portions of the stream section.

The hornblende schists are more coarsely crystalline than those above described, and show greater variation in their mineral composition. On the whole they are distinctly less felspathic. One narrow band near the Jasper Boundary Fault is an actinolite schist (Plate IV, fig. 2) made up entirely of amphiboles, which are pale green in hand specimens and colourless in thin section; sometimes, again, the rocks consist essentially of green hornblende along with much epidote and zoisite, and in these veins and segregations of epidote are common; biotite and iron ores occur as occasional additional accessories, and locally the rock is so rich in the former mineral as to become a biotite-hornblende schist. Felspar, although present, is largely replaced by colourless micas. Where those coarse hornblende schists appear again further south-west in a small tributary of the Corrie Burn they are rich in accessory rutile, and at one point they are traversed by pegmatitic veins of pink microcline.

In only one instance has a massive band been observed in the Corrie Burn. It consists of an epidiorite (Plate IV, fig. 3) richly charged with anhedral pink garnets and crossed by numerous quartz veins. When the rock is decomposed, both the garnets and the hornblende are replaced by chlorite. Iron oxides and apatite are rather abundant as accessory minerals, and the rock is much richer in quartz than any of the associated types.

The chlorite schists are paler in colour and finer in texture, and under the microscope they are seen to be much more felspathic than the hornblende schists. Hornblende is absent, the rocks consisting of an aggregate of albite, chlorite, carbonates, and iron oxides. In the field they recall the spilites, from which they are distinguished by the presence of fine foliation. For the most part, like the hornblende schists, they have undergone complete reconstruction. Locally, however, they contain narrow lath-shaped felspars, and those, together with the occasional appearance of micro-porphyritic texture, indicate that the original igneous structure is in part preserved (Plate IV, fig. 4). The lath-shaped felspars show also an apparent flow structure, which may, however, be due to movement. Like the sheared pillow lavas of Argyllshire,* too, the rocks are very rich in chlorite and carbonates. These textural and mineralogical peculiarities lead us to conclude that the chlorite schists represent effusive spilites, just as the hornblende schists are the equivalents of intrusive diabases and gabbros.

Intervening between the above calc-chlorite schists and the hornblende schists of the Corrie Burn section there is a belt of muscovite-chlorite schists. These may be readily recognised in the field from the development of silvery micas on the foliation planes. They are traversed by an anastomosing network of veins of ferruginous dolomite, and in all probability represent a zone in which the calc-chlorite schists have undergone subsequent shearing.

Schists of Sedimentary Origin.

As will be seen from the accompanying map, the metamorphosed sediments occur as an interrupted band along the northern margin of the hornblende schist complex. In the western part of the area they are found also within the belt occupied by the latter. The best and most continuous section is exposed by the roadside just beyond the course of the Old Loch Katrine aqueduct.

The sediments, like the associated igneous rocks, have undergone almost complete reconstruction. The dominating type perhaps is a black or dark-coloured, heavy crystalline quartz schist, consisting of a granulitic aggregate of quartz, iron oxides, and muscovite (Plate IV, fig. 5). The muscovite and iron oxides are often almost completely confined to definite layers, and the rocks take on a banded texture, lighter-coloured quartzose laminæ alternating with darker bands. Corrugated folding is well seen on weathered surfaces.

The quartz schists sometimes contain partially digested fragments of chert, and pass occasionally into brecciated cherts showing little trace of reconstruction. It is clear, therefore, that they represent metamorphosed highly siliceous sediments. We may note, however, that they are often so rich in iron ores as to suggest that they have been derived, not from the muddy cherts which overlie the local spilites, but from a zone of iron cherts, probably at a lower horizon. Such iron cherts are well developed as interbedded layers in the spilites between Craigeven Bay and Garron Point on the Kincardineshire coast.

Careful search was made for minerals indicative of contact metamorphism. Biotite occasionally accompanies the muscovite, but it is not of the type found in contact-altered rocks. Not infrequently, however, knots, the mineralogical character of which is uncertain, make their appearance, and in two slides they are seen to contain relics of garnet. The knots, as a rule, have been compressed into flattened

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* *Mem. Geol. Survey*: *Geology of Knapdale, etc.*, p. 88, 1911.

lenticular form, and have sometimes been fractured. We conclude, therefore, that the altered sediments exhibit dynamic metamorphism superposed on an earlier contact metamorphism induced by the intrusion of the diabases which are now in the condition of hornblende schists.

The sediments within the hornblende-schist area in the Corrie Burn region are in the form of intensely corrugated, fine-grained schists (Plate IV, fig. 6), partly of the nature of black phyllites, partly soft green schists, the original character of which is doubtful, but which may represent fine volcanic muds. The two types are sometimes interlaminated.

X. Comparison of the Margie Grits with the Leny Grits.

The Leny Grits immediately to the north of the Highland Border Rocks comprise a varied assemblage of sediments. Grits or greywackes, usually green in colour, less often red or dark grey, predominate. Locally, as in the belt which is well exposed in the Craigmore quarry, they became conglomeratic. They are accompanied by intercalations of blue- and purple-coloured slates.

The grits are, on the whole, very uniform in composition. Quartz, felspars, and micas are as a rule the only minerals found as pebbles and larger grains, and the matrix consists usually of minute clastic grains of the same minerals, together with a finely crystalline aggregate of authigenous chlorite and colourless micas. The relative proportions of the constituent fragments show considerable variation. Most frequently quartz predominates: sometimes, however, felspar grains are quite as numerous as those of quartz. Most of the grits are richly charged with large clastic muscovites and biotites. The quartz, as in the Margie Grits, is mainly granitic. The larger grains and pebbles of felspar are for the most part microcline, perthite, or orthoclase; plagioclase, ranging from albite to andesine, but mainly oligoclase, is dominant among the smaller grains. In the Craigmore conglomeratic grits red microcline is almost the only felspar present; on the other hand, among the finer grits occur types in which there is little or no microcline. The heavy constituents are chiefly zircon, green and brown tourmaline, and iron ores. Composite rock fragments are of somewhat rare occurrence except in the Craigmore grits, which are abundantly charged with large and small subangular pieces of a green mudstone closely resembling the mudstones interbedded with the Margie Grits in the Corrie Burn. Among the rock fragments have been noted also microcline granite, micropegmatite, spilite, chert (more crystalline than that of the local Highland Border Rocks), jasper, and quartzite. Schistose rocks have not been observed.

If we set aside the basement breccias, in which the constituents are for the most part of local origin, and consider the normal Margie Grits, we find that their most distinctive character (when compared with the Leny Grits) is the almost invariable occurrence of scattered fragments of black shale, which are absent from the latter series. The dominant constituents of the grits of both series, as already indicated, consist of quartz, microcline, orthoclase, oligoclase, muscovite and biotite, accompanied by abundant zircons and widely disseminated green tourmaline. The Margie Grits are richer in spilitic fragments, the Leny beds on the whole decidedly richer in clastic micas. In neither case has a single pebble or grain of a schistose rock been noted.

The associated mineral grains, taken together with the occasional occurrence of granite fragments, point to an area of granitic rocks as the ultimate source of the materials of both sets of grits. The occurrence of biotite and the fresh character of the soda-lime felspars suggest that the grits, which in both Series include types approaching arkoses, have been derived directly from such a source. The absence of schistose rocks, although a negative character, is noteworthy, since it implies in all probability the absence of such rocks at the surface in the region which was undergoing denudation.

The Leny Grits, on the whole, exhibit a higher degree of metamorphism. This appears most obviously in the frequent occurrence of pronounced foliation, accompanied often by a stronger development of authigenous green chlorite and quartz. In no case, however, has the clastic character been obliterated; and, indeed, it is possible to obtain from the Leny Series grits which show as little trace of metamorphism as the least altered Margie Grits. The argillaceous sediments of the Leny Series are characterised by well-marked slaty cleavage.

The above notes on the Leny Series are based on an examination of specimens collected during a number of traverses over the area immediately to the north of the Leny Boundary Fault. Setting aside the slight difference in the degree of metamorphism, and considering only the character of the original constituents, we confess that the data so far obtained do not do away with the difficulty which previous observers experienced in attempting to distinguish lithologically the grits of the Border Series from the grits to the north. The sediments of the Leny Series have not, so far, yielded fossils; the available petrographical evidence, although it suggests that the grits are an integral part of the Margie Series, is not conclusive; the age of the beds, therefore, may still be regarded as an open question.

XI. Later Intrusions.

In the area between the Leny Fault and the Highland Boundary Fault the post-Ordovician intrusive rocks include (*a*) Porphyrites of Lower Old Red Sandstone age, and (*b*) Quartz Dolerites which were intruded possibly in late Carboniferous times.

The larger of two porphyrite intrusions occurs opposite Lime Hill, extending for a distance of about half a mile in the direction of the strike of the beds of the surrounding Old Red Sandstone. Basic labradorite, usually with a narrow outer zone of more acid plagioclase, and ferro-magnesian minerals, including bastite pseudomorphs after hypersthene, chlorite and calcite replacing monoclinic pyroxene, and iddingsite after olivine, all appear as phenocrysts. The nature of the ground mass is somewhat obscured by alteration products; it contains stout laths of labradorite, granular calcite and chlorite doubtless representing original augite, iron oxides, apatite, and decomposed intersertal mesostasis. The rock is an olivine-enstatite porphyrite, and its petrographical characters point to community of origin with the local lavas of Lower Old Red Sandstone age. The other intrusion occurs further west in the Corrie Burn on the same line of strike.

The quartz dolerite dykes are seldom fresh, and their original characters are often obscured by the development of secondary chlorite and carbonates. The freshest specimens are seen to be free from or poor in olivine, and to contain quartz which is possibly, in part at least, primary. A dyke in the old limestone quarry north-east of Aberfoyle is rich in brown mesostasis, through which are scattered stout laths and forked microlites of labradorite, granular augite, iron oxides, and quartz. The distribution of the dykes is shown in the accompanying map (Plate VI). Their general trend is between north-east and south-west and east-north-east and west-south-west. In their direction and in their petrographical characters they recall the widely distributed quartz dolerites of Central Scotland, which are usually regarded as of late Carboniferous age.

XII. Tectonics.

From the account given in the preceding pages it will be seen that the rocks within the narrow belt between the main Highland Fault and the Leny Fault comprise a great diversity of types—igneous, sedimentary, and metamorphic. The structural relations are no less complicated. Our interpretation of the tectonics is set forth in the acompanying map and in a series of horizontal sections (figs. 3–10, pp. 206, 207) taken at intervals along the area from west to east. Some of the more important tectonic features have already been incidentally referred to; in the succeeding paragraphs it is proposed to discuss them in somewhat greater detail.

The Unconformability between the Lower or Black Shale and Chert Series and the Upper or Margie Series.—The rocks of the Lower Series, as we have seen, were laid down at and beyond the limits of terrigenous sedimentation; the Upper Series was deposited in close proximity to a land area. The basement breccias and grits of the latter contain fragments of the black shales and cherts and of the underlying spilitic lavas. It is clear, therefore, that the deposition of the Margie beds was preceded by a period of crustal movement and elevation. The old sea floor became a land area, the denudation of which supplied, in part at least, the materials for the sediments of the younger formation. That no inconsiderable amount of erosion was accomplished in that interval is shown by the presence in the basement beds and grits of the Margie Series of fragments of the spilites, which are the lowest visible part of the Black Shale and Chert succession. Materials derived from the Lower Series are scarcer in the grits than in the basement breccias. This points to a transgression of the Margie sea, the deposits of which were ultimately spread over the whole of the area occupied by the Lower Series. The relation of the beds of the two Series prior to the post-Margie folding is shown diagrammatically in fig. 2. The inclusion of fragments of the cherts, black shales, and spilites in the Margie breccias and grits is in itself good evidence of unconformity; the overlapping of the Margie beds from the black shales on to the spilites, as revealed by the detailed mapping (see map, and figs. 3 to 7), gives even more convincing proof of that relationship.

The Post-Margie Movements.—At a later period the rocks of both Series were involved in movements which produced intense folding, faulting, and crushing. The faults and crush lines are usually parallel to the general strike of the beds. The pressure came chiefly from the north-west, and has resulted at places in an intimate folding and faulting of the Margie Grits into the underlying cherts and shales. This is particularly well seen about 300 yards north of the spot at which the old Aqueduct crosses the valley north-west of the Drum of Clashmore. Occasionally the grits have snapped in the cores of nearly vertical folds, yielding phacoids or lenticles lying in crushed black and cherty shales,—as, for instance, along the northern margin of the belt half a mile north-east of Maol Ruadh, and again at the side of the Aqueduct road south-west of Clashbeg Wood, where the phacoids are sometimes over two feet in length. Sometimes lenticles of dark grit are seen in the cherty shales of Clashbeg Wood and also immediately south and west of the Bofrishlie Burn, where it makes a sharp bend to the north between the south-western ends of Arndrum and Dungarrow. The crush lines along which the phacoids are seen usually occur within a few yards of the line or lines of dislocation separating the Highland Border Rocks and the Leny Grits.

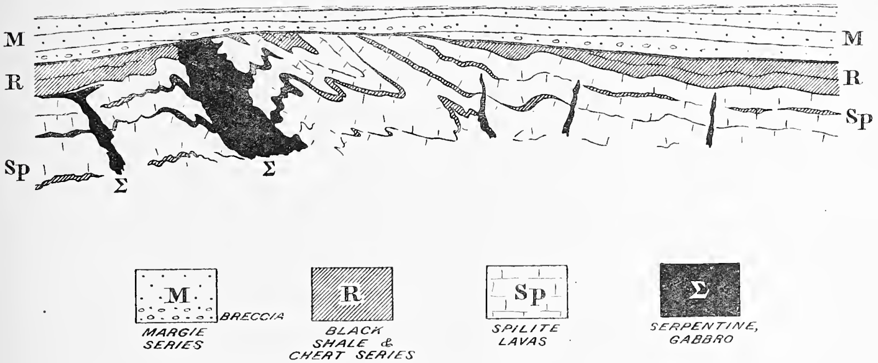


Fig. 2.—Diagrammatic section showing original relation of Upper to Lower Series.

The Belt of Metamorphic Rocks.—Intense shearing along a definite narrow belt, and probably at considerable depth, has resulted in the formation of schists both from hypabyssal and effusive igneous rocks and from cherty sediments associated with the Lower Series. The hornblende schists, which are the dominant rock type of the belt, represent, as has been already shown, original hypabyssal diabases and perhaps even gabbros; the calc-chlorite schists are altered spilitic lavas; the quartz schists are metamorphosed cherty sediments. The sediments underwent contact metamorphism prior to the development of foliation.

The extreme mineralogical and structural changes of those rocks, as compared with the corresponding rocks to the north-west, may be accounted for by the following factors: (*a*) intense local shearing; (*b*) probably an original greater cover, since the included metamorphosed lavas and iron cherts belong to a lower horizon than that of the unaltered lavas and cherts to the north; (*c*) the fact that the dynamic metamorphism may have followed close on the intrusion of the hypabyssal types, while these rocks and the adjoining sediments were still in a somewhat heated condition.

The period at which the shearing took place is an open question. Should the diabases and gabbros prove to have been intruded in pre-Margie times—as seems most likely,—then the shearing, which followed close on the intrusion, must belong to a phase of the pre-Margie movements of elevation and compression; on the other hand, it is possible that it may be a phase of the post-Margie Folding movements. Fragments of the rocks of the belt have not so far been recognised either in the Margie Grits or in the Leny Grits.

The belt is bounded on both sides by faults—on the south by the Jasper Fault, an overthrust which brings it in contact with the Lower Old Red Sandstone; on the north by a normal fault which brings it in juxtaposition sometimes with the Margie Grits, sometimes with different members of the Black Shale and Chert Series.

The Relation of the Highland Border Rocks to the Leny Grits.—The Leny Fault marks a line or lines of dislocation between the Highland Border Rocks and the Leny Grits. It hades at high angles to the north-west, and at places is almost vertical. As shown on the map and sections, figs. 3–10, the Leny Grits abut in some places against the Upper or Margie Series, and at others against the Lower or Black Shale and Chert Series. Cherts and Black Shales are nowhere seen *in situ* to the north-west of the Leny Fault.

The characters of the Margie Grits and Leny Grits have already been compared (pp. 200, 201) and their resemblances and differences discussed. It is important to note that clastic micas are common in the sediments of both series. The view held by Mr Barrow, that the Margie Series can be distinguished from the Highland Rocks to the north by the presence of clastic micas in the former and their absence in the latter, cannot be maintained, at any rate so far as the Aberfoyle district is concerned. If that is to be the criterion for separating the Highland Border Rocks from the more metamorphosed rocks of the Highlands in which the micas have been completely digested, the line separating the one from the other must be sought for further to the north-west.

The Serpentine-Gabbro-Dolomite Complex.—The serpentine-gabbro-dolomite complex, whose petrographical characters and affinities have already been discussed (pp. 195–197), can be traced almost continuously along the line of the main Highland Fault, which forms its southern boundary, from Gualann to the old limestone quarry north-east of Aberfoyle. Its delimitation northwards is also determined by a fault or faults. Its petrographical characters, as we have seen, leave little room for doubting that it represents an intrusive complex derived from the magma which gave rise to the spilites of the Black Shale and Chert Series. It may, therefore, be regarded as an integral part of the Highland Border group of rocks. As in the case of the albite diabase and the hornblende schists, its period of intrusion has not been established definitely. There can be no doubt that it is of pre-Lower Old Red Sandstone age, since its petrographical affinities are with the spilites and albite diabase rather than with the basic and ultra-basic facies of the newer granites of the Highlands. Again, since it is strongly foliated in places, it must be older than the post-Margie crustal movements. Further, as DU TOIT [*] has noted, in the region between Gualann and Balmaha well-rounded boulders, clearly derived from this complex, build up a serpentine conglomerate which may be the basement bed of the local Margie Series. It is possible, then, that the intrusion of the serpentines and gabbros took place in pre-Margie times. The dolomitisation and silicification of those rocks are, in part at least, of much later date, since dolomitic and siliceous ramifications from the main dolomite exposures penetrate the adjoining Lower Old Red Sandstone beds. Dolomite occurs as fault-rock on the line of the Highland Fault and the Gualann Fault, and the occurrence of jasper, which is seen from its microscopic characters to have resulted from the silicification of a ferruginous dolomite, is a feature characteristic of the course of the Jasper Fault.

Relation of the Highland Border Rocks to the Old Red Sandstone.—Along the whole area under consideration the Highland Border Rocks are separated from the main tract of the Lower Old Red Sandstone by the Highland Boundary Fault. From a point near the Boninty Burn opposite Clashbeg Wood westwards, however, a group of lower beds of the latter formation intervenes between the serpentine-gabbro complex and the zone of metamorphic rocks. Its southern boundary is determined by the Gualann Fault, its extension northwards by the Jasper Fault.

The outlier of rocks of Upper Old Red Sandstone age to the north-west of Gualann is faulted against the serpentine-gabbro mass along the line of the Gualann Fault. In the neighbourhood of that fault it is unconformable to the Lower Old Red Sandstone; to the north and west it overlaps successively the metamorphic belt, the black shales, cherts, and spilites of the Lower Series, and the beds of the Upper or Margie Series; finally is found resting directly on the Leny Grits.

[*] *Trans. Edin. Geol. Soc.*, vol. viii, p. 324, 1905.

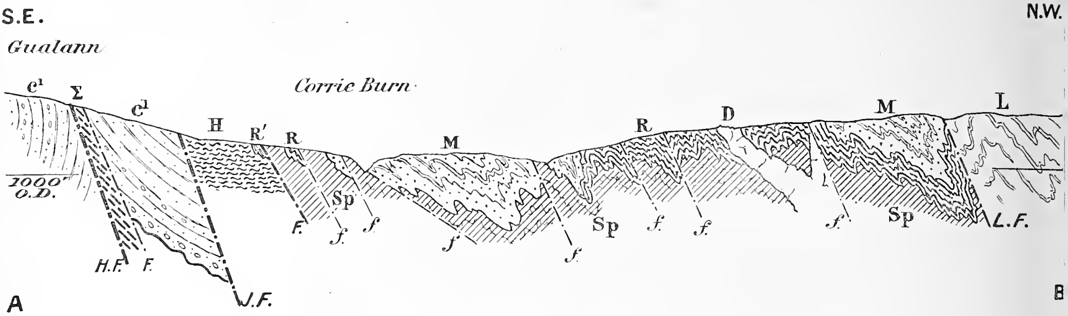


Fig. 3.

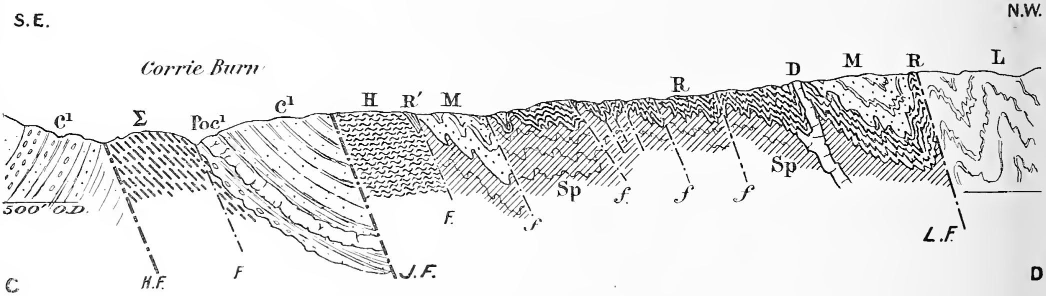


Fig. 4.

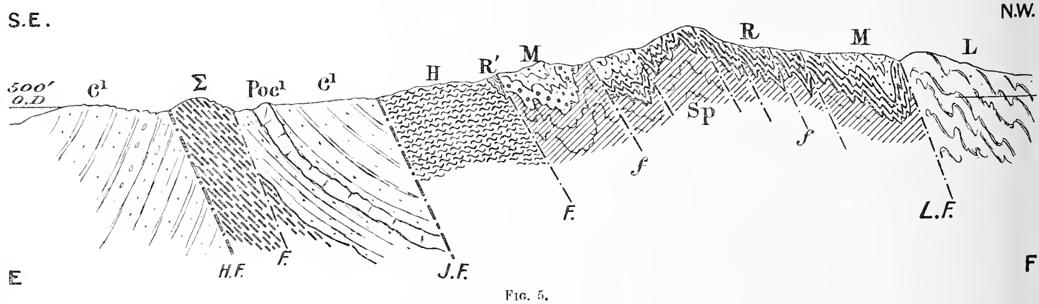


Fig. 5.

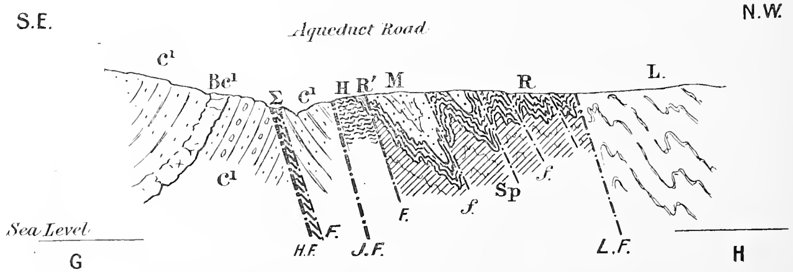


Fig. 6.

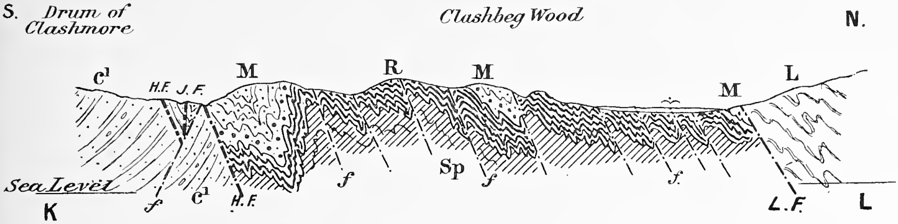


FIG. 7.

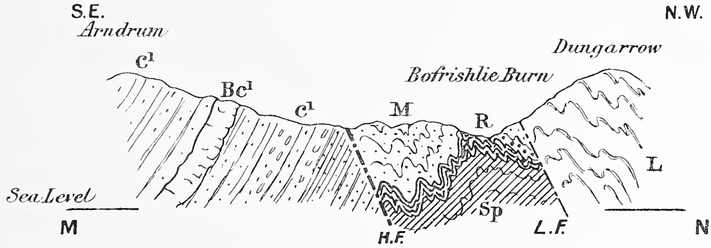


FIG. 8.

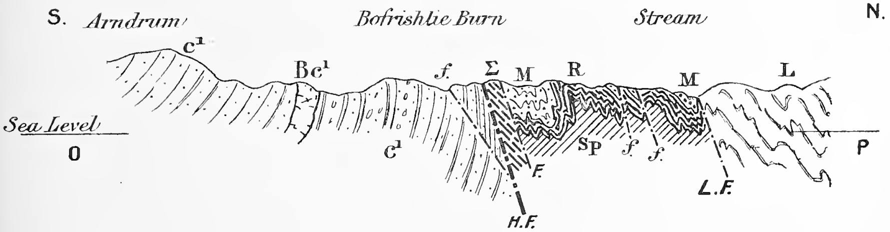


FIG. 9.

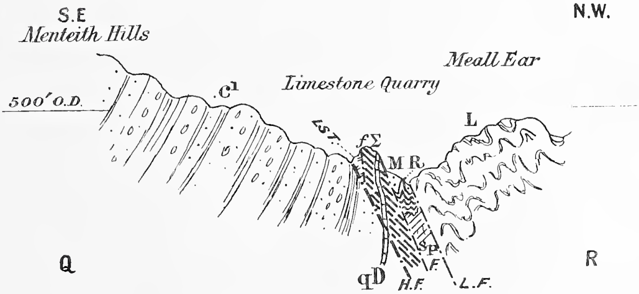


FIG. 10.

FIGS. 3–10.—Horizontal sections along the lines AB, CD, EF, GH, KL, MN, OP, and QR on map (Plate VI). Horizontal and vertical scales: 12 in. = 1 mile.

⌒⌒ = Superficial deposits; c^1 = Lower Old Red Sandstone; Bc^1 = Basaltic lavas; Poc^1 = Intrusive Porphyrite; qD = Quartz dolerite; M = Margie Series; Lst. = Aberfoyle limestone; R = Black Shale and Chert Series; R′ = Metamorphosed Black Shale and Chert; Sp. = Spilites; D = Albite diabase; Σ = Serpentine, gabbro and dolomite complex; H = Hornblende schist and chlorite schist; L = Leny Grits; H.F. = Highland Fault; J.F. = Jasper Fault; L.F. = Leny Fault; F = Major faults; f = minor faults.

Faults.—In the preceding pages mention has been made of the most important fault lines:—the Leny Fault, the Fault which forms the northern boundary of the belt of metamorphic rocks, the Jasper Fault, the Gualann Fault, and the Highland Fault, all of which trend north-east and south-west.

The Highland Fault and the Jasper Fault, which may be regarded as a branch of the former, are upthrusts from the north-west. The Jasper Fault can be traced eastwards from Gualann to a point in the Boninty Burn just south of Clashbeg Wood, where it is cut by a dip fault which shifts the main Highland Fault (see fig. 7). Beyond this point the Jasper Fault joins the main Fault. The Highland Fault, or rather complex of faults, is continuous along the southern margin of the Highland Border Rocks. It is of pre-Upper Old Red Sandstone age.

The Gualann Fault and the northern boundary Fault of the metamorphic belt are normal faults with downthrow to the north-west. From local evidence the former is seen to be of post-Upper Old Red Sandstone age; the later is subsequent to the folding of the Margie beds.

The Leny Fault may belong to the period of the post-Margie movements, which resulted in the folding, faulting, and crushing of the Highland Border Rocks, or it may be a normal fault of somewhat later origin.

In addition to the above strike faults, the rocks of the area are traversed by numerous dip faults which trend north-west and south-east. The courses of some of the more important of these are shown in the accompanying map (Plate VI).

XIII. Summary of Results.

1. The Highland Border Rocks in the district can be arranged in two divisions:—

   (*a*) The Lower Series, consisting of cherts, cherty shales, and black shales overlying and in less measure interleaved with spilitic lavas, and associated with igneous intrusions and with a group of highly metamorphosed rocks of both igneous and sedimentary origin.

   (*b*) The Upper or Margie Series, made up of grits, shales, and limestone, along with a remarkable basal breccia.

2. The sediments of the Lower Series point to deposition in clear water near the verge of sedimentation, from which coarse terrigenous material was excluded and in which *Radiolaria* thrived; the lavas indicate submarine volcanic eruptions. The beds of the Upper Series are unconformable to the Lower Series, and their constituent materials are in part the result of the denudation of the Lower Series. The Margie grits and shales are due to the accumulation of comparatively coarse terrigenous material laid down on a slowly subsiding land area. The basement breccia affords evidence of a recrudescence of volcanic activity at the beginning of Margie times.

3. The Lower Series is either of Upper Cambrian age or belongs to the Passage Beds between the Cambrian and the Ordovician.

The Upper Series includes a fossiliferous limestone, and may be placed with confidence on a higher horizon in the Ordovician system.

4. The igneous rocks, both lava-form and intrusive (including their metamorphosed representatives), which are associated with the Lower Series show certain affinities in mineralogical composition and in petrographical characters which lead to the conclusion that they have been derived from the same magma.

5. The hornblendic and chloritic schists are the result of the dynamic metamorphism of hypabyssal and volcanic rocks along a belt where these rocks were subjected to intense shearing. The metamorphosed sediments were affected by contact metamorphism prior to the dynamic metamorphism of the belt.

6. The whole belt of Highland Border Rocks is affected by lines of crushing and dislocation running in the direction of the general strike of the beds.

7. The age of the Leny Grits still remains an open question, and one on which further investigation is needed. But it is clear that a line or lines of dislocation separate these from the Highland Border Series.

XIV. Acknowledgments.

The area occupied by the Highland Border Rocks was mapped on the scale of six inches to a mile by Professor Jehu, who had the great advantage of having placed at his disposal by the late Dr C. T. Clough his field notes and the working copies of his map of the region. We wish to record here our indebtedness to Dr Clough not only for the assistance derived from perusal of his notes and maps, but also for the generous way in which he helped us from time to time in discussing difficulties in the light of his intimate knowledge of the district and of the problems involved.

The main boundary lines in the accompanying map coincide generally with those drawn by Dr Clough. The chief modifications are as follows: (*a*) the interpretation of the northern boundary of the hornblende-schist complex as a fault; (*b*) the mapping of a zone of spilitic lavas in the Gualann area, in part included by Dr Clough in the hornblende-schist complex; (*c*) the recognition of the breccias, which we regard as the basement beds of the Margie Series, on both sides of the main black shale and chert ridge; (*d*) numerous modifications of the boundary lines between the Black Shale and Chert Series and the Margie Series; (*e*) alteration of the position of the southern boundary line of the Leny Grits (particularly opposite Dungarrow) and its interpretation as a line or lines of dislocation: we understand that latterly Dr Clough adopted this interpretation for certain sections.

So far as we have been able to ascertain from his published and unpublished writings, our conclusions are different from those reached by Dr Clough in the following main particulars: (*a*) the definite separation of the Highland Border Rocks into a *Lower* and an *Upper Series* separated by an unconformity; (*b*) the discovery of fossils other than *Radiolaria* in the Lower (Black Shale and Chert)

Series and in the Aberfoyle limestone of the Upper (Margie) Series, and the consequent more definite determination of the age of the beds; (*c*) the recognition of spilitic lavas and intrusive albite diabases in the Lower Series and of albite gabbros associated with the serpentines; (*d*) the identification of the rocks of the hornblende-schist complex as metamorphosed representatives of the igneous and sedimentary rocks of the Lower (Black Shale and Chert) Series.

We wish also to express our thanks to Dr PEACH for the interest he has taken in our investigations, for many valuable suggestions, and particularly for his assistance in the determination of the fossils; to Dr FLETT for the opportunities he has given us of comparing our rocks with similar rocks from other districts; and to Mr CUTHBERT DAY for the trouble which he has taken in connection with the photographic illustrations.

Grateful acknowledgment must also be made to the Carnegie Trust for a grant to defray the expenses incurred in the preparation and reproduction of the illustrations.

XV. EXPLANATION OF PLATES.

PLATE I.

Acrothele (*Obolella*) *maculata*, Salter.

Fig. 1. Interior of dorsal valve; distorted.

Fig. 2. Exterior of the dorsal valve with the ventral valve appearing from underneath. (See p. 189.) [T. 2690^D, Geological Survey Collection.] Inset—*d* = dorsal valve; *v* = ventral valve.

Fig. 3. Interior of ventral valve.

Acrothele aff. *coriaceæ*, Linn. (See p. 190.)

Fig. 4. Exterior of ventral valve. Inset—part of surface much enlarged, showing the external ornamentation.

Acrothele (*Redlichella*) *granulata*, Linn. (See p. 190.)

Fig. 5. Exterior of ventral valve. Inset—part of surface much enlarged, showing the external ornamentation. *Radiolaria* are seen in the matrix of the rock. (See p. 187.)

Acrotreta nicholsoni, Dav. (See p. 190.)

Fig. 6. Interior of both valves.

Fig. 7. Exterior of ventral valve. *Radiolaria* are seen in the matrix of the rock. (See p. 187.)

Fig. 8. Exterior of ventral valve.

Fig. 9. Interior of ventral valve.

Fig. 10. Exterior of ventral valve.

Fig. 11. Interior of dorsal valve; wrinkled. *Radiolaria* are seen in the matrix of the rock.

Fig. 12. Exterior of ventral valve and interior of dorsal valve.

Acrotreta socialis, von Seebach.

Fig. 13. ? Cast of interior of ventral valve. *Radiolaria* showing spines radiating from centre (See p. 187.)

Fig. 14. Interior of dorsal valve. (See p. 190.) [T. 2621^D, Geological Survey Collection.]

Fig. 15. Interior of ventral valve. (See p. 190.)

Acrotreta aff. *sabrinæ*, Calloway.

Fig. 16. Interior of dorsal valve. (See p. 190.)

Siphonotreta aff. *micula*, M'Coy. (See p. 191.)

Fig. 17. Exterior of ventral valve.

Fig. 17A Drawing (enlarged) of above.

Siphonotreta aff. *scotica*, Dav. (See p. 191.)
Fig. 18. Cast of interior of ventral valve with part of rim of exterior of the valve.
Fig. 18A. Drawing (enlarged) of above.

?*Schizambon*, Walcott. (See p. 191.)
Fig. 19. Interior of dorsal valve.
Fig. 19A. Drawing (enlarged) of above.

Lingulella aff. *ferruginea*, Salter. (See p. 189.)
Fig. 20. Cast of interior of dorsal valve above and portion of interior of ventral valve below.
Fig. 21. Interior of ventral valve.
Fig. 22. Exterior of ventral valve.

Lingulella aff. *nicholsoni*, Calloway. (See p. 189.)
Fig. 23. Interior of dorsal valve; shell distorted and broken.

Photographs all magnified 5 diameters. Magnification of drawings 17A, 18A, 19A as shown on Plate. Figs. 17A, 18A, 19A, and the insets to figs. 2, 4, 5, are from drawings by Dr Peach. All the other figures are from untouched photographs.

Plate II.

Graptolitoidea. (See p. 187.)
Fig. 1. A Diplograptid—*Trigonograptus* or *Cryptograptus.* × 6½.
Fig. 1A. Counterpart of specimen shown in fig. 1. × 6½.
Fig. 2. A Diplograptid—*Trigonograptus* or *Cryptograptus.* × 5.
Fig. 2A. Counterpart of specimen shown in fig. 2. × 5.
Fig. 2B. Same specimen as that shown in fig. 2A. × 7.

Phyllocarida. (See p. 191.)
Fig. 3. *Modiolocaris dakynsi*, Peach. × 5.
Fig. 3A. Drawing of above.

Incertæ sedis. (See p. 192.)
Fig. 4. Fragment of some Arthropod. × 5.
Fig. 5. Punctate stain of some Arthropod. × 5.
Fig. 6. Jaw of an Annelid or one of the cheliceræ of an Arthropod. × 5.
Fig. 6A. Drawing of above (slightly enlarged as compared with fig. 6).
Figs. 7 and 8. Cercopods of a Phyllocarid Crustacean. × 5.
Fig. 9. Triangular plate, pitted, of an unknown form. × 5.

The Aberfoyle Limestone.
Fig. 10. Photograph of a hand specimen showing the columnal of a Crinoid. × 6.
Fig. 11. Photomicrograph of thin section of rock showing organisms. × 10. (See No. 1, p. 193.)
Fig. 12. Photomicrograph of thin section of rock showing organisms. × 25. (See No. 5, p. 193.)
Fig. 13. Photomicrograph of thin section of rock showing organisms. × 25. (See No. 2, p. 193.)

Figs. 3A and 6A are from drawings by Dr Peach. All the other figures are from untouched photographs.

Plate III.

Photomicrographs of Rocks.

Fig. 1. *Variolitic spilite*, Gualann, magnified 25 diameters. The variolitic arrangement of the albite laths is well seen. (See p. 181.)

Fig. 2. *Breccia* from exposure about ⅓ mile north-east of the ruins of Bofrishlie Farm, magnified 10 diameters. The white grains are quartz; the elliptical grain in the upper portion of the figure is orthoclase; the fragments with irregular margins are palagonite; the angular and subangular pieces of fine-grained sediments are cherty shales and mudstones. (See p. 183.)

Fig. 3. *Albite diabase*, from large intrusion north of Gualann, magnified 25 diameters; nicols crossed. Chief constituent is albite in large rectangular plates and in narrow laths enclosed in titanaugite in ophitic fashion. The black crystals are ilmenite. (See p. 195.)

Fig. 4. *Dunite serpentine*, Maol Ruadh, magnified 10 diameters. Most of the field is occupied by serpentine and carbonates after olivine with characteristic mesh structure. The black crystals are chrome spinels. On the extreme right is seen a vein of tufted anthophyllite. (See p. 195.)

Fig. 5. *Ferruginous dolomite*, south-west of old limestone quarry, north of Upper Dounans, Aberfoyle, magnified 10 diameters. Most of the rock consists of carbonates, with which is associated a little serpentine. The black crystals are chrome spinels. Mesh structure is preserved. (See p. 196.)

Fig. 6. *Hornblende schist*, opposite Maol Ruadh, magnified 10 diameters. The characteristic lenticular distribution of the felspar is shown. The veinlets traversing the schistose structures consist of albite and chlorite. (See p. 198.)

PLATE IV.

Photomicrographs of Rocks.

Fig. 1. *Hornblende schist*, opposite Maol Ruadh, magnified 25 diameters; nicols crossed. The centre of the field is occupied by an area of felspar. The equidimensional nature of the albite crystals is in sharp contrast with the elongated character of the crystals of hornblende. (See p. 198.)

Fig. 2. *Actinolite schist*, Corrie Burn, magnified 10 diameters. The rock consists of a coarsely crystalline schistose aggregate of colourless actinolite. (See p. 198.)

Fig. 3. *Garnetiferous epidiorite*, Corrie Burn, magnified 10 diameters. The anhedral garnets stand out in relief from the surrounding dark minerals (hornblende) and the lighter areas which are occupied by felspar and quartz. The narrow veinlet consists of chlorite. (See p. 198.)

Fig. 4. *Calc-chlorite schist*, Corrie Burn, magnified 25 diameters; nicols crossed. Lath-shaped crystals of albite, in parallel arrangement, associated with chlorite and carbonates. (See p. 199.)

Fig. 5. *Quartz schist*, from exposure by the roadside just beyond the Old Loch Katrine Aqueduct, magnified 25 diameters. The lighter bands consist of a granulitic mosaic of quartz with associated pale-green micas; the darker bands are made up largely of iron oxides. (See p. 199.)

Fig. 6. *Chloritic phyllite*, from lower slopes of Gualann, near the Corrie Burn, magnified 10 diameters. The photograph shows the corrugated folding which is characteristic of the fine sediments associated with the hornblende schists. (See p. 200.)

PLATE V.

Fig. 1. North-eastern side of old limestone quarry, north of Upper Dounans, Aberfoyle, showing from left to right quartz dolerite dyke on the line of a branch of the Highland Fault; serpentine-dolomite complex; and conglomerates of Lower Old Red Sandstone age.

Fig. 2. The Black Shale and Chert Series at the fossil locality on the right bank of the Bofrishlie Burn. The almost vertical folding of the beds is well seen.

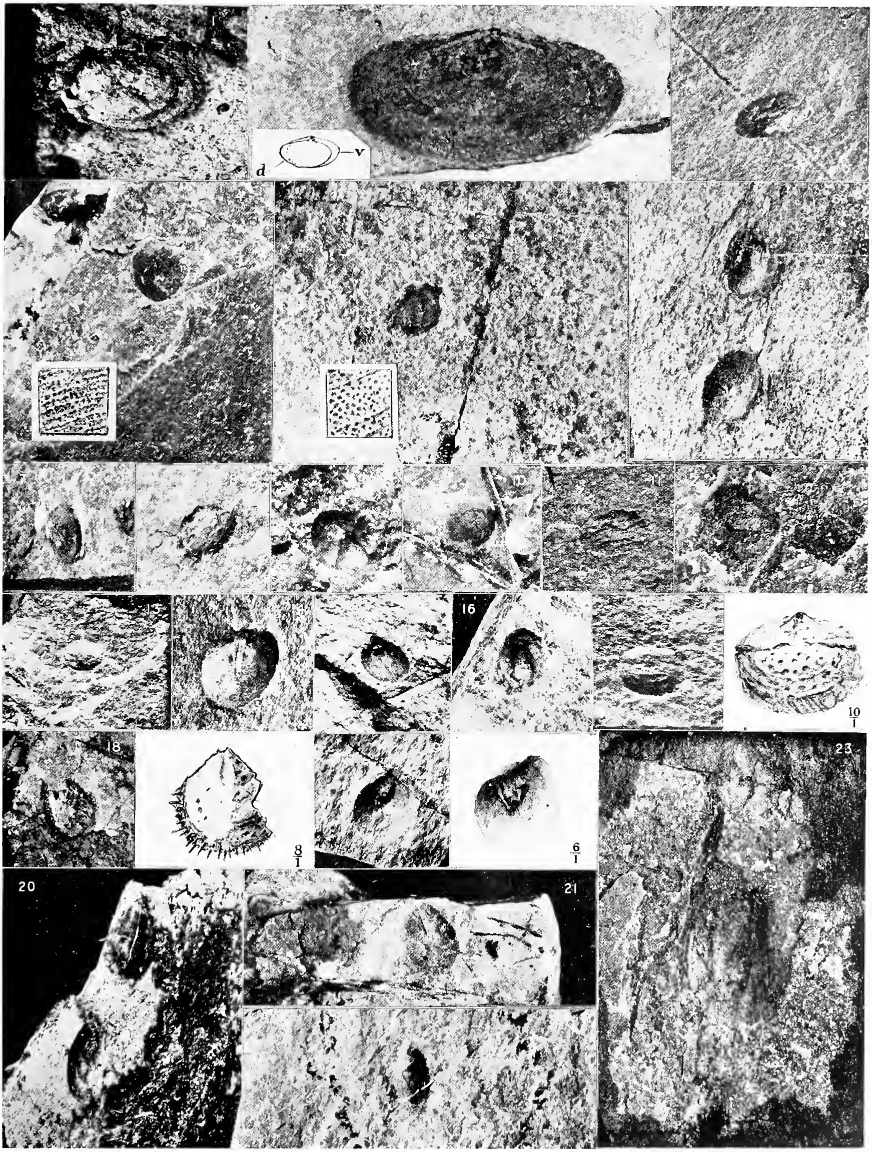
Fig. 3. Intensely folded and faulted interlaminated cherts and shales on the prominent ridge north-west of Lime Hill.

Fig. 4. Large included blocks of cherty shale in the basement breccia of the Margie Series at a knoll just south of a small stream about 300 yards north-west of the ruins of Bofrishlie Farm.

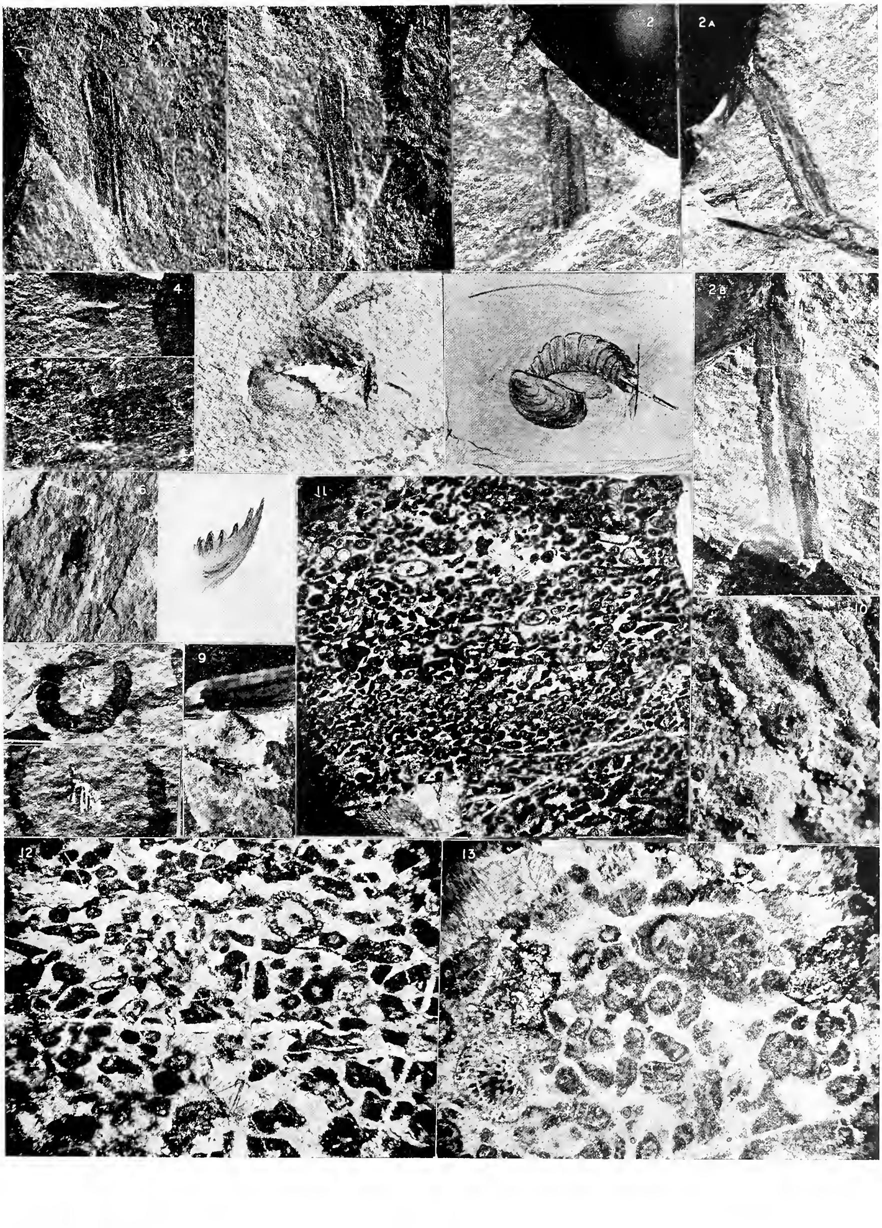
PLATE VI.

Geological map of the Aberfoyle district. [Geological lines on the area south of the Highland Boundary Fault are taken from the published map (scale one inch to a mile), Sheet 38, of H.M. Geological Survey.]

Professor T. J. Jehu and Dr R. Campbell: "The Highland Border Rocks of the Aberfoyle District."—Plate I.



Professor T. J. Jehu and Dr R. Campbell: "The Highland Border Rocks of the Aberfoyle District."—Plate II.



Professor T. J. Jehu and Dr R. Campbell: "The Highland Border Rocks of the Aberfoyle District."—Plate III.

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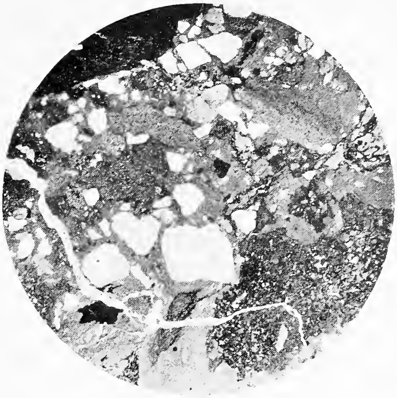

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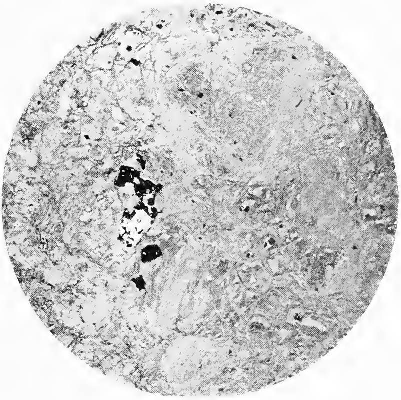

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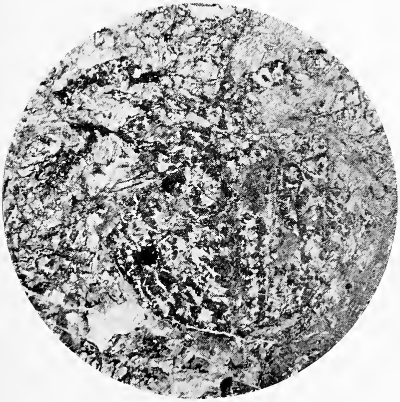

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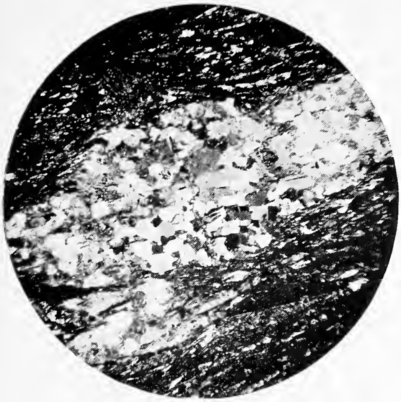
Professor T. J. Jehu and Dr R. Campbell: "The Highland Border Rocks of the Aberfoyle District."—Plate IV.



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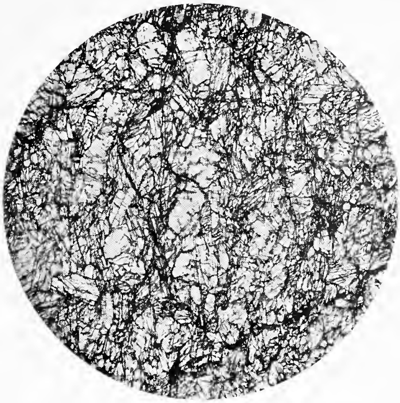

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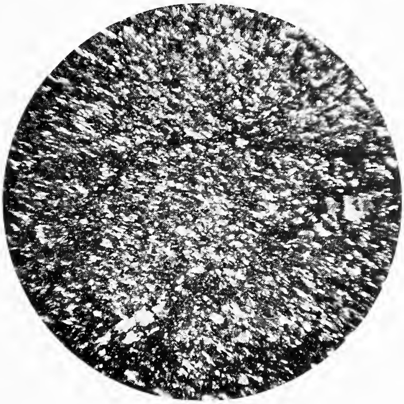

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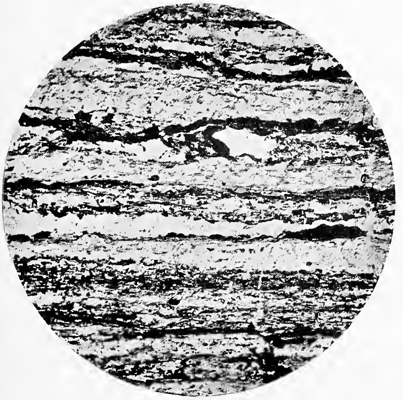

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Professor T. J. JEHU and Dr R. CAMPBELL: "The Highland Border Rocks of the Aberfoyle District."—PLATE V.

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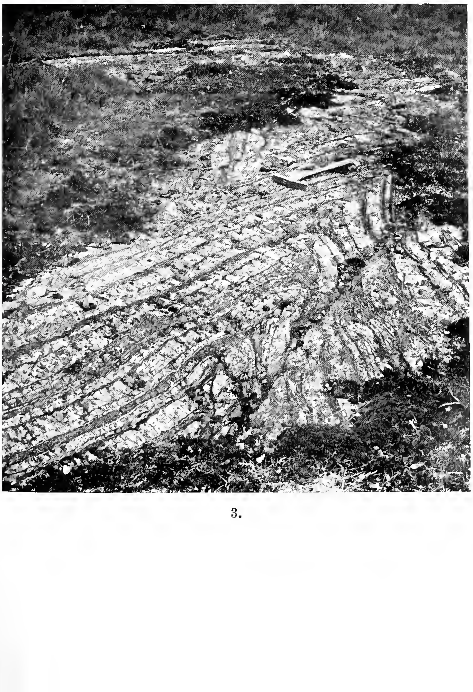

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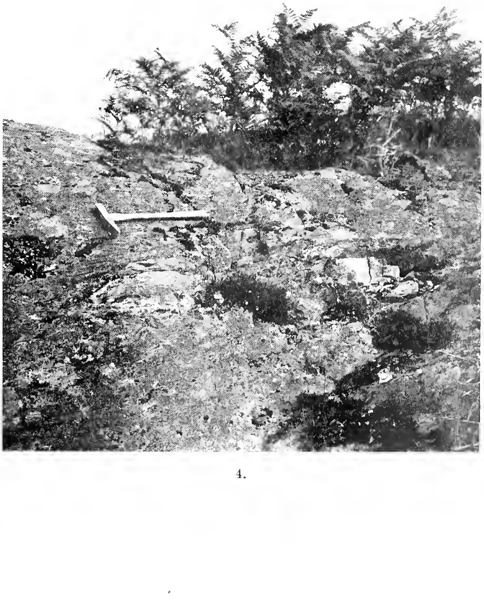

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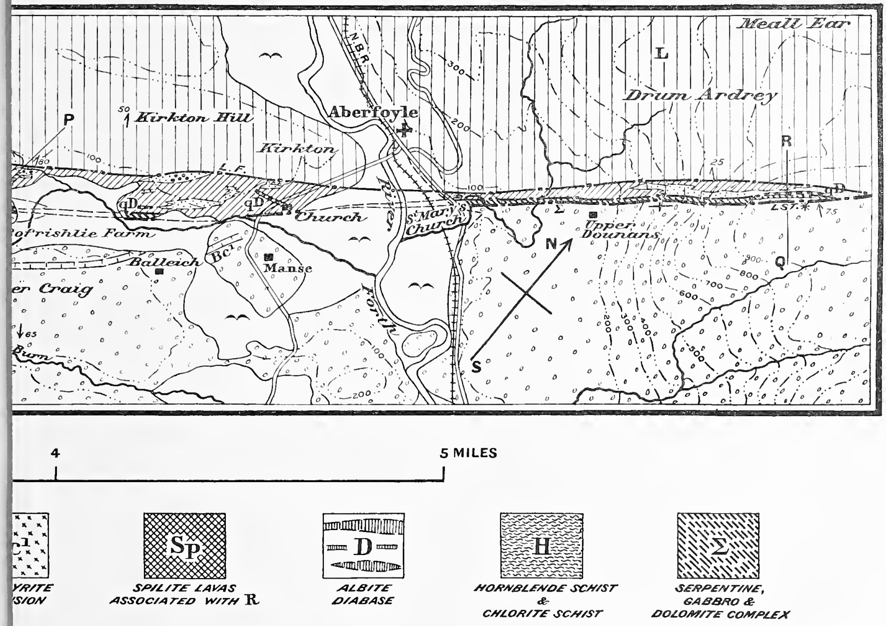
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Σ
SERPENTINE,
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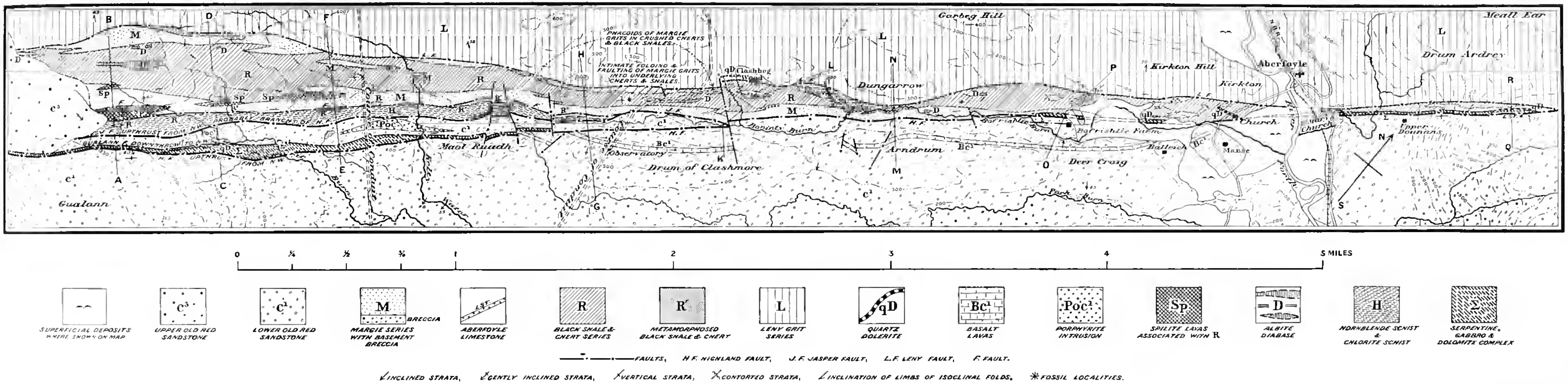
DOLOMITE COMPLEX

CALITIES.

Professor T. J. Jehu and Dr Robert Campbell: "The Highland Border Rocks of the Aberfoyle District."—Plate VI.



X.—The Structure, Bionomics, and Forest Importance of Myelophilus minor Hart.

By **Walter Ritchie**, B.Sc., B.Sc. (Agr.); Fullerton Scholar, University of Aberdeen; Research Scholar, University of Edinburgh. *Communicated by* Dr R. Stewart MacDougall. (With Two Plates.)

(Read January 22, 1917. MS. received March 31, 1917. Issued separately December 4, 1917.)

The two beetles *Myelophilus minor* Hart. and *Myelophilus piniperda* Linn. belong to the family Scolytidæ (the Ipidæ of Hagedorn), of the series *Rhynchophora* or snouted beetles.

The genus *Myelophilus* Eichhoff has the following characters: (1) the biting edges of the maxillæ are beset with spines, (2) third basal tarsal joint broadened out, (3) head with rostrum visible, (4) funiculus of antenna six-jointed, (5) club of antennæ not quite round but somewhat pointed at the apex, (6) head and thorax with outstanding hairs, (7) front edge of thorax not depressed in the middle.

The genus has four species, of which two are native of Britain, viz. *Myelophilus piniperda* (*Hylurgus* of the British catalogue), well known throughout Britain to the forester, and often called by him the "Pruner"; and *Myelophilus minor*, till now scarcely known at all in Britain, and described by Fowler * as very rare.

In the Aboyne district of Aberdeenshire, however, I have found this species occurring in very large numbers over an area of fifteen square miles. Later in this paper I give reasons for the references to this beetle in our British literature being so scanty.

To the forester these two species are of primary importance, as they prove very destructive to pine plantations in all stages of growth; firstly, by their attacking and boring into the tender shoots of pines; and secondly, by boring into pine stems for breeding purposes, the brood galleries in the bast and cambial regions ultimately causing the death of the trees.

The aim of the present paper is to describe the life-history, habits, and important anatomical features of *M. minor*, contrasting them with those of *M. piniperda*, so that its presence may be more readily recognised and preventive and remedial measures based on its life-history may be undertaken.

Description of the Two British Species of the Genus Myelophilus.

The following is Fowler's † description:—

M. piniperda L.—Black or pitchy black, or black with the elytra dull red, often entirely testaceous, shining; oblong, subcylindrical, clothed with a rather scanty

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* Fowler's *Coleoptera of the British Islands*, vol. v, p. 420.

† *Ibid.*

pilose pubescence; head somewhat strongly produced, distinctly punctured; antennæ ferruginous; thorax near base about as broad as or a little broader than long, much narrowed and somewhat compressed in front, rather finely punctured, the punctuation, however, being variable in different specimens and being closer and stronger at sides than on disc; scutellum rather large, punctured; elytra separately and broadly rounded at base, with comparatively fine punctured striæ; interstices punctured, somewhat granulose at base, and raised into asperate tubercles at apex; apex of second interstice depressed and without tubercles; legs black, tarsi red. Length 3½–4 mm.

M. minor Hart (fig. 1).—Very like the preceding, but on the average a little smaller (although according to Thomson it is of the same size), with the striæ of the elytra finer and more finely punctured, and the interstices more closely punctured, the second not being depressed and being furnished with a series of small tubercles on its apical declivity. It is also distinguished by the fact that of the teeth on the hind tibiæ one is situated about the centre of the tibiæ; the same tooth in *piniperda* is past the centre; the elytra are usually brownish red. Length 3½–3¾ mm.

In Fowler's description of *M. minor* no special mention is made of the shape of the prothorax. In what might be described as typical specimens the prothorax is cone-shaped and has a smooth middle line (fig. 2). In many specimens of *M. minor*, however, in the proportion perhaps of 1 to 30, there is a distinct variety where the shape of the prothorax differs from the above. In this variety the prothorax is markedly narrowed in front and has a distinct elevation along the middle line (fig. 3).

Further, while on the whole this is a slightly smaller species than *M. piniperda*, as its name *minor* indicates, yet I found not rarely specimens slightly exceeding Fowler's figures.

In the table which follows I contrast in two columns these two beetles, emphasising characters which have proved most helpful in my work with them.

	M. minor.	M. piniperda.
Size	3·5 mm. – 4·5 mm.	3·5 mm. – 5 mm.
Elytra of mature beetles	Reddish brown	Black, sometimes dark reddish brown
Apex of second interstice of elytra	Bears a row of tubercles and is not hollowed out (fig. 4)	Bears no tubercles and is hollowed out (fig. 5)
Posterior tibiæ	Tooth about centre (fig. 6)	Tooth past centre (fig. 7)

A rough-and-ready character which often proved useful to me in distinguishing the one species from the other is that, owing to the finer nature and hence greater transparency of the elytra of *M. minor*, the dorsal portion of the third segment of the thorax, *i.e.* the metanotum, can be seen showing through them as a dark triangular area, whereas in *M. piniperda* the elytra are coarser and not so transparent and no such dark area can be seen, although of course on removal of the elytra the metanotum is visible. At first it seems to be quite impossible to distinguish the two species with the naked eye, yet with a little practice the two beetles can be readily distinguished. If the insects be held between the first finger and thumb and be looked at sideways, the apical part of the elytra of *M. minor* appears shiny all over, since there are no hollowed-out portions on the second interstices. On the other hand, the apical part of *M. piniperda* held in a similar position appears shiny, except at the second interstices of the apical portion of the elytra; there it appears dull, due to the hollowing out of the second interstice on each side of the suture. This character is undoubtedly the chief differentiating character between the two species.

Sexual Differentiation in M. minor.

It is difficult to distinguish the two sexes of this beetle by external characters, yet with the aid of a binocular dissecting microscope the following differences can be noted:—

(1) The under surface of the last segment of the abdomen in the female is markedly convex from front to rear, while in the male this same part appears flattened or slightly concave.

(2) The ventral surface of the abdomen is much more convex from side to side in the females than in the males, in which the ventral surface is flattened.

These same two characters can be safely relied on for differentiating the sexes of *M. piniperda.*

A further aid in distinguishing the sexes in *M. piniperda*, pointed out by Eichhoff,* is that the apical part of the second interstice is narrower, deeper (more hollowed out) in the male, and in the female broader and shallower. I have repeatedly tested this and found it a most useful character.

Egg of M. minor.

The egg is oval in shape, smooth, and in colour shining white. It measures 1 mm.

The eggs of *M. piniperda* and *M. minor* are indistinguishable.

Larva of M. minor (fig. 8).

The larva of *M. minor* is a typical Scolytid larva, and is well adapted to its mode of life. It is a soft, cyclindrical grub, legless, with curved body. The colour is yellow-white, except the hard chitinous head and mouth parts, which are dark

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* W. J. Eichhoff, *Die europaischen Borkenkäfer*, p. 101.

brown in colour. The body is deeply wrinkled, with fine hairs scattered over it. The larva is made up of the chitinous head-piece and thirteen segments, the first three segments forming the thorax and the remaining ten the abdomen. The thoracic segments are slightly larger than the abdominal ones. The 8th and 9th abdominal segments are much smaller than the others, while the 10th is made up of three lobes around the anus. The 1st thoracic segment and the first eight abdominal segments bear each a pair of spiracles. The full-grown larva measures on an average 4·5 mm.

The Head (fig. 9).

The head of the larva of *M. minor*, viewed from above with the aid of a binocular microscope, shows the following:—In the centre of the chitinous head-piece may be seen a triangular region called the frons (*f.*); at the anterior corners of the triangular frons lie the antennæ (*a.*), each single-jointed and sunk in a pit; along the anterior base of the frons is a narrow area, the epistome (*e.*), composed of a thick band of chitin extending from one antennal pit to the other and supporting anteriorly the clypeus (*c.*); anterior and jointed on to the clypeus is the labrum (*l.*).

On either side of the frons posteriorly lies the epicranium (*ep.*), divided into two by the frontal sutures (*f.s.*) anteriorly, and by the epicranial suture posteriorly (*e.s.*).

Examined from above, the mandibles (*m.*) can be seen in part projecting beyond the labrum; their greater part, however, is overlapped by the labrum. Each mandible shows three prominent teeth, is dark brown in colour, and is highly chitinised.

As the shape of the epistome is often used as a means of distinguishing one species of larva from another, I have figured an enlarged view of this region of the head (fig. 10).

Looking at the head from the ventral side, one can see the maxillæ (fig. 11). The 1st maxillæ are the outermost parts in this view and are composed of three portions: posteriorly the cardo (*C.*), anterior to this the stipes (*S.*), which bears the three-jointed maxillary palp (*M.p.*) and a few bristles, and thirdly, the lacinial lobe (*l.l.*), which has fairly strong bristles. In the centre is the labium or fused 2nd maxillæ, which comprises the mentum (*M.*) anteriorly, bearing two labial palps (*l.p.*), each of which is two-jointed, and the ligulæ (*l.*) in the middle line. The submentum (*S.m.*) is posterior to the mentum, while still more further back is the submental area (*S.a.*).

The Thorax.

In a side view (fig. 8) of the thorax of the larva we have the prothoracic segment lying just behind the head, next the mesothoracic, and next the metathoracic segment. These are the three largest segments of the body.

The prothoracic segment in side view shows the following five folds[*]: the scutellar (*Sr.*) forming the dorso-lateral portion; the scutal (*Sc.*) and the epipleural (*e.*) forming the lateral portion, the latter being more anterior and ventral than the former; the hypopleural (*h.*) and sternellar (*St.*) forming the ventral portion, the sternellar fold being more ventral than the hypopleural. The scutal fold bears a spiracle which is situated in its most ventral part.

The mesothorax in side view shows six folds: the prescutal (*p.*) forms the anterior dorsal portion; the scutellar (*Sr.*) forms the dorso-lateral portion; the scutal (*Sc.*) and epipleural (*e.*) form the lateral portion; and the hypopleural (*h.*) and sternellar (*St.*) form the ventral portion. The metathoracic segment is similar to the mesothoracic.

The Abdomen.

The first seven segments of the abdomen of the larva (*c*, fig. 8) correspond in structure although they vary in size. In side view each shows six folds: the prescutal (*p.*), scutal (*Sc.*), and scutellar (*Sr.*) forming the dorso-lateral portion; the epipleural (*e.*) forming the lateral portion; while the hypopleural (*h.*) and sternellar (*St.*) form the ventral portion as before.

On each segment lying between the epipleural, and scutal, and scutellar folds there is an **S**-shaped groove in the anterior dorsal side of which lies a spiracle (*Sp.*).

The 8th abdominal segment is similar to the first seven, except that there is no prescutal fold; the scutellar fold is just traceable. The 9th abdominal segment is similar to the 8th, only it bears no spiracles. The 10th segment in side view shows three lobes surrounding the anus: the infra-anal lobe (*i.*) is situated ventral to the anus, the supra-anal (*Su.*) dorsal, while the para-anal (*pa.*) is between the above two.

In a ventral view of the larva two other folds may be seen, namely, the sternal and poststernellar. These two folds are present in all the segments of the thorax and abdomen, except in the last three of the abdomen. In the 8th and 9th the poststernellar is absent, while in the 10th both are wanting. The sternal fold comprises the anterior central portion of the ventral surface of each segment, while the poststernellar lies posterior to the sternellar. The poststernellar comprises the posterior portion of each segment; only the lateral portions of this fold are visible in the prothoracic segment.

COMPARISON BETWEEN HEAD OF LARVA OF M. MINOR AND M. PINIPERDA.

After careful microscopic examination of numerous preparations of the head and mouth parts of the two different larvæ, I have come to the conclusion that there is no satisfactory differentiating character. I have examined the parts mounted and unmounted, under cover-glasses where the pressure had the tendency to move the

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[*] In this description of the larva I have followed the terminology of HOPKINS, "The genus *Dendroctonus*," *U.S. Bureau of Entomology*, Bulletin No. 83, part i, p. 11, 1909.

parts slightly out of position, and without cover-glasses or pressure; preparations boiled in caustic potash, and untreated natural preparations, and without satisfactory differentiating results. In some cases it seemed that the shape of the labral edge of the clypeus—straight-edged or more rounded—would prove a helpful character for distinction, but examination of a large series of specimens proved that one could not rely absolutely on this character.

The close resemblance between the larvæ of the two species is not difficult to understand, as not only are they very near to one another in actual relationship, but their food habits are practically identical, both living below the bark and tunnelling in the bark and sometimes in the outermost layers of the sapwood.

The Pupa.

The pupa of *M. minor* in general size and form resembles the adult insect. It is white in colour, but soon becomes darker brown. The darkening of colour first reveals itself in the eyes, which show as two black spots, and in the mandibles, which show as two dark-brown patches.

In a ventral view of the pupa (fig. 12) the chief divisions of the body and their appendages are visible.

The vertex or front portion of the head bears on either side of it a few very small spines (*f.s.*) which are widely separated from one another. On each side of the head region there is present the antenna (*a.*), at the anterior base of which is situated the eye (*e.*). Posterior to the base of the antenna lies the gena (*g.*) or cheek region. Between the genæ lies the labrum (*l.*) or upper lip and the other mouth parts, viz. the mandibles (*m.*), the 1st maxillæ (*mx.*), and labium (*li.*).

The three pairs of legs are folded along the surface of the body, the last pair more or less overlapped by the elytra and wings (*el.* and *w.*), only the coxæ (*d*) and femora (*h*) being visible. The femora of the 1st and 2nd pairs of legs show small projecting spines (*f.sp.*) on their apical parts. Between the coxæ of the last pair of legs is situated the intercoxal area (*i.a.*).

Of the thorax the meso- and metasternum is visible; a deep groove (*o*) runs up the centre of the last-named portion.

Of the abdomen the sternal parts of the last eight segments are visible: the 9th segment bears two prominent fleshy projections or spines (*c.s.*), the presence of which is characteristic of Scolytid pupæ; the 10th segment (*r*) appears only as an oval patch intersected by grooves. On either side of the body the elytra (*el.*) are situated, while from under them project the tips of the flying wings (*w.*).

In the dorsal aspect of the pupa the noteworthy characters are the lateral spines on the pronotum, the scutellum at the base of the elytra, two rows of small fleshy spines along the dorsal part of the abdominal segments, and usually three rows of small fleshy spines—the pleural spines—parallel to the sides of the body.

The Brood Galleries of M. minor (fig. 13).

The brood galleries of *M. minor* are very characteristic, and, as will be seen by reference to fig. 13, it is quite impossible to confuse them with those of *M. piniperda*. Consequently, they are of great aid to the forester, in absence of beetles themselves, helping him to decide which species is at work. The typical mother gallery of *M. minor* is two-armed and runs in the transverse direction. The larval galleries run vertically upwards and downwards, and are not quite close to one another. There is a variation in the length of the mother galleries in my specimens from 1¼ to 6¼ inches. The long mother galleries were found on stems not so badly infested, and where therefore the beetles had room to work. The short mother galleries were found on very badly infested stems, the mother galleries in these conditions being shorter owing to overcrowding. As a rule a long mother gallery did not carry with it a larger number of eggs than the number in a shorter gallery: in the shorter galleries the eggs were closer together. The larval galleries were short, and at a greater distance from one another when the mother galleries were long.

The larval galleries also varied to some extent in length. The shortest measured was ⅜ inch in length, while the longest was 1 inch.

In my observations the female not only made the two-armed gallery in which she laid her eggs, but also the entrance portion of the gallery from the outside. While the female was in one arm of the gallery I often found the male in the other arm. The male works in throwing out the bore meal made by the female. In monogamous bark-boring species the female appears to do all the work of boring, and pairing takes place under cover or with the female half hidden. The female does not complete her gallery and then proceed to egg-laying, but lays her eggs in niches cut on either side as she continues to tunnel.

The two-armed gallery is completed in about 25 days to one month. In 50 separate cases which I recorded in my notebook the number of eggs laid was 21. The highest number I ever found was 31. Never in any completed gallery have I found a less number than 19.

When the eggs hatch the larvæ proceed to burrow along the inner bark layers at right angles to the mother gallery. The gnawed material from which they derive nourishment is passed through the alimentary canal. The undigested material is passed out behind and may be found lying in the tunnel, partly choking it up. Thus if a piece of bark be removed from the stem, the mother and larval galleries are very well marked on it.

When feeding is completed the larvæ pupate. Their place of pupation depends entirely on the thickness of the stems which have been chosen for brood purposes. Where the bark is very thin—for example, nearer the crown of the tree—the full-fed larvæ tunnel, it may be ¼ inch into the sapwood, where each larvæ excavates a bed in which pupation takes place. This pupal bed lies in the longitudinal direction.

Where the bark is somewhat thicker, pupation takes place in the bark or between the bark and the sapwood. Usually in the thicker-barked places pupation takes place in the bark itself. It was not uncommon, however, to find pupation in the bark even where the bark was thin, and in such places the pupæ were close to the outside. So near the outside were the pupæ in many cases that on the bark scales being removed pupæ fell away. After pupation the new beetles eat their way out through the bark or through sapwood and bark.

Overcrowding of mother galleries on badly infested stems occurs very frequently, and as a result these mother galleries are often very irregular in form (fig. 14). Some are one-armed, and, like the typical galleries, vary in length from 1¾ to 3 inches. In other cases one arm is much longer than the other; for example, in a few cases examined the left arm measured ½ inch, while the right arm measured 2½ inches. These galleries, though irregular, always showed on dissection a number of eggs equal to what were found in a normal two-armed mother gallery. Some mother galleries cut into adjacent galleries, linking up with them, and in this way form a network girdling the stem. In such cases the larval galleries are also quite irregular. Where larval galleries ran into other larval galleries, and these latter continued as single galleries, the weaker larvæ fell before the stronger.

Another kind of irregularity is that found where the beetles have used for brood purposes felled stems left lying. In such a case I found (see fig. 15) that the entrance-holes were made on the upper exposed surface, and the females cut single-armed galleries. These were long, and always down the shady side.

As will be seen from fig. 13, the brood galleries of *M. piniperda* are quite different from those of *M. minor*. The typical mother gallery is vertical, while the larval ones are horizontal. The length of the mother gallery of *M. piniperda* is variable. On standing stems I measured galleries varying in length from 3 to 7 inches. On felled stems the galleries were considerably longer. The mother gallery is somewhat bent at its commencement, broadening out slightly just underneath the bark for about ¼ inch. The female, as in the case of *M. minor*, does all the work, laying eggs as she bores, and placing them in niches on either side. The eggs in a single mother gallery are much more numerous than in the case of *M. minor*. They vary in number from 50 to 120. The male throws out the bore meal that results from the gnawing of the female, and is usually found in the gallery behind her.

The brood galleries, as in the case of *M. minor*, are in the inner bark layers, and are found more rarely cutting the sapwood. These larval galleries, like the mother galleries, vary also in length, measuring from 1½ to 3½ inches in length. When feeding is completed the larvæ pupate. This pupation takes place usually in the bark, but in cases where the bark is comparatively thin, between the bark and the sapwood. When ready to emerge the young beetles eat their way through the bark, leaving numerous flight holes.

As in the case of *M. minor*, where overcrowding has taken place, say, on a badly infested stem, irregular galleries are of frequent occurrence. A very interesting and puzzling form of mother gallery of *M. piniperda* may be found where the two species are breeding on the same stem. For example, in fig. 14 there is a mother gallery of *M. piniperda* loop- or inverted U-shaped. The female *piniperda* had made a gallery 2¼ inches in length, and, finding that she was about to cut across a gallery of *M. minor*, turned to the right, and continued the boring of the gallery vertically downwards.

Length of Life-Cycle in a Single Generation.

The number of days that it takes for the completion of a cycle from the laying of the egg to the issue of the young imago varies according to the season of the year at which the eggs are laid and the temperature, also on the quality of the food material and the position on the stem. Ratzeburg and Hess, writing of Central Europe, give 75 to 84 days as the time in favourable environments, the times stated being—egg stage, 14 days; larva, 49 to 56 days; pupa, 14 days. My observations at Aboyne in Aberdeenshire and my experiments in Edinburgh indicate rather a longer time. In January 1916 I found in the pine woods of the Aboyne district hundreds of adults of *M. minor* in young pine shoots lying on the ground. These shoots, tunnelled by the beetles, had been broken off from the trees by the winds, in the late part of December 1915. In sunny weather in April 1916 I observed the beetles leaving these shoots and flying off to the young shoots in the trees above: into these young shoots the beetles bored to feed. The most careful search failed to reveal any *minor* boring into stems for brood purposes, although large numbers of *M. piniperda* had begun their brood galleries.

On May 4, 1916, I found the first *minor* female commencing to bore an entrance and brood gallery for the purpose of egg-laying, and soon a male was found at the outside of the entrance-hole. Ten days later I dissected out this gallery, and found that it measured an inch in length and contained six eggs. Eggs hatched in times varying from 10 to 26 days. By May 15 numerous females had begun their mother galleries, and others continued to do so at intervals up to June 5. Females took a month to complete their two-armed gallery, and the first laid eggs had hatched before the gallery was completed and the last eggs laid.

The larvæ fed for 47 days and then pupated. The average time from the beginning of pupation to the exit of the imago in the latter part of August was 30 days.

From eggs laid at or about the end of May 1916 the first emergence of a new beetle was on August 25, 1916—that is, in 95 days. The time taken from the entrance of a female underneath the bark, in making the mother gallery, in laying her eggs, and in the completion of larval and pupal stage to the exit of beetles, was 102 days.

As exemplifying the effects which temperature and exposure have in hastening or retarding development, I may say that while on a stem, chosen for experiments and observations, adults were issuing after pupation from the sunny side of the stem in the latter half of August, a corresponding brood in the north side of the stem was still in the pupal stage in October.

Quality of Tree used for Brood Purposes by M. minor and M. piniperda.

I have no doubt whatever, from a very large series of observations, that *M. minor* for brood purposes seeks a better quality of food material than *M. piniperda*.

In a thirty-year-old suppressed stem, where I found the two species at work, *M. piniperda* for brood purposes had chosen the lower parts of the stem of the tree, *M. minor* the upper, thinner-barked parts. In another pine stem similar to the last mentioned, which I felled for purposes of minute examination, *M. piniperda* brood galleries were plentiful below the bark of the lowermost 4 feet of the stem, without a trace of *M. minor*; whereas, from this height upwards to the crown, *M. minor* brood galleries were very plentiful. In another stem of a similar age, minutely examined, there was no trace of *M. piniperda* brood galleries, *M. minor* galleries commenced at 1 foot above the surface of the ground and continued upwards to the crown. In still another stem of similar age examined, which was comparatively thin barked throughout its whole length, *M. minor* galleries were very plentiful from the surface of the ground to the crown of the tree. In a number of fifty-year-old-tree stems examined, the foliage of which was much reduced, partly by the beetles themselves, *M. minor* galleries were very plentiful from 3 feet above the surface of the ground to the crown. No galleries of any kind were found below that height.

I conclude from these and other observations that *M. minor* prefers the thinner-barked portions of standing stems, *i.e.* the upper and middle portions, avoiding the thicker-barked portions nearer the surface of the ground. This does not exclude altogether the use of thicker-barked parts. This is also the experience of Continental foresters.

M. piniperda, on the other hand, prefers these lower portions of standing stems where the bark is thicker. In older stems, with thick bark, *M. piniperda* may be found breeding almost throughout the whole length of the stem.

To ascertain whether *M. minor* bred on stumps of felled trees, I examined in June 1916 a large number of stumps of trees which had been felled in the previous year. Some of these stumps were situated at intervals throughout a wood, where I found *M. minor* breeding freely on weakened stems which were still standing: others were in an area of clear felling adjacent to this wood. In none of these stumps could I find any trace of *M. minor*. On the other hand, I repeatedly found *M. piniperda* breeding on them. *M. minor* does not breed on stumps, whereas *M. piniperda* breeds quite freely on them.

As a result of very careful observation and comparison in the woods, I do not hesitate to say that *piniperda* swarms earlier in the spring than *minor*: on an average there may be a month of difference in the appearance of the two species.

Host Trees.

In the Continental forest literature *M. minor* is reported as attacking a number of species of pine; in Scotland I have found it only on Scots pine. *M. piniperda* is also typically a pine species, but I have frequently found it working on felled spruce and larch.

Length of Life of M. minor and the Number of Generations in a Year.

The old view, championed for example by Eichhoff, was that these forest beetles had not only a comparatively short life as adults, but that the newly issued imagos, once their external chitinous covering had hardened, were able to proceed at once to an efficient copulation followed by egg-laying. This was disproved by von Oppen,[*] Nusslin,[†] and MacDougall[‡] for Curculionidæ. It has been further disproved for a number of Scolytid species in a series of papers by Pauly, Nusslin,[§] Knocke,[||] and Fuchs.[¶] An excellent summary of results is given by Hagedorn.[**] From the researches of the four last-named authors, we now ascertain that several, indeed a number of Scolytid species do not die after pairing and a fresh egg-laying, but can proceed, after a period of renewed feeding, necessary in order to recuperate and render their sexual organs once more functional, to a further pairing, followed by a second egg-laying and second brood. It has also been satisfactorily demonstrated for a number of Scolytid species that the imago on its first appearance from the pupal condition is, owing to the unripeness of the sexual organs, unable to proceed to an efficient copulation followed by egg-laying, but that a feeding period must intervene in order that the reproductive organs may be properly matured. In relation, then, to the sexual organs, two periods of feeding have to be distinguished, viz. a feeding preliminary to the first efficient pairing and egg-laying, and a renewal of feeding for recuperation purposes that follows the exhaustion due to the egg-laying and rearing of the first brood.

As regards the feeding of the imago necessary to bring the sexual organs to

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[*] Von Oppen, "Zur Lebensdauer des *Hylobius abietis*," in *Zeitschr. f. Forst. und Jagdwesen*, vol. xv, 1883, and vol. xvii, 1885.

[†] Nusslin, "Über Generation und Fortplanzung der Pissodesarten," in *Forstlich naturwissenschaftlichen Zeitschrift*, 1897.

[‡] MacDougall, "Ueber Biologie und Generation von *Pissodes notatus*," in *Forstlich naturwissenschaftlichen Zeitschrift*, part v, 1898. "The Biology of the Genus *Pissodes*," in the *Proceedings of the Royal Society of Edinburgh*, 1900.

[§] Nusslin, *Leitfaden der Forstinsektenkunde*, 1905 and 1913.

[||] Knocke, "Beiträge zur Generationsfrage der Borkenkäfer," *Fortwiss. Centralblatt*, 1900 and 1904.

[¶] Fuchs, *Über die Fortplanzungs verhältnisse der rindenbrutenden Borkenkäfer*, 1907.

[**] Hagedorn, "Fam. Ipidæ," in *Genera Insectorum*, 1910.

maturity, this feeding may take place in the place below the bark where the beetle was reared, *i.e.* in the neighbourhood of its birthplace, or in other species the imago makes an exit hole through the bark, and flies to a feeding place on another part of the tree. *Myelophilus minor* and *M. piniperda* are two excellent examples of this latter habit.

It is clear, too, that the question of whether two broods—broods in the relationship of parents, children, grandchildren—are possible in a year is to a great extent dependent on two things, viz. whether a preliminary feeding is necessary before brooding, and if this feeding time be short or long. If a Scolytid species can, as soon as the imago stage is attained, issue and proceed without a preliminary feeding period to rear a brood, then in favourable environment this brood may issue and at once proceed to pair and lay eggs from which adults will be developed in the same year. That is, we can have two generations in the year, in the succession of parents, children, grandchildren. This seems possible with our elm-bark beetles and with *Hylesinus crenatus* of the ash. If the feeding, however, that follows the fresh appearance of the imago takes only a short time, a second generation in the year is also possible. But if the feeding preliminary to first pairing extends over a long time, then a second generation in the year will not be possible. This last seems to be the case in *M. minor*. KNOCKE, working in Central Europe, declared that this applied to *M. minor*, *M. piniperda*, and *Hylesinus fraxini*. It was part of the purpose of this research to verify KNOCKE's statement for Britain, and later in this paper I give reasons in favour of the view that two generations in a year of *M. minor* or of *M. piniperda* are not found in Scotland. The proving of this is not so easy as it looks at first sight, because there is the possible complication that there may be two broods in a year in the relationship of parents and children and a second brood of brothers and sisters, the parents of the first brood having fed and bred again. The facts can only be satisfactorily proved by a careful dissection and examination of the reproductive organs of young and old beetles. To NUSSLIN and KNOCKE belongs the credit of first directing attention to the need for anatomical information. For the proper understanding of the problem a knowledge of the structure of the reproductive organs of Scolytid beetles is necessary, and I take the reproductive organs of *M. minor* for illustration.

THE MALE REPRODUCTIVE ORGANS.

Fig. 16 is a drawing of the male reproductive apparatus after dissection: testes, vasa deferentia, seminal vesicles, accessory glands, common vas deferens or duct, and penis.

The testes are transparent glandular bodies, one lying on either side of the abdomen, ventrally. In side view they appear flattened from above downwards and rounded at the edges; by these the sperms are produced. From the under side of each testis a duct passes, known as the vas deferens. The two vasa deferentia unite and form a common duct which leads to the penis.

About halfway between each testis and the union of the vasa deferentia each duct is much swollen, appearing in side view as a lens-shaped receptacle known as the seminal vesicle. Two blind diverticula,—the accessory glands—after uniting with each other, open into the vasa deferentia just before the latter swell out to form the seminal vesicles.

The chitinous supporting part of the penis consists of fork, ring, and sheath. The ring is circular in shape, and partly surrounds the sheath of the penis. The sheath is made up of a sheet of chitin, the edges of which overlap at the sides. The sheath anteriorly is prolonged into two rods known as the femora. The lower part of the common vas deferens passes between the femora, through the ring, and down the centre of the sheath.

Repeated dissections of the male reproductive organs were made; the structures were examined in various media. In this way the male reproductive organs of *minor* and *piniperda* were compared. No reliable differences were observed in the softer parts, but the chitinous fork afforded an excellent means of distinguishing the males of the two species.

The fork of *M. minor* (F., fig. 16) is visible to the naked eye. It is a stout chitinous rod, breaking up at the posterior end into two short branches which are slightly curved. Anteriorly it ends in a blunt, triangular-shaped knob. In a few cases this triangular knob was prolonged on either side into short thin branches, which were slightly curved.

Compared with this, the fork in *M. piniperda* is not nearly so stout (fig. 17). Posteriorly it diverges into two short branches which are more curved. Anteriorly the main rod is bent almost at right angles, and it tapers gradually to a point.

The ripeness or unripeness of the male reproductive organs may be thus distinguished under the microscope:—

Unripe.	*Ripe.*
Testes white and without spermatozoa.	Testes yellowish and with spermatozoa.
No spermatozoa in the vasa deferentia.	
Seminal vesicles small.	Seminal vesicles small and full of spermatozoa.
No spermatozoa in the seminal vesicles.	
Accessory glands short and thin and only slightly developed.	Accessory glands greatly lengthened and swollen and with spermatozoa.

I verified the main points in the above differences, the variation in size of the seminal vesicles and the accessory glands being of distinct help in determining the ripeness or unripeness.

Female Reproductive Organs of M. minor.

The parts may be followed in fig. 19, which shows them as dissected from a female *minor* ready to lay eggs. There are two ovaries, one on each side of the abdomen. Each ovary consists of two egg tubes, with a terminal nutritive chamber and terminal filament at their apex. The eggs pass from the ovaries to the oviducts, which join to form a common portion, the uterus. Associated with the lower portion of the uterus we have the bursa copulatrix, receptaculum seminis, accessory gland, and slime glands. The bursa copulatrix, along with the lowest part of the uterus, forms a structure for the admission of the sperms to the receptaculum seminis; communication is by means of a small duct. An accessory gland produces a secretion which mixes with the sperms that are stored in the seminal receptacle. On each side of the lowest portion of the uterus (the vagina), and prior to the entrance of the bursa copulatrix, is a slime or cement gland.

Repeated dissection and comparison of the female reproductive organs of *minor* and *piniperda* yielded no reliable differences. Sometimes it seemed that such a difference might be found in the receptaculum seminis (spermatheca), the only chitinous part of the female reproductive organs of the two beetles; but while this varied slightly in appearance at different seasons, there was no specific differentiating character.

The variation in appearance of the female reproductive organs may be gathered from the following comparisons drawn by Nusslin and Knocke:—

Unripe.	*Ripe.*
The nutritive chamber at the apex of the egg tubes is small, and apparently seated directly on the oviduct.	Nutritive chambers large.
Egg tubes diminutive, short, not prominent, not separated up into ovarian chambers.	Egg tubes long and jointed, so as to suggest strings of beads. The egg chambers increase in size gradually from the nutritive chamber to the oviduct.
Bursa copulatrix empty. Seminal receptacle empty. The gland associated with the seminal receptacle empty.	Bursa copulatrix, seminal receptacle, gland associated with seminal receptacle well filled, and the sperms present.
Cement or slime glands empty.	Cement or slime glands filled with a white secretion and then a citron-yellow secretion.

The above characters proved of very great value in determining the age of the *minor* or *piniperda*, and in illustration I figure with notes four stages of the female reproductive organs of *minor* drawn from preparations made of the dissected-out organs.

Fig. 18. The immature organs, unripe, and before any egg-laying has taken place. The imagos after pupation issue through a flight hole in the bark and fly to the young shoots at the top of the tree. Into these shoots the young beetles tunnel and feed. As a result the reproductive organs fill out, and efficient pairing and egg-laying follow.

It will be specially noticed in this figure that the egg tubes are not separated up into ovarian chambers. In the natural preparations the bursa copulatrix and slime glands are empty, and white in colour.

Fig. 19 shows the reproductive organs of a female about to lay. The egg tubes here are divided up into ovarian chambers, while in the natural preparation the bursa copulatrix and slime glands are somewhat yellow in colour.

Fig. 20 shows the reproductive organs of a female dissected out while egg-laying was in process. Attention may be directed here to the so-called "corpora lutea." When a ripe egg has passed through the oviduct the epithelial cells collect at the base of the egg chamber, showing and remaining as a little heap of degenerate dirty yellow tissue. In the natural preparation the bursa copulatrix and slime glands are citron yellow in colour.

Fig. 21 shows the reproductive organs, dissected out for examination, from a beetle which had laid its eggs.

It is noticeable in this figure that, owing to the completion of egg-laying, the ovarian chambers are empty (contracted), containing no eggs, and that the so-called corpora lutea is now very conspicuous. In the natural preparation the bursa copulatrix and slime glands are dirty yellow in colour.

Question of Number of Generations in a Year.

A question which has importance for the forester is whether two generations of a bark-boring species are possible in a year or not, a fact which has also to be reckoned with in combating these pests.

From my own observations, both in the open and from experiments, I am convinced that in Scotland, in the case of *M. minor*, the occurrence of a double generation in the succession, parents, children, grandchildren in a year, is impossible.

The following is a short account of my observations from experiments carried out during the years 1915 and 1916 :—

On August 12, 1915, I was permitted to fell a thirty-year-old Scots pine stem on which *M. minor* had bred. On examination of the galleries on it I found immature beetles chiefly, about to emerge from their pupal chambers. No parent beetles were present in the mother galleries. I collected these young, immature adults as they issued from the bark, and later liberated them in a muslin cage in which I had planted young pines. At the same time I placed vertically in the cage fresh logs of Scots pine, some thick barked, other thin barked, in which the beetles could breed if they chose. A few days later I found these young beetles tunnelling in the shoots of the young pines. There they had gone to feed in order to ripen their reproductive organs. I examined the pine logs, caged with the young pines, at intervals of a few days, but still the beetles remained in the shoots. During the later months of the year—November and December 1915,—on examining some of the beetles in the shoots they appeared quite dormant, evidently feeding very little and using the shoots for hibernating purposes. This cage was kept outside, but all the beetles died in January 1916 because of unfavourable circumstances. In no case did they ever attempt to make a brood gallery on the pieces of stem supplied during the year 1915, a fact proved by external examination and dissection of the logs.

In August 1916 I repeated this experiment, collecting the young beetles as before which emerged from their breeding stems, commencing August 25, 1916. Now I examined, after dissection, the reproductive organs of some of the females just as they emerged from their brood galleries. The reproductive organs were found to be quite immature (see fig. 18) and the beetles quite unready for egg-laying. The rest of these beetles I liberated on young pines protected against the entry of any other insects, and they proceeded to tunnel in the pine shoots for feeding and for the ripening of their reproductive organs. On November 3, 1916, I killed some, and dissected out the reproductive organs, which were found to have undergone little further development and were still unripe.

One must remember that with severer weather conditions in late October, November, and December the beetles feed very little, remaining dormant for most of the time. The daily temperature by this time is now much lowered, so that feeding practically ceases until the warmer weather in the following spring. It is impossible, then, that in the case of *M. minor*, whose first brood emerges in August, the reproductive organs of the females can be in a fit state for efficient copulation and egg-laying in the same year. They cannot be in such a state until the following spring. From the results of these experiments and dissections, I conclude that only one generation is possible in a year.

In experiments similar to those already mentioned, which I carried out to obtain information as evidence on this particular point, in the case of *M. piniperda* I found that the young beetles did not breed in the same year as they emerged from their pupal chambers, but remained in the shoots throughout the winter months, breeding in the following spring.

The Occurrence of Two Broods in a Year.

While two generations in a year are impossible, the occurrence of two broods in a year is possible: that is to say, the adult beetles, after the laying of the eggs from which the first brood will develop, leave the parent galleries and return to the young pine shoots at the top of the tree with their reproductive organs in an exhausted state. On a nutritious diet the organs are restored, and a second egg-laying may follow in a new-made mother gallery. If the beetles, the parents of the first brood, recuperate in time, then from their second laying it is possible that a second issue of adults may take place in a calendar year.

On pieces of stem infested with *M. minor*, which I cut in the beginning of June 1916, I found adult beetles in the galleries and also their eggs. I enclosed these pine logs in a sack secured at the ends to prevent escape of beetles. In this sack later on in June I caught the beetles as they left their completed galleries, egg-laying having been completed. At the time of exit a number of their eggs were still unhatched, while other eggs had given out their larvæ which were still very small.

The first of these beetles emerged on June 20, and they continued to do so up to July 12. The males emerged from the galleries first, the females following. These beetles were removed and placed on young potted pines, and were prevented from escaping by means of muslin sacks. In this muslin cage I placed fresh pine logs with their ends paraffined, some thin barked, others thicker barked. In a few days I found a number of the beetles in the shoots of the young pines. Their reason for going there was to feed for recuperation after rearing their first brood.

In over three weeks' time (the first on July 12, others following in considerable numbers on the 14th and 16th) the beetles had left these pine shoots and burrowed into the pine logs which I had provided. They proceeded to make typical double-armed galleries. In my experiment I found that these old beetles left the pine shoots in a period on an average of three to five weeks. These beetles entered the pine logs to breed, as was evident from frass, and proceeded to make their typical two-armed galleries.

There is considerable mortality among the beetles which have reared a brood, a certain portion only of these individuals being able after feeding in shoots to proceed to a new egg-laying.

In the previous year I had performed the same experiment with adults of *M. piniperda* that had already bred; some died, but others succeeded in rearing a second brood after entering the stems supplied. These galleries I examined on October 12, 1915, and found larvæ about to pupate. These specimens were placed in the laboratory, where, owing to artificial temperature, the adults emerged in January 1916. The females which proceeded to a second egg-laying made mother galleries slightly shorter and laid a smaller number of eggs.

The Economic Importance of M. minor in Scottish Forestry.

Both *minor* and *piniperda* are dangerous enemies, and in a strong attack sound trees can be brought to their death. If not immediately destroyed the trees are being continuously weakened and predisposed to the attack of other enemies. The most damage is caused by the beetles feeding in the young shoots of pines in order to ripen their reproductive organs or for recuperation after egg-laying. The result of this tunnelling in the shoots of healthy trees leads to great loss of foliage, as the tunnelled shoots are broken off by the wind. There are two main attacks on the shoots, the first by newly escaped beetles, which have to feed in order to develop their reproductive organs before egg-laying, and the second, by the beetles which have paired and laid eggs, and which previous to a second egg-laying renew their feeding in the shoots. The former takes place from mid August onwards, the latter from late June onwards. The damage by these attacks greatly reduces the vitality of the trees, and the weakening of the trees prepares their stems for successful attack by this beetle for brood purposes.

The characteristic shape of the crown of the pine becomes quite altered by the blow-down of the tunnelled young shoots, so that it becomes like, and mimics the form of spruce. Such damage and such misshapen trees are commonest at the edges and exposed parts of the wood, but are not altogether confined to these parts. Trees here and there in the middle of the wood show the same damage, and gaps are visible to the eye. The result is not only a direct loss to the tree, but an indirect loss to the forest owing to soil deterioration by opening the way for light. There is considerable loss in wood increment also from the loss of shoots and foliage.

Then there is the damage done by the mother and larval galleries. The mother galleries of *minor* run in the transverse direction, and sometimes quite encircle the young stem; in thicker places such galleries link up with others, and as a result the passage of sap is interfered with. Small dry dead patches of bark are found here and there on the stem as the result of *minor* attack. In the case of *piniperda* large sheets of bark covering the place of attack can be pulled away easily.

It is of great importance to the forester to know where *M. minor* breeds, inasmuch as it is while breeding that this species can be most successfully attacked and its numbers reduced. *M. minor* breeds on standing Scots pine trees from thirty to fifty years of age. It may also use the smaller side branches in the crown. As far as I have found, the beetle prefers standing trees: only in one case have I found *M. minor* breeding on a felled Scots pine stem. While this is my experience over a considerably large area examined in Aberdeenshire, it is quite possible that in different conditions *M. minor* may use more freely than I have found it to do so, felled or blown stems for brood purposes: for example, BORODAEWSKIJ * states that in the State forests of the province of Minsk (Russia) *M. minor* breeds very frequently on felled trees, even preferring them to standing ones.

In plantations of Scots pine where *M. minor* was very prevalent I arranged felled trees as traps in April 1916. These were thin-barked stems of about thirty years old,

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* BORODAEWSKIJ, P., in *Liesnoj Journal* (*Forestry Review*), year xlv, part 8–9, pp. 1222–1247, Petrograd, 1915.

which had been quite recently felled. I examined these later, during July onwards, but only *M. piniperda* was found breeding on them.

If the woods be properly managed the increase of *M. minor* may be readily checked and their numbers reduced. The method of preparing trap-trees should be adopted, but these trap-trees should be standing trees, selected at intervals throughout the wood. Trees with badly shaped crowns, unhealthy, damaged, or those suppressed by taller surrounding trees, should be selected if possible as trap-trees. If such trees as these cannot be found in the wood, certain comparatively thin-barked trees may be selected and artificially be brought into an unhealthy condition by removing a ring of bark just above the surface of the ground. The use of trap-trees should be continuous from March to October to ensure success, so that suitable places at all times would be offered the beetles for their egg-laying. At regular intervals these traps, after examination, should be felled and the bark removed and destroyed, taking care that this is done before the larvæ have become full grown, otherwise in the thin-barked portions of stems some of the pupæ might be deep in the sapwood and not so easily reached.

NATURAL ENEMIES OF M. MINOR.

The chief natural enemies of *M. minor* are predaceous and parasitic insects, and these do much to keep our species in control.

The predaceous insects belong for the most part to two Coleopterous families, viz. the Cleridæ and the Nitidulidæ.

I found *Clerus formicarius* L. both in the larval and adult stages feeding on larvæ, pupæ, and adults of both *M. minor* and *M. piniperda.* The four Nitulids* were *Rhizophagus ferrugineus* Payk., *Rhizophagus depressus* F., *Pityophagus ferrugineus* F., and *Ips. quadripustulata* L. In a number of cases the galleries of *M. minor* had been almost completely stripped of eggs by these beetles.

A small Staphylinid beetle was an active predaceous form in the *minor* and *piniperda* galleries, feeding on the eggs.

The larvæ of Rhaphidia sp. (a Neuropterous genus) were also found destroying the eggs of *minor* and *piniperda.*

A Hymenopterous parasite was not uncommon, feeding externally as larva on the larvæ and pupæ of *minor* and *piniperda.*

Fungi.—Examination of infested trees in the open and close observation of *M. minor* and *piniperda* during the past years gave me the opinion that there is little mortality of *minor* due to fungus attack. On the other hand, whole broods of *piniperda* on the stumps of felled trees may be wiped out by fungus mycelia.

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* These Nitulid beetles feed on a number of bark-boring and bark-infesting species, Curculionid and Scolytid. See MACDOUGALL, "On the Life-history and Habits of *Rhizophagus depressus* F.," *Notes of Royal Botanic Garden*, No. iii, 1900 ; also the same Journal for the life-history and habits of *Clerus formicarius*, by MACDOUGALL.

A point worthy of consideration is to what extent fungi are encouraged through the destructive work of the beetles. If *M. minor* is present in numbers and attacks healthy standing trees, there is no doubt that the reduction of foliage, as well as the wounds caused by borings, reduce the vitality of the trees and predispose them to fungus attack, while the wounds and exit holes serve as entrance-places for wound parasites.

Symptoms of Attack of the Two Species.

The large numbers of tunnelled young pine shoots lying on the ground, broken off by high winds from the tree-tops above, is quite sufficient evidence of the presence of this species in a wood. The tree-tops above, as a result of the loss of shoots, appear as if they had been pruned, and pruned badly, while a number of withered shoots may be still found hanging on the trees.

The presence of beetles boring below the bark can be readily detected by the occurrence of bore meal thrown out at the entrance-holes of the mother galleries. During May and June this bore meal should be looked for on standing trees. Later this sawdust can be traced in streaks down the bark, and can even occur in little heaps either at the surface of the ground or on the bark scales.

Although the foregoing observations on *M. minor* are confined to the Aboyne district of Aberdeenshire, where in some places the species occurs in very large numbers and equally as common as its congener *M. piniperda*, yet I believe the occurrence of *M. minor* is more widespread throughout Scotland than is generally supposed. Its so-called rarity is probably due to the fact that in appearance it is so similar to the much commoner *M. piniperda*. Further, the damage done by *M. minor* to the young shoots through its feeding habits is similar to that of *M. piniperda*, and so the misdeeds of the known *piniperda* are ascribed to the scarcely known *minor*. In the woods where observations were made, the damage to the shoots by *M. minor* was equal to, if not greater than, that by *M. piniperda.* While the two species damage the shoots in the same way, *minor* may be a worse enemy than *piniperda*, inasmuch as it asks for a better quality for rearing its brood, and attacks standing trees. It has been stated before that *minor* favours rather the upper thinner-barked parts for brood purposes, and this can be a reason for its comparative rarity on felled stems, since these favourite places, the thin-barked parts, dry quicker, and therefore cease to provide the better quality which *minor* asks.

The study of the two species and their work is further interesting, as showing that closely similar and nearly related species may sometimes be more easily distinguished by their behaviour than by their external specific characters. Thus, while the trained entomologist, armed with a lens, would have little or no difficulty in determining the two species by examination, both to trained entomologist and forester the distinction between the two, as shown by their work, is extremely easy.

In conclusion, it is with great pleasure that I acknowledge the help, advice, encouragement, and facilities which have been given me by Dr R. Stewart MacDougall throughout this work.

DESCRIPTIONS OF FIGURES OF M. MINOR.

Fig. 1. The smaller pine beetle, *Myelophilus minor* Hart. Adult. (Greatly magnified.)

Fig. 2. Prothorax of *M. minor*. (Greatly magnified.)

Fig. 3. Prothorax of *M. minor* var. (Greatly magnified.)

Fig. 4. Apex of elytra of *M. minor*. (Greatly magnified.) *a* = second interstice.

Fig. 5. Apex of elytra of *M. piniperda*. (Greatly magnified.) a_1 = second interstice.

Fig. 6. Hind leg of *M. minor*. (Greatly magnified.) *a* = base of tibia; *b* = tooth about centre of tibia; *c* = apex of tibia.

Fig. 7. Hind leg of *M. piniperda*. (Greatly magnified.) a_1 = base of tibia; b_1 = middle of tibia; c_1 = apex of tibia.

Fig. 8. Larva of *Myelophilus minor*, side view. (Greatly magnified.) *a* = head; *b* = thorax; *c* = abdomen; *e.* = epipleural fold; *h.* = hypopleural fold; *i.* = infra-anal lobe; *M.* = mandible; *Mx.* = maxillæ; *p.* = prescutal fold; *pa.* = para-anal lobe; *Sc.* = scutal fold; *Sp.* = spiracle; *Sr.* = scutellar fold; *St.* = sternellar fold; *Sa.* = supra-anal lobe.

Fig. 9. Head of larva, *M. minor*, seen from above. (Greatly magnified.) *a.* = antenna; *c.* = clypeus; *e.* = epistome; *ep.* = epicranium; *e.s.* = epicranial suture; *f.* = frons; *f.s.* = frontal suture; *l.* = labrum; *m.* = mandible.

Fig. 10. Region of epistome, *M. minor* larva. *a.* = antenna; *c.* = clypeus; *ep.* = epistome; *f.* = frons; *l.* = labrum.

Fig. 11. Maxillæ and labium of *M. minor*. (Greatly magnified.) *C.* = cardo; *l.* = ligulæ; *l.l.* = lacinial lobe; *l.p.* = labial palp; *M.* = mentum; *M.p.* = maxillary palp; *S.* = stipes; *S.a.* = submental area; *S.m.* = submentum.

Fig. 12. Pupa of *M. minor*, ventral view. (Greatly magnified.) *a.* = antenna; *c.* = coxa of front leg; $c._1$ = coxa of middle leg; *c.s.* = caudal spine; *d.* = coxa of hind leg; *e.* = eye; *el.* = elytra; *f.* = frons; *fe.* = femur; *f.s.* = frontal spines; *f.sp.* = femoral spines; *g.* = gena; *h.* = femur of hind leg; *i.a.* = intercoxal area; *l.* = labrum; *li.* = labium; *m.* = mandible; *ms.* = mesosternum; *mt.* = metasternum; *mx.* = maxilla; *o.* = medial groove; *r.* = tenth abdominal segment; *w.* = flying wing.

Fig. 13. Galleries of *M. minor* and *M. piniperda* on a thin-barked piece of Scots pine stem; the pupation in the case of *M. minor* larvæ has taken place in the wood. *a* = mother gallery of *M. piniperda*; a_1 = mother gallery of *M. minor*; *b* = larval gallery of *M. piniperda*; b_1 = larval gallery of *M. minor*; *c* = pupal chamber of *M. piniperda*; c_1 entrance to pupal bed, *M. minor*; *d* = entrance to mother gallery, *M. piniperda*; d_1 = entrance to mother gallery, *M. minor*; *e* = exit hole through which a young *M. minor* adult had escaped from its pupal chamber.

Fig. 14. Piece of pine bark with crowded workings of *minor*; pupation of the *minor* larvæ here took place in the bark; the inverted U-shaped gallery is an irregular *piniperda* gallery, the irregularity being due to overcrowding.

Fig. 15. Galleries of *M. minor* made on a piece of felled pine stem: the long arms have been formed in a direction away from the sun.

Fig. 16. Male reproductive organs of *M. minor*. (Greatly magnified.) *A.g.* = accessory gland; *C.d.* = common duct; *F.* = fork; *Fe.* = a femur of penis; *P.* = penis; *R.* = ring; *S.* = sheath; *S.v.* = seminal vesicles; *T.* = testes; *V.d.* = vas deferens.

Fig. 17. Fork of penis, *M. piniperda.* (Greatly magnified.)
Fig. 18. Immature female reproductive organs of *M. minor*, ventral view. (Greatly magnified.)
Fig. 19. Reproductive organs of female *M. minor* about to lay eggs, ventral view. (Greatly magnified.)
Fig. 20. Reproductive organs of female *M. minor*, egg-laying, ventral view. (Greatly magnified.)
Fig. 21. Reproductive organs of female *M. minor*, after egg-laying, dorsal view. (Greatly magnified.)

LETTERING FOR LAST FOUR FIGURES.

A.g. = accessory gland; *B.c.* = bursa copulatrix; *C.l.* = corpora lutea; *O.* = ovarian tubules; *Od.* = oviduct; *R.* = receptaculum seminis (spermatheca); *S.g.* = slime gland; *T.c.* = terminal chamber; *T.f.* = terminal filament; *U.* = uterus; *V.* = vagina.

WALTER RITCHIE: "The Structure, Bionomics, and Forest Importance of *Myelophilus minor* Hart."—PLATE I.

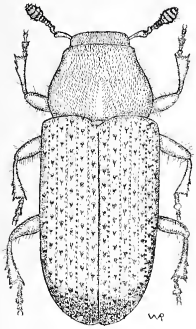

FIG. 1.

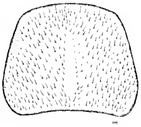

FIG. 2.

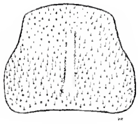

FIG. 3.

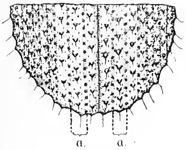

FIG. 4.

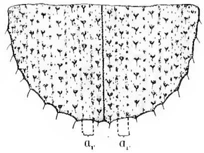

FIG. 5.

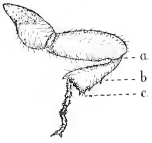

FIG. 6.

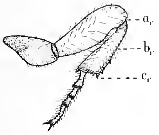

FIG. 7.

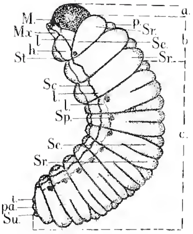

FIG. 8.

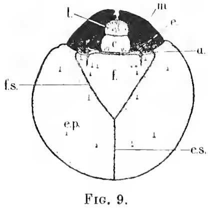

FIG. 9.

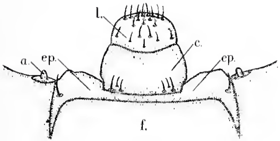

FIG. 10.

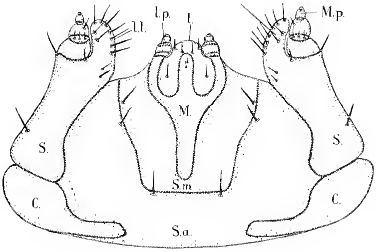

FIG. 11.

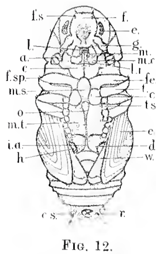

FIG. 12.

Walter Ritchie: "The Structure, Bionomics, and Forest Importance of *Myelophilus minor* Hart."—Plate II.

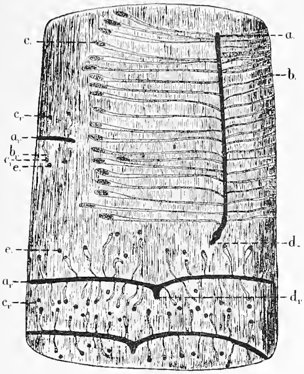

Fig. 13.

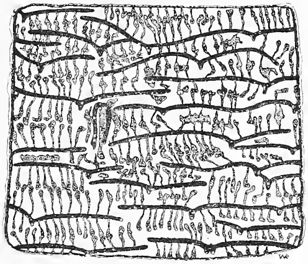

Fig. 14.

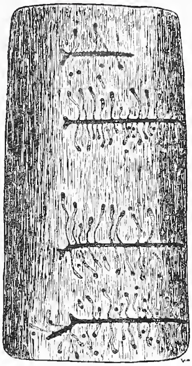

Fig. 15.

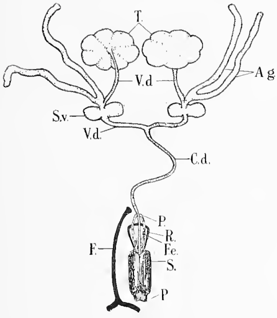

Fig. 16.

Fig. 17.

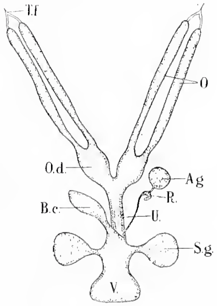

Fig. 18.

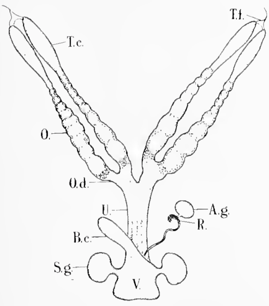

Fig. 19.

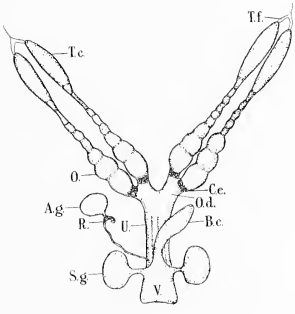

Fig. 20.

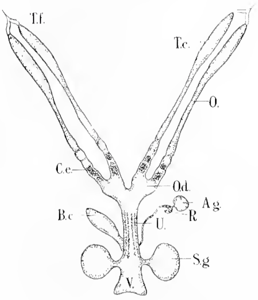

Fig. 21.

XI.—On Knots, with a Census of the Amphicheirals with Twelve Crossings.

By Mary Gertrude Haseman. *Communicated by* Dr C. G. Knott, *General Secretary.* (With One Plate.)

(MS. received March 28, 1917. Read June 4, 1917. Issued separately February 1, 1918.)

The theory of the knotting of curves, except for a few elementary theorems due to Listing,* was entirely neglected until Tait † was led to a consideration of knots by Sir W. Thomson's (Lord Kelvin's) work on the Theory of Vortex Atoms. He attacked chiefly the problem ‡ of constructing knots with any number of crossings, and obtained a census of the knots of not more than ten crossings. Those knots which exhibit a special kind of symmetry—the amphicheiral knots—offer certain points of interest.

§ 1. Knot Schemes.

Tait has introduced two schemes for representing knots: the alphabetical and compartment symbols.

Alphabetical Symbol.—The alphabetical scheme of a knot is based upon the idea of the sequence of the crossings which exist on the plane projection of the knot. In the case of the alternating knot, the thread passes alternately over and under at the crossings. It is convenient to distinguish between the over and under crossings by means of the signs + and − respectively. Starting with an over crossing $\underset{+}{a}$, the alternate crossings may be denoted by $\underset{+}{b}$, $\underset{+}{c}$, $\underset{+}{d}$, etc. In this way there is obtained a definite sequence of the letters a, b, c, arranged so that those occupying the odd places represent over crossings, while those in the even places denote under crossings. Thus Tait's problem of constructing the plane knots with n crossings reduced itself to a question of the essentially different ways in which the even places of the sequence

$$\underset{+}{a}\;\underset{+}{b}\;\underset{+}{c}\;\ldots\;\underset{+}{n}$$

may be filled in with the same letters so as to form unipartite closed curves. For example, the only arrangement in the case of three crossings is

$$\underset{+}{a}\;\underset{-}{c}\;\underset{+}{b}\;\underset{-}{a}\;\underset{+}{c}\;\underset{-}{b}\;\Big|\;\underset{+}{a}$$

Hence the "trefoil" knot is the only knot of order 3.

Compartment Symbol.—Tait obtained his idea of the compartment symbol from the Listing type-symbol, which depends upon the division of the plane into $n+2$

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[*] Listing, *Vorstudien zur Topologie* (1874).

[†] Tait, *Trans. Roy. Soc. Edin.*, xxviii (1876–77), pp. 145–191; xxxii (1882–86), pp. 327–342, 493–506. See also *Scientific Papers*, vol. i, pp. 273–347.

[‡] The same problem has been considered by Kirkman, *Trans. Roy. Soc. Edin.*, xxxii (1882–86), pp. 281–309; and by Little, *Proc. Conn. Academy*, vii (1885–88), pp. 27–43.

compartments by the projection of the knot of order n. Both LISTING and TAIT showed that, of these compartments, no one contained less than 2 or more than n angles. Following LISTING's notation, the angle on the left along with its vertical, as a crossing is passed by the upper thread, is denoted by δ and the remaining pair by λ. The various compartments of an alternating knot are monotype; that is to say, the angles are of the same character, as shown in fig. 1. The Listing type-symbol is merely an enumeration of the two sets of compartments, in which an exponent is used to indicate the number of angles in a compartment and a coefficient to represent the number of such compartments. Thus the Listing type-symbol for the knot given in fig. 1 is

$$2\delta^2 + 2\delta^3 + \delta^4 + 2\delta^5$$
$$2\lambda^2 + 2\lambda^3 + 2\lambda^4 + \lambda^6$$

In general, each part of the Listing type-symbol for a knot of order n amounts to nothing more than a set of partitions of the number $2n$, where each member of the partition indicates the presence of a compartment with the same number of angles as there are units in this member. For example, the partitions corresponding to the type-symbol above are:

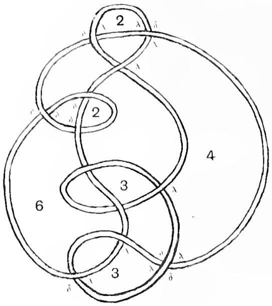
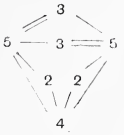


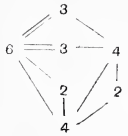
FIG. 1.

2 2 3 3 4 5 5
2 2 3 3 4 4 6

But it is not sufficient for the determination of the knot to know simply the number of compartments and the number of angles in each. It is necessary to know the number of joins between the various compartments as well as the arrangement of these joins. The number and arrangement of these joins is expressed by the compartment symbol, in which the joining lines indicate the number as well as the arrangement of the crossings connecting the set of δ compartments and the number as well as the arrangement of the laps of the thread bounding the set of λ compartments, or *vice versa*. We may assume that TAIT recognised the importance of the order of the crossings, for his symbols conform to the above definition of the compartment symbol. Little mentions the fact that the knot is not uniquely determined unless its so-called partition symbol, which is the same as the compartment symbol, as defined above, indicates the sequence of the crossings on the knot.

The compartment symbol of the knot (fig. 1) is





where the first refers to the set of δ compartments and the second to the set of λ compartments. In the following pages these symbols are referred to as primary and secondary. As Tait showed, the knot may be constructed from either the primary or secondary symbol by connecting the mid-points of the joins with a line which intersects itself only at these points.

§ 2. Methods of Varying a Given Knot.

Since the positions of the apparent double points of a twisted wire in space vary as the point of view changes, the plane projection is susceptible of two types of variation, which Tait calls deformation and distortion respectively.

By deformation of the knot Tait means a projection which leaves unaltered the relative positions of the compartments, as well as the number of angles in each compartment. For instance, any compartment may be made the amplexus, or infinite compartment, by turning the knot into this compartment; or, which is precisely equivalent, by inversion of the knot with respect to a point of this compartment as origin. But the knot scheme is unaltered by deformation, and the two knots are said to be equivalent.

Distortion, on the other hand, is a projection which changes the position of one or more of the crossings, so that, in general, it is impossible to represent the distorted form by the same scheme. In certain cases the number of angles and the arrangement of the joins of the various compartments is unaltered by a distortion. Such a distortion, therefore, reduces to a deformation, and the distorted form is equivalent to the original. As regards the knot in the plane, distortion is the process of shifting a crossing from one lap of the thread to another by a twist through two right angles of a limited portion of the knot. For example, by a rotation through two right angles about an axis in the plane of the paper, downwards through the crossing a, fig. 2 is distorted into fig. 2′.

Effect of Distortion on the Alphabetical Symbol.—If from a limited portion of a knot there emerge two free ends, that is to say, if a single part of the complete thread exhibits a certain number of crossings, then the knot consists of two or more separate knots on the one thread, and is said to be composite.

But a distortion[*] of a non-composite knot is possible if there emerge from a limited portion of it, four free ends, of which an adjacent pair is crossed. The four free ends indicate that the portion considered is made by a number of crossings of two distinct parts of the complete thread, and hence may be called a "reversible two-thread[†] tangle"—or, more simply, a "reversible tangle." Denote by x, y, p, q the four free ends, and let the adjacent pair x, y be crossed at a point α. By a rotation through two right angles as above, the two threads x, y are untwisted, and the threads p, q are crossed at a point α'. Hence, as LITTLE points out, there will be no change in the number of compartments involved in the primary and secondary symbols, although the order in which they are joined may be disturbed.

A distortion is of order n if it involves $n+2$ crossings. Denote by D_n^{α} a distortion of order n which operates on the crossing α. The reversible tangle R_n is the portion of the knot which admits the possibility of a distortion D_n^{α}.

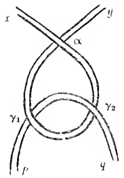


FIG. 2.

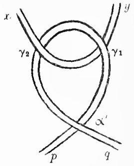


FIG. 2'.

Let the knot be described in such a direction that the reversible tangle R_n is entered by the thread x over the crossing α, and denote by $\gamma_1, \gamma_2, \ldots\ldots \gamma_{n+1}$ the remaining $n+1$ crossings in the order in which they are met. To leave the reversible tangle it is necessary either to return to the crossing α and pass out along the thread y, or to leave by one of the two remaining threads, say p. Accordingly, the alphabetical schemes for the reversible tangle R_n are respectively

$$\underset{-}{x}\ \underset{+}{\alpha}\ \underset{-}{\gamma_1}\ \underset{+}{\gamma_2} \ \ldots\ldots\ \gamma_{n+1}\ \alpha\ y\ \ldots\ldots\ q\ \gamma_j\ \ldots\ldots\ \gamma_i\ p$$

or

$$\underset{-}{x}\ \underset{+}{\alpha}\ \underset{-}{\gamma_1}\ \underset{+}{\gamma_2} \ \ldots\ldots\ \gamma_{n}\quad \alpha\ y\ \ldots\ldots\ p\ \gamma_i\ \ldots\ldots\ \gamma_j\ q$$

and

$$\underset{-}{x}\ \underset{+}{\alpha}\ \underset{-}{\gamma_1}\ \underset{+}{\gamma_2} \ \ldots\ldots\ \gamma_{n+1}\ p\ \ldots\ldots\ y\ \alpha\ \gamma_i\ \ldots\ldots\ \gamma_j\ q$$

$$\underset{-}{x}\ \underset{+}{\alpha}\ \underset{-}{\gamma_1}\ \underset{+}{\gamma_2} \ \ldots\ldots\ \gamma_{n+1}\ p\ \ldots\ldots\ q\ \gamma_j\ \ldots\ldots\ \gamma_i\ \alpha\ y$$

where $\gamma_i, \ldots\ldots \gamma_j (i \neq j)$ denotes the γ's in some order. If a crossing $\gamma_\mu (\mu = 1, 2, \ldots\ldots n+1)$ occurs twice on one thread of the reversible tangle R_n, then only the remaining n crossings exist on the second thread. The effect of a distortion on the alphabetical

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[*] TAIT, *Trans. Roy Soc. Edin.*, xxxii (1882–83), p. 328, or *Scientific Papers*, i, p. 320, recognises the possibility of such distortions; to LITTLE, *Proc. Conn. Acad.*, vii (1885), p. 44, § 10, is due the formulation of necessary conditions in the appearance of the knot.

[†] In the case of the alternating knot the possibility of a distortion is limited to the two-thread tangle; for non-alternating knots there may exist distortions of reversible tangles of more than two threads.

schemes is made clear by a consideration of the representation in figs. 3 and 3′ of a reversible tangle R_n, where the crossings $\gamma_1, \gamma_2, \ldots . \gamma_{n+1}$ are supposed to lie within the circle drawn in both figures. By the application of the distortion $\overset{\alpha}{D}_n$, the alphabetical scheme becomes in the first case

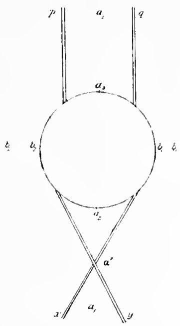


FIG. 3.

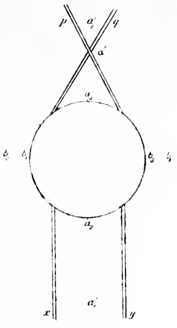


FIG. 3′.

$$\underset{-}{x}\ \underset{+}{\gamma_1}\ \underset{-}{\gamma_2} \ldots . \gamma_{n+1}\ y \ldots . p\ \alpha\ \gamma_i \ldots . \gamma_j\ \alpha\ q$$

or

$$\underset{-}{x}\ \underset{+}{\gamma_1}\ \underset{-}{\gamma_2} \ldots . \gamma_{n+1}\ y \ldots . q\ \alpha\ \gamma_j \ldots . \gamma_i\ \alpha\ p$$

and in the second case

$$\underset{-}{x}\ \underset{+}{\gamma_1}\ \underset{-}{\gamma_2} \ldots . \gamma_{n+1}\ \alpha\ p \ldots . y\ \gamma_i \ldots . \gamma_j\ \alpha\ q$$

or

$$\underset{-}{x}\ \underset{+}{\gamma_1}\ \underset{-}{\gamma_2} \ldots . \gamma_{n+1}\ \alpha\ p \ldots . q\ \alpha\ \gamma_j \ldots \gamma_i\ y$$

Within a reversible tangle R_n, may exist the possibility of distortions D_{n-1}, D_{n-2}, ... D_2, D_1, D_0, which may be applied singly or in combination with others. A knot is invariant under a distortion $\overset{\alpha}{D}_0$, since by it, the two threads of the reversible tangle R_0 are untwisted at a point α preceding γ_1, to be twisted at a point α' beyond γ_1, and consequently the general arrangement of the crossings is undisturbed. Hence in a consideration of the different forms of a given scheme the distortion of lowest order to be considered is the distortion D_1. The reason that makes the consideration of D_0 unnecessary applies also to a similar distortion $\overset{\gamma'}{D}_n$ on the sequence

$$\ldots . \gamma_1\ \gamma_2 \ldots . \gamma_{n+2} \ldots . \gamma_1\quad \gamma_2\quad \ldots . \gamma_{n+2} \ldots$$

or

$$\ldots . \gamma_1\ \gamma_2 \ldots . \gamma_{n+2} \ldots . \gamma_{n+2}\ \gamma_{n+1} \ldots . \gamma_1 \ldots .$$

Also it is unnecessary to consider a distortion affecting more than one-half of the total number of crossings, since it is equivalent to a distortion applied to the remainder of the knot. Hence the different knots of orders 3, 4, and 5 have but one form.

Consider the knot given by the alphabetical symbol :—

(1)
$$\begin{array}{cccccccccccccccccccc|c} a & f & b & g & c & j & d & h & e & b & f & a & g & i & h & e & i & c & j & d & a \\ + & - & + & - & + & - & + & - & + & - & + & - & + & - & + & - & + & - & + & - & \end{array}$$

The symbol shows the possibility of the following distortions :—

$$\begin{array}{llccccccccccc}
D_0^{a \text{ or } f} & ; & \cdots & a & f & & & \cdots & f & a & & & \cdots \\
 & & & + & - & & & & + & - & & & \\
D_0^{f \text{ or } b} & : & \cdots & f & b & & & \cdots & b & f & & & \cdots \\
 & & & - & + & & & & - & + & & & \\
D_0^{c \text{ or } j} & ; & \cdots & c & j & & & \cdots & c & j & & & \cdots \\
 & & & + & - & & & & - & + & & & \\
D_0^{j \text{ or } d} & ; & \cdots & j & d & & & \cdots & j & d & & & \cdots \\
 & & & - & + & & & & + & - & & & \\
D_0^{e \text{ or } h} & ; & \cdots & h & e & & & \cdots & h & e & & & \cdots \\
 & & & - & + & & & & + & - & & & \\
D_1^{i} & : & \cdots & h & e & & & \cdots & i & h & e & i & \cdots \\
 & & & - & + & & & & - & + & - & + & \\
D_1^{c \text{ or } d} & ; & \cdots & c & j & d & & \cdots & c & j & d & & \cdots \\
 & & & + & - & + & & & - & + & - & & \\
D_2^{g} & ; & \cdots & a & f & b & g & \cdots & b & f & a & g & \cdots \\
 & & & + & - & + & - & & - & + & - & + &
\end{array}$$

Of these distortions only D_1^i and D_2^g can produce a change of form, since a knot is invariant under a distortion D_0 or a continuation of distortions D_0; that is to say, $D_1^{c \text{ or } d}$. The application of the distortions D_1^i, D_2^g produce the symbols :—

(2)
$$\begin{array}{cccccccccccccccccccc|c} a & f & b & g & c & j & d & i' & h & e & i' & b & f & a & g & h & e & c & j & d & a \\ + & - & + & - & + & - & + & - & + & - & + & - & + & - & + & - & + & - & + & - & + \end{array}$$

and

(3)
$$\begin{array}{cccccccccccccccccccc|c} g' & a & f & b & c & j & d & h & e & g' & b & f & a & i & h & e & i & c & j & d & a \\ + & - & + & - & + & - & + & - & + & - & + & - & + & - & + & - & + & - & + & - & + \end{array}$$

respectively. The distortion $D_1^i D_2^g$, that is to say the distortion D_1^i, followed by the distortion D_2^g, gives the symbol

(4)
$$\begin{array}{cccccccccccccccccccc|c} g' & a & f & b & c & j & d & i' & h & e & i' & g' & b & f & a & h & e & c & j & d & g' \\ + & - & + & - & + & - & + & - & + & - & + & - & + & - & + & - & + & - & + & - & \end{array}$$

While it is a simple matter to recognise in any alphabetical scheme the existence of reversible tangles, R_n, and the effect thereon of the corresponding distortions, D_n, it is not so easy to say whether the distorted form and the original are the same or different. To meet this difficulty, the alphabetical symbol may be replaced by an equivalent numerical symbol * in which for each letter is substituted a number equal to one-half the number of crossings intervening before the next occurrence of the letter as the knot is described. For some purposes it is convenient to write also in a second row the numbers that arise when the knot is described in the reverse direction; but for a knot of order n, the sum of the numbers immediately above and below any letter is equal to $n-1$. Thus the symbol (1) becomes :—

(1′)
5 4 3 4 6 6 6 3 3 6 5 4 5 1 6 6 8 3 3 3
4 5 6 5 3 3 3 6 6 3 4 5 4 8 3 3 1 6 6 6

or more simply

5 4 3 4 6 6 6 3 3 6 5 4 5 1 6 6 8 3 3 3

---

* Suggested by Professor C. A. Scott, who calls it the intrinsic symbol.

while the variants become

(2′) 6 5 4 5 6 6 6 1 3 3 8 5 4 3 4 6 6 3 3 3
(3′) 4 5 4 3 6 6 6 3 3 5 6 5 4 1 6 6 8 3 3 3
(4′) 5 6 5 4 6 6 6 1 3 3 8 4 5 4 3 6 6 3 3 3

Since the set of numbers (1′) is the same as a set of numbers complementary to (4′), but in the reverse order, the forms (1) and (4) are equivalent. Likewise (2) and (3) represent the same knot.

Effect of Distortion on the Compartment Symbol.—In a consideration of the different forms of a given knot, the compartment symbol is more convenient than the alphabetical symbol, although the statement of the effect of a given distortion is now not quite so simple. It is clear from figs. 4 and 4′ that a reversible tangle R_n exists when a compartment δ_i is joined once, and only once, to a compartment δ_j, which in turn is joined at any number of vertices to a compartment δ_k, and the entire configuration is bounded on the right and left by the compartments λ_r, λ_s respectively, λ_r, λ_s being joined at the same crossing as δ_i, δ_j, let the compartments δ_i, δ_j, δ_k, λ_r, λ_s be joined to the reversible tangle R_n by 0, a_2, a_3, b_1, b_2 crossings, and to the remainder of the knot by a_1', 0, a_3', b_1', b_2' crossings respectively, so that

$$\begin{aligned} i &= a_1' + 1 \\ j &= a_2 + 1 \\ k &= a_3 + a_3' \\ r &= b_1 + b_1' + 1 \\ s &= b_2 + b_2' + 1 \end{aligned}$$

Then the symbol for this portion of the knot becomes

$$\begin{tikzcd} \delta_{a_1'+1} \arrow[d, no head] & & \\ \delta_{a_2+1} \arrow[d, leftrightarrow, "\Phi" description] & \lambda_{b_2+b_2'+1} \arrow[r, no head] & \lambda_{b_1+b_1+1} \\ \delta_{a_3}+\delta_{a_3'} & & \end{tikzcd}$$

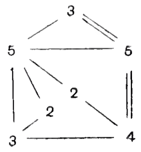
where $\overset{\uparrow}{\underset{\downarrow}{\Phi}}$ indicates that the two compartments may be joined directly or indirectly. By the application of the distortion D_n, this symbol becomes

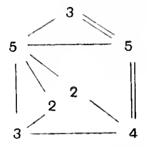
$$\begin{tikzcd} \delta_{a_1'+a_2} \arrow[d, leftrightarrow, "\Phi" description] & & \\ \delta_{a_3+1} \arrow[d, no head] & \lambda_{b_1+b_2'+1} \arrow[r, no head] & \lambda_{b_1'+b_2+1} \\ \delta_{a_3'+1} & & \end{tikzcd}$$

When $a_1' = a_3'$, $a_2 = a_3$, $b_1 = b_2$, the number of compartments and the number of angles in each is undisturbed. If the order in which these compartments are joined is the same as for the original knot, then the distortion reduces to a deformation, since the two forms are equivalent.

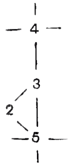
Both the primary and secondary symbol admit the possibility of distortions. The simple distortion D on the primary symbol merely changes the position of two joins in the secondary symbol.

As a simple illustration of the effect of a distortion on the compartment symbol, consider the knot whose primary and secondary symbols are

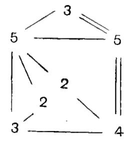


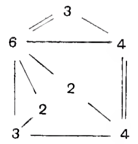


The primary symbol shows the presence of the reversible tangle R_2:

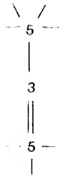


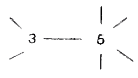
for which $a_1' = b_1' = 3$, $a_2' = a_3 = a_3' = b_2 = b_2' = 2$, $b_1 = 1$. Hence the application of the corresponding distortion D_2 gives the symbol



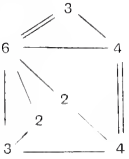


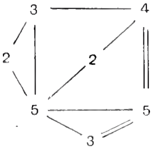
In addition to the reversible tangle R_2, the primary symbol exhibits the reversible tangle R_1:

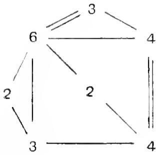


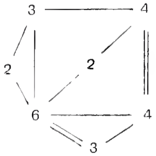


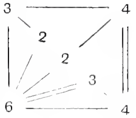
Similarly, the secondary symbol shows the presence of the reversible tangles R_1' and R_2'. Hence there exists the possibility of distortions D_1, D_1', D_2, D_2', and all possible combinations of these. It is found that the above form possesses only the four variants—

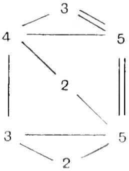


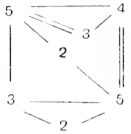


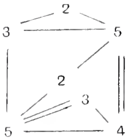












§ 3. Amphicheiralism.

The perversion of a knot is the form obtained by replacing each crossing with one of the opposite character. The amphicheiral knot was originally defined by Tait as one which can be deformed into its own perversion. From this definition it is to be inferred that to every compartment δ_i there corresponds a similar and similarly placed compartment λ_i; that is to say, a necessary condition for an amphicheiral knot is the identity of the primary and secondary symbols.

Since the primary and secondary symbols of the amphicheiral knot are the same, the plane is divided into an even number of compartments by the plane projection of the knot, and consequently an even number of crossings is involved.

If such a knot is fitted on the surface of a sphere so that the corresponding arcual boundaries are made equal, a spherical compartment δ_i and its corresponding compartment λ_i must either be congruent or symmetrical* (where symmetrical is used in the sense of symmetrical triangles on a sphere). An amphicheiral knot whose corresponding compartments are congruent is called by TAIT an amphicheiral of the first order, as distinguished from one of the second order, in which the corresponding compartments are merely symmetrical.

From the definition of an amphicheiral knot it is seen that every distortion D_n carries with it a conjugate distortion $\overline{D}_n$ such that the product $D_n\overline{D}_n$—that is to say, the simultaneous application of the two distortions—gives an amphicheiral knot. The form obtained by the single operation D_n can be *distorted* into its own perversion by the operator $D_n^{-1}\overline{D}_n$, and is said to be of the second class, while one which can be *deformed* into its own perversion belongs to the first class. Therefore TAIT divides the amphicheirals of each order into those of the first or second class, according as they are the result of operating on the knot with conjugate or non-conjugate distortions.

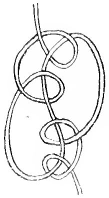


FIG. 4.

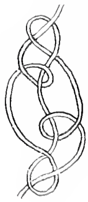


FIG. 4′.

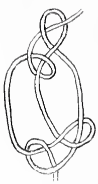


FIG. 4″.

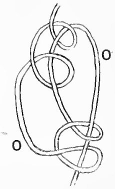
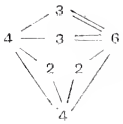
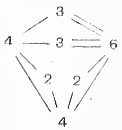


FIG. 4‴.

In an investigation of the amphicheiral knots of order 12 it appears that a third classification of amphicheiral knots of the first and second orders is necessary, namely, amphicheirals which are obtained as the product of two or more non-conjugate distortions. For example, consider the amphicheiral knot (fig. 4) whose compartment symbol is





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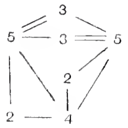
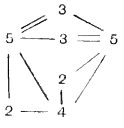
* (*Trans. R.S.E.*, xxxii, p. 494; or *Scientific Papers*, i, p. 336.) In his third paper TAIT deliberately limits himself to this view; but he remarks—"We shall afterwards find that there are at least three other senses in which a knot may be called amphicheiral, and shall thus be led to speak of different *orders* and *classes* of amphicheirals." (See below, § 6.)

There exist four reversible tangles R_1, $\bar{R}_1$, R_1', $\bar{R}_1'$ of the type

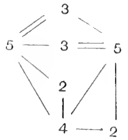
R_1, R_1' being conjugate to $\bar{R}_1$, $\bar{R}_1'$ respectively. The distortions $D_1\bar{D}_1$, $D_1'\bar{D}_1'$ transform the knot into the amphicheiral form

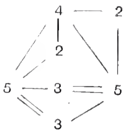




as shown in fig. 4′.

The knot shown in fig. 4″ is obtained from the original by means of the distortion $D_1\bar{D}_1'$. Its compartment symbol is





but the knot is not an amphicheiral knot of the first class.

The distortion $\bar{D}_1\bar{D}_1'$ reproduces the original amphicheiral with amphicheiral centres O, O′, as shown in fig 4‴. In this case the distortion $\bar{D}_1\bar{D}_1'$ amounts to a deformation of the knot. Possibly the effect of the above distortion may be accounted for by the peculiar symmetry of the knot.

§ 4. Amphicheirals of the First Order.

A census of the twelvefold amphicheiral knots of the first and second orders is given on pp. 253–255 (shown also on the Plate); in the construction of these the methods of Tait[*] have been used.

Tait's Method of Construction.—When an amphicheiral knot is fitted on the surface of a sphere, as stated on p. 244, the part of the knot on one hemisphere is congruent to the part on the other. This congruence persists when the knot is subjected to symmetrical deformations by shortening or lengthening corresponding

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[*] *Trans. Roy. Soc. Edin.*, xxxii, pp. 494–497; or *Scientific Papers*, i, 336–340.

laps of the thread, and consequently any path drawn across the knot can be made a great circle.

Since the two parts of the knot are congruent, rotation about a certain diameter will bring the first part of the knot into the position originally occupied by the second part. Tait shows that this diameter must terminate in the mid-points of corresponding laps of the thread. But a rotation about such a diameter necessitates the existence of two pairs of adjacent corresponding compartments, in order that each compartment of the sphere may be rotated into the position of its corresponding compartment. The number of such diameters depends on the number of pairs of adjacent corresponding compartments. Now deform the knot so that the path from O to O′, which meets the knot in the minimum number, p, of points exclusive of O, O′, shall become the arc of a great circle S of the sphere, but in such a way as to keep corresponding crossings at equal arcual distances from the points O, O′. Since all great circles through the points O, O′ divide the knot into congruent halves, the projection of the knot from the point O′ on the tangent plane to the sphere at O will be divided into halves by all the straight lines through O, and in particular by the straight line s, which corresponds to the great circle S of the sphere. Of the $2p+2$ points of intersection of the line s and the knot, one, corresponding to the point O′, lies at infinity, and the rest by pairs at equal distances from the amphicheiral centre O. A part of the thread which joins two of these points is a bend. The framework for one half of the knot, that is, the framework on either side of the line s, consists of $p+1$ bends, of which one is infinite, since one point of intersection lies at infinity. Every possible arrangement of the bends must be considered; and in every admissible arrangement the bends are made to intersect so as to exhibit one half of the total number of crossings. The congruent half completes the knot (*cf.* fig. 5).

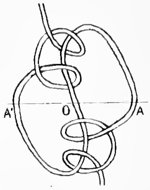

Fig. 5.

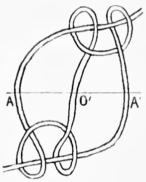

Fig. 5′.

Inasmuch as two entirely different paths, O, O′, through the knot may give the proper number of intersections, $2p+2$, the knot* may be built upon an entirely different framework, and in such a case the eye may be deceived. The equivalence of the two is immediately detected by means of the compartment or intrinsic symbol.

If the knot is projected from the point O, on the tangent plane at the point O′, the figure exhibits symmetry about the point O′. This projection may be said to be

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* Tait, *Trans. Roy. Soc. Edin.*, xxxii, p. 496; or *Scientific Papers*, i, p. 338.

the complementary form of the knot. For example, the complementary form given by fig. 5 is fig. 5′; the identity of this with fig. 5 may be recognised either from the compartment symbol or from the intrinsic symbol (p. 240).

Tait points out how, in the structure of the framework, m-filar knots can be avoided, and that composite knots, which are at once detected, must be discarded.

By the index of a knot, with respect to the pair of amphicheiral centres O, O′, is meant the number p which has been defined earlier. For a knot of order n, it may be shown that n is not less than $4p$; hence, for $n=12$, the only values of p to consider are 1, 2, 3. That is, in the construction of the amphicheiral knots of order 12, it is unnecessary to consider frameworks with more than four bends, including the infinite bend.

If a knot has a second pair of amphicheiral centres, not necessarily on the line OO′, the corresponding index may be the same as or different from p, and hence the knot may be constructed on a different framework. For example, knot No. 31 on the Plate, shown also in fig. 6, is of index 2 with respect to the pair of amphicheiral centres O, O′, but of index 3 with respect to the pair O_1, O'_1. Also Nos. 34, 35, for which $p=2$, belong to the set $p=3$ (see the Plate).

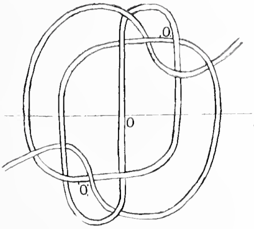

Fig. 6.

§ 5. Amphicheirals of the Second Order.

Tait's Method of Construction.—When an amphicheiral knot of the second order is fitted on the surface of a sphere, a compartment δ_i must either be diametrically opposite to its corresponding compartment λ_i, or it must be the image of the compartment λ_i in a diametral plane.

In the first case the desired arrangement of compartments may be obtained by means of a closed curve on a sphere and its diametrically opposite curve, together with a great circle. Such an arrangement can only lead to a trifilar knot. Further, the knot is bifilar if the curve is taken as its own opposite.

As may be seen by a projection from one pole of the great circle on to the tangent plane to the sphere at the other, the proper correspondence of compartments in a plane is secured by means of a circle, a closed curve, and its inverse as to the circle, but reflected in the origin. If now the closed curve is made to touch the circle in a point, the inverse curve will touch it at the diametrically opposite point, and it is necessary only to replace the contacts by crossings to secure the representation of a unifilar knot which exhibits amphicheiralism.

The second method of producing compartments δ_i and λ_i of the desired nature is rejected by TAIT, since it leads to a link solution. While a closed curve and its image in a diametral plane, together with the great circle of the sphere in this plane, will give the desired arrangement of compartments, it is impossible to fuse the curves into a single circuit as in the first case, for the process introduces triple points which cannot be replaced by three dps without destroying the amphicheiral symmetry. Hence, only the simplest trifilar link can result from such an arrangement. If the curve is taken as its own image, a bifilar knot is represented.

Before applying this method of construction, some preliminary considerations are necessary.

A closed curve on a sphere is either * a simple circuit or one member of a twin circuit. The simple circuit, which is its own opposite on the sphere, is met by a great circle in an odd number of pairs of points. In TAIT's method of construction a simple circuit leads always to an m-filar knot.

The twin circuit, which consists of a closed curve and its opposite on the sphere, intersects a great circle in an even number, 2ι, of pairs of points. There are two types of twin circuits which may present themselves. First, if $\iota = 0$, each member of the twin circuit is confined to a single hemisphere. Second, if $\iota \neq 0$, each member exceeds that hemisphere, and therefore the two members may intersect, necessarily in an even number, $2\sigma'$ of points where $\sigma' = 0, 1, 2, \ldots$

The projection, f, of any closed plane curve on to the sphere from its centre gives a twin circuit of the first type. A twin circuit of the second type is obtained by a similar projection of a plane curve of even order, which cannot be projected entirely into the finite part of the plane, as, for example, the Cayley non-singular sextic,† for which $\iota = 6$, $\sigma' = 0$. Every non-singular twin circuit divides the sphere into three regions, in one of which an odd circuit may lie.

Each member of the twin circuit may have σ dps, thus giving rise to σ pairs of crossings in the resulting knot. The only other cause that can produce crossings in the knot is the presence of κ pairs of contacts of the circle and the twin circuit. For a knot of order n, κ may not be greater than $\frac{n}{2}$. Hence for $n = 12$, $\kappa \not> 6$.

The few numerical possibilities for the above numbers to be considered are given in the following table :—

κ	1	1	1	2	2	2	2	3	3	3	4	4	4	5	6
ι	4	2	2	4	2	2	0	2	0	0	2	0	0	0	0
σ	1	3	1	0	0	2	4	1	3	1	0	2	0	1	0
σ'	0	0	2	0	2	0	0	0	0	2	0	0	2	0	0

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* MÖBIUS, *Über die Grundformen der Linien der dritten Ordnung*, ii, p. 90.

† CAYLEY, vol. v, op. 361, p. 468.

Of the hundreds of cases arising from the different arrangements of these points, and the different ways of joining them, the greater number lead to composite or m-filar knots. Also Nos. 19, 21, 22, 24 ($p=2$) of the amphicheirals of the first order (see Plate) appear among those of the second order, since the arrangement of the δ and λ compartments is symmetrical, and hence unaltered by reversion (Tait, iii, § 12). Rejection of these reduces the amphicheirals of the second order with twelve crossings to the following two:—

(5) *f j g i b e l d a c h k* $[\mathrm{D}_1^e]$
(6) *f k b i a d l e h c g j* $[\mathrm{D}_1^b]$

These two knots can be constructed on models involving more than one pair of contacts, and hence may be expected to present themselves several times in the course of the construction. Starting with a given knot of the second order, the different models on which the knot may be constructed are obtained by transferring one or more compartments to the inside of the circle, and therefore their correspondents to the outside of the circle. This amounts merely to a deformation of the knot so as to make any desired path into a circle.

If small letters are used to denote the intersections of the circle and the twin pair, while capital letters indicate the points of contact, that is, the crossings at which a change of thread takes place, then the different models for the above knots may be represented as follows:—

(5′)
(1) A *f b j c* G *l h d i*
(2) I *e* B *j* C *k* H *d*
(3) A *f b* J C G *l h* D I
(4) A F E B *j c* G L K H *d i*
(5) A F B J C G L H D I
(6) A F E B J C G L K H D I

(6′)
(1) A *f d* G *l j*
(2) *a f* D *b c* K *g l* J *h i* E
(3) A *f* B C *k* G *l* H I *e*
(4) A F D *b* C *k* G L J *h i* E
(5) A F D B K G L J H E

§ 6. Skew Amphicheirals of the Second Order.

In a note added to his last paper on knots, Tait gives a special knot* of order 8 which he classes as an amphicheiral of the second order; although, strictly speaking, it does not belong to the second order, since corresponding compartments are not opposite when fitted on a sphere.

In the investigation of amphicheirals with twelve crossings this type assumes

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* *Trans. Roy. Soc. Edin.*, xxxii, p. 500; *Scientific Papers*, i, p. 342.

sufficient importance to be worth separate treatment. Knots of this character have, however, so much in common with the regular amphicheirals of the second order, that it seems convenient to call them skew amphicheirals of the second order.

Following TAIT's construction for the special knot in question, consider on a sphere a non-singular closed curve that has, in common with a great circle, no points except μ points of contact, conveniently placed at the alternate vertices $V_1, V_2, \ldots . V_\mu$ of a regular polygon with 2μ sides; and a similar curve on the opposite hemisphere to touch the circle at the remaining vertices $V_1', V_2', \ldots . V_\mu'$. Projection from either pole of the great circle shows that this construction may be accomplished in the plane by drawing inside a circle a non-singular closed curve C which touches the circle at the alternate vertices $v_1, v_2, \ldots . v_\mu$ of a regular polygon, of 2μ sides and a corresponding curve C′, to touch at the remaining vertices $v_1', v_2', \ldots . v_\mu'$. When the points of contact are regarded as crossings, the figure that results possesses the desired amphicheiral symmetry, although it is not necessarily unifilar. The plane projection of such a knot from the mid-point of an arc $| V_1V_1' |$ of the great circle on the tangent plane at the diametrically opposite point exhibits symmetry about a point, as in the case of the amphicheirals of the first order.

In the case when μ is odd, a point of contact v_1 of the curve C is opposite to a point of contact of the curve C′, and the curve C is opposite to the curve C′. Hence the resulting knot is an amphicheiral of the second order.

On the other hand, if μ is even, the point of contact v_1 is opposite to the point $v_{\mu/2}$. Corresponding arcs are no longer opposite as to the circle. Nevertheless the corresponding compartments of the resulting knot are equal and non-congruent, as in the amphicheirals of the second order.

If $\mu = 4$, the peculiar eightfold knot given by TAIT is obtained.

The special case $\mu \equiv 0 \bmod 3$ leads always to a trifilar link. For suppose the knot to be described by a point P in a fixed direction, starting from the point v_1 along the arc $| v_1v_2 |$ of the curve C. It leaves this arc at the point v_2 along the circle, only to return to the curve C after the elapse of four vertices of the regular polygon; that is to say, in going once around the circle, every third arc $| v_i v_j |$ of the curve C is described. If therefore the number of such arcs is a multiple of 3, the point P returns to the position v_1 along the arc $| v_1v_2 |$ by which it left, before the complete knot has been described. A second thread of the knot is traversed if the point P starts from the point v_2 along the arc $| v_2v_3 |$. And, starting from the point v_3 along the arc $| v_3v_4 |$, a third thread is obtained, thus completing the description of the knot. On the other hand, $\mu \equiv 0 \bmod k$, where k is any other number, must lead to unifilar knots, since it will be necessary for the point P to go around the circle three times before returning to the starting-point along the same arc by which it left. The primary compartment symbol for such a knot contains $2\mu + 1$ compartments, one with μ angles and μ with three angles each. The compartment δ_μ is joined once to each of the compartments δ_3, any two adjacent compartments δ_3 being joined singly.

In the construction of these amphicheirals it is not, however, necessary that the curve used be non-singular; it is possible to obtain a figure which exhibits the

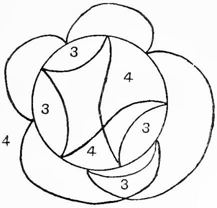
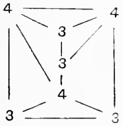
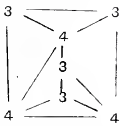


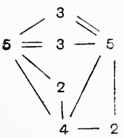
FIG. 7.

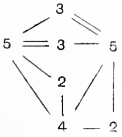
amphicheiral property by means of two singular curves arranged as above. For example, fig. 7 represents the amphicheiral knot whose compartment symbol is





Corresponding compartments are not opposite on the sphere; nevertheless the primary and secondary symbols exhibit the identity as to the number and arrangement of the joins, differentiated only by the right- and left-handed property peculiar to an amphicheiral of the second order. By reversal of the one set of compartments the amphicheiralism is undisturbed, and this knot is found to be No. 22 ($p=2$) of the amphicheirals of the first order. However, the skew amphicheiral constructed as shown in No. 61 in the plate of knots is not an amphicheiral of the first class as defined by TAIT. It is equivalent to the knot shown in fig. 4‴, p. 244, which is the result of applying to the amphicheiral knot shown in fig. 4, p. 244, two non-conjugate distortions. Consequently TAIT would call it an amphicheiral of the first order and second class. But its compartment symbol





shows the particular character that belongs to an amphicheiral of the second order. It is prevented from being classed as an amphicheiral of the second order by the fact that it is not obtained by means of a twin circuit in contact with a circle; that is to say, corresponding compartments are not opposite.

Thus it is seen that TAIT* is not justified in stating that there are but two possible ways in which corresponding spherical compartments of a knot may be equal. Further, contrary to TAIT,† it is possible for an amphicheiral knot to belong to the first class of one order and to the second class of another; as, for example, the skew amphicheiral (No. 61), which belongs to the second class of the amphicheirals of the first order, and first class of the skew amphicheirals of the second order.

The explanation of the difficulty is that the set of λ compartments cannot be moved on the sphere without affecting the set of δ compartments; hence it is not always possible to place the whole knot in one of the two ways considered by TAIT. Inasmuch as all possible cases of amphicheiralism do exhibit themselves in the compartment symbol, it seems highly advisable to use this in the definition, which may then be formulated as follows:—

Definition.—An amphicheiral knot of the first class is one whose primary and secondary symbols are identical as to numbers and arrangement, but with rotation in the same sense for those of the first order, in the opposite sense for those of the second order. Any form obtained from an amphicheiral of the first class by non-conjugate distortions ‡ is an amphicheiral of that same order, but of the second class. It is, however, possible for a knot to belong to the first class of one order and to the second class of the other. Since the two symbols are alike, it is possible by a deformation to replace the amplexus δ_i with the corresponding compartment λ_i, and the perversion is obtained.

With one exception (No. 61) the skew amphicheiral with twelve crossings turn out to be amphicheirals of the first order. This overlapping of the different divisions has been detected by TAIT for knots with ten crossings, where there are no amphicheirals of the second order that are not also of the first order. As shown here for twelve crossings, there are some of the second order not included under those of the first order; presumably with a greater number of crossings there may exist amphicheirals of the second order that escape any of the other divisions.

This completes the census of the twelvefold amphicheirals, of which there are sixty-one, as compared with one fourfold, one sixfold, five eightfold, and thirteen tenfold amphicheirals.

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* TAIT, *Trans. Roy. Soc. Edin.*, xxxii, p. 498; or *Scientific Papers*, i, p. 340.

† TAIT, *Trans. Roy. Soc. Edin.*, xxxii, p. 499; or *Scientific Papers*, i, p. 341.

‡ It must be remembered that if a knot is amphicheiral of the first order, with more than one pair of centres, distortions that are non-conjugate for one pair may be conjugate for another pair.

§ 7. Census of Amphicheirals with Twelve Crossings.

In the census of the amphicheiral knots of the first order with twelve crossings the alternate crossings which occur as the knot is described in a fixed direction from the amphicheiral centre at infinity are denoted by a, b, c, . . . The first crossing a in the amphicheirals of the second order has been assigned arbitrarily. Only the letters which occupy the even places in the sequence of the alphabetical symbol of the knot are given, although the distortions D_n, given in brackets, are detected only in the complete scheme. The number of different forms of a given knot is indicated by the number of distinct distortions D_n in the brackets following the knot scheme; the different forms are obtained by the product of a distortion D_n and its conjugate $\overline{\mathrm{D}}_n$, which occurs at the same distance from the amphicheiral centres as D_n.

In the determination of the pairs of amphicheiral centres of a knot the intrinsic symbol is very convenient. It may be shown that the sum of the numbers at equal distances from an amphicheiral centre is equal to $n-1$, where n is the order of the knot. From the reduced alphabetical symbols given, it is a simple matter to write down the complete alphabetical and therefore the intrinsic symbols of the knots; hence the pairs of amphicheiral centres are known, and the knot may be constructed.

There exist the following amphicheirals with twelve crossings :—

I. Amphicheirals of the First Order :

$p=1$, Nos. 1–18 ; $p=2$, Nos. 19–54 ; $p=3$, Nos. 55–58.

(1) $i\ h\ g\ l\ j\ k\ c\ b\ a\ f\ e\ d$

(2) $h\ i\ g\ k\ l\ j\ a\ b\ c\ d\ e\ f$

(3) $i\ g\ h\ l\ j\ k\ c\ a\ b\ f\ d\ e$

(4) $h\ i\ g\ k\ l\ j\ b\ a\ c\ d\ f\ e$ $[\mathrm{D}_2^k, \mathrm{D}_2^k\mathrm{D}_3^d]$

(5) $i\ g\ h\ l\ j\ k\ c\ b\ a\ f\ e\ d$ $[\mathrm{D}_2^b]$

(6) $h\ a\ g\ c\ l\ j\ d\ b\ f\ i\ e\ k$ $[\mathrm{D}_1^a]$

(7) $d\ h\ g\ a\ k\ j\ b\ c\ l\ e\ f\ i$ $[\mathrm{D}_2^g, \mathrm{D}_3^d]$

(8) $d\ h\ b\ g\ k\ i\ a\ c\ l\ e\ j\ f$ $[\mathrm{D}_1^b, \mathrm{D}_1^d, \mathrm{D}_3^a, \mathrm{D}_1^b\mathrm{D}_3^a, \mathrm{D}_1^d\mathrm{D}_3^a]$

(9) $g\ h\ b\ a\ k\ l\ d\ c\ f\ e\ j\ i$ $[\mathrm{D}_1^b, \mathrm{D}_2^d, \mathrm{D}_3^g, \mathrm{D}_4^a, \mathrm{D}_1^b\mathrm{D}_3^g, \mathrm{D}_2^d\mathrm{D}_3^g, \mathrm{D}_3^g\mathrm{D}_4^a, \mathrm{D}_2^d\mathrm{D}_3^g\mathrm{D}_4^a, \mathrm{D}_1^b\mathrm{D}_2^d\mathrm{D}_3^g]$

(10) $c\ h\ a\ g\ k\ i\ d\ b\ f\ l\ e\ k$ $[\mathrm{D}_1^c, \mathrm{D}_1^a, \mathrm{D}_3^d; \mathrm{D}_1^c\mathrm{D}_3^d, \mathrm{D}_3^d\mathrm{D}_4^g]$

(11) $i\ h\ f\ l\ k\ c\ j\ b\ a\ g\ e\ d$ $[\mathrm{D}_3^f]$

(12) $c\ h\ i\ j\ k\ d\ a\ b\ g\ l\ d\ f$ $[\mathrm{D}_1^c, \mathrm{D}_2^i, \mathrm{D}_2^a, \mathrm{D}_1^c\mathrm{D}_2^i, \mathrm{D}_1^c\mathrm{D}_3^a, \mathrm{D}_1^c\mathrm{D}_2^i\mathrm{D}_4^d]$

(13) $e\ a\ g\ b\ c\ j\ d\ l\ f\ h\ i\ k$ $[\mathrm{D}_1^a, \mathrm{D}_2^c, \mathrm{D}_1^a\mathrm{D}_2^c]$

(14) $e\ d\ g\ a\ b\ j\ c\ l\ k\ f\ h\ i$ $[\mathrm{D}_1^d, \mathrm{D}_2^d]$

(15) $e\ g\ b\ a\ d\ k\ c\ l\ h\ f\ j\ i$ $[\mathrm{D}_1^d, \mathrm{D}_1^b, \mathrm{D}_2^b, \mathrm{D}_1^d\mathrm{D}_1^b, \mathrm{D}_1^d\mathrm{D}_2^b]$

(16) $i\ d\ f\ l\ b\ c\ j\ a\ k\ g\ h\ e$
(17) $j\ e\ l\ f\ b\ d\ i\ k\ g\ a\ h\ c$ $[\mathrm{D}_1^i, \mathrm{D}_1^g]$
(18) $i\ f\ e\ l\ c\ b\ k\ j\ a\ h\ g\ d$ $[\mathrm{D}_1^f, \mathrm{D}_1^e]$
(19) $d\ h\ f\ a\ k\ c\ j\ b\ l\ g\ e\ i$
(20) $f\ d\ h\ a\ j\ b\ l\ c\ k\ e\ g\ i$ $[\mathrm{D}_1^d]$
(21) $j\ e\ l\ g\ b\ i\ d\ k\ f\ a\ h\ c$
(22) $f\ e\ h\ g\ j\ i\ l\ k\ b\ a\ d\ c$
(23) $i\ e\ h\ l\ j\ b\ d\ k\ f\ a\ g\ c$
(24) $f\ j\ k\ g\ b\ i\ l\ d\ e\ a\ h\ c$
(25) $e\ i\ g\ k\ a\ j\ b\ l\ c\ d\ f\ h$
(26) $j\ h\ l\ g\ k\ i\ b\ d\ e\ a\ f\ c$
(27) $f\ a\ i\ j\ b\ d\ l\ c\ g\ e\ h\ k$ $[\mathrm{D}_1^a]$
(28) $i\ a\ g\ l\ c\ j\ d\ b\ f\ h\ e\ k$ $[\mathrm{D}_1^a]$
(29) $f\ h\ i\ j\ k\ b\ l\ c\ a\ e\ g\ d$
(30) $i\ f\ h\ l\ j\ c\ k\ b\ a\ g\ e\ d$
(31) $e\ f\ h\ g\ j\ i\ k\ l\ b\ a\ d\ c$
(32) $j\ f\ l\ g\ b\ i\ k\ d\ e\ a\ h\ c$
(33) $i\ f\ a\ l\ b\ e\ k\ g\ c\ d\ h\ j$ $[\mathrm{D}_1^e]$
(34) $e\ h\ f\ a\ k\ c\ j\ l\ b\ g\ d\ i$
(35) $d\ i\ f\ k\ a\ b\ j\ c\ l\ e\ g\ h$
(36) $f\ i\ b\ k\ a\ d\ l\ c\ g\ e\ j\ h$ $[\mathrm{D}_1^b]$
(37) $k\ l\ h\ c\ j\ b\ d\ a\ f\ i\ g\ e$ $[\mathrm{D}_1^e]$
(38) $e\ f\ g\ a\ b\ j\ k\ l\ c\ d\ h\ i$
(39) $e\ f\ g\ b\ a\ j\ k\ l\ c\ d\ i\ h$ $[\mathrm{D}_2^k]$
(40) $e\ f\ h\ a\ j\ c\ k\ l\ b\ g\ d\ i$
(41) $e\ j\ k\ a\ b\ c\ d\ l\ f\ g\ h\ i$
(42) $e\ j\ k\ b\ a\ c\ d\ l\ f\ g\ i\ h$
(43) $f\ j\ k\ h\ i\ c\ l\ a\ b\ g\ d\ e$
(44) $j\ f\ l\ g\ a\ i\ k\ c\ b\ e\ d\ h$
(45) $j\ i\ l\ k\ a\ b\ d\ c\ f\ e\ g\ h$
(46) $i\ f\ g\ l\ b\ j\ k\ a\ c\ d\ h\ e$
(47) $f\ i\ h\ k\ j\ b\ l\ c\ a\ e\ g\ d$
(48) $i\ j\ k\ l\ a\ c\ e\ f\ b\ g\ d\ h$
(49) $j\ i\ l\ k\ a\ c\ e\ f\ b\ g\ d\ h$
(50) $c\ f\ a\ g\ b\ i\ k\ d\ e\ l\ h\ j$ $[\mathrm{D}_1^e, \mathrm{D}_1^a]$
(51) $d\ f\ b\ h\ i\ c\ k\ a\ l\ g\ j\ e$ $[\mathrm{D}_1^b, \mathrm{D}_1^d]$
(52) $e\ g\ h\ a\ j\ k\ c\ l\ b\ f\ d\ i$
(53) $j\ g\ l\ a\ b\ k\ c\ d\ e\ f\ h\ i$
(54) $j\ g\ l\ h\ i\ k\ d\ a\ f\ b\ c\ e$
(55) $k\ f\ g\ b\ l\ j\ k\ a\ c\ d\ i\ e$
(56) $h\ j\ k\ b\ l\ c\ d\ a\ f\ g\ i\ e$
(57) $h\ j\ k\ a\ l\ c\ b\ d\ e\ g\ f\ i$
(58) $d\ j\ k\ h\ i\ c\ b\ a\ l\ g\ f\ e$

II. Amphicheirals of the Second Order :—

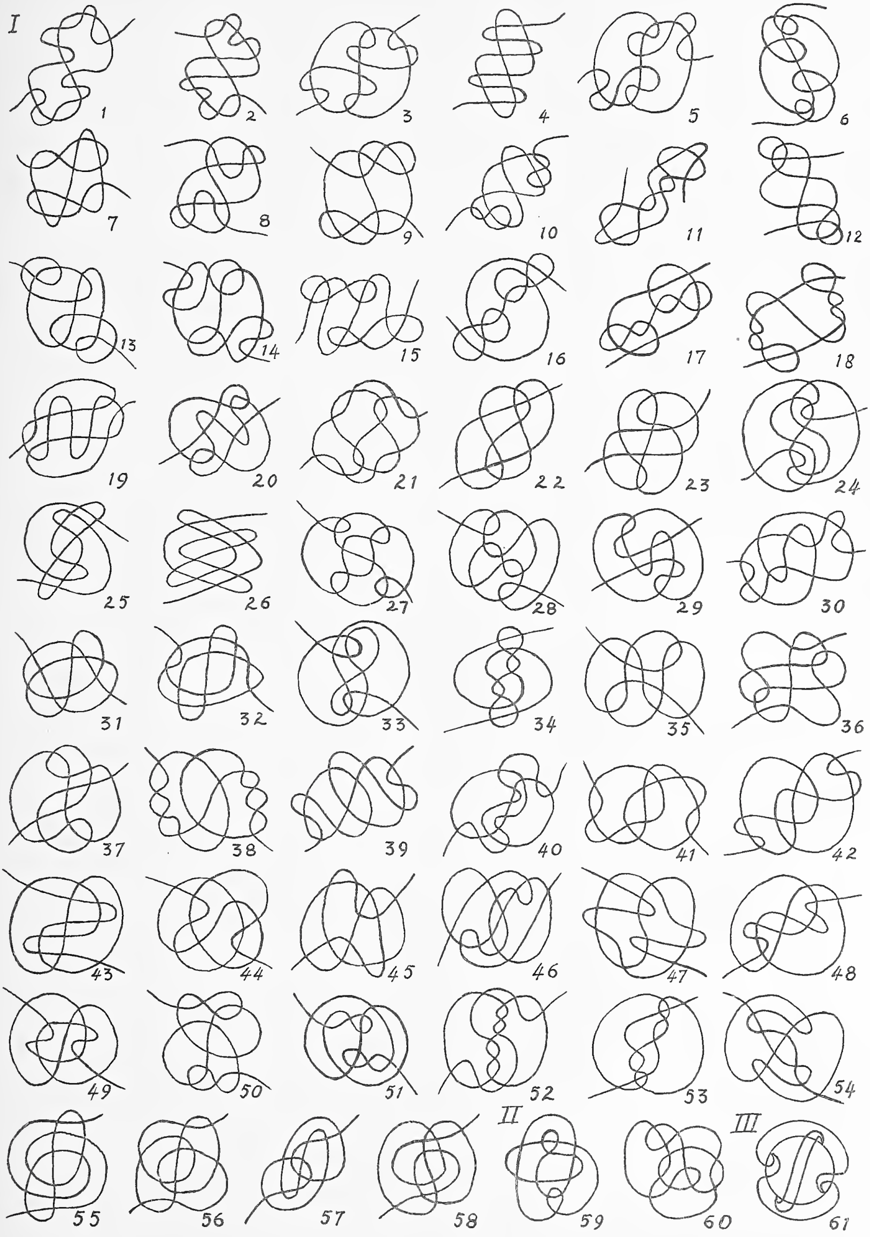
(59) $f\ j\ g\ i\ b\ e\ l\ d\ a\ c\ h\ k$ $[\mathrm{D}_1^e]$
(60) $f\ k\ b\ i\ a\ d\ l\ e\ h\ c\ g\ j$ $[\mathrm{D}_1^b]$

III. Skew Amphicheirals of the Second Order :—

(61) $i\ g\ b\ l\ j\ e\ c\ a\ h\ f\ d\ k$

I am indebted to Dr J. R. Conner and Professor Huff of Bryn Mawr College for their interest and encouragement; particularly to Dr Conner for his helpful criticisms. I am especially glad to have this opportunity of expressing to Professor Scott my sincere gratitude for her valuable help and unfailing encouragement during the writing of this dissertation as well as throughout my graduate course.

MARY G. HASEMAN: AMPHICHEIRAL KNOTS OF TWELVE CROSSINGS.



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XII.—The Development of the Heart in Man. By Prof. D. Waterston, M.D., Bute Medical School, University of St Andrews. (With Eighteen Text-figures and Sixteen Plate-figures.)

(Read July 9, 1917. MS. received December 26, 1917. Issued separately August 1, 1918.)

Introduction.

Examination of living embryos has shown that the heart is a functionally active organ from a very early stage of its development. At all periods of life the result of the functional activity is in essentials the same, viz. the propulsion of the blood in a definite direction through the heart into the vessels arising from it; but the mechanism for effecting this propulsion undergoes profound alterations, and the heart becomes transformed from a simple continuous tube, destitute of valves, whose walls contract in a rhythmic peristaltic wave, into a complex four-chambered organ, divided into right and left portions, which are ultimately completely separated from one another, possessing valves, and contracting not in a peristaltic wave but in alternating consecutive contractions of the atria and ventricles of the right and left sides simultaneously. Coincidently with the changes in the heart itself, profound alterations occur in the vessels leading to and from the heart. In this combination of simultaneous development and functional activity the heart differs from the other organs of the body, and hence its development presents special problems involving the function as well as the structure of the different parts. Our knowledge of the development of the heart in man cannot yet be said to be complete.

The discovery by Kent and His of connections between the atria and ventricles, and that by Keith and Flack of the sinu-atrial node, with the consequent altered views of the mechanism of the heart-beat which are now generally accepted, have imparted a new interest and value to the study of the development of the heart.

The development of the atrio-ventricular bundle has been worked out by Mall, but the records of examination of at all complete series of the hearts of human embryos are as yet scanty. The introduction of the plate method of reconstruction provided a new method of great value to embryologists, particularly in the study of the development of the heart, since without accurate plastic reconstructions it is almost impossible to follow the complex three-dimensional changes which occur, and hence those descriptions alone are of special value in which this method has been employed.

The embryonic material examined in this investigation includes human embryos from 3 mm. to 30 mm. in length (maximum) cut in serial section, and a number of larger embryos.

The principal developmental changes have been completed at the 30-mm. stage, though complete separation of the atria does not occur until birth.

The embryos examined in section include the following specimens :—

1.	Embryo	2W1,	3	mm. in length	(maximum).
2.	,,	S1,	6	,,	,,
3.	,,	B1,	8	,,	,,
4.	,,	M1,	9	,,	,,
5.	,,	S4,	12·5	,,	,,
6.	,,	B2,	13	,,	,,
7.	,,		16	,,	,,
8.	,,	S3,	20	,,	,,
9.	,,	B3,	22	,,	,,
10.	,,		30	,,	,,
11.	,,	E1,	28·5	,,	,,

All of these embryos showed good histological condition, and most of them almost perfect histological detail.

I am indebted to Prof. Symington for the embryos B1, B2, and B3, and to Prof. Peter Thompson and to Prof. Bryce respectively for the opportunity of examining and reconstructing from their sections the heart in the embryos 7 and 10 of the list.

In addition, I have examined series of sections of embryos of the cat, guinea-pig, and mouse, and I am greatly indebted to my colleague, Prof. W. C. M'Intosh, for the opportunity of examining specimens of the adult heart in the shark, dogfish, boa, and crocodile, examination of which gives considerable help in the correct interpretation of the conditions found in different stages of the development of the mammalian heart.

Prof. Peter Thompson also kindly allowed me to examine several of his reconstructions of developing hearts, and particularly his model of the 2·5-mm. embryo of R. Meyer's collection, which is a most valuable specimen.

The earliest stages of the development of the human heart are as yet unknown, as the material necessary for investigating them does not exist in any collection ; but it is presumed that the heart follows the lines of development exhibited in the earliest stages of other mammals, in whom the primitive heart is formed by the fusion of two parallel longitudinal vessels, which unite to form a single tube, receiving at its caudal extremity the afferent veins, and terminating orally in a single vessel, the truncus arteriosus, which divides almost at once into the two ventral aortæ.

The heart tube becomes bent upon itself and twisted into the shape of an S. Alternate dilatations and constrictions make their appearance, so that it comes to show a series of dilatations, viz. the sinus venosus, the atrium, the ventricle, and the "bulbus cordis" in succession from the caudal to the oral end. The atrium and ventricle are joined to one another by a short narrow channel of great importance in the later stages of development, termed the atrial canal. In describing these chambers the terms "proximal" and "distal" may be used, the former indicating the sinus end and the latter the truncus arteriosus end of the heart.

The stage at which the following description begins is that at which the heart has the form of a twisted tube, showing the constrictions and dilatations referred to above.

It is convenient to begin the description of the successive stages by giving an account of the heart in the youngest specimen examined, an embryo of twenty-seven pairs of somites (2W1) (1), maximum length (from sections) about 3 mm., from which models of the heart and trunk at a magnification of 100 and 200 diameters were made.

The larger model of the heart of this embryo is shown in the Plate-fig. 1. Viewed from the front, a portion of the atrium, the atrial canal, the ventricle and "bulbus cordis," leading to the commencement of the truncus arteriosus, are visible. In its general shape the heart bears a resemblance to the model constructed and figured by P. Thompson from the R. Meyer embryo (No. 399) of eighteen pairs of somites (2).

At this stage the heart tube is twisted so that the atrium lies oral and dorsal to the ventricle, the atrial canal lies on the left side, and the ventricle and "bulbus" are sharply bent upon one another. The ventricle lies on the left side and at the apex, and the "bulbus" extends along the right margin and curves orally to the left.

The heart tube has become divided into segments, viz. sinus venosus, atrium, ventricle, and bulbus cordis, separated from one another by constrictions, and the principal bendings have occurred at the constrictions separating these chambers. The sinus venosus and atrium are not sharply bent upon one another, but the atrial canal marks the position of a sharp bend, in an oblique plane, between atrium and ventricle. At the bulbo-ventricular constriction a bend has been formed in an almost vertical plane. The bulbus is slightly curved to the left, and another bend is found at the junction of bulbus and truncus arteriosus.

The terms "ventricle" and "bulbus cordis" are used here following Tandler (3). The terms and the significance of the chambers which they denote are discussed later.

Table I.

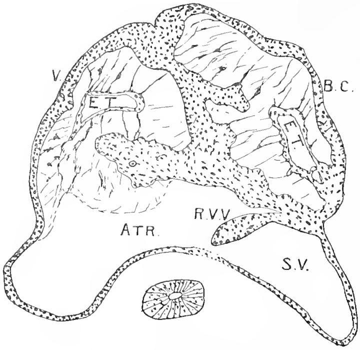
Dimensions of Heart Model of 2W1. × 200.

Vertical height		150	mm.
Transverse width of atrium		85	,,
Vertical height of atrium		110	,,
Sinu-atrial orifice, height		50	,,
Atrial canal, width		15	,,
Ventricle, dorso-ventral width		70	,,
,, transverse width		60	,,
,, thickness of wall		13	,,
Bulbus cordis, thickness of wall	lower part	13	,,
	upper ,,	6	,,

Chambers.—The sinus venosus consists of a short and comparatively narrow transverse portion, and of a right and left horn. The left horn, the smaller of the two, lies in the upper margin of the left portion of the septum transversum, whence the transverse portion passes to the right and terminates in a large right horn, which is partly embedded in the septum transversum and partly has risen out of it.

The right horn of the sinus venosus lies dorsally and to the right of the atrium. It is roughly triangular on section, and its wall is continuous with that of the atrium (text-fig. 1).

Sinu-atrial Orifice.—The communication between sinus and atrium is a vertical slit-like orifice, opening from right to left, and slightly ventrally. The ventral junction of sinus venosus and atrial walls is infolded, forming a prominent right venous valve, but there is no left venous valve.



TEXT-FIG. 1.—Transverse section (slide 103, section 3) of heart of 3-mm. embryo, showing the chambers and the narrow endothelial tube within the myo-epicardial mantle. × 100.

Atrium.—The atrium is a large, capacious chamber, lying dorsal and oral to the ventricle, and extending at its oral end across the whole width of the heart; the sinu-atrial opening is placed at the dorsal right margin, while the atrial canal opens from the caudal and left ventral corner.

The dorsal wall is incurved towards the cavity, but there is no trace of the atrial septum.

The muscular wall is deficient over a small area of the dorsal wall; the "area interposita" and the myocardial and endocardial walls are in contact. The muscle wall is extremely thin.

Atrial Canal.—This short channel extends from the left ventral and caudal corner of the atrium to the oral left portion of the ventricle. Its width in the model, at 200 diameters magnification, is 15 mm., and it is almost cylindrical.

In this portion is found that separation of the myocardial and epicardial walls by a space containing a loose reticulum of tissue, whose features have been worked out in similar specimens by MALL (4).

The endothelial tube containing the blood stream is a very narrow channel indeed, lying centrally within the lumen of the myocardial wall.

The sub-endocardial reticulum shows no division into separate cushions. It extends uniformly round the lumen of the tube, and is continuous with a similar reticulum in the upper part of the ventricle and in the bulbus.

The next portion of the heart, from the atrial canal to the root of the truncus arteriosus, is divided into two segments, separated from one another by a deep groove which traverses obliquely the ventral surface from the left to the caudal right margin, and is produced by the acute flexion of the heart tube (Plate-fig. 1).

The homologies of these portions and the successive development of each will be traced later; but for the present the proximal limb may be termed the ventricle, while the distal segment is termed the "bulbus cordis."

The ventricle is of the shape of an inverted triangle, the apex forming the apex of the heart. Its muscle wall, of considerably greater thickness than that of the atrium, is reticulated and separated in the greater part from the endothelial tube within by a space containing fine fibrils. Only at the caudally-placed apex are these two walls, myocardium and endocardium, in apposition. The atrial canal opens at the oral left angle, while the exit to the bulbus is at the corresponding oral and right corner.

At the junction of bulbus and ventricle the lumen of the heart tube is narrowed, and a short surface constriction is formed, partially separating them.

From the interior, this separation of bulbus and ventricle is seen to be due to the infolding by the bulbo-ventricular groove of the ventral wall, so that a prominent ridge is formed on the ventral and oral aspect extending to the caudal border of the lumen.

The bulbus cordis possesses a myocardial wall of some thickness, a delicate reticulum, and in the interior a narrow endothelial blood tube.

As in the atrial canal a reticulum of this nature precedes the formation of endocardial cushions, so apparently here also the reticulum precedes the formation of definite bulbar cushions.

The reticulum ceases abruptly at the commencement of the truncus arteriosus, and the endothelial tube widens out to line the external wall; and at this point the muscle wall of the heart ceases abruptly, and is replaced by fibrous tissue on the wall of the truncus arteriosus.

The bulbus is roughly of a triangular outline, for near its middle the oral right wall is considerably distended. It lies in the ventral surface of the atrium.

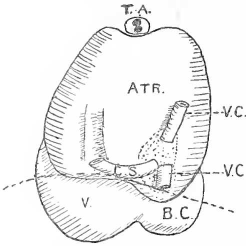
If this specimen be compared with the rather younger embryo heart modelled by THOMPSON (2), a close resemblance of the specimens can be noted, and corresponding divisions of the heart tube are present. In his specimen, however, while the ventricle and bulbus have generally the same features as in mine, their relative position is different—the ventricle lying caudally in his specimen, and the bulbus lying orally, the two chambers separated by a bulbo-ventricular groove which is nearly horizontal in direction.

The condition in my specimen has been reached by a rotation of the bulbo-ventricular groove from the horizontal to the oblique axis, and later specimens show that this rotation is continued until the groove is vertical in direction.

HEART OF EMBRYO S1 (6 MM. IN LENGTH).

The external form and the internal structures are shown in Plate-figs. 2, 3, and 4.

At this stage the sinus venosus has risen out of the substance of the septum transversum, and in place of the vitelline and umbilical veins there is a single large vessel (vena cava inferior) which opens into the right horn of the sinus venosus. The left duct of Cuvier runs into a comparatively narrow channel, and the transverse portion of the sinus venosus passes along the posterior surface of the heart and opens by a narrow orifice into the right horn. The right horn forms a small chamber, into which opens the right duct of Cuvier and the vena cava inferior. The sinus venosus opens into the atrium by a narrow slit-like orifice, measuring in the model 25 mm. vertically and 5 mm. transversely at its widest part. The sinus wall is smoothly and evenly continued into the atrial wall.



TEXT-FIG. 2.—Dorsal view of heart of 6-mm. embryo.

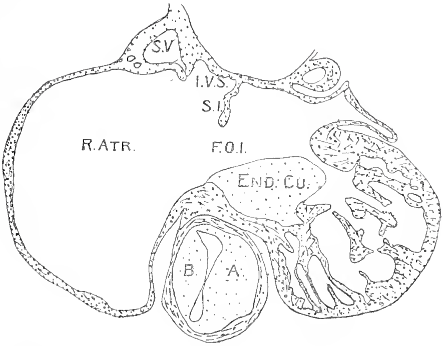
The right venous valve—the more prominent of the two—measures 8 mm. in length, and in structure consists of a more loosely reticular tissue than the adjacent heart wall, and vacuoles or spaces are present within it. The two venous valves united orally to the orifice form a long, narrow "tensor valvulæ," prolonged on to the roof of the atrium (Plate-fig. 3).

Atrium.—The shape of this chamber is considerably altered, and it forms a large crescentic cavity, enclosing in its bay the tubular portion of the bulbus cordis. The dorsal convex wall of the crescent is indented centrally by the dorsal body wall.

Near the middle line there is an almost complete septum primum atriorum uniting the dorsal and ventral walls. It does not reach the ventral portion of the floor of the atrium, and there is present the foramen ovale primum, measuring in the model some 20 mm. in vertical height (text-fig. 3).

In the upper part of the septum primum there is a small orifice with ragged edges—the foramen ovale secundum.

The septum primum terminates caudally and ventrally in the cushion tissue of the atrio-ventricular canal. The right portion of the atrium is much larger than the left, and forms a very large chamber lying to the right of the septum primum.



TEXT-FIG. 3.—Transverse section (slide 11) of heart of 6-mm. embryo.

Between the septum primum and the sinu-atrial orifice is a distinct recess, the intersepto-valvular space.

TABLE II.

Dimensions of Heart of S1. × 100.

Vertical height	170	mm.
Atrium, transverse width	150	,,
,, vertical height	150	,,
Sinu-atrial orifice, height	25	,,
Distance between right and left venous ostia	40	,,
Ventricle, left, vertical height	115	,,
,, ,, transverse width	50	,,
,, ,, thickness of wall	12 to 18	,,
,, right, transverse width	60	,,
,, ,, thickness of wall	7 to 12	,,
Interventricular foramen { dorso-ventrally	21	,,
Interventricular foramen { vertically	30	,,
Distance of interventricular foramen from interventricular cleft	45	,,

Atrial Canal.—The exit from atrium to ventricle is now divided into two minute channels by the union with one another of the endocardial cushions of the atrial canal.

The interval between these orifices, or venous ostia, represents the single atrial canal of the former specimen, which has moved to the right and lies almost ventral to the sinu-atrial inlet into the atrium.

The atrial septum, prolonged forward, would lie nearer to the right than to the left orifice. The fused endocardial cushions form a mass, extending into the floor of the atrium to the base of the septum primum.

The left orifice opens into the left ventricle, and the right into the bulbus cordis; and the right margin of the right atrio-ventricular opening is limited by one of the two bulbar cushions (Plate-fig. 3).

Ventricular and Bulbus Portions.—This portion shows a partial division into right and left ventricles by a thick, rounded muscular partition which projects into the interior from the ventricle wall, and is represented on the surface by a groove on the ventral aspect and a notch upon the caudal margin of this portion of the heart. Of the two chambers, the left ventricle forms a spherical, thick-walled chamber, with reticulated muscle tissue in its interior, receiving the left atrio-ventricular orifice in its dorsal cephalic wall. The interventricular foramen forms the sole outlet for this chamber, and by it the blood can pass to the distal portion of the bulbus cordis (Plate-fig. 3).

The wall of the right ventricle is of less thickness, and is not so fully reticulated. The ventricle is flask-shaped, and the lower portion, dilated and capacious, leads into a narrow tubular portion, where the lumen shows incomplete division into two channels. Within the lower portion are found the terminations of the two chief bulbar cushions, one on the interventricular septum, the other forming a prominence on the right of the right atrio-ventricular orifice.

Within the tubular portion are found the distal portions of the bulbar cushions.

The spiral course and the general shape and arrangement of these cushions may be gathered from the reconstruction figured in Plate-fig. 4.

The ultimate derivatives of these two portions of this chamber are very different, and the nature of the two portions is discussed later.

For the present, the names of conical portion and tubular portion may be given to distinguish the two parts from one another.

HEART OF EMBRYO B1 (8 MM. IN LENGTH). Plate-figs. 5, 6, and 7.

External Form.—The heart in this embryo and that in embryo M1 (9 mm.) resemble one another very closely indeed.

The large ventricular portion shows clear indication upon its surface of the internal division into right and left chambers by the interventricular furrow and the notched caudal border.

The interventricular furrow continues in a caudal direction the left margin of the tubular "bulbus cordis" portion.

The right ventricle and its tubular continuation have the same flask shape noted in S1.

Internal Structure.—Sinus venosus.—The right horn of the sinus venosus forms a chamber lying near the dorsal right corner of the atrium, and marked off from it externally by a vertical groove extending between the right margins of the venæ cavæ superior and inferior. The superior vena cava (right duct of Cuvier) opens into it high up on the dorsal wall, while the vena cava inferior and the transverse portion of the sinus venosus open into its floor; between the latter two orifices is a small ridge.

Sinu-atrial Junction.—The venous valves are much larger than in the former specimen, the right one particularly so, and it projects so far into the atrium as almost entirely to cut off the portion on its right from that on its left side. Along the floor of the atrium it extends as far as to the cushions of the atrial canal (text-fig. 4, and Plate-fig. 6).

The left venous valve is shorter, but it also is prolonged for some distance along the floor of the atrium. Orally it blends with the right valve and forms a large "tensor valvulæ."

The orifice between the two valves is a vertical slit. The right venous valve shows again a recognisable difference in structure from the remainder of the heart wall, and is loose in texture.

Atrium.—A wide bay on the outer surface of the roof of the atrium corresponds to the upper attachment of the septum primum.

TABLE III.

Dimensions of Model of the Heart of B1. × 100.

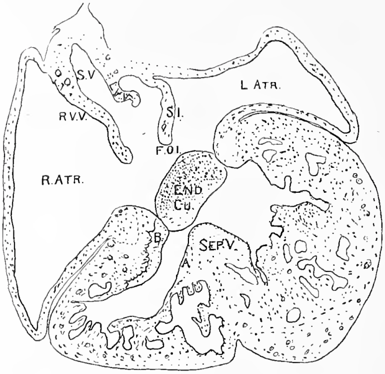
Vertical height		130	mm.
Atrium, transverse width	right	100	,,
	left	90	,,
,, vertical height		140	,,
Sinu-atrial orifice, vertical height		50	,,
Right venous valve, depth		65	,,
Left ,, ,,		20	,,
F. ovale primum still present, diameter		10	,,
,, secundum, vertically		25	,,
Distance between right and left venous orifices		42	,,
Ventricle, left, vertical height		105	,,
,, ,, transverse width		90	,,
,, ,, thickness of wall		40–60	,,
,, right, transverse width		90	,,
,, ,, vertical height (conical portion)		65	,,
,, ,, thickness of wall		25	,,
Interventricular foramen, diameter		35	,,
,, ,, vertically		similar.	
Distance of interventricular foramen from interventricular cleft		75	mm.

Right and left venous valves united caudally and orally.

On a transverse section the atria are crescentic in shape, and they are very capacious—many times more so than the ventricles. It is probable that the atrium has been fixed in diastole and the ventricle in systole.

The septum primum is not complete, for there is a small foramen ovale primum close to the region of the atrial canal. The septum is S-shaped in section, and shaped so as to direct the inflowing blood from the vena cava inferior towards the foramen ovale secundum, an orifice of some size in the upper part of the septum, with irregular margins.

Atrio-ventricular Openings.—These orifices resemble closely the orifices seen in S1. They are very small indeed, and lie on either side of the fused mass of the endocardial cushions. The extent and arrangement of these cushions are shown diagrammatically in text-fig. 5.

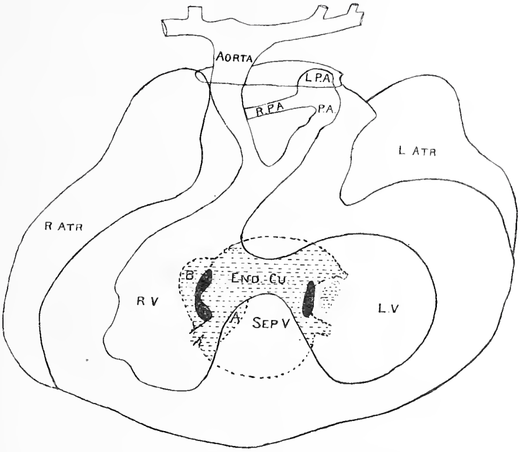


TEXT-FIG. 4.—Transverse section (slide 10, section 20) of heart of 8-mm. embryo.

The upper cushion is of loose texture, and the nuclei are widely separated from one another, but there are small areas where they are closely packed together.

The margins of the cushion stain more deeply and are marked off distinctly from adjacent muscular tissue. The upper endocardial cushion begins high up in the ventricle and on the ventral surface of the septum primum of the atria. At this level it lies embedded in the muscle substance of the ventricles. Traced downwards, it passes to the free margin of the interventricular septum and projects on each side into the lumen of the right and left ventricles. Its right margin extends to blend with the lateral bulbar cushion above the level of the right atrio-ventricular orifice, and to the left it joins the trabecular musculature of the left side of the ventricle above the left atrio-ventricular orifice. On the left of the left atrio-ventricular orifice there is a small patch of cushion tissue. Slightly caudally this upper endocardial cushion diminishes in size, and the right and left atrio-ventricular orifices appear on each side of it. At this level a transverse area of closely packed, deeply staining nuclei runs across the mass of cushion tissue, but probably this area may indicate the line or junction of the upper and lower cushions. This area can be traced from the dorsal surface of the cushion, where it begins in the floor of the atrium, onwards to the apex of the interventricular septum, and hence corresponds to the region of the atrio-ventricular node and bundle.

At the external atrio-ventricular groove on the surface of the heart there is a very distinct region of loose connective tissue, intervening partially between the atrial and the ventricular musculature.



Text-fig. 5.—Linear frontal reconstruction of heart of 8-mm. embryo B1. × 50.

The lower endocardial cushion, between the right and left atrio-ventricular orifices, lies against the base of the septum primum, and is continued below the septum primum in the floor of the atrium to reach the margin of the orifice of the vena cava inferior, and is prolonged also towards the wall of the coronary sinus.

On the ventricular side it passes on to the interventricular septum below the interventricular opening. To the right it blends with bulbar cushion B below the right atrio-ventricular orifice, and to the left it merges into the trabecular musculature of the left ventricle (text-fig. 5).

The right ventricle is triangular in shape and is smaller than the left, but has a larger cavity and thinner walls.

The muscle wall is irregularly reticulated.

The cavity is narrow, and passes gradually into the cavity of the distal portion.

The displacement of the atrio-ventricular orifice towards the right, so that its right extremity opens into the bulbus, has produced a corresponding alteration in the muscle coats, and the atrial muscle wall at the right side is now directly continued into the muscle tissue of the bulbus wall, from which it was primarily separated by the whole width of the base of the ventricle.

Septum.—The interventricular septum springs from the floor and ventral wall of the ventricle, and extends on the dorsal wall as high up as to the endocardial cushions.

The interventricular foramen is an almost circular opening lying between the apex of the muscular interventricular septum on the one side and the fused endocardial cushions on the other (Plate-fig. 7). The opening leads from the cavity of the left ventricle into that of the right at the junction of the conical and cylindrical portions.

The arrangement of the tissues around the venous ostia is particularly instructive, for it shows these openings before any definite valve apparatus has been formed.

The transverse width of the atrial canal measures rather less than 90 mm., while the atrium and the ventricle are more than twice this diameter. The canal is very short, forming an annular narrow constriction, and there the muscle walls of the atrium and ventricle are directly continuous with one another.

The connective tissue of the annulus fibrosus is considerably thicker than on other parts of the heart, and on section it forms a large oval mass.

The inner part of the wall of the left ventricle, beside the left venous ostium, forms a loose network, and is becoming undermined in the fashion described by His.

At the right ostium a more definite lateral valve cusp is formed. Here the mass of cushion tissue formed by the downward prolongation of the bulbar cushion B forms a large oval swelling in the inner surface of the wall. This cushion extends nearly to the lowest part of the ventricle, and there it lies on a band of muscle tissue which has become undermined and passes to the right surface of the ventricular septum, like the "moderator band" of the adult heart.

There are no indications of medial cusps at either the right or the left orifice. The interventricular septum passes downwards with smooth walls from the medial border of each ostium.

Nor are there any definite indications of the formation of papillary muscles, with the exception of the strand already referred to in the right ventricle.

The arrangements and attachments of the endocardial cushions, which form the medial boundaries of the venous ostia, are shown in the linear reconstruction (text-fig. 5).

Right Ventricle.—The figure of the external form at this stage (Plate-fig. 5, compared with Plate-fig. 2) shows the nature of the considerable changes which have taken place.

(1) The conical basal portion or right ventricle proper has increased in its relative size.

(2) The upper cylindrical portion is now oblique in direction, and slopes from right to left and towards the dorsum as it ascends.

(3) The termination of the heart tube, *i.e.* the junction with the truncus arteriosus, can be clearly determined by the structure of the wall.

The lumen of the truncus is divided into two separate channels, aorta and pulmonary artery, and each of them is continuous with a portion of the incompletely divided lumen of the cylindrical portion of the bulbus cordis.

The increasing obliquity of the region has led to a lengthening of the convex portion. The bulbar cushions are distinct, though only two can be made out (see also embryo M1).

Text-fig. 6.—Transverse section (slide 10, section 10) of heart of embryo M1.

Embryo 9 mm. in Length (M1).

Reconstruction at 100 *Diameters.*—The heart of this embryo resembles closely the former specimen (B1) both in size and in shape. The external form is almost identical with that of B1 (Plate-fig. 5). There are the same wing-like expansion of the atria, the surface division between right and left ventricles, and the modified flask-like character of the right ventricle passing orally into a tubular portion.

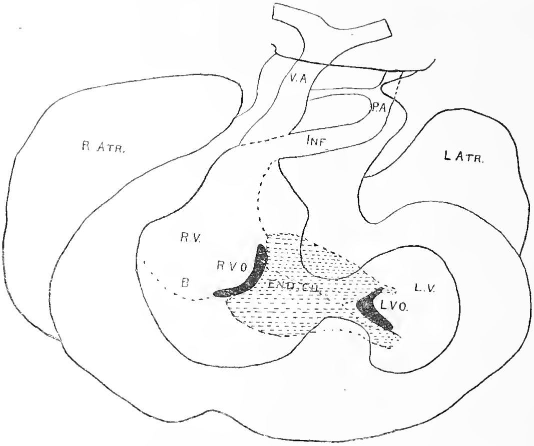
Internal Structure.—The relationship of sinus venosus to atrium resembles so closely that in B1 that it requires no further description. The disposition of the venous valves and septum primum is practically identical with the former specimen (text-figs. 4 and 6).

Sections in this specimen stained with picro-indigo-carmine indicate very clearly the extent and connections of the muscle coat.

Atrio-ventricular Junction (text-fig. 6).—The upper endocardial cushion, as before, lies against the septum primum dorsally, while ventrally its upper part forms the dorsal wall of the ventricle.

Within this cushion are shown very clearly strands of closely packed, deeply staining nuclei, which traverse the loose general tissue of the cushion and extend from beneath the lumen of the atrium downwards and forwards towards the ventricle. This upper cushion blends on the right with the bulbar cushion B, both above and below the atrio-ventricular orifice. To the left it blends with the trabecular tissue in the wall of the ventricle, ventrally with the interventricular septum, and on the surface of this septum there is seen exactly the same arrangement of the bulbar cushion A as was seen in B1.

The lower cushion makes its appearance first to the left of the right atrio-ventricular orifice, where it forms a round tubercle, and the line of junction of the upper and lower cushions runs obliquely from right to left and caudally. There is a similar extension of this lower cushion across the floor of the atrium to the dorsal wall, and also similar strand-like arrangements of nuclei within its substance. This cushion forms the right margin of the right atrio-ventricular orifice, and below that orifice its left extremity is attached to the trabecular musculature of the ventricles. It descends for some little distance on the left side of the interventricular septum.



TEXT-FIG. 7.—Linear frontal reconstruction of heart of embryo M1. × 50.

The extent and connections of these cushions are shown in the frontal reconstruction, text-fig. 7.

The interior of the cylindrical portion of the right ventricle is shown in Plate-fig. 8.

In the proximal portion the lumen is undivided, and the prominent bulbar cushion A projects into it. More distally the lumen is divided into two, and the bulbar cushion is prolonged into each as a projection on the interior.

The whole extent of the cushion tissue is uniform, and there is no indication whatsoever of "distal" as contrasted with "proximal" bulbar cushions.

Embryo B2 (13 mm. in Length).

In this heart the condition of the upper part of the bulbus cordis resembles, on the whole, the condition found in B1 and M1. The pulmonary artery and the aorta are separated from one another in the upper part of their extent; proximally the stems of these two vessels unite and are continued as a single stem into the upper part of the right ventricle. The bulbar cushions A and B are prolonged downwards on to the lateral ventricle wall and to the septum respectively.

Atrio-ventricular Junction.—The right bulbar cushion (B) joins with the right margin of the upper endocardial cushion above the right atrio-ventricular orifice. This orifice is of some size, and its lower boundary is formed by a tubercle of the lower endocardial cushion. The upper endocardial cushion extends to the base of the septum primum atriorum and passes across to the left side, forming the upper boundary of the left atrio-ventricular orifice. The lower endocardial cushion is prolonged to the apex of the interventricular septum, below the level of the interventricular foramen, and forms a large mass extending from the dorsal wall of the atrium across the floor to the interventricular septum. From its left extremity a tubercle projects into the cavity of the left ventricle and forms the right margin of the left atrio-ventricular orifice.

A small accessory left endocardial cushion forms the left boundary of that opening.

The muscle wall of the ventricles shows a complex network of trabeculæ, and a cortical layer which is considerably thicker in the left than in the right ventricle.

In this specimen the endocardial cushions are very distinct, as the nuclei alone are stained, while the muscle wall is of a pinkish colour.

The atrio-ventricular valve apparatus is rudimentary, but the stage of development is only slightly more advanced than in B1.

In other details the heart in this specimen resembles closely the heart in S4; and as the latter shows more perfect histological detail, a fuller account need not be given of B2.

Heart of Embryo S4 (12·5 mm. in Length).

The heart of this embryo was modelled at a magnification of 100 diameters, from sections 10μ in thickness.

External Form.—The figure (Plate-fig. 9) shows the external form from the front. The atria, greatly expanded, enclose the upper segment of the bulbus cordis in a deep groove, and this portion of the bulbus lies almost horizontally.

The ventricular portion resembles generally that of the earlier specimens. The left ventricle, somewhat spherical in shape, is separated from the right ventricle by a deep interventricular sulcus and by a notch on the caudal margin.

The proximal conical portion of the right ventricle is continued uninterruptedly into a distal tubular portion, on which an almost vertical furrow, lying on the right side, forms an external constriction corresponding to an internal division of the lumen. The portion behind the constriction contains the ascending aorta, and that in front the infundibulum leading to the pulmonary artery.

TABLE IV.

Dimensions of Heart of S4. × 100.

Vertical height	200 mm.	
Transverse width, left ventricle	125 ,,	
,, ,, right ,,	125 ,,	
Dorso-ventral width, atria (middle)	112 ,,	
Left ventricle	205 ,,	
Right ,,	155 ,,	
,, venous ostium	45 ,,	× 15.
Thickness of wall, compact	25 ,,	
Interventricular opening	20 ,,	× 15 mm.
Distance from apex	120 ,,	

Internal Structure.—The incorporation of the sinus into the atrium has advanced, and the position and attachments of the venous valves and of the atrial septum are of great interest (text-figs. 8, 9, and 10).

The venous valves stretch from the dorsal to the ventral wall of the atrium both orally and caudally, and they enclose between them a central narrow slit-like chamber which receives blood from the venæ cavæ and the coronary sinus. On each side is the widely dilated atrium proper. The central chamber communicates with each of these by a small somewhat oval opening, and they in turn lead into the ventricle on each side. This central chamber may be termed the sinu-atrial chamber. The venous valves meet and blend with one another in both the roof and floor of the chamber. The vena cava superior opens by a narrow orifice through the upper part of its dorsal wall, and the vena cava inferior and the coronary sinus open in the floor separately, the latter far forward.

The right venous ostium lies on the right side of the base of the right venous valve.

Closely blended with the left venous valve is the septum primum atriorum.

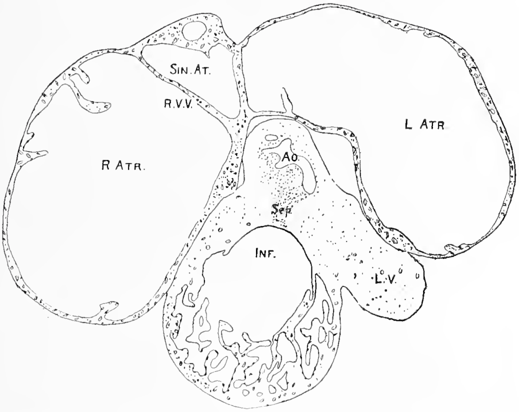
From the left side of the septum primum the wall of the left atrium slopes sharply to the left ostium.

The septum primum forms a complete ring round the interior of the circumference of the atrium, but the foramen ovale secundum is so large that nowhere is the septum of any considerable height. The septum and the venous valves are shown in Plate-fig. 10 viewed from the left side. It is deepest in the ventral inferior portion and very shallow indeed on the dorsal wall, and at its dorsal and inferior attachments it is largely blended with the left venous valve.

The single large pulmonary vein opens into the left atrium immediately to the left side of the septum primum.

Atrio-ventricular Junction.—The ostia from the right and left divisions of the atrium into the corresponding ventricles are large, and around these orifices there is a definite though rudimentary arrangement of valves. The right ostium is a long vertical slit, 50 mm. long and 12–15 mm. in width; while the left is slightly smaller but is wider, measuring some 30 mm. by 20 mm. The right ostium is bounded on the right by a large flap formed by an infolding of the tissues into the interior of the ventricle.

Similarly in the left ventricle there is an early "mitral" valve, the lateral cusp formed by an infolding from the left side, while the medial (aortic) cusp is derived from the cushion tissue between the left and right atrio-ventricular orifices.



TEXT-FIG. 8.—Transverse section (slide 38, section 7) of heart of embryo S4.

The cusps of the valves are attached by a network of muscle tissue to the ventricular wall. Some bands are specially distinct. In the right ventricle one sweeps from the lateral cusp already described on to the interventricular septum, and it is clearly derived from the similar band seen in B1.

There is an advance in the condition in B1, but the differences are not so great as to prevent the recognition of corresponding structures.

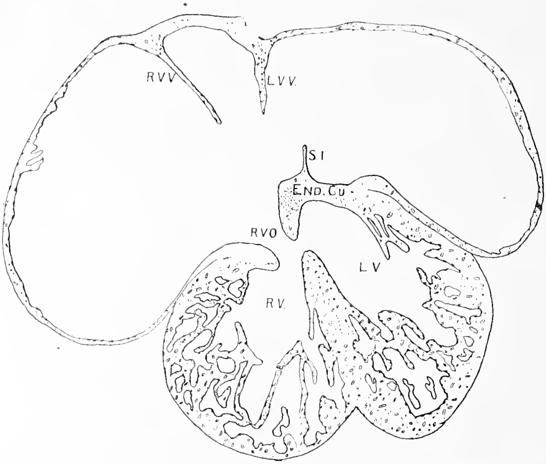
The transverse width of the muscular wall of the atrial canal is, in this specimen, 180 mm.

At the right venous ostium, the atrio-ventricular junction is infolded into the interior of the ventricle so as to form a large curved flap, undermined and concave on the ventricular aspect, extending from the caudal border of the ostium along its right side to its cephalic border and on to the interventricular septum. In the caudal portion this flap forms a cusp of some thickness and is attached to the interventricular septum (text-figs. 9 and 10).

More orally, its margin is free, and above it sweeps above the level of the interventricular foramen and is connected to the bulbar septum, as described later.

The muscle wall of the ventricle is trabecular, and many of the strands are undermined. The anterior papillary muscle is foreshadowed as a thick strand of muscle incompletely separated from the wall of the ventricle, united at one end to the ventricular surface of the cusp, and at the other attached to the lateral wall of the ventricle. Its base is connected to the septum by a short, stout band of muscle.

The "tricuspid" valve at this stage possesses but a single cusp, representing the anterior and posterior cusps of the adult heart. Its most oral part gives rise to the tendinous cord attaching the anterior cusp to the bulbar septum.

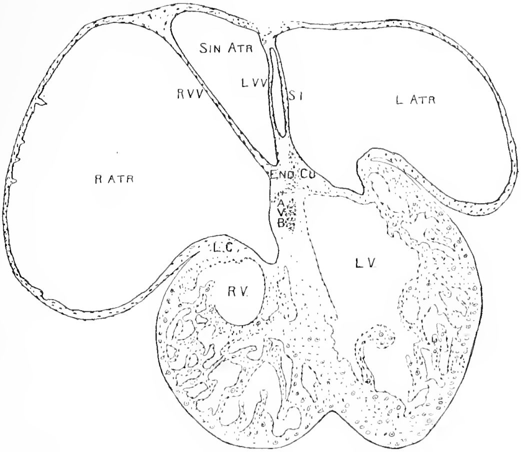


TEXT-FIG. 9.—Transverse section (slide 40, section 7) of heart of embryo S4.

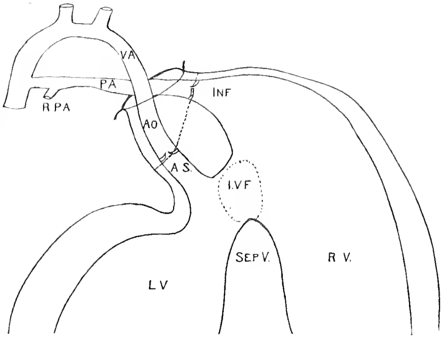
On the left side the structures are simpler both in the valve cusps and the papillary muscles. Medial and lateral cusps are present—the medial a thick rounded projection from the central endocardial cushions attached to a prominent muscle bundle in the floor of the ventricle, and orally prolonged on to the lateral wall. The lateral cusp overhangs into the cavity from the atrio-ventricular junction, and it extends to both the anterior and posterior papillary muscles.

Right Ventricle.—The tubular portion lies even more horizontally than that in the former specimen, and it is flattened from side to side. The proximal end has widened out and extends towards the right ventricle. A short partial spiral groove, distinct on the right side, marks off a more dorsal and vertical portion from the ventral oblique portion.

The accompanying figure (text-fig. 11) shows the extent of the septum dividing the lumen into two portions, the position of the pulmonary and aortic valves, and the position of the interventricular foramen. The extent of the muscular coat is indicated, and the pulmonary and aortic valves are seen to lie at the distal extremity of the heart tube. These valves, and especially the pulmonary valve, are plump and well developed.



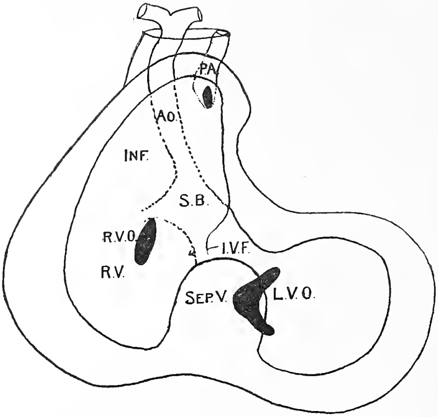
TEXT-FIG. 10.—Transverse section (slide 41, section 14) of heart of embryo S4.



TEXT-FIG. 11.—Linear reconstruction (lateral) of portion of heart of embryo S4.

As has been stated, there is an interventricular foramen of some size. Its position and exact boundaries are of considerable interest. It lies close to the basal portion of the ventricles, and it is between the two venous ostia. It is bounded dorsally by the cushion tissue between the ostia, and ventrally by the concave free margin of the interventricular septum (text-figs. 11 and 12).

The boundaries are rendered more complex by the approximation and extensions of the bulbar septum. The proximal edge of this septum is concave, and the ventral right end is continued on to the ventral and upper part of the interventricular septum; while the other end, dorsal and to the right, joins with the tissue between the venous ostia and is continued on to the interventricular septum. From its right margin a prolongation of this septum of the bulb extends towards the right side above the right venous ostium, and joins the flap which sweeps on to the interventricular septum. The interventricular opening is, in this specimen, unobscured by valve cusps on the septal wall, and its boundaries are shown with remarkable clearness in the model.



TEXT-FIG. 12.—Linear reconstruction of heart of embryo S4.

Tubular Portion.—There is a complete separation of the aorta from the infundibulum of the right ventricle.

There is a considerable change, however, in the general position and diameter of the infundibulum of the right ventricle from the condition found in the earlier stages. Comparison of the linear reconstructions of these specimens shows the changes.

The lumen within the tubular portion of the bulbus cordis has expanded and now forms a chamber continuous with the cavity of the lower part of the right ventricle.

EMBRYO (16 MM. IN LENGTH), PROF. PETER THOMPSON'S SPECIMEN.

Plate-figs. 11 and 12.

In this specimen, and in all the later ones, a definite advance in the development of the heart is marked by the closure of the interventricular orifice. It was pointed out that in the earlier specimens the sole outlet for the blood from the left ventricle was the interventricular foramen. With the closure of that foramen the left ventricle is brought into direct continuity with the aortic channel in the cylindrical portion of the right ventricle.

External Form (model at 50 diameters magnification).—The heart is relatively small in comparison with that of the 12·5 mm. specimen, and measures only 110 mm. vertically, 95 mm. transversely, and 130 mm. dorso-ventrally in the model. The atria are small and in systole. The left ventricle exceeds in vertical depth the right ventricle. The external form of the ventricular portion is similar to that part of S4, and there are similarly distinct interventricular furrow and notch.

Interior of the Heart.—Sinus Venosus and Atrium.—The sinus is now largely merged into the atrium. The vena cava superior has a long oblique course through the dorsal wall. The orifice of the vena cava inferior is directly caudal to it.

The right venous valve shows an arrangement similar to that in S4, and forms a long vertical and almost complete partition extending across the atrium from the right of the venæ cavæ to the left side of the right venous ostium.

The inferior attachments of the right and left venous valves are completely separated from one another (Plate-fig. 12).

Sinu-atrial Chamber.—This chamber is distinct, but is modified in its shape from that of S4, partly by the condition of systole. Into it there open the vena cava superior dorsally and the vena cava inferior and coronary sinus caudally, well separated from one another. The lateral boundaries are the venous valves. The left venous valve forms a ring-like fold, attached around its circumference to the wall of the atrium. The caudal attachment is blended with the septum primum, and orally the attachment of these two folds to the wall forms a stout mass.

For the rest, the septum primum also forms a ring-like projection into the atrium, with a large central orifice, the foramen ovale secundum, towards which the lower part of the septum is inclined. The interval between this deflected portion and the left venous valve constitutes the remains of the intersepto-valvular space.

Ventricles.—The ventricles were apparently fixed in systole, and their cavities are extremely small, hence the specimen is not a favourable one for determining the arrangement of the atrio-ventricular valves.

The position of the interventricular orifice is found to be occupied by a fibrous septum continuous orally with the septum separating the aorta from the right ventricle.

The wall of the right ventricle is not so thick as that of the left ventricle.

Within the upper part of the muscular interventricular septum there is a rounded mass of deeply-staining nuclei embedded in loose connective tissue which is a definite rudiment of the atrio-ventricular bundle, but its connection with other portions could not be traced.

The heart in the following embryo (S3), of approximately a similar stage of development, affords a clearer picture of the condition of the chambers at this stage.

HEART OF 20-MM. EMBRYO (S3).

Model of the Heart magnified 50 *diameters* (Plate-fig. 13).

Dimensions.—1. Vertical (of ventricles)		150 mm.
2. Transverse width	right ventricle	50 ,,
	left ,,	60 ,,
3. Dorso-ventral, whole heart		165 ,,

The heart was modelled within the pericardium and the body wall, and the external appearances reproduce accurately the shape of the heart within the embryo.

In external form the heart resembles the former specimen, but is somewhat flattened in an oblique direction. The impression on the under aspect of the right ventricle is caused by the projection of the right lobe of the liver against the floor of the pericardium.

The heart appears to have been fixed in systole, and the cavities are small, particularly those of the ventricles.

The atria form vertically elongated narrow channels enclosing the dorsal half of the upper portion of the heart.

The right and left ventricles are separated by an oblique furrow, and the upper part of the right ventricle forms a bulging prominence whose upper margin lies horizontally.

The aorta occupies very much the same position as in the adult heart.

Interior of the Heart (Plate-fig. 13).—The incorporation of the sinus and atrium is far advanced, and the venous valves and the septum primum are so prominent that in cross-section the three-chambered appearance of the atrium is very striking. At each side lie the expanded lateral portions of the atria, and between them lies the sinu-atrial chamber.

The vena cava superior opens by an oblique channel through the dorsal wall, and then turns forwards; and the vena cava inferior and the coronary sinus open separately on the floor.

The right venous valve again forms a large vertical septum stretching dorso-ventrally across the right atrium, perforated only by a small orifice which allows blood to escape from the sinu-atrial chamber into the right atrium proper and so to the right ventricle. The condition of the left venous valve is not easily determined in this specimen, for only a small portion of it is at all distinct. It forms a small flap on the left side of the orifice of the vena cava superior. That orifice is a narrow one, and the small flap blends with the right venous valve both oral and caudal to the opening.

The septum primum is separate and distinct. Its lower part forms an S-shaped fold, the bay of the S leading to the foramen ovale II, and directing the blood stream from the vena cava inferior directly to it.

The septum is more complete than in the former specimen, and the orifice of the foramen ovale II is only a small hole in a nearly complete partition, and it lies close to the oral border.

The arrangement of these structures is further modified by the size and shape of the atria, which are of great vertical height.

The wide bay which existed in the earlier specimens in the roof of the atrium, and which indicated the line of the division, is now replaced by a deep, narrow cleft, at the bottom of which the septum primum is attached. The apparent infolding of the wall of the atrium constitutes an early stage of the formation of the septum secundum, but it is produced not by a downgrowth of a septum but by the upgrowth of the atria.

A large pulmonary vein opens immediately to the left of the septum primum; and further to the left side there is an elevation of the floor of the left atrium, apparently marking off the quadrilateral sinus of the left atrium from the appendix (auricle).

Atrio-ventricular Junction.—The atrio-ventricular junction shows now an almost complete separation of the muscle wall of the atrium from that of the ventricle. Connective tissue from the atrio-ventricular orifice passes deeply into the interior of the substance of the flaps forming the lateral boundaries of the atrio-ventricular orifices: so that the tissue on the atrial surface of the valve cusps is continuous with the atrial musculature, while that on the ventricular surface is continuous with the trabecular musculature of the ventricles.

Rudimentary or embryonic muscle tissue is recognisable on the atrial surface of these valve cusps. The rudimentary medial or septal cusp of the tricuspid valve is present as a rounded projection on the right surface of the interventricular septum, consisting mostly of endocardial cushion tissue.

The interventricular septum is now complete, but where it joins the region of the endocardial cushions its texture is very loose, while in the centre of this loose tissue is a very distinct rounded rudiment of the atrio-ventricular bundle.

The medial (anterior or aortic) cusp of the mitral valve (not shown in the figure) is very distinct and projects from the left side of the atrio-ventricular septum, with which its ventricular surface is continuous; but this flap throughout is less muscular in texture than the opposite cusp.

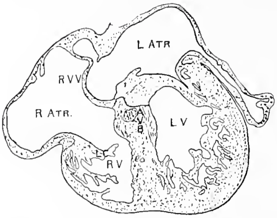
The pulmonary artery and the aorta are completely separated from each other, and the semilunar valves of each of them are well formed. The semilunar valves of the aorta lie immediately above the level of the interventricular septum; while the pulmonary valves, on the other hand, lie 50 mm. orally at the termination of the tubular part of the bulbus cordis.

The condition of the whole of the right ventricle is very similar to the condition found in S4. There is, for example, the same narrowing of the lumen of the most distal portion near the root of the semilunar valves; proximal to this a more dilated but still tubular part; and, finally, the lower part of the cavity of the ventricle with the valve cusps, papillary muscles, and trabeculæ of the ventricular cavity proper.

Heart of 22-mm. Embryo (B3).

Both ventricles present a rounded outline; the wall of the left ventricle is almost twice as thick as that of the right; both show extensive trabeculæ; the cusps of the aortic valve are well formed and plump; and the interventricular septum is completely formed, though extremely thin in the membranous part.

The right atrio-ventricular orifice, widely open, possesses right and left cusps, both of which, especially the right, are undermined by trabecular musculature, and their apices are continued by stout muscle bundles to the ventricular wall. A wedge or cone of rudimentary connective tissue penetrates for a short distance into this marginal cusp, and on the atrial surface of the cusp an oval area of cushion tissue is present. The septal cusp shows a condition similar to those seen in S3.



Text-fig. 13.—Transverse section (slide 26, section 23) of heart of embryo B3. × 20.

Left Atrio-ventricular Orifice.—Shows very clearly the origin of the anterior cusp of the mitral valve from the endocardial cushion tissue of the atrio-ventricular junction, and as yet shows no muscular tissue in its substance; while the posterior or marginal cusp is distinctly muscular in structure.

Atrio-ventricular Bundle.—Rudiments of this are very clearly seen within the loose endocardial tissue of the atrio-ventricular junction (text-fig. 13).

The condition of the atria is, on the whole, similar to that shown in S3.

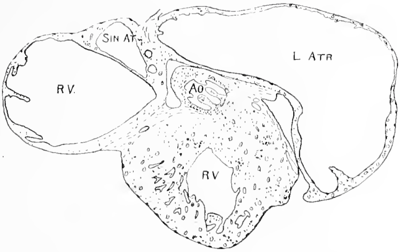
30-mm. Embryo, Prof. Bryce's Specimens. Plate-figs. 14 and 15.

The anterior view of the model of this heart, reconstructed 50 diameters, is shown in Plate-fig. 14.

External Form.—The external form of the heart shows it to have advanced considerably towards the adult form, and the internal structure of the ventricle is practically the same as is found in the adult, the right and left ventricles being completely separated. The atria, however, communicate freely with one another.

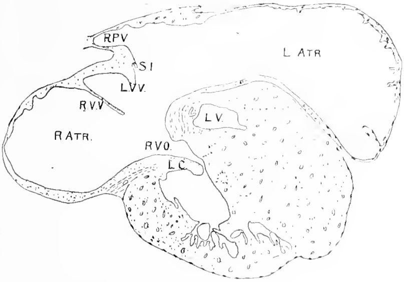
The right ventricle considerably exceeds in the anterior view the left ventricle, and its upper part, widely dilated, leads to the pulmonary stem, which lies horizontally.

The atria are of relatively enormous size, enclosing the ventricular portion on each side, are of irregular outline, and are apparently in diastole; while the small size of the cavity of the ventricles and their thick walls point to the condition of systole of the ventricles. The wall of the left ventricle is very considerably thicker than that of the right ventricle.



TEXT-FIG. 14.—Transverse section (slide B13) of heart of 30-mm. embryo (BRYCE).

Internal Structure.—The Interior of the Right Atrium.—The auricular portion of this cavity—large, wide, and with trabeculæ of muscle tissue upon its wall—forms by far the greater part of this cavity. The right venous valve forms a large, almost vertical partition, stretching from the dorsal wall along the floor to the anterior wall and shutting off a small cavity on its left side from the large cavity on the right; there being only a small, rounded orifice between the anterior concave margin of the central part of this valve on the one hand, and the anterior wall of the atrium on the other hand (text-figs. 14, 15, and 16).



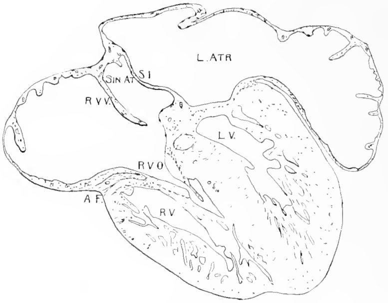
TEXT-FIG. 15.—Transverse section (slide B17) of same heart as fig. 14.

The anterior attachment of the base of the right venous valve is split into two thin laminæ for a distance of 25 mm., and between these two limbs is the rounded orifice of the coronary sinus.

To the left of the right venous valve the vena cava inferior opens into the floor of the atrium, while the opening of the vena cava superior is directed vertically downwards and about 75 mm. orally. The arrangement of the left venous valve and of the septum primum shows considerable modification towards the adult form.

The left venous valve forms a small sickle-shaped ridge, 30 mm. in maximum height, projecting from the atrial wall especially dorsally and orally. It extends forwards on the roof of the atrium, and its anterior end merges into the right venous valve.

The intersepto-valvular space has very largely disappeared, and the left surface of the left venous valve is in contact partly with the right surface of the septum primum. The arrangement of these parts is shown in Plate-fig. 15.



Text-fig. 16.—Transverse section (slide B17) of the same heart as figs. 14 and 15.

Two pulmonary veins, a right and a left, separated by a considerable interval, open into the left atrium. On the left side of the left vein is an enormous dilatation forming the cavity of the auricular portion. The ventricular orifice from the left atrium lies ventrally to the openings of the pulmonary veins. The opening into the right ventricle lies to the right of the right venous valve (text-fig. 16).

Right Ventricle.—The cavity of the right ventricle is narrow but much elongated, and rudimentary valves are present around the right atrio-ventricular orifice in the form of a large muscular flap passing from the right margin of the atrio-ventricular junction towards the interventricular septum, while on the opposite side of the orifice there is a similar thinner cusp resting on the interventricular septum. The minute structure of the right cusp shows that it consists near its base of (1) a layer of muscle tissue continuous with the muscle tissue of the ventricle; (2) a layer of embryonic connective tissue passing in a wedge-shaped manner from the atrio-ventricular ring into the interior of the cusp; (3) a layer of rudimentary muscle tissue continuous with the atrial wall.

The first and third layers merge into one another, and beyond that level the valve cusp consists of a single rather thick layer of muscle tissue, and it is covered on its atrial surface by an oval mass of endocardial cushion tissue.

There are no chordæ tendineæ, but the muscle tissue of the flap is attached by a number of muscle strands to the trabecular tissue of the ventricle. The septal cusp shows a somewhat similar arrangement, its ventricular surface being formed of muscle tissue covered by a large mass of endocardial cushion tissue, but the auricular wall does not form any part of the substance of this valve cusp.

The cavity of the right ventricle is continued upwards in a spiral fashion to become continuous with the pulmonary artery; the trabecular arrangement of fibres being distinct on the ventral wall, while the dorsal wall is largely composed, not of muscle tissue, but of fibrous tissue derived from the septum separating it from the aortic stem. The muscle wall is continued to the base of the semilunar cusps of the pulmonary valve and ceases abruptly, the wall of the pulmonary artery and of the ascending aorta consisting quite definitely of fibrous tissue only. Proximal to the semilunar cusps for a distance of less than an inch there is the same narrowing of the lumen noticed in earlier specimens; the stem of the pulmonary artery to its bifurcation now measures 45 to 50 mm. The wall of this part is undulating, showing two constrictions, as was seen in earlier specimens.

The cavity of the left ventricle is very small; medial and lateral cusps can be recognised at the atrio-ventricular orifice, and the aorta takes origin from a definite infundibulum corresponding in extent to the pars membranacea septi (text-figs. 15 and 16).

The aortic valves lie again immediately above the upper margin of the membranous part.

The wall of the right ventricle is in the model 30 mm. in thickness, while that of the left is 45 mm.

Embryo 28·6 mm. in Length (E1). (Text-figs. 17 and 18.)

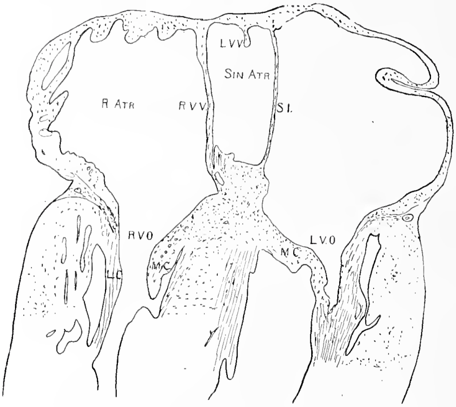
The sections and the model of this singularly perfect specimen constitute a good picture of the heart at the close of the period of development specially studied, a stage when all the principal developmental changes of intrauterine life have been completed.

In general shape the heart externally resembles that in the 30-mm. embryo.

Internal Structure.—The atrial portion is partly divided into three portions—a central and two lateral, of which the central smaller chamber communicates with those on either side, while they in turn open into the corresponding ventricles.

The right venous valve, as in the former specimen, forms a large vertical septum. In structure, especially at its basal attached margin, it differs from the atrial wall—the tissue is not striated, the cells are larger, and vacuoles are present. Along its left margin is a continuous line of large, very darkly staining cells similar to those seen in the endocardial lining of some portions of the ventricles, and which probably afterwards form Purkinje cells.

The ventral attachments of both the right and left venous valves run into a mass of indefinite cushion tissue at the central portion of the atrio-ventricular junction, and especially into a mass of deeply-staining cells lying immediately to the left of the orifice of the coronary sinus, in the position of the atrio-ventricular node of the adult heart. This mass in turn is connected with a mass of similar cells lying in the interior of loose vacuolated tissue in the apex of the interventricular septum, similar to the structure seen in earlier specimens already described. This structure is identical with that described by Mall as the rudiment of the atrio-ventricular bundle in the embryonic heart.



Text-fig. 17.—Transverse section (slide 64, section 9) of heart of 28·5-mm. embryo.

The structure described above constitutes a continuous medium of communication between the nodal tissue, or rather pre-nodal tissue, which from an early stage is recognisable at the base of the right venous valve, and the definite atrio-ventricular node lying near the coronary sinus.

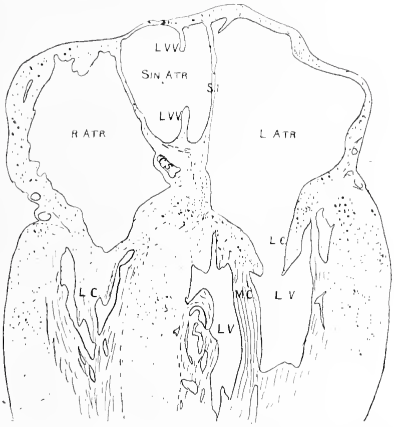
The lower part of the septum primum forms a partition of considerable height, and it forms the lower left boundary of the sinu-atrial chamber. Its lower attachment is separate and distinct from that of the left venous valve, but the two structures gradually approach one another orally.

The foramen ovale secundum is placed so far ventrally that its ventral boundary is the level of the wall of the atrium. Dorsally, however, the foramen does not extend to the dorsal wall of the atrium, but here the remains of the septum primum form a slight ridge, which merges into the left venous valve.

The dorsal attachments of the left venous valve and of the septum primum are fused, and at their origin from the wall of the atrium there is an infolding of the atrial wall, consisting of two layers of muscle tissue in apposition, separated only by a small amount of connective tissue. This slight invagination is the rudiment of the septum secundum.

The embryo was specially examined to determine the presence of any conducting tissue between atrial and ventricular muscle in other regions.

At the circumference of the atrial canal, at the junction of atrium and ventricle, an apparent infolding of the wall takes place, involving both the atrium and the ventricle; and as a result a wedge-shaped mass of connective tissue is formed, its base at the free surface and its apex passing into the interior of the lateral valve flaps of the venous ostia.



TEXT-FIG. 18.—Transverse section (slide 65, section 9) of heart of same embryo as fig. 17. × 25.

These lateral valve cusps are formed of embryonic heart muscle, and there is also present in each of them a mass of cushion tissue lying on the atrial surface of the cusps.

This infolding was traceable around the lateral margins of the atrial canal; and as the muscle tissue present in the cusps is later transformed into connective tissue, there cannot be any continuity between the atrial and ventricular muscle at these levels. Orally and caudally there is not the same infolding, but in these regions also there appeared to be a complete break between the muscle wall of the atria and that of the ventricle and bulbus.

The Atrio-ventricular Valves.—The valve apparatus of the right and left sides forms a clear illustration of the formation of these structures.

On the right side there is a single large lateral cusp attached to the septal wall and to the anterior and posterior walls of the ventricle. This cusp contains a portion of bulbar cushion B, and also the extension to the right of the septum of the bulb, and this cusp forms an investment for the right and for the oral margin of the right ostium.

On the opposite side—namely, on the septal aspect—there is as yet no cusp, but a large oval prominence is present on the septal wall, which probably becomes undermined later and forms the medial cusp. The moderator band of the adult heart is formed from a portion of the septal wall on which lay bulbar cushion A, which is gradually undermined.

At the left ostium two cusps are present, forming practically the adult arrangement—the medial cusp derived from the endocardial cushions of the atrial canal, and the lateral from the infolding of the atrio-ventricular junction.

These cusps are large, and there is already fully developed the apparatus connected with them of papillary muscles.

The medial cusp extends from the oral to the caudal margin of the orifice, and its apex is widely separated from the septum.

Comparison of this specimen with S4 shows the changes which have occurred in the structures found in the earlier specimen. As in the former, the right venous ostium has a valve of one cusp, viz. a large right or lateral cusp, representing the two cusps, lateral and anterior, of the adult heart. The most oral attachment of this cusp is effected by muscular cords which pass to the infundibulum of the pulmonary artery, and are attached to the region of the former septum of the bulb.

There is no proper septal cusp, but its position is indicated by prominent rounded elevation.

On the left side the cusps of the mitral valve are attached, the medial cusp to a large anterior papillary muscle, to which the marginal cusp also is attached, and also to a small anterior papillary muscle.

The interventricular foramen is barely closed.

There is a large "vestibule" in the left ventricle, below the root of the aorta.

Discussion.

The series of specimens is sufficiently comprehensive to afford an almost complete account of the successive stages in the development of the heart from the stage at which the heart tube is formed.

The transition from the 3-mm. to the 6-mm. stage is perhaps rather less completely illustrated than the others, but the gap is adequately filled by specimens described in the literature of the subject, among which I would refer particularly to the 4·5-mm. embryo described by Ingalls, as well as by specimens figured by Tandler from the Vienna collection.

The developmental changes which occur in the heart subsequent to the earliest stage described here may conveniently be discussed in the following groups :—

1. Changes in the external form of the heart.
2. Changes affecting the sinu-atrial junction.
3. The division of the atrium.
4. The atrial canal and the bulbus cordis.
5. Changes in the primitive bulbus cordis.
6. The atrio-ventricular junction, the formation of the atrio-ventricular valves and of the conducting mechanism.

1. *Developmental Changes in the External Form of the Heart.*

The changes in the external form of the heart indicate successive changes in the size and position of the various segments of the primitive heart tube.

Atrium.—The atrium is from the first placed dorsally, and extends across the whole transverse width of the heart. Its cephalic surface is rounded and only slightly indented centrally by the truncus arteriosus. The atrium is everywhere separated by a deep groove from the ventricle and from the bulbus cordis. Throughout it retains this dorsal position. Wing-like expansions grow out on either side, curving round and partly enclosing the bulbus and, later, the pulmonary artery and the aorta.

After the formation of the septum primum, the atria increase greatly in their relative vertical depth, but the region of the attachment of the primitive septum grows less rapidly, and hence an infolding of the wall is produced in that region.

Ventricle.—The ventricular portion of the heart consists at first of a V-shaped loop, with right and left limbs, separated from one another, except at the apex, by an oblique groove, the bulbo-ventricular groove. These limbs at a still earlier stage lie—the one cephalic, the other caudal—in position, and the intervening groove is horizontal; but a gradual rotation occurs, so that the groove becomes oblique and eventually vertical in position. The bulbo-ventricular groove extends nearly to the opposite margin of the heart, and its termination lies opposite to a slight notch upon that border.

The left limb of the ventricle is at first triangular in outline, but later becomes more spherical in shape and forms the left ventricle. The right portion becomes flask-shaped, the caudal portion being spherical and the oral tubular in form.

The right and left ventricles are from the first clearly demarcated from one another by the groove upon the ventral surface and by the notch upon the caudal margin of the connecting piece. The notch may persist and be present even in the adult heart.

The right ventricle, at first placed with its long axis vertical, becomes slightly oblique from right to left orally, and the distal portion slopes more and more obliquely in the dorsal direction. The deep cleft between the oral portion of the two ventricles becomes shallower, especially dorsally, and the dorsal half of the tubular portion of the right ventricle becomes directly continuous with the left ventricle.

The ventral surface of the right ventricle shows a groove at the junction of the two parts forming it, but this groove gradually becomes shallower and disappears by the 12·5-mm. stage.

The proximal portion of the right ventricle retains a triangular form; the distal tubular portion becomes more and more oblique. The groove on the surface of the conus arteriosus which marks the septum dividing that vessel into the pulmonary artery and the aorta, becomes deeper and is prolonged spirally on to the bulbus cordis, marking off a dorsal from a ventral portion. The dorsal portion becomes reduced in length, and its root passes to the left side and joins the base of the left ventricle. The ventral portion, at first tubular, dilates to a marked extent and forms the infundibulum of the adult right ventricle.

Dorsally the sinus venosus and the atrium become largely incorporate at the 9-mm. stage. The transverse portion of the sinus venosus become applied to the dorsal surface of the heart and lies obliquely on the dorsal surface of the atrium.

The dorsal wall of the atrium expands with the formation of the pulmonary veins, and the sinus venosus (transverse portion) is displaced and comes to lie in the atrioventricular groove, or circular sulcus of the adult heart.

The adult arrangement of four pulmonary veins has been reached in the 28·6-mm. embryo.

2. *Developmental Changes affecting the Junction of the Sinus Venosus and Atrium.*

The portion of the sinus venosus which participates in these changes is the right horn, and to a lesser degree the transverse portion.

The changes which occur in this part of the heart are known to consist largely in the incorporation of the right horn into the atrium, so that these two portions come to form in the adult a single chamber in which only slight demarcation can be determined of the sinus portion from the atrium proper.

Stated briefly, the changes involved in this incorporation are as follows:—

At the junction of the sinus and atrium there is externally a slight groove, a narrow smaller chamber joining on to one of larger size. The groove becomes invaginated at each side, producing in the interior two loose flaps of tissue—the right and left venous valves, the right one being formed before the left. Whether these valves are formed merely by a passive invagination or by active ingrowth cannot be determined. In histological structure, however, the right venous valve, and to a less degree the left one, differ from the wall of the sinus or atrium; the cells are larger and less fibrillated, and numerous vacuoles are present.

The sinus opening into the atrium resembles the "valvula coli" of human anatomy in being merely a slit on the summit of a prominent ridge, and the ridge is prolonged on the wall of the atrium, especially orally, forming the septum spurium, better termed the "tensor valvulæ."

The right venous valve grows rapidly forwards, and the slit-like sinu-atrial orifice enlarges orally and caudally, reaching to the floor of the atrium. The right valve extends forwards on the floor as far as to the atrio-ventricular cushions. It extends orally along the roof of the atrium and forms an almost complete partition, shutting off the portion of the atrium lying to its right side from the portion on the left. The prolongation of this venous valve extends to the left side of the atrio-ventricular orifice.

The wall of the atrium to the right of this partial septum is smooth internally, but at 12·5 mm. muscle bands are present, and these increase in number and in size and constitute the musculi pectinati of the atrium. Up to a late stage of development these bands do not spring from the venous valve, but arise some short distance from it. They run obliquely down to the region of the atrio-ventricular junction.

The further development of the portion of the atrium lying to the right of the right venous valve need not be more fully described. Its size varies in different specimens, depending largely upon whether the atrium is in systole or diastole at the time of fixation.

The views of the external surface of the various hearts show how, on both the right and left sides of the heart, the marginal portions of the atrium expand and form two wing-like processes lying on either side of the cylindrical bulbus cordis. In the adult heart they form the auricles or appendices of the atria.

The most important and most complex developmental changes occur in the portion of the atrium lying to the left side of the right venous valve.

The extension forwards of the right—and later of the left—venous valves into the cavity of the atrium and the septum primum atriorum mark off clearly a chamber to which it seems advisable to give a special name, since it can be recognised through all the later stages of development, and in the adult heart forms the "sinus venarum." To this chamber of the embryonic heart I propose to give the name of the sinu-atrial chamber. Its limits are: on the right, the right venous valve; on the left, the left venous valve and the septum primum; the roof formed by the wall of the atrium between the upper diverging limbs, and the floor formed by the area between the lower attachments of the venous valves. In the adult heart this chamber includes the whole of the posterior part of the right atrium from the vena cava superior to the vena cava inferior, its right margin formed by the crista terminalis, and its continuation the valve of the vena cava inferior, the left wall formed by the fossa ovalis and the limbus above it as far as to the roof of the atrium. The left wall is a composite wall, formed, as will be shown, by the septum primum in the floor of the fossa ovalis, by left venous valves merged into it, and by a partial fusion of the adjacent walls of the two atria. The lower attachment of the right venous valve to the floor of the atrium becomes modified after the 20-mm. stage.

At the stage of the 8-mm. embryo the vena cava inferior and the coronary sinus open into the sinus venosus dorsal to the atrium. The widening of the sinu-atrial orifice caudally allows the opening of both of these vessels to move forwards so that their orifices come to lie in the floor of the sinu-atrial chamber near the atrio-ventricular opening.

This attachment extends as far as to the atrio-ventricular junction, and thence on the ventral wall of the atrium, and divides into two limbs. This splitting is connected with a change in the position of the opening of the coronary sinus, which moves forwards in the floor of the sinu-atrial chamber and comes to open between the two limbs. Its orifice therefore is separated from that of the vena cava inferior by the left limb of the attached margin. This limb forms the valve of the coronary sinus, while the right limb forms the valve of the vena cava inferior.

The vena cava superior does not move forwards to the same extent, nor do the venous valves diverge so much from one another orally. For a time, at about the 20-mm. stage, the orifice of the vena cava superior appears to be guarded by a definite valve, formed by the right venous valve and a portion of the left venous valve. This condition is well illustrated in the figure of the 20-mm. embryo. The left venous valve later is displaced to the left, and the narrow orifice becomes a wide one.

There can be little doubt that the terminal parts of the venæ cavæ superior and inferior are formed from portions of the sinus venosus, for the orifices of these vessels widen out and merge very gradually into the atrium.

Left Venous Valve.—In the 6-mm. embryo the left venous valve forms a small flap united to the right valve at its upper and lower ends.

In the 8-mm. specimen the two valves are more widely separated. Subsequently their union caudally is divided and each valve is attached separately to the floor of the atrium.

The left venous valve is at first separated from the septum primum of the atrium by an interval which forms a small bay in the posterior part of the atrium, the inter-septo-valvular space. This interval gradually disappears, and the left venous valve and septum primum come into contact with one another. In the 12·5-mm. specimen these two folds are united caudally for a short distance and form a single vertical fold. Above the level of this union the left valve is continued along the roof of the atrium, and forms there a ridge which extends as far forwards as to the atrio-ventricular junction. In the 16-mm. embryo the left valve is attached caudally to the septum primum, but orally passes to the roof of the atrium and on to the ventral wall, forming a complete ring separating the sinu-atrial chamber from the inter-septo-valvular space. In the 20-mm. embryo a portion of the left venous valve forms a small flap limiting on the left the opening of the vena cava superior into the sinu-atrial chamber. Caudally it is fused with the base of the septum primum, which now forms the left margin of the orifice of the vena cava inferior (Plate-fig. 15).

In the embryo of 30-mm. length the left venous valve is merged at its root with the septum primum, but at a higher level it projects as a crescentic ridge along the roof of the atrium, and extends to the ventral wall.

3. *The Formation of the Atrial Septum.*

The specimens show the origin of the septum primum as usually described and the formation of the foramina ovalia primum and secundum.

The septum primum is fairly completely formed, even at the 6-mm. stage, and it forms an almost vertical septum, joining the dorsal and ventral walls of the atrium to one another near their middle. The septum appears to form orally and grows downwards to the floor of the atrium, and it unites with the dorsal portion of the floor of the atrium at an early stage. It is, however, for some time incomplete caudally and ventrally, where it fails to reach the floor of the atrium, leaving a channel between the two halves (foramen ovale primum). This orifice is shown in the 6- and 8-mm. embryos, but has closed at 12·5 mm. The lower margin of the foramen ovale primum is formed by the cushion tissue of the endocardial cushions of that atrial canal, and its closure is probably due largely to the increase in size of those structures and their extension dorsally.

I have, however, found a specimen of the heart of a fully-developed human embryo in which the foramen ovale primum had not become closed, but persisted with a foramen ovale secundum (Plate-fig. 16).

The foramen ovale secundum is formed, even at the 6-mm. stage, as an irregular orifice with ragged edges in the upper part of the septum primum. It gradually increases in size, and at 8 mm. it is large, and only a small portion of the septum primum is found inferiorly to it. It is, in many specimens, placed in the hollow of a bay in the septum by which the current from the vena cava inferior is conducted to the foramen.

In structure the septum primum seems for a long time to be fibrous instead of muscular.

It is convenient here to describe the exact conditions of the fold known as the septum secundum atrium.

Retzer states in regard to it that in the pig "the septum secundum in Born's sense does not exist. Search for it was made in vain in the embryonic hearts of man, monkey, and rabbit.

"The conus arteriosus is the fixed point physically, and the growing atria, in their efforts to expand and form auricles, grow around the fixed point and cause a bulging inwards of the wall. It is, therefore, a passive formation, and never attains such a size that one is justified in calling it a septum. The septum primum of Born remains the ultimate septum."

In the same paper Retzer describes and figures the attachment to the floor of the atrium of the right venous valve as it occurs in my own specimens, and his figure I can corroborate.

The formation of the septum atriorum as illustrated in the models is as follows :—

The Oral Surface of the Roof of the Atrium.—In the 6-mm. embryo there is a central slight indentation of the roof of the atrium at the point where the septum primum and left venous valve are present. This surface indentation is more distinct in the 8-mm. embryo, in which there is a wide dorso-ventral groove of considerable depth, and on each side of it the roof of the atrium forms a large cupola.

In the later stages these lateral cupolæ increase greatly in size, and form narrow, long vertical chambers, quite separate from one another.

At a still later stage the two adjacent walls of the two dilated portions meet and become slightly attached to one another. Thus the appearance is produced of a narrow communication between the right and left atria situated caudally, bounded cephalad and dorsally by an area of atrial wall of considerable extent.

This area consists of a narrow margin—the edge of the "limbus fossæ ovalis," formed by the fused left venous valve and the remains of the upper portion of the septum primum, and of an area where the walls of the two atria are in coaptation.

In this region there is no true blending of the atrial walls, for even in the adult heart the walls of the right and left chambers can be separated from one another without the division of any muscle tissue as far as practically to the margin of the limbus fossæ ovalis.

To show this it is only necessary to incise the epicardium on the dorsal wall of the atria along a vertical line between the right pulmonary veins on the one hand, and a line joining the left borders of the venæ cavæ inferior and superior on the other. The walls of the right and left atria can then be separated from one another by merely dividing a little loose connective tissue, and the separation can be carried as far as practically to the margin of the limbus fossæ ovalis. The whole of the dorsal and oral portion of the so-called septum secundum atriorum is therefore merely the result of the coaptation of adjacent portions of the walls of the two atria, and is not a true septum comparable to the septum primum.

To this extent I can confirm the view expressed by Retzer, in so far as he states that the septum secundum is not a true septum comparable to the septum primum.

The sections of the more advanced embryonic hearts show the infolding of the wall quite clearly.

4. *The Atrial Canal and the Bulbus Cordis.*

Born has pointed out the importance of the change which occurs in the position of the opening of the atrial canal into the ventricle. At first that canal lies on the left side of the heart, but it gradually moves to the right, and at the same time the orifice elongates in the same direction and becomes a horizontal slit. This alteration in position is due probably as much to a growth change in the atrium and in the ventricle, extending them to the left side, as to an actual transition in the position of the canal; but there is also an actual extension of the orifice. At the same time the loose reticular tissue lying beneath the endocardium (seen in embryo 2W1) becomes arranged into two definite masses which form the upper and lower cushions of the atrial canal. The extension of the orifice to the right side passes beyond the bulbo-ventricular septum and beyond the limits of the original ventricle, so that the right portion of the opening leads from the atrium into the chamber termed the bulbus cordis. The endocardial cushions of the atrial canal also extend in the same direction, and their right margins come into contact with the bulbar cushion lying on the right and dorsal aspect of this portion of the bulbus.

This is a morphological fact of considerable importance, since it justifies the statement that the right atrium comes to open into the bulbus cordis. This fact is clearly shown in some of Born's figures, but its morphological significance has not been pointed out. The upper portion of the bulbo-ventricular furrow remains as an infolding of the wall, marking the separation between ventricle and bulbus cordis. The contact of the bulbar cushion with the cushions of the atrial canal is well seen in the 6-mm. as well as in the 8- and 9-mm. specimens.

It is convenient at this stage to turn to the bulbus cordis and to consider the part which it plays in the formation of the adult heart and its homologies.

Considerable uncertainty exists as to the exact relationship of the bulbus cordis and ventricular portions respectively of the early embryonic heart to the chambers and vessels of the adult heart.

Since the time of His it has been recognised that the ventricular portion of the early embryonic heart is in the form of a V, the two limbs being separated by a deep groove.

In an early specimen described by His, similar to the youngest specimen of my series, such an arrangement exists. His gave to the left or descending limb the name of "conus venosus," and to the right or ascending limb the name of "conus arteriosus." Such a terminology has obvious drawbacks, such as the fact that the name of conus arteriosus is used in adult human anatomy for a definite structure, not the same as the structure so named in the embryonic heart.

Considerable light is thrown upon the significance of these portions of the heart by the study of the hearts in embryo as well as in adult fishes and reptiles.

Boas, working on the heart in the Anamnia, recognised "a clearly separated independent portion of the heart, which should be added as a third chamber to the auricle and ventricle," and termed it in Anamnia the conus arteriosus.

Kolliker and Born termed a similar portion of the heart in embryo Amniota the bulbus aortæ, or bulbus arteriosus.

Langer, working on embryo fishes and reptiles and later on birds and mammals, identified a chamber in the heart possessing similar characters, and gave to it the name of bulbus cordis, a term which has been generally recognised and adopted. Thus Born at a later date substitutes the term bulbus cordis for the portion termed by His the conus arteriosus; and Tandler, in describing the development of the human heart at an early stage, terms the descending limb of the V-shaped loop the ventricular limb and the ascending the bulbus limb.

The distinctive features of the bulbus cordis chamber in embryo hearts can be clearly laid down.

(1) Its wall is composed of a muscular tissue similar to that of the myocardium of the ventricle.

(2) It contains in its interior thickenings of subendocardial tissue, which form the "bulbar cushions."

(3) In position it lies between the ventricle and the truncus arteriosus.

Greil has followed the changes which occur in the bulbus cordis in the developing heart of Lacerta, and in the crocodile; and he has shown that in Lacerta it forms in its caudal portion a definite chamber in the ventricular part of the heart, from which arise the pulmonary artery and the left systemic aorta.

It has also been recognised that in the mammalian heart, including man, the bulbus cordis forms at least a portion of the right ventricle (Keith, etc.); and Born derives from its upper part a portion at least of the pulmonary artery, as well as of the right ventricle.

By some writers it is assumed that the bulbo-ventricular is synonymous with the interventricular furrow of the heart.

Thus Mall (*Amer. Journ. of Anat.*, vol. xiii, p. 252), describing the heart of an embryo 3·5 mm. in length, states: "The lower connecting piece unites the left ventricle with the bulb, which later on gives rise to the right ventricle." And again, in reference to the heart of an embryo 4¼ mm. in length, he states: "The trabecular system has extended into the bulbus—that is, into the right ventricle."

In examining a series of embryos such as the present one, one is very much struck by the definite characters shown throughout all the early stages of development by the "bulbus cordis."

Its wall is composed of muscle tissue similar to that of the left ventricle, and this muscle tissue ceases abruptly at the line of junction of the bulbus with the truncus arteriosus. The interior shows at the earliest stages the loose subendocardial reticulum, which is later replaced by definite masses, the bulbar cushions, and it lies between the left ventricle and the truncus arteriosus.

The principal features to be discussed are: (1) alteration in the direction of the bulbo-ventricular groove; (2) the extent of the bulbar cushions; and (3) the relation of the bulbar cushions to the right ventricle and to the definite muscular interventricular septum.

Relation of the Conus Arteriosus to the Chambers in the Adult Heart.

From the condition shown in Thompson's model (2), in which the bulbo-ventricular groove lies horizontally, through the specimen 2W1 and onwards to the stage of the 5·2-mm. embryo figured by Tandler, the bulbo-ventricular groove is seen to rotate gradually from a horizontal to an oblique, and finally to an almost vertical position. In the last specimen mentioned the groove forms a practically vertical furrow on the ventral surface of the heart, extending from the left side of the base of the truncus arteriosus to the caudal margin of the ventricle, where a notch is found on this border of the heart. Such a notch is present at earlier stages also, and is present even in the model prepared by Thompson, though not shown in the figures.

Born's models of this region of the heart in the rabbit are not at all conclusive. In two hearts closely resembling one another, he shows in the younger a bulbo-ventricular cleft running obliquely on the heart wall; and in a slightly older specimen a similar furrow is present, from which a depression extends across to the right side, and the latter is taken to be the bulbo-ventricular furrow, while the former is termed the interventricular furrow.

He states repeatedly, however, that there was no clear indication of the division of the bulbus from the ventricle.

Of my own specimens, the heart of the embryo of 6-mm. length follows closely upon the Tandler specimen from a 5·2-mm. embryo, so far as the external form is concerned. In it the figure shows a vertical furrow extending on the anterior surface of the heart to the caudal border. It corresponds internally to the interventricular septum, and the appearances suggest that it is no more than a deepened bulbo-ventricular furrow.

It must further be noted that in the lower part of the interventricular septum (septum ventriculorum inferius) there is to be found the termination of one of the proximal bulbar cushions. This fact seems to afford strong support for the view that this portion of the interventricular septum is derived from the bulbo-ventricular ridge; for were the interventricular septum formed to the left side of the bulbo-ventricular septum, and within the cavity of the primitive ventricle, it is difficult to see how the bulbar cushion could be prolonged on to it.

From the 6-mm. stage onwards through the 7- and 8-mm. and on to the 12-mm. specimens, the evidence from the study of the position of the bulbar cushions and the muscle wall goes to show that the bulbo-ventricular groove is the same as the interventricular groove of later stages.

The right atrio-ventricular orifice is enclosed on its right side by one of the bulbar cushions, and the septal wall of the ventricle supports the other proximal bulbar cushion.

It is true that neither of these cushions reaches to the very apex of the right ventricle, but that fact is not sufficient in itself to justify the division of the right ventricle into two parts of separate developmental origin. The appearances strongly suggest that the mammalian right ventricle is formed entirely from a primitive chamber homologous with the bulbus cordis of fishes and reptiles. If the mammalian right ventricle is derived solely from the bulbus cordis, and if the mammalian muscular interventricular septum be the bulbo-ventricular septum, then the muscular interventricular septum of the reptilian heart is not represented as such in the heart of mammals, and the anterior and posterior ventricles of the reptile are not homologous with the right and left ventricles of the human heart.

Greil has pointed out also that in Varanidæ there is no question of the division of the ventricle into a right and a left ventricle, for both of the atrio-ventricular openings belong to the dorsal chamber (the ventricles being dorsal and ventral, and not left and right). It must, however, be pointed out that the anterior ventricle of the reptilian heart, consisting as it does of bulbar and ventricular portions, separated partially from one another by a muscular ridge, gives rise not only to the pulmonary artery but also to the left systemic aorta, and hence it is not entirely comparable with the right ventricle of the mammalian heart.

It can, moreover, be shown that in the development of the heart of man the bulbus is divisible into two portions—an upper cephalic and a lower caudal; and that these two parts give rise to different parts of the adult right ventricle—the upper to the infundibulum, and the lower to the expanded portion of the ventricle.

5. *Developmental Changes in the Bulbus Cordis.*

If we assume, on the grounds previously stated, that the chamber in embryo S1 which forms the right portion of the ventricle is the bulbus cordis, this specimen affords a convenient starting-point from which to trace the subsequent changes in this part of the heart tube.

In this specimen, as in other specimens of similar age described by other writers, that portion of the heart is flask-shaped, and is divisible into a caudal spherical and an oral cylindrical portion. In the latter the lumen is almost completely divided into two channels by the projection into the interior of the bulbar cushions, while in the former the bulbar cushions are widely separated from one another and diverge on opposite sides of the ventricular cavity.

Distal Portion.—Plate-fig. 4 shows a reconstruction of a portion of the distal part of the bulbus, with one of the two large cushions found in it. This cushion begins above at the separation of the root of the combined sixth aortic arches from the truncus arteriosus, and extends uninterruptedly downwards in a clockwise spiral. On the opposite wall, which has been removed, there was another cushion of similar extent.

The upper portion of these cushions corresponds precisely to the "distal bulbar swellings" 1 and 3 respectively figured by Tandler in the heart of an embryo

6·5 mm. in length. In my specimen, however, there is no separation such as he describes between proximal and distal cushions. Between the cushions 1 and 3 of Tandler there lie two additional cushions, namely, the distal bulbar cushions 2 and 4. Successive sections of the bulbus in my specimen show that these swellings are extremely small and indefinite, and, were it not for the fact that four such cushions are readily recognisable in the developing hearts of lower forms, it is extremely doubtful whether they would be described as occurring at all in the human heart.

In short, it is extremely doubtful whether there are distal bulbar cushions as distinct from the large proximal cushions in the human embryo at all.

The cushions described above pass as far distally as to the root of the aortico-pulmonic septum.

The figures from reconstructions of this portion of the heart in embryos from 6 to 12·5 mm. show the successive transitions which occur.

Thus in the 6-mm. embryo the distal portion of the bulbus cordis forms a cylindrical tube, lying within the pericardium and obliquely crossing the upper part of the atrium (Plate-fig. 2).

The muscle coat does not extend as far as to the pericardium, and beyond the muscle-coated part is the truncus arteriosus. At the junction of bulbus and truncus the right and left sixth arterial arches arise dorsally very close to one another.

Within the bulbus there are two distinct and large endocardial cushions, which almost meet with one another, so as to divide the lumen into two channels. These channels form the exit from the heart for the blood from both the left and the right ventricles, and at this stage the whole of the blood from the left ventricle must pass through the narrow interventricular foramen.

In the next specimen (B1) the portion of the bulbus is more oblique in position and lies more horizontally on the roof of the atrium, and its muscle coat ceases at a greater distance from the pericardial wall.

Within the terminal portion the lumen of the bulbus is divided into two channels—one, ventral and to the left, is continuous with the orifice of the fused sixth arterial arches; and the other, dorsal and to the right, is continued into the truncus arteriosus.

Proximal to this region, within the bulbus, are two large, plump spirally arranged cushions, one of which passes to the interventricular septum, and the other to the right margin of the atrio-ventricular opening.

In the succeeding specimen (M1) the condition is very similar, and does not require special description. The figure shows that the large cushions are continued along the walls of the two separated vessels in the terminal part of the bulbus, and, in addition, some small intermediate swellings of a similar character have appeared there (bulbar cushions 2 and 4) (Plate-fig. 8).

There is at this stage no definite formation of either aortic or pulmonary valves.

In the next specimen modelled (12·5 mm.) a considerable change has occurred.

The muscle coat of the bulbus can be traced quite definitely to a point where it abruptly becomes continuous with the fibrous coat of the truncus arteriosus, and at that level are found the commencing pulmonary and aortic valves.

The terminal part of the bulbus has now become more horizontal, and there is a marked inequality in the length of the ventral and dorsal walls: the ventral wall has increased in length, while the dorsal wall has remained stationary or has even shortened.

Hence the valves (pulmonary) of the more ventral vessel lie some distance above the heart, while the aortic valves are near to it.

Within the bulbus the division of the lumen into two vessels now extends along practically its whole length, and there are two distinct channels, both of which, however, communicate with the right ventricle below.

Perhaps the more striking change—it certainly directed my own attention specially to this region—is the dilatation of the channel leading to the pulmonary artery.

Up to the 12·5-mm. stage the lumen was narrow and inconspicuous. Now it is large and dilated, and the orifice into the pulmonary artery is placed upon the dorsal wall, not at the termination (text-figs. 11 and 12).

The ventral wall is lined with a reticulated formation of muscle continuous with that of the ventricle. Thus the "infundibulum" of the right ventral is formed.

The so-called congenital stenosis of the pulmonary artery is due to failure in the dilatation of this part of the right ventricle.

The development of this region of the heart may be summarised:—

1. The pulmonary artery of the adult is developed from a portion of the truncus arteriosus, the lumen of the truncus arteriosus being divided into:

(*a*) The pulmonary artery, from which arise the sixth pair of arches, very close together.

(*b*) The ascending aorta.

2. The pulmonary and the aortic valves are formed at the distal extremity of the bulbus cordis. The infundibulum of the right ventricle is formed from a portion of the bulbus cordis, and is at first merely a narrow channel, but becomes distended.

3. The increasing obliquity and the consequent relative elongation of the ventral wall causes the pulmonary valves to lie some distance above the right ventricle, while the aortic valves lie near the base of the left ventricle.

The septum of the bulbus is continued downwards in a spiral and oblique direction to join the upper margin of the septum of the ventricle, in such a way that the dorsally placed vessel (the aorta) is in continuity with the left ventricle, while the infundibulum communicates with the right ventricle only.

6. *The Atrio-ventricular Junction, the Formation of the Atrio-ventricular Valves and of the Conducting Mechanism.*

The atrial canal is at first a short channel lying on the left side of the heart, but it moves to the right and comes to lie centrally, and it is no longer visible from the surface but is concealed by the overlapping atria and ventricles.

The upper and lower cushions of the canal fuse with one another centrally, and the lateral margins of the channel remain as the venous ostia. All these changes are exactly as are shown in Born's models and figures.

The orifices are at first destitute of valves, but soon rudiments of valves appear on both sides, right and left; the first to appear being a large laterally placed cusp formed by the infolding of the atrio-ventricular junction into the interior, and by its undermining on the ventricular side.

This cusp represents, on the right side, the lateral and anterior cusps of the tricuspid valve, and on the left side the lateral cusp of the mitral valve.

This cusp formation, by infolding, has an important bearing upon the loss of continuity between the muscle walls of the atrium and the ventricles.

The structure of the infolded cusp is a centrally placed wedge-shaped mass of connective tissue derived from the external surface of the atrio-ventricular junction, with a layer of muscle tissue continuous with the atrial muscle coat on the atrial surface, and of ventricular muscle substance on the ventricular aspect. On the atrial surface there may, in addition, be small masses of cushion tissue.

At the margin of the cusp the two layers of muscle tissue are continuous with one another. As the tissue of the cusp becomes altered into fibrous tissue this continuity is destroyed.

The right lateral cusp is of large size, and it is attached to the ventricular wall by muscle bands of considerable size. Orally it gains an attachment to the infundibulum, close to the region of the septum which divided this channel from the aorta, and this attachment as a rule remains fibrous and can be readily identified in the adult heart.

At each orifice later a second cusp is formed, the medial cusp being in each case derived from the central mass of tissue representing the fused cushions of the atrial canal, and from the adjacent muscle tissue of the septum of the ventricles.

The endocardial cushions of the atrial canal form a central mass of considerable size, connected dorsally with the atrium, and especially with the atrial septum, and ventrally with the ventricle muscle tissue.

The cushion mass extends widely on either side, and on the right side a prolongation of the upper cushion extends above the right venous ostium and joins with the bulbar cushion B.

On the left side, the upper and lower cushions send prolongations to the ventricle muscle wall above and below the left venous ostium.

Development of Nodal Tissue and Connecting Tissue (Atrio-ventricular Bundle).

Nodal tissue possessing the adult characteristics cannot be definitely recognised in the developing heart at the stages described, probably because its histological features are not sufficiently differentiated.

The right venous valve from an early stage, however, shows histological characters which distinguish it from adjacent portions of the heart wall, such as a loose texture and vacuoles, and this may precede the formation of the sinu-atrial muscle of Keith and Hoch.

Neither does the atrio-ventricular bundle present in the young embryonic heart the features which allow it to be recognised in the adult.

The most that can be said, from the specimens examined, is that from an early stage a structure can be identified which has special histological characters, and which lies in the position afterwards occupied by a part of the atrio-ventricular bundle.

This structure is recognisable in the 16-mm. embryo, and is very distinct in the 20-mm. embryo as well as in later specimens.

It consists of a rounded mass of cells whose nuclei stain rather darkly and are more closely packed together, surrounded by a ring of very loose tissue.

This structure is most clearly seen in the upper part of the muscular interventricular septum, close to the apex, and it appears to run into and to be connected with the cushion tissue of the atrio-ventricular canal. The peripheral connections of this structure with the walls of the ventricles cannot be discovered, except that on the right side it appears to pass towards the origin of the "moderator band."

This band is in part covered by the continuation of the bulbar cushion to the ventricular septum, and it is interesting to find that the path in the adult heart of the principal limb of the atrio-ventricular bundle lies in tissue immediately underlying a layer derived from cushion tissue.

The histological characters of this mass have been fully described and figured by Mall, and his figures represent accurately the condition found in my specimens from 20 mm. onwards.

Towards the atria I have not been able to trace definitely any connections of this bundle, beyond the fact that it runs into or below the cushion tissue of the atrio-ventricular canal and joins with the right and left venous valves.

It may here be pointed out that the process of development of the heart as described here shows a short-circuiting of part of the blood stream. In the early stages the blood passes from atrium to ventricle, and thence to bulbus cordis.

The alteration in the position of the atrial canal allows part of the blood stream to pass from the right division of the atrium into the bulbus cordis and so to the truncus arteriosus, without passing through the primitive ventricle at all.

At the stage when the right and left ventricles become completely closed off from one another, this short-circuiting of part of the blood stream necessitates an alteration in the original peristaltic wave, so that the left and right ventricles may beat simultaneously, and it is when this separation has been affected that in my specimens there is the first indication of the presence of the atrio-ventricular bundle.

Towards the expenses of preparing the models a grant was received from the Royal Society of London, and the expenses connected with the illustrations have been largely defrayed by a grant from the Carnegie Trust for the Scottish Universities.

To these two bodies I wish to express my thanks for this assistance.

LITERATURE.

The literature of the development of the heart is an extensive one, and need not be referred to in detail here, as adequate summaries are found in the KEIBEL-MALL *Textbook of Embryology* and in TANDLER'S *Das Herz*, as well as in HOCHSTETTER'S comprehensive bibliography in HERTWIG'S *Handbuch der vergleichenden und experimentellen Entwickelungslehre.*

The works to which reference has been specially made, in addition to those above mentioned, are the following:—

(1) WATERSTON, *Journ. of Anat. and Phys.*, vol. xlix.
(2) THOMPSON, P., *Brit. Med. Journ.*, 1909.
(3) TANDLER, *Anatomie des Herzen*; and KEIBEL-MALL, *Manual of Human Embryology*, vol. ii.
(4) MALL, *Amer. Journ. of Anat.*, vol. xiii.
(5) KEITH, *Journ. of Anat. and Phys.*, vol. xli.

LIST OF PLATE ILLUSTRATIONS.

PLATE I.

Fig. 1. Ventral view of wax-plate model of heart of 3-mm. embryo (2W1).
Fig. 2. Ventral view of model of heart of 6-mm. embryo (S1).
Fig. 3. Interior of the above model.
Fig. 4. Dorsal wall of distal portion of the bulbus cordis in the same model.
Fig. 5. Ventral view of model of heart of 8-mm. embryo (B1).
Fig. 6. View from the right of the interior of the right atrium and ventricle of the same model.
Fig. 8. Interior of a model of the distal portion of the bulbus cordis of embryo M1 (9 mm.) to show the endocardial cushion B, the root of the pulmonary artery and of the aorta.
Fig. 9. Ventral aspect of model of the heart of 12·5-mm. embryo (S4).

PLATE II.

Fig. 7. Caudal half of the same model divided horizontally.
Fig. 10. View from the left of the same model after removal of the lateral wall of the left atrium.
Fig. 11. Ventral aspect of model of 16-mm. embryo.

Fig. 12. The same model from the right side after removal of the lateral wall of the right atrium and ventricle, and of the right venous valve.

Fig. 13. Caudal portion of model of heart of 20-mm. embryo, divided horizontally.

Fig. 14. Ventral aspect of model of 30-mm. embryo.

Fig. 15. Same model viewed from the right after removal of the lateral wall of the atrium and of the right venous valve.

Fig. 16. Interior of the left atrium of heart of a fully developed child, with foramen ovale I persisting in addition to foramen ovale II.

The lettering in the figures is as follows:—

A. = Bulbar cushion A.
Ao. = Aorta.
A.S. = Aortic sinus.
Atr. = Atrium.
A.-V.V. = Atrio-ventricular valve.
A.-V.B. = Atrio-ventricular bundle.
A.F. = Annulus fibrosus.
B.Cu. = Bulbar cushion.
B. = Bulbar cushion B.
B.C. = Bulbus cordis.
B.V. = Bulbo-ventricular.
C.S. = Coronary sinus.
E.T. = Endothelial tube.
End. Cu. = Endocardial cushions of the atrial canal.
F.O. I and F.O. II = Foramen ovale primum and secundum.
Inf. = Infundibulum of right ventricle.
I.V.C. = Inferior vena cava.
I.-V.S. = Intersepto-valvular space.
I.V.F. = Interventricular foramen.
L.A. = Left atrium.
R.A. = Right atrium.
L.C. = Lateral cusp of atrio-ventricular valve.
M.C. = Medial cusp of atrio-ventricular valve.
L.V. = Left ventricle.
L.A.-V.O. R.A.-V.O. = Left and right atrio-ventricular openings.
L.V.O. = Left venous ostium.
R.V.O. = Right venous ostium.
L.V.V. and R.V.V. = Left and right venous valves.
O. = Opening of sinu-atrial chamber into the right atrium.
P.A. = Pulmonary artery.
P.V. = Pulmonary vein.
R.V. = Right ventricle.
R.P.V. = Right pulmonary vein.
S. I = Septum primum atriorum.
S.-A.O. = Sinu-atrial orifice.
S.B. = Septum of the bulbus cordis.
S.V. = Sinus venosus.
S.V.C. = Superior vena cava.
Sin. At. = Sinu-atrial chamber.
T.A. = Truncus arteriosus.
T.V. = Tensor valvulæ.
V.Ao. = Ventral aorta.
V.C.S. = Vena cava superior.

Professor D. WATERSTON on "The Development of the Heart in Man."—PLATE I.

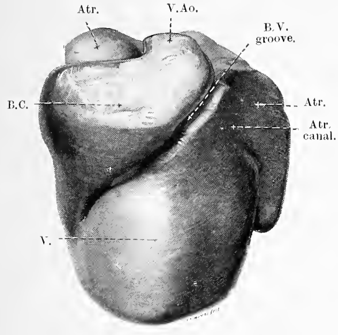
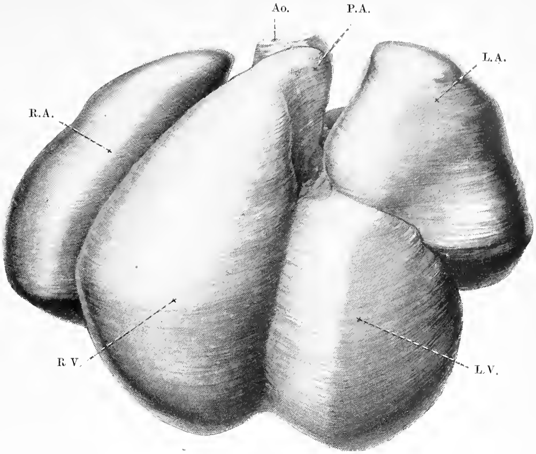


FIG. 1.



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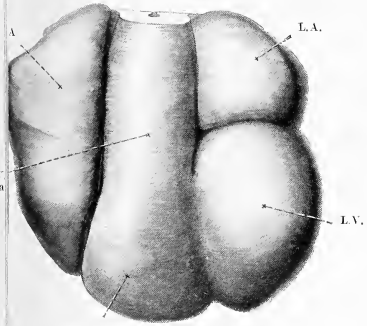
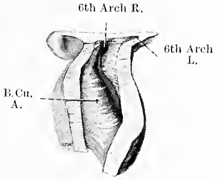


FIG. 2.



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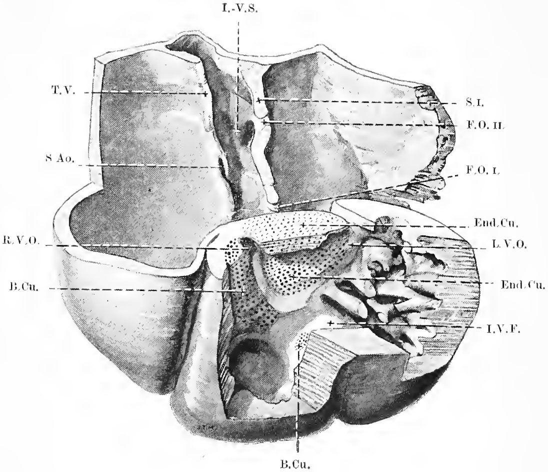
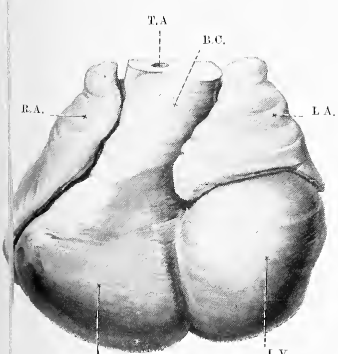


FIG. 3.



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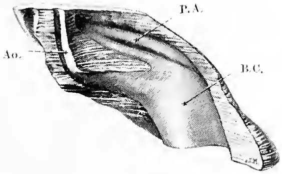


FIG. 8.

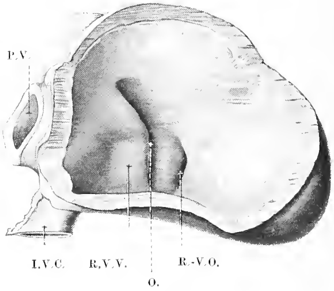


FIG. 6.

Professor D. WATERSTON on "The Development of the Heart in Man."—PLATE II.

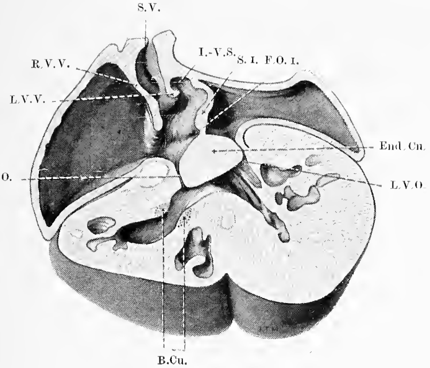


FIG. 7.

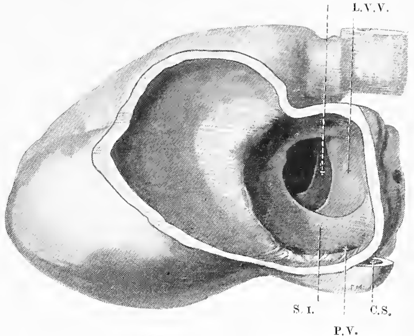


FIG. 10.

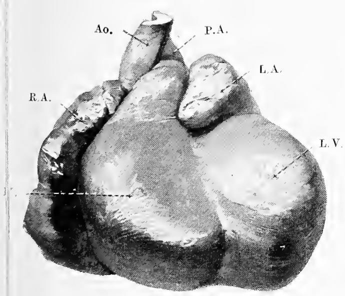
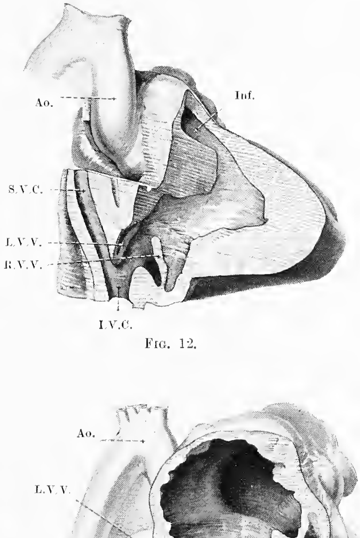


FIG. 11.



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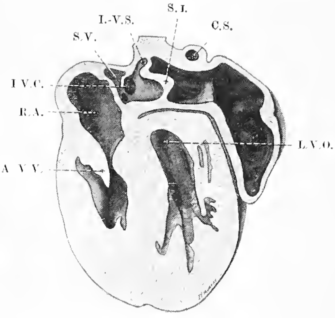
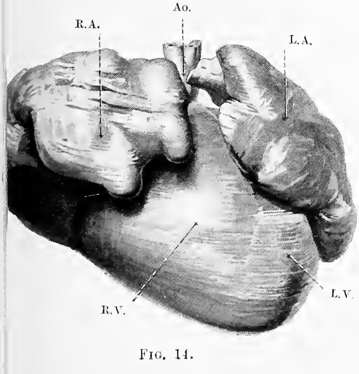


FIG. 13.



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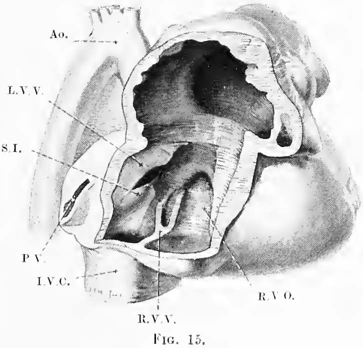

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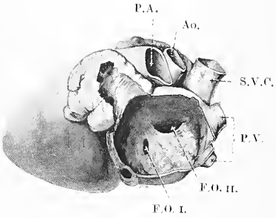

FIG. 16.

XIII.—The Formation, Rupture, and Closure of Ovarian Follicles in Ferrets and Ferret-Polecat Hybrids, and some Associated Phenomena. By Professor Arthur Robinson, University of Edinburgh. (With Ten Plates.)

(Read July 9, 1917. MS. received April 26, 1918. Issued separately September 18, 1918.)

Introduction.

A few words of explanation are necessary at the outset in connection with the terms used in association with the animals upon which these investigations were made.

Dealers in ferrets supply two types of animals—one with yellowish-white fur and pink eyes, which they call "ferrets," and a second type in which the yellowish fur is intermingled with a varying admixture of brownish or brown-black hairs; the second type they call "polecats." The polecats of the ferret-dealers are not, however, true polecats, for Miss Frances Pitt, who has bred ferrets and polecats and ferret-polecat hybrids in a scientific manner, and to whom I am indebted for the greater and best part of my information on this subject, points out that the so-called polecat of the dealers is never so dark and handsome in colour as the true polecat. Moreover, as Miss Pitt states, in the true polecat the light marks in front of the ears do not usually join across the forehead, whereas in the polecat of the dealers they form a band across the face; further, when viewed from in front and above, the head of the true polecat has the form of a fairly equilateral triangle, whilst in ferrets and the so-called polecats of the dealers the head, on the whole, has the form of an isosceles triangle.

The polecat is classified as a sub-genus of the Mustelinæ, and is termed *M. putorius*; and the ordinary ferret is generally looked upon as a white variety of the same sub-genus. Doubt has been cast upon this assumption by Miller (26), who states that, on account of some cranial features, the common ferret is more closely allied with the Siberian *M. eversmanni* than it is with *M. putorius*. The features to which Miller draws attention cannot be denied, but Miss Pitt says that reddish specimens of the polecat are not uncommon in the Aberystwith district, and the red colouring is also met with in the common ferret; this fact appears to point to a reversion of both forms to an ancestral type, though it in no sense substantiates the view that the ferret is a white variety of the polecat. Though the zoological position is of interest, it is not of great importance from the point of view of this investigation, for whatever the zoological affinities of the ferret and the polecat may be, it is certain, from the results of Miss Pitt's observations, which are confirmed by my own experience, that ferrets and polecats breed freely together, and their progeny are fertile among themselves, with ferrets and with polecats; moreover, the structure of the ovaries is the same in all, therefore, for the purpose in hand, they may be looked upon as one group; but for convenience of description, and to indicate clearly in the following account whether a ferret in the ordinary sense or a so-called "polecat," which I believe to be a hybrid, is being described I have termed the so-called "polecat" in all cases a ferret-polecat hybrid.

In the course of the investigation 266 animals were used, but in many cases the ovaries of the animals were in functional stages, which have only indirect bearing on the points to be considered now, or they offered evidence only on subsidiary points, therefore I have selected 118 animals from which 232 ovaries, obtained in satisfactory condition, were cut into continuous sections. Details with regard to these animals are given in the accompanying tables; at the same time it is to be understood that one or both the ovaries of all the 266 animals have been cut into continuous sections and have been examined, and that the statements to be made with regard to conditions which are found at different periods are based upon the whole group.

Some of the animals were obtained from a dealer in Norfolk, others from a dealer in Kent. Some of the animals were reserved for me at the end of one breeding season, were kept separate from the male, and were sent to me either before signs of œstrus appeared or immediately thereafter; these animals were inseminated by healthy, vigorous males in my own laboratory, and under my own observation. Other animals were inseminated under the dealers' observation, and were sent to me immediately thereafter or some days later, care being taken to prevent access to the male after the insemination. Both dealers thoroughly understood what was required of them, and as the results obtained from the animals inseminated under their observation correspond with the results obtained from the animals inseminated in my laboratory, there can be no doubt that they carried out the instructions given to them effectively.

The ferret possesses certain advantages for the purposes of investigations dealing with the phenomena of early development in mammals, for it is one of the few highly specialised carnivora which are obtainable in considerable numbers, and which are small and easily dealt with. It is also one of the group of animals which possess an almost completely closed ovarian capsule of the type present in the racoon and the badger, to which I have previously directed attention (32), (figs. 1, 2, Pl. I), and in which, therefore, it might be hoped that all the ova shed at an ovulation would almost certainly be found in the genital passages; this hope has, for the main part, been fulfilled; though, as will be seen later, it is possible for an ovum to escape through the opening in the peritoneal capsule into the peritoneum. The presence of the peritoneal capsule is also an advantage, inasmuch as it protects the surface of the ovary from injury during the manipulations which are necessary in association with the fixation, hardening, and embedding of the ovaries preparatory to cutting; and although the ovaries, oviducts, and uterine cornua are not so small as in some other mammals, yet they are so small that the cutting of them into serial sections does not entail an excessive expenditure of labour or time. Further, the ferret is an animal in which ovulation only occurs after insemination.* Therefore it was hoped that it would be possible to establish precisely the time at which ovulation and fertilisation occurred. This hope has not been entirely fulfilled for reasons which will be explained later.

Methods.

Food and Condition.

I made no stipulations with the dealers as to the feeding of the animals, and I understand that whilst they were in their hands they were fed on milk, bread, and scraps of rabbits, rats, mice, and birds. Whilst they were in my laboratory they were fed on bread and milk only, and they were all healthy and in good condition at the time of death, except one which suffered from rupture of the uterus during parturition and died twelve hours afterwards.

All the animals were killed by chloroform narcosis. They were placed in a jar full of chloroform vapour; in it they showed no fear and very little excitement; in a few seconds they were unconscious, and they were dead within ten minutes. The method was chosen because one of the points to be determined was whether or not there was effusion of blood into the cavity of the ovarian follicles at the time of rupture, and it was essential, therefore, to have as little as possible of excitement and struggling at the time of death.

Fixation.

Immediately after death the abdomen was opened; each uterine cornu was cut through close to the body of the uterus, which is very short in the ferret; the cut end of the cornu was held in the forceps, the broad ligament was divided with scissors to a point cranial to the attachment of the ovary, and the uterine cornu, with the ovary and the oviduct, were placed in the fixation fluid, care being taken to avoid any contact of the ovarian capsule with anything outside the body of the animal except the fixing fluid. In some cases the fixing fluid was heated to body temperature, and in other cases it was at the temperature of the laboratory; the results obtained by the two methods were not essentially different.

The fixing fluids were: Zenker; Maximow; strong Flemming, with from 2 to 3 per cent. of acetic acid; Mann's picro-corrosive sublimate, without and with formol; Perenyi; picro-nitric acid solution, with 5 per cent. formol; Lenhossek's fluid.

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* Marshall made the same statement in 1904 (21); but in 1910 (22, p. 136) he seems to have modified his opinion, for he writes: "In the ferret ovulation occurs during œstrus, but postponement of coition may bring about the degeneration of the ripe follicles, since they do not always discharge spontaneously."

The ovaries of opposite sides were, as a rule, placed in different fluids, and the fluid used in the case of each ovary is stated in the appended tables.

The post-fixation processes were those in ordinary use in association with the fixatives used, and in all cases in which the fixative fluid contained mercuric perchloride the mercury salt was removed by iodine in 75 per cent. alcohol.

Embedding and Staining.

All the ovaries were embedded in paraffin after being passed through alcohol in increasing strength, into alcohol and xylol, xylol, xylol and paraffin, and finally pure paraffin melting at 55·5° C.

Some of the ovaries were stained in bulk in Meyer's hæmalum before being embedded. This method cannot be recommended, in spite of the fact that it gives beautiful differentiation, because it is apt to shrink and harden the fibrous stroma of the ovary to too great an extent.

The majority of the ovaries, which were not stained in bulk with hæmalum, were faintly stained with eosin, placed in the various alcohols through which they were passed. This facilitates the selection of the sections, which are to be treated by various staining methods, before the paraffin is removed from them. The stain is, in most cases, completely washed out in the subsequent processes.

The majority of the sections were cut 10μ thick, some were 7μ, still fewer 5μ, for I found it practically impossible to get a satisfactory series of sections of 5μ.

The sections were fixed to the slides with egg albumen.

Most of the sections of the various ovaries were stained by Heidenhain's iron-hæmatoxylin method, sometimes in the ordinary way, but more frequently, and with better results, with the modification suggested by Rubaschkin (33)—that is, the sections were placed for one minute in a ·25 per cent. solution of potassium permanganate, washed in water, placed for one minute in a solution containing ·5 per cent. of potassium sulphite and ·5 per cent. of oxalic acid, and then washed for one hour in running water before they were mordanted in iron alum.

After the iron-hæmatoxylin process was completed some of the sections were mounted without further treatment; others were counter-stained with anilin blue, with orange green, or with a mixture of the two; with eosin, or with light green, or with erythrosin and light green.

Other sections, not treated by the iron-hæmatoxylin process, were stained with erythrosin and light green, with Mallory's connective-tissue stain, with safranin and light green.

Special sections were selected for treatment with the various elastic-tissue stains, and others, for the demonstration of mitochondria, by Meves' and Benda's methods.

Description.

In the course of the observations upon the growth of the ovarian follicles of the ferret and other phenomena associated with the development of the ova of ferrets certain points have been noted which have little or no direct bearing upon the question at present under consideration; they are perhaps not of sufficient importance to justify a separate communication, but they have a certain amount of morphological or histological interest, and to these points attention will be directed, incidentally, in the course of the description.

The Ovaries.

The ovaries of ferrets are of irregular ovoid form, the cranio-caudal length always exceeding the dorso-ventral and the side-to-side measurements, and, as a rule, but not always, the dorso-ventral diameter exceeds the side-to-side measurement.

The size of the ovary naturally varies at different periods; it is smallest in the anœstrus period, and largest about the middle of pregnancy; the average size, measured upon 366 ovaries taken from 183 animals killed between the early part of November and the middle of July, measured, after fixation and hardening, and stated in cubic millimetres, was 30·095996866 mm.^{3}, the smallest ovary of the anœstrus period being 9 mm.^{3}, and the largest 44 mm.^{3} There is some relationship between the weight of the animal and the size of the ovary, but it is by no means constant, and the smallest ovary, 9 mm.^{3}, was obtained from an animal which weighed 19 ounces, whilst ovaries of double that size were obtained from animals weighing only 16 ounces.

The average size of twenty ovaries, taken from ten anœstrus ferrets, killed in November, December, and January, was 20·238 mm.^{3}, and the size of the largest ovary taken from a pregnant animal was 66·87 mm.^{3}; it may be assumed, therefore, that the ovary may increase to at least three times its average anœstrus size during pregnancy.

The ovaries of the left side are as a whole larger than those of the right side, the average size of the ovaries of the 183 animals before mentioned being 28·626 mm.^{3}, the average size of the left ovaries was 31·565 mm.^{3} The point is of no particular importance, but it is noticeable in association with the disappearance of the right ovary in birds, the greater size of the left ovary of monotremes, and the tendency, which is so constant in mammals, for the persistence of the left of any two organs which are formed bilaterally during embryonic life, and of which one disappears during development, the ventral rudiments of the pancreas being an exception. It must be noted, however, that in ferrets, in a proportion of cases which constitute somewhat less than a third of the whole, the right ovary is larger than the left. The difference is not due to the fixative and hardening processes, for though, in the majority of the cases, the ovaries of opposite sides were fixed in different fluids, the proportion of right and left ovaries fixed in similar fluids was about the same.

Structure.

The cortex and the medulla of the ovary of the ferret are very sharply defined (fig. 61, Pl. X). The medulla is reticular in character, and it is continuous with the extra-peritoneal connective tissue at the hilum of the ovary. Through it pass numerous blood and lymph vessels, and in it lie cords of interstitial cells which are connected with the interstitial substance of the cortex, and two sets of tubules. The tubules of one group, which are irregular in number and size, are similar to the occasional tubules which are met with in the cortex (fig. 63, Pl. X). The other set, consisting of tubules which are of smaller size, lie near the hilum, and are continuous, through it, with the tubules of the epovarium, which lies in the mesentery of the uterine cornu. The latter are similar, in all essential respects, to the tubules described by WINIWARTER (43) in the cat.

The cortex is surrounded by the so-called germinal epithelium, internal to which is a definite tunica albuginea. The tunica albuginea consists of spindle-shaped cells, and of fibrils which run, for the most part, parallel with the surface of the ovary, but which bend inwards, at intervals, to become continuous with strands of spindle-shaped cells which pass through the cortex from the tunica albuginea to the medulla, with both of which they are continuous. Most of the primitive ovarian follicles lie in the spindle-cell strands of the cortex, which are particularly numerous near the hilum of the ovary, but some are found also in the tunica albuginea (fig. 3, Pl. I).

The main mass of the cortex consists of interstitial cells, which are divided into columns and nests by lamellæ of spindle cells (figs. 61, 63, Pl. X).

The interstitial cells vary considerably in size, but they all possess the typical polygonal body and the large round nucleus.

The blood and lymph vessels of the cortex lie either in the tunica albuginea or in the spindle-cell strands, into which they penetrate after passing through the medulla of the ovary.

THE OVARIAN FOLLICLES.

When the primitive ovarian follicles are first recognisable, as such, in the adult ovary, each follicle consists of an ovum, surrounded by a single layer of flattened cells, which constitute the primitive capsule, and which are the progenitors of the follicular epithelium.

The ovum is spherical or ovoid; its nucleus is large, round, and excentric; it always contains one large spherical nucleolus; and sometimes, though rarely, two nucleoli are present. In the portion of the ovum not occupied by the nucleus there are numerous granules of varying shape, size, and chemical constitution (figs. 4, 4A, 5, Pl. I). The granules are especially numerous at the pole opposite to the nucleus, where they form the vitellogenous crescent of VAN DER STRICHT (40), in which a centrosome is not uncommonly visible (fig. 4, Pl. I). I propose to deal with the structure of the ova in another communication, and therefore content myself with the remark that so far as the ova of the primitive follicles are concerned they correspond, generally, with the primitive ova of the cat, as described by VAN DER STRICHT (39A).

The cells of the capsule are flattened plates, and they are not distinguishable from the cells of the stroma amidst which they lie, except by their position, their arrangement, and by the fact that they stain less vigorously.

As the follicles grow the follicle cells increase in number, and they gradually attain first a cubical and then a columnar form, whilst their nuclei become fairly spherical. At this period, when the follicle cells are seen in surface view, or in sections at right angles to their long axes, the cell bodies are polygonal, and neither in surface views nor in sections, which are either longitudinal or transverse, is there any definite indication of the presence of limiting membranes round the cell bodies; indeed, in many cases the cell bodies appear to be fused to a greater or less extent into a nucleated synctium.

It is difficult to say whether the increase of the number of the follicle cells, in the early stages, is due to mitotic or to amitotic division, and, as a matter of fact, although I have examined many thousands of primitive follicles, I have never seen any clear indications of mitotic division of the young follicle cells, although mitotic divisions were numerous in larger follicles of the same ovary. Neither, on the other hand, have I been able to convince myself that the increase is due to amitosis, though such indications as are present are more in favour of amitosis than of mitosis.

The primitive follicles, as already stated, lie occasionally in the tunica albuginea, but the majority are in the spindle strands which intervene between the columns and nests of interstitial cells, and neither the older nor the younger follicles are always the more superficially placed, for not uncommonly a follicle, in which the follicular cells have attained a columnar form, lies quite close to the tunica albuginea, whilst follicles which are still quite primitive are situated much more deeply. In some places and at certain times the primitive follicles are so numerous that they form definite nests, and this is most commonly the case in the neighbourhood of the hilum. In such nests two adjacent ova may be separated by only a single layer of follicle cells (fig. 4, Pl. I), but as a rule each ovum has its own capsule of flattened cells.

When the follicles have attained a size of ·0009 mm.^{3} the nuclei of the follicular epithelium begin to arrange themselves in two layers—an internal, adjacent to the oolemma of the ovum, and an external, next the external limiting membrane; and whenever the cell territories, associated with each nucleus, can be distinguished, at this stage, they extend from the oolemma to the external limiting membrane. At this period the majority of the follicles are distinctly ovoid in form, and the multiplication of the nuclei is most rapid at the poles of the follicles (figs. 9, 10, 11, Pl. II). This condition persists until some time after the follicles become vesicular, then, as the follicles are distended by the accumulation of the liquor folliculi in their cavities, they become more spherical, but are never completely spherical. As the antrum folliculi grows the rapidity of the multiplication of the nuclei of the follicular epithelium increases, and it is most rapid in the region of the ovular cumulus; simultaneously the outlines of the follicle cells become more distinctly defined, and the nucleus of the ovum migrates to a peripheral position (fig. 16, Pl. III; figs. 40, 41, 42, Pl. VII).

Antrum Folliculi and Primary Liquor Folliculi.

The majority of the follicles begin to become vesicular as soon as the nuclei of the follicular epithelium are arranged in three layers in the greater part of the area of the follicle, and, as a rule, the first indications of cavity formation take place at the poles of the follicles (figs. 10, 11, 12, Pl. II).

The first indications of the formation of the cavity of a follicle are the appearance of numerous small independent spaces at one or other, or both, poles of the follicle. Presumably the spaces are formed by the accumulation of a more fluid substance between the cell territories; at all events the spaces are separated from one another by strands of protoplasm which are continuous with the protoplasmic substance around the adjacent nuclei. As the fluid-filled spaces distend the protoplasmic strands between them become reduced to extreme tenuity; but, even when the follicle has attained the full growth of which it is capable before insemination, and its cavity is fully distended, it is obvious, when the fixation and staining have been successful, that the so-called liquor folliculi is in reality a fluid-filled meshwork (fig. 13, Pl. II; fig. 14, Pl. III). The extremely fine strands of the reticulum anastomose freely with one another, and they are connected on the one hand with the cells of the ovular cumulus, and on the other with the follicle cells which form, together with the cumulus cells, the peripheral wall of the cavity of the follicle. As the term liquor folliculi is established, and as the fluid part of the content of the cavity is undoubtedly preponderant, I propose to call this first formed, fluid-filled, meshwork the *primary liquor folliculi*, for, as I shall show later, a secondary and a tertiary content of the cavity can be distinguished, each of which has its distinctive characteristics.

The ovarian cumulus, as is well known, is the mass of cells in which the ovum is embedded. The greater part of it projects into the cavity of the follicle, and the remainder, which forms the base of the cumulus, is directly continuous, either over a broad area or by means of a relatively narrow stalk, with the lining follicular cells.

In ferrets and ferret-polcat hybrids the ovular cumulus is generally situated in the deeper part of the follicle, that is, the part furthest away from the surface of the ovary, but in some cases it lies at the most superficial part of the follicle.

As the cavity of the follicle attains its full growth a membrane, which may be called the *membrana limitans interna*, is formed on the inner surface of the follicular epithelium and on the projecting part of the cumulus. It consists, mainly, of a condensation of the stroma of the primary liquor folliculi, and in it are incorporated the remnants of degenerated follicle cells (fig. 17, Pl. III; figs. 52, 55, 57, Pl. IX).

In the earlier stages of its formation the membrana interna is continuous, towards the interior of the cavity, with the stroma of the primary liquor folliculi, and, externally, it is connected with protoplasmic processes of the more internal follicle and cumulus cells.

As the membrana limitans interna forms, the stroma of the more central part of the primary liquor folliculi is broken up into a granular detritus, and, under the influence of some of the fixative fluids, especially Zenker's fluid, the remnants of the stroma and the fluid in which it lies tend to form a granular coagulum. In some cases the more solid part of the coagulum separates from the more fluid part without any disturbance of the connection of the membrana interna with the follicle and cumulus cells, but in other cases, as the coagulum shrinks the membrana interna is torn away from its peripheral attachments, and always more from the follicle than from the cumulus cells. It is probable that the shrinkage of the coagulum and the attendant displacement of the membrana interna are not normal processes but are due entirely to the reagents used, but I can offer no direct proof in support of this supposition.

At an early stage in the growth of the follicle an external limiting membrane, the "basal membrane" of many investigators, appears at the outer periphery of the follicular epithelium; it is quite distinct when the follicular epithelium consists of a single layer of more or less well-defined cubical cells, and it persists until shortly before the rupture of the follicle, when it is broken up by the penetration of blood-vessels into the follicular epithelium (figs. 49, 50, Pl. VIII).

As the follicle reaches the full growth which it is capable of attaining, independently of insemination, a growth which may, for convenience, be termed the *pre-inseminal growth*, the outlines of the follicle cells, which were more or less indefinite in the early stages, become more distinctly defined. At this stage the outermost cells of the general epithelial lining and the cells adjacent to the oolemma in the cumulus are columnar, conical, or spindle shaped (figs. 52, 54, 55, 56, 57, Pl. IX; figs. 58, 60, Pl. X; fig. 53, Pl. IX; fig. 16, Pl. III). The outer ends of the follicular epithelium cells, which are always the more distinctly defined, are attached to the external limiting membrane, and the inner ends blend with processes of the more internal cells, which assume stellate and irregular outlines, to form a cellular reticulum. It is to the inner portion of this cellular reticulum that the internal limiting membrane is attached.

The only further change of importance which takes place, in the follicular epithelium, during the pre-inseminal growth of the follicle, and which occurs as the growth is completed, is the separation of the cumulus cells into an ovular layer next the oolemma, and a more external layer next the cavity of the follicle and the base of the cumulus, by the appearance of fluid-filled spaces between the two groups of the cumulus cells (fig. 16, Pl. III; fig. 53, Pl. IX). The appearance produced in the cumulus by these changes is not dissimilar to that seen during the formation of the primary liquor folliculi, but there are differences of importance. During the formation of the primary liquor folliculi the spaces which appear amidst the follicular cells are separated from one another, from the first, by thin strands of protoplasmic substance, which become finer and finer as the cavity of the follicle enlarges. The spaces which appear in the midst of the cumulus cells, and which contain the fluid part of a new fluid, the *secondary liquor folliculi*, have at first a very similar appearance to those associated with the formation of the primary liquor folliculi, and they are similarly separated by fine strands of protoplasmic substance, but the protoplasmic strands are more granular and less filamentous than those of the primary liquor folliculi; moreover, as the cells of the basal part of the cumulus are pushed apart by the increasing fluid, masses of granular substance are formed which are not seen during the formation of the primary liquor. These masses are devoid of nuclei, they are surrounded by groups of fluid-filled spaces, and they are connected with the protoplasm of the adjacent cells by granular protoplasmic strands (fig. 40, Pl. VII; fig. 48, Pl. VIII). The mode of formation of the protoplasmic masses is uncertain; they must be evolved from the protoplasm of the cumulus cells, but there is no evidence of the breaking down of cells, and no evidence of the migration of nuclei from the masses to adjacent parts. Eventually, after insemination, the protoplasmic masses break down and disappear. Another difference between the primary and the secondary liquor folliculi is, that the secondary liquor does not coagulate and shrink under the influence of certain fixatives as the primary liquor does in the later stages of the growth of the follicle.

The Sheaths of the Follicles.

It is customary to state that each fully developed ovarian follicle is surrounded by two sheaths, the theca interna and the theca externa. The theca interna, which lies immediately outside the external limiting membrane, is said to consist of a somewhat loose cellular stroma interspersed with blood-vessels and with plasma cells, which, apparently, is the name applied by some authors to what are undoubtedly interstitial cells. The theca externa is described as being denser, more fibrillated, and less vascular than the theca interna, and as containing few or no interstitial cells.

In the ferret the stroma surrounding follicles, which have attained their full pre-inseminal growth, is sometimes arranged in the so-called typical manner; more commonly, however, the circumfollicular stroma is not clearly separated into an inner and an outer theca. It is a fibro-cellular layer of very varying thickness, in which the cells and fibrils run parallel with the external surface of the follicular epithelium, and in which are embedded small clumps of interstitial cells (fig. 49, Pl. VIII). It differs from the other parts of the cortex only because the fibrillar tissue is more marked, the interstitial cells are less numerous, and as the follicle attains its full pre-inseminal size the small blood-vessels in the immediate neighbourhood of the external limiting membrane of the follicle become so numerous that they constitute a definite vascular layer (figs. 19, 20, Pl. III; fig. 24, Pl. IV; fig. 48, Pl. VIII; figs. 54, 57, Pl. IX; figs. 59, 60, Pl. X).

The Sizes of Full-grown Follicles of the Pre-inseminal Stages.

The sizes of the follicles in the pre-inseminal stages are of interest in connection with the changes which occur after insemination. They have been estimated by taking the largest follicles in each ovary of the various groups. In the accompanying tables the sizes of the follicles are given, and the number of the follicles of the largest size are stated. In that number are included follicles which were slightly smaller than the largest, but the smaller follicles of the group differed only by a few microns from the larger in one or more of the three diameters. The condition of the largest follicles, whether normal or degenerate, is noted in the tables.

It will be seen that the follicles differ considerably in size in different ovaries, and that the difference is independent of the size of the animal, as judged by its weight.

The average size of the largest follicles in 35 ovaries taken from 16 animals in the anœstrus period (Table I) is ·0404 mm.^{3}, the smallest follicle being ·0025 mm.^{3}, and the largest ·1561 mm.^{3} If the anœstrus series of largest follicles is broken up into two groups, one consisting of the largest follicles in the ovaries of animals killed between 11th November and 9th December of the following year, and a second group consisting of the largest follicles in animals killed between 5th February and 6th May, it is found that the average size of the largest follicles of the first group is ·0049 mm.^{3}, and the average size of the largest follicles of the second group is ·0598 mm.^{3}

The average size of the largest follicles in the ovaries in animals in heat, and in which no attempt at insemination was made (Table III), is ·3215 mm.^{3}, and if to this group are added the follicles of two animals which were in heat after parturition (Table IV), the average size of the œstrus follicles is increased to ·3627 mm.^{3}

The average size of the largest follicles in the ovaries taken from 13 animals in full œstrus in which insemination was attempted, but unsuccessfully (Table V), is ·9567 mm.^{3}; and the average in the group of ovaries taken from animals in the post-partum or post-abortion condition, and which were not in heat, is ·2830 mm.^{3}

The most important changes in the constituents of the follicles during the pre-inseminal period are increase in size of the ovum and alterations in its constitution, especially associated with the accumulation of lipoid substances; increase of the thickness of the oolemma; and the migration of the nucleus to the periphery of the ovum, where it lies in close apposition with the oolemma.

It has already been noticed that during the same period the outlines of the follicle cells become gradually more distinct; other changes which occur in the follicle cells, including changes of structure and alterations in the positions of the nuclei, will be dealt with more fully in a subsequent section.

The Post-inseminal Growth and the Rupture of the Follicles.

After insemination the most obvious changes occur in the region of the ovarian cumulus. So far as the ovum is concerned the essential changes are the formation of the first maturation spindle, followed by the formation of the first polar body and the second maturation spindle. These changes only occur, normally, after insemination; they may occur, however, in ova in the follicles of non-inseminated animals, but only occasionally, and then always accompanied by other phenomena which indicate abnormal conditions.

The most striking changes, independently of the maturation phenomena in the ovum, are those which take place in and amidst the cumulus epithelium.

About eighteen hours after insemination, or later, the secondary liquor folliculi, which had already appeared in small amount in the later period of pre-inseminal growth, increases rapidly. As the secondary liquor folliculi is augmented the peripheral cells of the projecting part of the cumulus and the more internal cells of the basal portion are dispersed in all directions (figs. 17, 18, 19, 20, Pl. III; figs. 21, 22, 23, 24, Pl. IV). The nuclei of the dispersed cells show indications of degeneration, the protoplasmic processes by which the cells were connected are destroyed, and many of the cells break down and disappear. At the same time the periovular cells of the cumulus are transformed into a very beautiful corona radiata. As the corona radiata is developed all the periovular cells become club-shaped. The thin ovular ends of the cells remain connected with the oolemma, and the nuclei migrate to the enlarged peripheral ends of the cells (figs. 41, 42, 43, 44, Pl. VII; fig. 45, Pl. VIII).

By the continued increase of the secondary liquor folliculi the membrana interna is separated from the follicular cells. Sometimes this separation is complete, but in the majority of cases it is, probably, only partial. When the cumulus is situated at the superficial part of the follicle the membrana interna, as it is stripped from the follicular epithelium, is simply pushed towards the deeper part of the follicle (fig. 22, Pl. IV), but when the cumulus lies in the deeper part of the follicle, the secondary liquor folliculi pushes its way between the separated membrana interna and the follicular epithelium till it reaches the superficial part of the follicle (figs. 18, 19, 20, Pl. III; figs. 21, 23, 24, 25, Pl. IV). In the meantime the superficial part of the wall of the follicle becomes thinner and thinner as the distension of the follicle proceeds, and ultimately it ruptures at the most projecting point.

The time which intervenes between insemination and rupture of the follicles varies considerably; the shortest time in my series of animals was $30\frac{1}{2}$ hours, and in one, an animal killed $93\frac{1}{2}$ hours after insemination, rupture had not yet occurred (9 and 10, Table IX).

When rupture takes place the ovum with its corona, the secondary liquor folliculi with the remnants of the dispersed cumulus epithelium, and the primary liquor folliculi with the greater part of the membrana interna, are evacuated, and they are carried, apparently at once, into the cranial part of the middle third of the oviduct. I have found four extruded ova in the space between the ovarian capsule and the ovary, and one escaping through the opening from the interior of the capsule into the peritoneum (fig. 2, Pl. I; fig. 46, Pl. VIII), but all the others, which were still unfertilised, or which were in the earliest stages after fertilisation, were in the cranial part of the middle third of the oviduct, where fertilisation usually occurs. None of the ova which were in the cavity of the ovarian capsule were fertilised, and I have never found spermatozoa beyond the cranial part of the middle third of the oviduct.

Not uncommonly, as in the case of the ovum shown escaping into the peritoneal cavity (fig. 2, Pl. I; figs. 46, 47, Pl. VIII), the extruded ovum and its corona become enveloped by portions of the liquor folliculi, which, judging from its reactions to stains, and from the fact that parts of the membrana interna are associated with it, is the primary liquor; but quite as frequently the ovum and its corona are accompanied and surrounded by numerous cells, which are, apparently, those which were adjacent to it in the cumulus. In other cases the ovum and its corona lie quite free in the fluid in the oviduct. The differences appear to be due to the amount and the character of the dispersion of the cumulus cells which takes place after insemination. In all cases some of the cumulus cells remain attached for a time to the corona cells by fine protoplasmic filaments. In many cases the membrana limitans interna is entirely displaced from the cumulus cells, but in others parts of the membrana interna remain attached to the cumulus cells, which are themselves connected with the corona cells.

When rupture occurs and the cavity of the follicle is evacuated the walls of the follicle contract and fold (fig. 26, Pl. IV; figs. 27, 28, 30, Pl. V), but, as a rule, a considerable part of the cavity of the follicle remains, and only occasionally is it almost entirely obliterated, as in the follicle shown in fig. 29, Pl. V. The differences appear to be associated with the extent to which the membrana limitans interna is detached from the follicular epithelium by the secondary liquor folliculi. If the separation is complete, as in the specimen shown in fig. 24, Pl. IV, all the contents are evacuated and the cavity almost entirely disappears; but if part of the membrana interna retains its connection with the follicular epithelium until the time of rupture—and this is usually the case—then when the rupture takes place this still attached portion of the membrana interna is forced from its anchorage, and, as it is extruded, it carries with it long filamentous processes of the follicular cells, which frequently drag with them some of the more internal follicular cells; these processes and cells, together with a rapidly exuded fluid which forms a granular coagulum under the action of the fixative reagents, and with which white blood corpuscles are intermingled, constitutes a *tertiary liquor folliculi* (figs. 26, 26A, Pl. IV; figs. 27, 27B, 27C, Pl. V).

For some time after its formation the tertiary liquor folliculi forms an adhesive tenacious coagulum which fills that part of the cavity of the follicle which remains after the rupture has taken place; it also plugs the aperture of rupture, and extends beyond it into the cavity of the ovarian capsule, its terminal portion always inclining towards the orifice of the oviduct (figs. 27, 27A, Pl. V; figs. 31, 33, Pl. VI).

Immediately after the rupture the orifice of the follicle is comparatively large, but as the plug which occupies it shrinks, the opening gradually becomes smaller until it closes. The closure commences externally and terminates internally (see figs. 26, 26A, Pl. IV; figs. 27, 27A, 28, 30, Pl. V; figs. 31–33, 34–37, Pl. VI).

As the orifice in the wall of the follicle closes, the cavity in its anterior usually enlarges (figs. 32, 34, 35, Pl. VI), though exceptions are met with, as in the specimen shown in fig. 29, Pl. V. As the re-enlargement of the cavity proceeds the filamentous coagulum of the tertiary liquor folliculi breaks down into a granular detritus, in which the granules, which are at first relatively coarse, become finer as the fluid content of the redistending follicle increases (figs. 36, 37, 38, Pl. VI).

It has already been noted that vascularisation of the follicular epithelium commences before the rupture of the follicle occurs (figs. 49, 50, Pl. VIII). After the rupture has taken place the blood-vessels amidst the follicular epithelium cells increase in number, and they penetrate further towards the interior of the follicle, until in some cases they approach close to the inner surface of the follicular epithelium (fig. 28, Pl. V; figs. 32, 33, 33A, Pl. VI).

Bleeding into the cavity of the follicle does not occur at the time of rupture, and, in the majority of cases, no blood enters the cavity of the follicle at any period, but hæmorrhage occasionally takes place into the cavity of the follicle after the redistension is completed.

The redistended follicle, which is the rudiment of the corpus luteum, contains a cavity as large as that which was present before rupture. The cavity is filled with a fluid containing granules, which are the remnants of the filaments of the tertiary liquor folliculi, and amidst the granules there are, not uncommonly, a few white blood corpuscles and a few isolated follicle cells in a state of degeneration.

The Post-inseminal Growth of the Follicles.

It has been pointed out that the average size of the ovarian follicles of animals in full heat, in which no attempt at insemination was made, the first œstrus of the season, is ·3215 $mm.^3$, and that the average size of the largest follicles in animals in which insemination had been unsuccessfully attempted is ·9567 $mm.^3$

After insemination, on account of the rapid formation of the secondary liquor folliculi, the average size of the largest follicles increases to 1·7815 $mm.^3$, as estimated from the largest follicle of each of twenty ovaries (Tables VI–IX), the ova in the follicles being either in the first maturation spindle stage or in the first polar body stage of development; therefore in a period varying from 19 to 41 hours after insemination the follicles increase to over five times their original size.

After rupture, and before redistension, the average size of the largest follicles falls to ·7800 $mm.^3$, as measured in 14 ovaries in which rupture of the follicles had occurred, and in which it was noted that redistension had not recommenced (Tables VII–XII). Measurements made upon the largest follicles of 35 ovaries in which the follicles had ruptured, closed, and redistended give the average size of the redistended follicles as 1·9478 $mm.^3$—that is, somewhat larger than the average size of the ripe unruptured follicles.

The redistension of the ruptured follicles may commence 41 hours after insemination, but it may not have commenced 10 hours later. The redistension may be completed at any time between 61 and 120 hours after insemination.

Changes in the Follicular Epithelium during the Maturation and the Distension of the Follicles.

At all periods of the growth of the follicles the protoplasm of the follicle cells contains a considerable amount of substance which assumes a grey, or greyish-black, or bluish-black appearance when treated by iron-hæmatoxylin methods, and which stains a more or less definite violet under the influence of Benda's alizarine stain; presumably, therefore, it is of mitochondrial nature. This substance may be either in the form of granules or filaments, and the filaments may form a more or less definite reticulum.

In the primitive follicles, in which the follicular epithelium has the form of flattened curved plates, the mitochondrial substance is granular, the nuclei of the cells are ovoid: their chromatic substance is distributed throughout the bodies of the nuclei; it has the form of spheroids of varying size, of which one is usually somewhat larger than the others. The spheroids are scattered irregularly in the interior of the nuclei, but it is not possible to say that any definite nucleoli are present (figs. 4, 5, Pl. I).

When the follicle cells become cubical or columnar the granules of the cell protoplasm become collected into the form of granular filaments, and although the position of the filaments varies, they tend on the whole to lie parallel with the long axes of the cells (fig. 6, Pl. I). The nuclei of the cubical or columnar cells are spherical or slightly oval, and whilst the cells form only a single layer, the nuclei lie close to the external limiting membrane. When the nuclei form two rows, those of the inner row lie close to the oolemma, and those of the outer row close to the external limiting membrane (fig. 7, Pl. I; figs. 8, 10, 11, 12, Pl. II). The chromatin of the nuclei, as in the previous stage, is still in the form of spheroids, and it is not possible, except occasionally, to distinguish nucleoli. The tendency for the chromatic substance of the nuclei to form spheroidal masses of varying size continues throughout the whole period of the growth, rupture, and closure of the follicles in the nuclei which are in the resting condition, and, at any given moment, they form the majority of the nuclei. After the nuclei have increased considerably in number and are arranged in several layers it is possible to find here and there a nucleus which contains a definite nucleolus, but the appearance of a definite nucleolus in a follicle cell is uncommon, and in that respect the follicle nuclei differ markedly from the nuclei of the ova. The rarity of nucleoli in the nuclei of the follicle cells is as marked as the rarity of mitotic figures in any given section, and it is possible that the formation of a nucleolus is precedent to the commencement of mitotis, when the spheroidal masses of chromatin are transformed into short rods.

As the follicles increase in size the chondriosomes in all the cells, including those which have become stellate or irregular in shape, assume the form of granular rods or filaments (fig. 6, Pl. I; fig. 10, Pl. II; figs. 54, 57, Pl. IX; figs. 58, 59, 60, Pl. X), which appear as granules when cut at right angles to their long axes, and this condition is maintained until the follicle cells begin to assume luteal characters, a condition which may occur before, but which more usually does not take place until after the rupture and closure of the follicle. As the luteal condition is assumed, nucleoli become more and more a feature of the nuclei of the follicle cells.

During the whole period of the pre-inseminal growth of the follicle a layer of nuclei lies close to the external limiting membrane, and a similar layer lies close to the oolemma of the ovum (figs. 48, 49, Pl. VIII; fig. 40, Pl. VII; fig. 57, Pl. IX; fig. 16, Pl. III; fig. 53, Pl. IX); but as the pre-inseminal maturity of the follicle is attained, the number of nuclei which lie close to the external limiting membrane is gradually reduced, for the majority of the nuclei migrate towards the interior of the cavity (fig. 58, 60, Pl. X), though the external ends of the cells to which they belong still maintain their association with the external limiting membrane (figs. 58, 59, 60, Pl. X), and as the pre-inseminal maturity of the follicle approaches, granules of osmic-blackening fat appear in the bodies of the cells (fig. 51, Pl. VIII).

The appearance of spherules of fat in the follicle cells during the pre-inseminal maturation of the follicles is a constant and normal phenomenon, but the amount of fat which is deposited varies considerably in different follicles. The deposition of fat spherules in the follicle cells is also a constant phenomenon of the commencing degeneration of follicle cells; but when the deposition of fat takes place in commencing degeneration the spherules are always of larger size, more numerous in proportion to the size of the cell in which they are deposited, and they tend to fuse together to form globules of relatively large size, and under low magnification of osmic preparations the dense, black, degenerate follicular epithelium is easily distinguished from normal epithelium (compare the left and right follicles, fig. 39, Pl. VII).

After insemination no very definite changes beyond the nuclear migration occur in the general follicular cells, except in the region of the cumulus. There the dispersion of the follicle cell by the secondary liquor folliculi is a marked phenomenon, and the migration of the nuclei, which lay close to the oolemma, commences and proceeds regularly till the corona radiata is fully developed, when all the nuclei of the corona lie in the peripheral ends of the cells to which they belong (figs. 41, 42, 43, 44, Pl. VII). At the same time the corona cells become greatly, but unequally, elongated, with the result that the surface of the corona appears to be formed by a number of projecting spokes of different lengths, a condition which probably facilitates the effect of the rush of fluid which sweeps the ovum through the cavity of the ovarian capsule into the oviduct.

The chondriosomes of the corona epithelium are similar to those of the general follicle cells, that is, they are rods and filaments of varying size which lie parallel with the long axes of the cells, and, where the inner ends of the corona cells blend with the outer part of the oolemma, the chondriosomes appear to pass into the substance of the oolemma (fig. 43, Pl. VII; fig. 45, Pl. VIII).

Discussion.

Membrana limitans externa.

Unlike the membrana limitans interna, the external limiting membrane (fig. 52, Pl. IX; fig. 59, Pl. X) has received a large amount of attention. It seems to be universally present, for although Benckiser (3), Schottländer (36), and Sandes (35) say that it is absent in the pig, Monterosso (27) figures and describes ovarian follicles of that animal, and says that "Tra la membrana basilare o propria folliculi e la theca interna è interposto uno strato quasi continuo di cellule grandi," a statement which indicates that interstitial cells are present in the pig, and which is not in accord with Frankel's account of the ovaries of the pig.

Whilst the presence of the external limiting membrane is well known, there is difference of opinion regarding its constitution. Wagener (41), Schottländer (36), and Limon (18) look upon it as a connective tissue structure, though they differ in details as to the mode of its formation; whilst WALDEYER (42) and NAGEL (28) believe that it is formed by the follicle cells, and NAGEL says that it is structureless, non-nucleated, and is similar at first to the oolemma.

In the ferret its reaction to stains is not the same as the reaction of the oolemma, and when the follicular epithelium is detached from the internal theca by the action of the fixative reagents, the membrana external separates into two layers (figs. 58, 60, Pl. X). The inner of the two layers is connected with the outer ends of the follicle cells, and is possibly formed by them, in the same way that the external limiting membrane of the central nervous system is formed by the outer ends of the neuroglial cells. The outer layer is connected with the innermost flattened cells of the internal theca, and it reacts like other connective-tissue structures to connective-tissue stains.

The external limiting membrane is present at a very early stage of the life-history of the follicle, being formed when the follicular epithelium is a single layer of cubical cells. Its function is unknown, but its constant presence indicates utility, and it possibly regulates the passage of different materials in opposite directions to and from the follicle.

Membrana limitans interna.

So far as I am aware, the only observers who have noted the presence of an internal limiting membrane in ovarian follicles are BOUIN and ANCEL (4), who describe it as occurring in the ovarian follicles of the bitch. One of LONGLEY'S figures of part of an ovarian follicle of a cat (20) suggests that it is present in that animal also, and one of RUSSO'S photographs (34) indicates that it may be present in the mature follicles of the rabbit.

According to BOUIN and ANCEL'S account of the internal limiting membrane in the bitch, it is formed, in that animal, by the flattening out of the internal cells of the granulosa, which are transformed into a series of closely applied lamellæ. They also state that when it is definitely established it reacts to stains in the same manner as the external limiting membrane, and they conclude, therefore, that some external membranes may also be of epithelial origin. They do not discuss the function of the internal membrane, but they say that as the corpus luteum is formed the internal membrane becomes delaminated, and its various laminæ constitute a more or less dense feltwork in the interior of the cavity of the corpus luteum, "*tout à fait semblable à des fibres conjonctives enlacées.*" If the membrane which BOUIN and ANCEL describe in the bitch is formed and reacts to stains as they say, and if it takes part in the fibrillar network which afterwards appears in the interior of the corpus luteum, it is quite a different structure from that which I have noted in ferrets. In the latter animals the membrana interna does not react to stains in the same way as the membrana externa, and it never presents the vitreous appearance which is so distinctive of the external membrane; moreover, it takes no part in the formation of the reticulum which appears in the interior of the corpus luteum; on the contrary, it is ejected from the follicle at the time of rupture. Before it is ejected the greater part is separated from its connections with the follicular epithelium by the formation and extension of the secondary liquor folliculi, and when the part which is not so displaced is forced out at the rupture of the follicle, it carries with it filamentous processes of the bodies of the follicle cells, and sometimes also strands of displaced cells, which take part in the formation of the tertiary liquor folliculi which fills the remnant of the cavity of the ruptured follicle.

As to the function of the membrane little can be said, because there is no definite evidence, but it is possible that it may serve to regulate the constituents of the substances which pass into the antrum to form the fluid portion of the primary liquor folliculi.

Antrum folliculi and Primary liquor folliculi.

There has been considerable discussion as to the mode of formation of the antrum and the primary liquor folliculi, and there is a fairly general agreement that part of the fluid which appears is derived, either by osmosis or by secretion, through the follicle cells from the contents of the blood-vessels of the internal theca, but as to whether the fluid which appears, and by its appearance produces the beginnings of the antrum, is at first inter- or intracellular there is difference of opinion, and there is also difference of opinion as to whether or not the dissolution of the follicle cells plays a considerable part in the formation of the fluid. Amongst those who hold that the breaking down of the follicle cells plays an important part in the formation of the fluid are ALEXANDO (1), JANOSIK (14), SCHOTTLÄNDER (36), NAGEL (28), VAN DER STRICHT (40), and SANDES (35), whilst HONORÉ (13) holds that it is an intercellular secretion, and he shows that the so-called bodies of CALL and EXNER are not, as JANOSIK thought, vacuoles in cells but, in reality, intercellular spaces. My own observations entirely support HONORÉ's point of view, and I believe, moreover, that the central parts of the bodies are merely isolated portions of the general antrum. The point is one upon which it is difficult to form a positive opinion, and indeed it can scarcely be definitely settled until some improved methods of differential staining are evolved, for the photographs given by VAN DER STRICHT of the bats' ovaries, and those which SANDES gives of the ovaries of *Dasyurus viverrinus*, which are supposed to demonstrate the breaking down of follicle cells, can be equally well used to support an opposite opinion. The phenomena met with in the ferret, under the methods of preparation which I have adopted, indicate an inter- rather than an intracellular origin of the fluid portion of the primary liquor. The matter is of importance in association with the real nature of the primary liquor; for if it is formed by the dissolution of the follicle cells, it is primarily a fluid in which may be found here and there the remnants of destroyed cells; but if, as appears to be the case in the ferret, it is formed by an intercellular secretion which forces apart the bodies of the cells and extends their substance into long intercommunicating filamentous processes, then the primary liquor folliculi is primarily a reticulum filled with fluid secreted by the cells, and it bears, therefore, a close structural resemblance to the primitive vitreous body of the eyeball. That such a reticulum is formed in the ferret is obvious, and I am inclined to think, judging from the photographs of VAN DER STRICHT (40) and SANDES (35), that it may be found in bats and Dasyurus; but my specimens of ovaries of dogs, cats, rabbits, guinea-pigs, mice, and rats, though prepared in the same manner as those of ferrets' ovaries, do not show the reticulum in the same clear manner, and I am inclined to believe, therefore, that modifications of the process found in ferrets may be present in other animals.

Secondary liquor folliculi.

So far as I am aware, no one has drawn attention to the formation of the secondary liquor folliculi in ovarian follicles. There is no doubt in the case of the ferret that it is present, that it is formed more rapidly, and that it is of more fluid consistence than the primary liquor, and that it takes part in the final distension of the follicle which precedes the rupture. But although the formation of the secondary liquor appears to have escaped the attention of observers who have paid special attention to the development of ovarian follicles, some of the figures they have given to illustrate other points of follicular development indicate that the secondary liquor is formed in the ovarian follicles of other animals besides the ferret. Thus the figure which LONGLEY (20) gives to illustrate the conditions of the cumulus region of a normal follicle of the cat, just before rupture, depicts essentially the same details as are shown in follicles of the ferret at the same stage of development, and which are represented in the photographs which constitute figs. 18 and 20, Pl. III. Further, RUSSO's photograph (fig. 6, pl. xxxiv) suggests that something of the same kind takes place at all events in some ovarian follicles of rabbits. Indeed, unless the process is one of fairly common occurrence it is difficult to account for the extrusion of the ovum and its corona from follicles, such as those of the human female, the sheep, the bat, and *Dasyurus viverrinus*, in which the cumulus oophorus is merely a more or less prominent rounded elevation of the general follicular epithelium; for there seems to be no reason why the evacuation of the primary liquor, which does not disturb anything more than the superficial part of the stratum granulosum, should break up and displace the somewhat dense mass of cells which forms the primitive cumulus, though it might readily break down the retinaculæ which maintain the cumulus in position in some of the follicles of rabbits and some other rodents.

The Growth of Ovarian Follicles.

For many years after PFLUGER's descriptions of the tubes and nests of cells, which are present in the ovaries of the female embryos of all mammals, became generally known, it was presumed that the ova and the follicle cells which surrounded them were the cells of the tubes and nests, gradually isolated into follicles by the interposition of stroma cells. Further, it was asserted, and generally believed, that all the ova which come to maturity were formed in the ovary during the embryonic period; elaborate calculations of their numbers were made, and the results are still at times quoted.

After "germ cells" were discovered, and their migrations from their seats of origin to the ovary were traced, the assumption previously adopted was modified, and it became usual to accept the "germ cells" as the progenitors of the ova, whilst the follicle cells were considered to be the descendants of the germinal epithelium which covers the surface of the ovary. Definite proof that ova are derived from "germ cells" in mammals has never been produced, but the suggestion was enticing, and it received ready acceptance, although it was unaccompanied by any explanation of the reason why of all the ova and follicles, formed at approximately the same time, some proceeded to further growth and development at relatively long periods, in some cases years, before the others, whilst all were presumably subjected to the same influences at all periods.

In 1905 Miss LANE-CLAYPON (16) made a series of observations, on the ovaries of rabbits, which led her to propound the conclusion that the ova, the follicle cells, and the interstitial cells of the ovary are all formed by the germinal epithelium, and that the interstitial cells are potential ova. Her general conclusions have not been confirmed by other observers, but it has become increasingly evident from the researches of WINIWARTER and SAINMONT on the cat (43), RUBASCHKIN on the guinea-pig (33), and KINGERY (15) on the white mouse, that the ova formed by the early embryonic proliferation, whether they are descendants of the germinal epithelium cells or of special germ cells, are not those which attain to maturity and become the rudiments of a new generation of animals, for they all die before they have attained any advanced stage of development, and many of them before they become enclosed in follicles.

According to RUBASCHKIN (33), the ova which attain to maturity are formed by a proliferation of the cells of the germinal epithelium which takes place before birth, but which is, at all events, a third and not a first generation; whilst WINIWARTER and SAINMONT (43) found, in the cat, that the ova which reach maturity are formed by a proliferation of cells, starting from the germinal epithelium and taking place from three and a half to four months after birth. If this is the case, explanation is still wanting as to why certain numbers of the follicles and their contained ova mature for each ovulation period; for all being formed at the same time are of the same age, are situated in practically similar situations, and are subjected to the same influences which bring about the maturation of only a small number at any given ovulation period.

It seems improbable that of a large number of ova and follicles formed at the same time only a few shall attain maturity at an early epoch, whilst the majority remain quiescent for relatively long periods, in some animals for years, when, throughout the whole period, all are under the influence of exactly similar conditions.

In the course of my investigations into the history of the follicles in the ferret I have noted a number of facts, which I hope to publish as soon as photographs of the specimens can be made, which are entirely opposed to the idea that the ova and follicles which become mature at different periods are all formed at one period of proliferation of the germinal epithelium; and, although the work is not yet completed, I may state here that the results so far obtained not only confirm in all essential respects those arrived at by KINGERY during his investigations on the development of ova in the white mouse, *i.e.* "that the new formation of germ cells from the germinal epithelium is prolonged and extends from birth or shortly afterwards to approximately sexual maturity," but that they lead me to the conclusion that new groups of ova and follicle cells are formed throughout the whole period of the functional life of the ovary.

My observations do not extend over the period from the beginning of August to the end of October; but during the remaining period of the year, that is, from the early part of November to the end of July, it may be said, speaking generally, that in ferrets and ferret-polecat hybrids the growth and death of groups of ovarian follicles proceeds continuously, and that it is not interfered with by pregnancy, but the statement, though it is true in its broad outlines, requires qualifications.

In the first place, if the corpora lutea are numerous and large they may occupy practically the whole of the cortex; stroma, interstitial tissue, and follicles being reduced to a minimum. In these cases the follicles which are present, normal and degenerate, are either quite primitive or but slightly advanced beyond that condition, and it is probable that it is in cases of this kind that the animal has no second œstrus period during the breeding season; this, however, is merely a supposition, and it is not supported by the material at my disposal, for five post-partum animals bearing upon the point of which I have definite notes give the following results:—

F.D. X/16 (Table II). 11 days post-partum. Cast 7 young on 29th May. All young dead on 1st June. Killed 10th June, when showing slight signs of pro-œstrum. Corpora lutea corresponding with last pregnancy, 10 in one ovary and 6 in the other ovary. Both ovaries contained follicles of full pre-inseminal growth.

P.D.A. 40/15 (Table IV). Cast 8 young on 8th May. In full heat 27th May. Killed 1st June. Corpora lutea corresponding with last pregnancy, 8 in one and 4 in the other ovary. Both ovaries contained follicles of full pre-inseminal growth.

F.D. Z^2/16 (Table II). Cast 7 young on 6th May, and ate them all the same day. Was not in heat when killed on 2nd July. Corpora lutea corresponding with previous pregnancy, 8 in one and 4 in the other ovary. No follicles of full growth in either ovary.

D.A. 42/15 (Table II). Cast 11 young on 11th May, and was not in heat when killed on 8th June. Corpora lutea corresponding with last pregnancy, 3 in one and 5 in the other ovary. Both ovaries contained follicles of full pre-inseminal growth, and the animal would probably have shown signs of the pro-œstrum in a few days.

F.D.A. 45/15 (Table IV). Cast 8 young on 21st May, which were all dead the next day. In full heat on 7th June. Killed 2nd July. Corpora lutea corresponding with the previous pregnancy, 10 in one and 8 in the other ovary. Both ovaries contained follicles of full pre-inseminal growth.

The ovaries of all five animals contained a considerable amount of cortical tissue not encroached upon by the degenerating corpora lutea.

In spite of these apparently adverse facts a survey of the ovaries of all the animals at my disposal shows that the sizes of the corpora lutea vary greatly both in the same and in different animals. They also show that although the space occupied by the corpora lutea is relatively large, a considerable portion of the cortical tissue remains in most cases as in the above mentioned for animals, and that it frequently contains follicles of considerable size, whilst in a certain number of cases, as already stated, the corpora lutea practically usurp the whole of the cortical area, and only a few very rudimentary follicles can be found. In these latter cases it seems impossible to believe that the cortex can be reconstituted and follicles developed in time for a second œstrus.

There are other factors, with which this inquiry is not concerned, which interfere with the occurrence of a second œstrus in one season, but the point already noted raises the question of the amount of time occupied by the follicle in passing from its initiation to its full pre-inseminal growth. The data at disposal cannot, of course, give a positive answer to the question, for it is not possible to follow the life-history of any given follicle, but they offer interesting suggestions.

Table I shows that the size of the largest follicles in the ovaries of anœstrus animals gradually rises from the middle of November to the early part of April, the breaks in the series being due in all probability to the fact that some of the animals were young adults born late in the previous season. It shows further that of the follicles of largest size, or about largest size, a considerable proportion are in a state of degeneration, and that that proportion is relatively the same throughout the whole period. Under these circumstances it seems scarcely possible to assume that the largest normal follicles of the earlier part of the period persist and become the largest normal follicles of the later part of the period; on the contrary, it seems more reasonable to suppose that all the largest follicles of the earlier part of the period die and are replaced by other follicles, which, as the œstrus period approaches, are able to attain a more advanced stage of development, until, finally, some attain to full pre-inseminal growth, but not to full pre-inseminal development. This supposition is supported by the specimen F.D.A. 45/15 (Table IV), which was killed on the thirtieth day of her second œstrus, for in her ovaries were not only follicles of full pre-inseminal growth-size, both normal and degenerate, but also follicles which had evidently attained that stage and had then undergone atrophy as well as other follicles of comparatively large size, apparently approaching to full growth.

After insemination and the rupture of the mature follicles, follicles of full post-inseminal and pre-ruptural growth-size are found in a certain number of ovaries; but such follicles always show definite signs of abnormal conditions, and though they may become luteal, they do not rupture (fig. 38, Pl. VI).

Follicles of full pre-inseminal growth-size are present in the ovaries of pregnant animals up to the twentieth day of pregnancy. From the twentieth to the thirtieth day no follicles of that size were found. They are present again at the thirty-sixth day, and in increasing numbers to the forty-second day, which is the termination of the full period. Among the largest follicles present at any given day of pregnancy, some are always normal and some degenerate. It appears, therefore, that throughout the whole period of pregnancy, growth and death of groups of follicles continues with a diminution of the largest size attainable during the middle of the period. But whilst the size of the largest follicles during the middle of the period of pregnancy is less than the size of the largest follicles in the early and late parts of that period, it is never so small as the size of the largest follicles of the early part of the anœstrus period. It is obvious, therefore, that the largest follicles present at the beginning of pregnancy all disappear by the middle of pregnancy, and that they are replaced by younger follicles; but there is no evidence to show which of the younger follicles, the primitive or those more advanced of the early period, become the largest follicles of the later period. The facts as they stand, however, lend basis to the assumption that a follicle takes at least half the time of the period of pregnancy, that is, twenty-one days, to pass from its primitive condition to the condition of full pre-inseminal growth.

The conditions met with in the ovaries of ferrets during the gestation period are similar in all essential respects to those described by Loeb (19, 19a) in guinea-pigs, and it is obvious that in both groups of animals corpora lutea, as such, have no detrimental effect on the growth of the follicles; but whilst they do not prevent the growth, they do, in the guinea-pig, prevent the ripening; for Loeb finds that when the corpora lutea are totally extirpated in that animal, in a certain number of cases ovulation may occur during pregnancy. But whilst under ordinary circumstances the corpora lutea do not prevent the growth of follicles, there are cases in the ferret where the number and sizes of the corpora lutea are so great that the remaining part of the cortex of the ovary is reduced to a minimum; in those cases the growth of the follicles is interfered with, but that is due to the circumstance that there is neither room nor, probably, is there pabulum sufficient for the growth which is more usually met with at the corresponding periods of gestation.

In other animals, such as rats, mice, and rabbits, in which ovulation does, or can, take place immediately after parturition, it is very probable that the growth of the follicles occurs during pregnancy, much in the same way as in guinea-pigs and ferrets, the only difference between the various animals being that, in those in which ovulation is not dependent on insemination, some follicles reach full maturity during gestation, whilst in the ferret they only attain to full or almost full pre-inseminal growth, a point which will be referred to again in the consideration of the causation of œstrus.

Whether the conditions met with in the ovaries of ferrets, during the gestation which intervenes between two œstrus periods, occur also in the ovaries of polyœstrus animals is doubtful, and, so far as the human subject is concerned, the statements made by different observers are extremely contradictory. Unfortunately, most of the observers who have dealt with human material have been chiefly concerned in inquiring as to whether or not ovulation occurs during pregnancy, and on that point they are practically all agreed; it either does not occur or is very exceptional; neither does it occur in any other animal, being prevented, according to Loeb's observations, by the corpora lutea; but ovulation is only the termination of completed follicle growth, and there is considerable difference of opinion as to what extent follicle growth takes place in the human ovary during pregnancy.

Seitz (37), who examined the ovaries of thirty-six pregnant women, was unable to find ripe or nearly ripe follicles in any of them, and he throws doubt on a case of Consentino's, which he quotes, in which a recently ruptured follicle was found in the ovary of a woman in the sixth month of gestation. The more recent researches of Leopold and Raveno (17) and those of Raveno (31), which were carried out on a large number of cases, do not support Seitz.

Raveno, as the result of his observation of a series of sixty cases, writes: "In allen Eierstocken fanden sich Graafsche Follikel auf dem Wege der Reife; ei einige schon reif und im Begriff zu platzen, aber ein frisch angebrochener Follikel wurde niemals beobachtet" (31).

Hill and O'Donoghue (12) state that the rupture of a group of follicles in *Dasyurus viverrinus*, which is monœstrus, and which ovulates spontaneously, is not followed by the growth of a fresh batch of follicles, whether the animal becomes pregnant or not; but they do not state that follicle growth completely ceases either after ovulation without pregnancy or during pregnancy, and it appears, from what is known with regard to other animals, that follicle growth proceeds throughout the whole or the greater part of extrauterine life—even in the human female, after the menopause, according to Leopold and Raveno (17). But whilst this must be admitted in view of the evidence which is available, it must be noted that the state of development to which the follicles can attain varies considerably at different periods of life.

In association with these facts three questions at least arise: 1. What is the cause of the growth of the follicles? 2. Why do many follicles die before attaining maturity? 3. What is the cause of the rupture of the follicles? To these questions the conditions met with in the ovaries of ferrets suggest certain answers, but they furnish no absolutely conclusive proofs that those answers are correct. Such absolute proof can only be obtained by experiments, which will be very difficult to carry out on account of the intimate relations of the parts of the ovary which are involved.

The cause of the growth of the follicles is either intraovarian, extraovarian, or partly one and partly the other.

It is possible to suppose that the cause of the growth of the follicles is extraovarian, and that it is due to some supposititious substance, such as the "gonadin" invoked by HEAPE as the cause of the general phenomena of the pro-œstrum and œstrus; but if that supposition is admitted, it is necessary to account for the fact that the majority of the follicles formed fail to become mature; for whilst it may be granted that some of the follicles die because their positions in the ovary are unfavourable to complete development, as both HEAPE (11) and LOEB (19) suggest, that explanation does not account for the fact that, both in the guinea-pig and the ferret, many generations of follicles, which appear in the ovaries at certain periods, die before attaining to maturity, unless it is assumed that the substance formed outside the ovary and carried to it by the blood-vessels is first formed in small quantity sufficient to produce a moderate amount of development and then fails, later in larger but still insufficient amount and again the supply fails, until finally an amount sufficient to carry the follicles to their maturity is provided; and that these conditions recur again and again in regular sequence. This is a supposition difficult to entertain, and although extraovarian influence has not been excluded, no series of observations or experiments hitherto made has provided it with any appreciable basis of support. If, therefore, we leave aside the possibility of extraovarian influence and turn to the ovary for an explanation of the growth of its follicles, there are three parts of the organ which at once suggest possibilities: (1) the interstitial tissue, (2) the corpora lutea, and (3) the follicles themselves. It is generally admitted that both the interstitial tissue and the corpora lutea do produce secretions which pass into the blood and influence the activities of other organs, but it is not so generally admitted that the follicles are also endocrine organs. Nevertheless it is possible, as I will attempt to show, that the follicles, once formed, are the cause of their own further evolution.

A certain number of primitive follicles of any given group or generation are capable of obtaining from the surrounding blood and lymph vessels sufficient nutriment to enable them to grow until they become follicles with a single layer of cubicular or columnar follicle cells. As the follicle cells assume their cubical or columnar shape they acquire also all the characteristic features of secreting cells (figs. 6 and 7, Pl. I). It may be argued, and it is frequently assumed, that any secretive capabilities which the follicle cells possess at this stage are utilised for transmitting to the ovum the material which is necessary for its growth and development. It cannot be doubted that the secreting power of the follicular epithelium is used for this purpose, but there is no evidence that it is not utilised also for the transmission to the exterior of the follicle of substances formed in the follicular cells; indeed there are indications, long before the pro-œstrum appears, that this is the case.

When a follicle becomes vesicular, on the appearance of its antrum, the follicle cells separate into two groups—the peripheral group, which forms the boundary wall of the antrum, and the cumulus group, which projects from the peripheral group into the antrum. One of the functions of the cells of both groups is to form the liquor folliculi. The function of some of the cells of the cumulus group is to transmit nutritive material to the ovum, for there is no other way than by and through the cumulus cells that the ovum can obtain the nutriment necessary for its growth and development. The protoplasm of the innermost cells of the cumulus blends with the outermost layer of the oolemma (figs. 41 and 43, Pl. VII; fig. 45, Pl. VIII), and the nuclei of many of the cumulus cells lie in close contact with the oolemma until after insemination has taken place, then they all rapidly move away to the peripheral ends of the cells (figs. 41, 42, 43, Pl. VII; figs. 45, 47, Pl. VIII). The peripheral cells of the general follicular epithelium exhibit the same peculiarities, but the positions of the cells are reversed, that is, the peripheral ends of the cells are in contact and fused with the external limiting membrane (figs. 58, 59, 60, Pl. X), and the nuclei of many of the peripheral cells lie in close apposition with the external limiting membrane until the development of the follicle is completed (figs. 48, 49, Pl. VIII; figs. 54, 57, Pl. IX).

It is certain that the inner cells of the cumulus are transmitting material to the ovum, and it is not unfair to assume therefore that the cells which bear the same relationship to the external limiting membrane that the innermost cumulus cells do to the ovum may be transmitting material to the exterior of the follicle.

The material transmitted to the exterior of the follicles in the period shortly before the rupture plays a part, and probably the chief part, in the production of the phenomena of the pro-œstrum and the œstrus, and it is to be presumed that the material transmitted to the exterior of the follicle in the earlier stages of follicular development also has some function; that function is, I believe, to facilitate the growth of the follicles themselves. The secretion produced by an earlier generation of follicles enables that generation to grow to a certain stage, but it is not sufficient, when the demand comes to carry it on to the next stage; therefore the generation dies, but part of the secretion remains, and that remainder, together with the supply produced by itself, enables the next generation to attain a further stage of development; again the supply is not sufficient for the demand at a certain period, and the generation dies, but the amount of secretion left is greater than it was at the preceding stage, and so the process proceeds until the amount of secretion present is sufficient to enable the next or some succeeding generation to attain to maturity.

In other words, the earlier generations of follicles are the pioneers which blaze out the pathway along which the succeeding generations advance to the promised land of maturity.

In some animals, such as *Dasyurus viverrinus*, the secretion produced by groups of follicles which have died is so exhausted by the production of the maturity of what may be called a terminal group, that, whether pregnancy occurs or not, a long anœstrus period is necessary during which numerous groups of follicles may grow and die before sufficient secretion is accumulated to induce the maturation of another terminal group.

In the guinea-pig the regular production of groups of follicles, which grow to a certain extent and then die, continues throughout the period of pregnancy, and although it is interfered with by the corpora lutea, as Beard (2) suggested it was in all mammals, and as Loeb (19) has proved it to be in guinea-pigs, still it occurs to an extent necessary to bring a terminal group of follicles to maturity at or about the period of parturition, and it is practically certain that the same conditions occur in rats and mice.

It appears probable, therefore, that in all mammals groups of follicles are produced and grow and die throughout the whole period of sexual life, and that the majority of the groups have no possibility of attaining maturity; nevertheless they have a definite function, which is to form the secretion which is necessary for the maturation of a terminal group of follicles. A time comes, however, at all events in the case of the human female, when the production of groups of follicle, or their growth, or their capability to form the necessary secretion, is so reduced that ovulation first becomes irregular and then ceases, and the menopause occurs.

The suggestion is not invalidated by the fact that ovulation occurs after the menopause in a certain number of cases, for the occurrence is rare, and it is probable that the follicles which rupture them are not normal, inasmuch as the ova they extrude are rarely, if ever, capable of fertilisation.

The Relation of the Follicles to the Pro-œstrum and Œstrus.

In some of the preceding pages I have shown the necessity for the repeated production of groups of ovarian follicles, and have attempted to show that the attainment of maturity by special groups depends upon the life-work of the groups of follicles which preceded them and failed to reach maturity; but in addition to their work of preparing the means for their own development, the follicles at a certain period of their history appear to take on the function of providing the secretion which is responsible for the phenomena of the pro-œstrum and the œstrus. This function, considered in the light of the evidence furnished by the ferret, may now be considered.

The contention that it is a secretion produced by the ovarian follicles which is responsible for the phenomena of the pro-œstrum and the œstrus does not receive universal acceptance.

Heape (11), as the result of extensive observations on rabbits, arrived at the conclusion that "it does not seem possible to accept the view that the stimulus which induces pro-œstrum and œstrus has its origin in the ovary," and he believes that the phenomena are due to a substance of extraneous origin ("gonadin"), "due to a change in the condition of the blood brought about by climatic influences and food."

Heape (9, 10, 11) has shown that in monkeys ovulation may occur without menstruation, and that menstruation may occur without, in some cases, a precedent, and in others any subsequent, ovulation. Leopold (17) has demonstrated the same facts in the case of the human female. It seems to be mainly on these two groups of circumstances that Heape bases his belief that the ovary cannot possibly play a part in the production of the phenomena of heat; but whilst he is convinced of the impossibility of looking upon the ovaries as causative agents in the production of the phenomena of the pro-œstrum and the œstrus, he makes no attempt to show how it is that the phenomena cease in sexually mature females after the ovaries are removed.

Marshall (23) acknowledges the influence of the ovaries, but denies that the follicles are the responsible agents. He bases his objection to the follicles on the results of two experiments made on bitches, in which he pricked the protruding follicles of the ovaries, in one case from one to three weeks before the expected period, and in the other two months before the period was due. In both cases œstrus appeared at about the expected time. The first animal was killed a week after the appearance of œstrus, and it was found that "the ruptured follicles were very abnormal, since they contained large cavities surrounded by tissue resembling degenerate luteal tissue." "The probable conclusion is that heat is not brought about by the ripening follicles, but that the process of maturation and the phenomena of the pro-œstrum and œstrus are both the results of some further factor which is probably to be sought for in the ovarian interstitial cells."

To this conclusion O'Donoghue (29) rightly objects that interstitial tissue is not present in many mammals which ovulate regularly; and although it may be doubted if interstitial tissue, or at all events cells which play the part of interstitial cells, are absent as frequently as is supposed, they are undoubtedly not present in many mammals in the typical glandular form met with in the rabbit, cat, and ferret. It is stated that they are absent in the bitch—that is, in the animal on which Marshall experimented—but in some bitch ovaries in my possession interstitial cells are undoubtedly present in considerable numbers in the form of strands of cells and scattered cells, but they do not form so prominent a feature of the ovarian structure as in the cat and ferret.

Moreover, MARSHALL's experiment, though it is apparently accepted by PATON (30) as conclusive, is not adequate to support the contention based upon it. It provides no proof that the capabilities of the cells of the ruptured follicles were interfered with, and there is every reason to suppose they were not. The intra-follicular pressure was temporarily reduced, but it was, obviously, soon re-established, for MARSHALL notes what he takes to be the abnormal size of the follicles in the first animal when it was killed, a week after œstrus had commenced and three and a half weeks after the operation. Such considerable redistension of the normally ruptured follicles is not unusual in ferrets, and is only one of the phases met with in the formation of the corpora lutea.

In all young animals group after group of follicles grows and dies, but no signs of heat appear, because none of the groups have attained to the phase of growth during which they form the heat-producing secretion. Again, in sexually mature and adult guinea-pigs and ferrets group after group of follicles grows and dies without attaining the stage at which the heat-producing secretion is formed; but once a group of follicles has attained to that stage which is shown in the ferret (fig. 13, Pl. II; figs. 15, 16, Pl. III), when the cumulus epithelium begins to show signs of separation into an outer and an inner group of cells, the phenomena of the pro-œstrum followed by those of the œstrus appear. It was probably just before this stage was attained that MARSHALL punctured the follicles, but it is obvious that the puncture did not prevent the subsequent growth and the transformation of the follicle cells into luteal cells, which MARSHALL describes, and thinks, were of abnormal character. Even if that was the case, it is clear that the follicle cells had passed successfully through the phases which precede their transition into luteal cells, and it is in those phases that they produce the secretion which gives rise to the phenomena of heat.

The preceding statement is not merely the expression of a supposition, for the ferret furnishes practically conclusive information with regard to the point at issue.

I have shown, and a reference to the accompanying tables of notes will confirm the statement, that the ferret does not ovulate unless it is properly inseminated, and by proper insemination I mean unless spermatozoa enter the caudal third of the oviduct, for the excitement of the act of copulation may occur without subsequent ovulation (see Table V), although the follicles in the ovaries are at the stage of growth at which rupture would occur if insemination were successful. After insemination has been unsuccessfully attempted the phenomena of heat continue, and if the female is placed with another male, successful insemination can be attained. If insemination is successful, the phenomena of heat disappear as the follicles pass to their later phases of development; but if the female in heat is kept separate from the male, the phenomena of heat continue. In one of MARSHALL's specimens it lasted for a period of five weeks (21) and then terminated; in another it was still present at the end of six weeks, when the animal was killed (21). In one of my specimens it had lasted thirty-two days when the animal had to be killed, in the summer of 1914, and I have not since then had an opportunity to carry the investigation further. It is, therefore, uncertain how long heat may continue in the case of the ferret. The time is obviously variable, and is no doubt associated with the fact that some ferrets produce one brood, others two, and a few three in the sexual season; which probably means that the substance necessary for the maturation is present in the first case only in sufficient amount to bring one group of follicles to pre-inseminal maturation, and is then so used up that there is not time, during the succeeding forty-two days of pregnancy, for the necessary recuperation to an extent sufficient for the production of the maturation of another group of follicles during the season; or that the groups of follicles which grow and die during the gestation are not sufficient to produce the necessary amount of material, whilst in the second and third group of cases the conditions are more favourable.

Marshall gives no account of the ovaries of his two ferret specimens referred to which were kept separate from the male. In my specimen, which was killed in the thirty-second day of œstrus, the ovaries contained fourteen large follicles, of which five were in a state of degeneration; the remainder were in the stage of development always found associated with the condition of heat (fig. 39, Pl. VII).

In ferrets, therefore, œstrus only occurs when the ovaries contain follicles in a certain stage of development, and such follicles are present as long as œstrus continues (see Tables III, IV, V). Under these circumstances it can scarcely be doubted that the phenomena of heat are due to something produced by the follicles, and Marshall's experiments prove not that the follicles take no part in the production of the phenomena of the pro-œstrum and the œstrus, but that puncture of follicles of considerable size, which have not yet attained the proper stage, does not prevent the follicular epithelium reaching the necessary stage and performing the functions associated with it.

This part of the subject cannot be dismissed without some reference to the events which occur in the bats, for they have been used as an argument against the possibility that the follicles can play any part in the production of the phenomena of heat. It is known from the researches of Van Beneden (38) and Van der Stricht (39) that the majority if not all the sexually mature females are inseminated in autumn, and that the spermatozoa lie dormant till the following spring; then some of the ovarian follicles ripen, ovulation occurs, and fertilisation follows. This evidence, so far as it goes, tells against the position I have taken; but, unfortunately, we have no clear knowledge of the condition of the ovaries of bats in autumn, when it must be assumed that heat occurs, and until that is furnished, the evidence offered by bats has no great weight either one way or the other. There are also other possible explanations of the phenomena which occur in bats to which it will be necessary to refer in connection with the next section of this discussion; but before passing to that, it should be noted that the suggestion that the follicles produce the substance which facilitates their own growth, and also that on which the phenomena of heat depend, is not in disaccord with HEAPE's contention that the phenomena of the œstrus period are dependent on climatic and food conditions, for it is obvious that the necessary pabulum must be provided for both purposes, and, under ordinary conditions of life, it is probable that the proper pabulum is only attainable at certain seasons, whilst in the cases of domesticated animals it is provided all the year round; thus by the artificial alteration of external conditions it is possible that a normally monœstrus animal might be converted into a polyœstrus animal.

The Cause of the Rupture of the Follicles in Ferret and Ferret-Polecat Hybrids.

In ferrets and ferret-polecat hybrids no ovarian follicles rupture unless spermatozoa are present in the caudal third of the oviduct; moreover, the rupture does not take place at the same time after copulation in all animals. It may occur about thirty hours after copulation, and it may be delayed for over ninety hours (see Tables VII, IX).

In the specimens in which ovulation was delayed, follicles of normal size and structure were present in the ovaries, but the ova in some had not passed into the stage of the first maturation division, and in others were only attaining that stage at a later period.

It is well known that animals will not permit sexual congress unless they are in heat, and heat is always associated with follicles which contain ova which are in the first maturation division phase, or which are ready to pass into that phase as soon as the necessary stimulus is provided. Therefore the animals in which spermatozoa were found in the oviducts must have been in œstrus; their ovaries all contained follicles in the stage of pre-inseminal maturity. The only difference which could be detected between those in which ovulation followed insemination after a relatively short period and those in which ovulation was delayed was the number of spermatozoa in the caudal thirds of the oviducts.

In those cases in which the spermatozoa were numerous ovulation occurred relatively soon, and in those in which the spermatozoa were few in number ovulation was delayed.

In those animals in which the spermatozoa in the oviducts are numerous the dispersion of the cumulus epithelium, the formation and extension of the secondary liquor folliculi, the phenomena of the first maturation division of the ovum, and the rupture of the follicles take place relatively quickly, whilst in those in which few spermatozoa are present all the phenomena are retarded.

It appears, therefore, that, in the case of the ferret, the final phenomena of the maturation of the follicles and their rupture are due either to the spermatozoa or to the seminal fluid.

It is possible, however, that other factors may be at work, for I find that in the cases of females inseminated by the same male ovulation may occur in all, but fertilisation may fail in one or more. Thus if it is possible for the seminal fluid to produce ovulation in two females and fertilisation in only one of the two, it is also possible that the seminal fluid of a given male, independently of the number of spermatozoa, may be less potent in producing ovulation in one female than in another. The evidence at present available on this matter is quite insufficient to justify a positive statement, and the point must be left open.

A question which naturally arises in association with the points which have already been noted is, is there any significant structural difference between the ovaries of the animals which ovulate spontaneously and the ovaries of animals which only ovulate after coitus? It may be admitted at once that the evidence available does not justify a definite answer, but it suggests assumptions and indicates paths along which further investigations might be made, and on that account it deserves consideration.

In the cat and ferret, which ovulate only after successful insemination, the interstitial tissue forms a preponderant part of the cortex of the ovary. In the human female, on the other hand, and in monkeys, mares, asses, pigs, and in *Dasyurus viverrinus*, all of which ovulate spontaneously, the interstitial tissue is either absent or it is present in only small amount, and not in the typical glandular form in which it occurs in the animals first mentioned; but although there are two widely different types of ovaries so far as the presence of interstitial tissue is concerned, that tissue cannot be responsible for the different modes of ovulation, for it is present in the typical form and in large amount in guinea-pigs, which ovulate spontaneously, and in the rabbit, which sometimes, though rarely, ovulates spontaneously (25A), and in the bitch, which regularly ovulates spontaneously; for although FRANKEL denies its presence in that animal, it is present in considerable amount in some of my specimens. The bats give, at present, as little help in the solution of the question of the relation of ovarian structure to ovulation as they do to the question of the relation of follicular growth to follicular development. Their ovaries contain a very large amount of interstitial tissue, and we know that the majority, if not all, of the sexually mature females are inseminated in autumn and do not ovulate till the following spring; but we also know that some females are inseminated in spring, and with regard to them there is no evidence as to whether they ovulate spontaneously or not. Moreover, it must not be forgotten that the arrangements in bats may be a case of special adaptation developed to assure the majority of the females being inseminated, in autumn, by vigorous, well-fed males rather than by males which have recently passed through a long period of hibernation.

That such special adaptations do occur is evidenced by conditions met with in birds. In the case of the ordinary fowl the male takes no part in the incubation of the eggs, and ovulation occurs independently of the presence of the male. In pigeons, the male pigeon takes his fair share in the process of incubation. It would obviously be a disadvantage, therefore, if the female began to lay before pairing; and CRAIG (6) has shown that if pairing is prevented, ovulation is delayed for a very considerable period. In this particular case the influence of the male appears to be purely of psychic character, and it is certainly unassociated with coition.

The present knowledge which we possess of marsupials also helps very little towards the solution of the question at issue, for though O'DONOGHUE (29) has pointed out that interstitial tissue is absent from the ovaries of the polyprotodonts, and is present in the ovaries of the diprotodonts, and HILL and O'DONOGHUE (12) have found that in the polyprotodont *Dasyurus viverrinus* ovulation is spontaneous, we do not yet know whether it is spontaneous or not in other marsupials.

There is still another structural difference between the ovaries of polyœstrus spontaneously ovulating animals and the ovaries of the animals which only ovulate after copulation, that is, the presence in the former group of periodic corpora lutea, which develop after ovulations which are not followed by pregnancy. Periodic corpora lutea are structurally similar to the corpora lutea of gestation, but they persist for a much shorter time. In 1909 BOUIN and ANCEL (5) formulated the opinion that the interstitial gland is not present in spontaneously ovulating animals, and that its place is taken by the periodic corpora lutea, both structures presiding over the development of the secondary female sexual characters. The opinion cannot be sustained, since the base on which it rests is unsound; for the guinea-pig, which ovulates spontaneously, and therefore can form periodic corpora lutea, also possesses a very large amount of interstitial gland tissue, and many other spontaneously ovulating animals have a considerable amount of interstitial tissue in their ovaries.

So far as the evidence available goes, it seems to exclude interstitial tissue as an active agent in the control of ovulation, and we are driven towards the tentative conclusion that in animals that ovulate spontaneously something is present or something is absent as contrasted with animals which ovulate only after coition.

If something is present in the first group which favours spontaneous ovulation, it must be absent in the animals which ovulate only after coition, and must be provided by coition; and if something is present in animals which ovulate only after coition, which interferes with ovulation, it must be neutralised by coition, and it must be absent in animals which ovulate spontaneously. If either inference is correct, the question arises, How is the substance provided by coition, and is the end attained by chemical means, or by psychic means, as in the case of pigeons?

The evidence afforded by ferrets is opposed to the idea of psychic influence, for, in their case, sterile coition is not followed by ovulation, and it is difficult to believe that an alteration of the nervous system produced by sexual congress can produce results in some animals of a species in about thirty hours, when in other animals, of the same species, placed under similar conditions, the result may be delayed for more than ninety hours, whilst if the coition is sterile, the result aimed at is not attained.

If the influence is a nervous phenomenon, which acts by producing vascular engorgement of the generative glands, and so provides an increase of pabulum for the developing follicles, it might be expected to be fairly regular in its effects, as it seems to be in rabbits, which usually ovulate about ten hours after coition, whether the coition is sterile or not. This possibility cannot at present be definitely excluded, and it must be noted in association with it that, in my series of thirteen ferrets, in which coition was attempted, and was apparently successful, but in which ovulation did not follow (Table V), the average size of the largest follicles is $\cdot 9567$ mm.^{3}, that is, somewhat less than three times as large as the average size of the largest follicles in animals in full heat but in which no attempt at insemination was made, a fact which points to the conclusion that although the coition was sterile and was not followed by ovulation, it had nevertheless a definite influence on the growth of the follicles.

If the influence produced by coition is a chemical influence, then it must be due either to the spermatozoa or to other constituents of the seminal fluid.

In bats, coition produces no results, with which we are acquainted, until several months after its occurrence, and it is difficult to imagine that the fluid portion of the seminal fluid can lie in the uterus for so long a period without diffusing into the lymph or blood-vessels and then be suddenly absorbed in the early months of spring, whilst it is less difficult to realise that the spermatozoa might lie dormant.

The influence of spermatozoa is more or less excluded, however, by the conditions met with in rabbits. Some, but very few, of those animals ovulate, on rare occasions, spontaneously (25A). The majority ovulate about ten hours after coition, but ovulation may occur when coition has been rendered sterile by a previous operation, either on the male or on the female, the result, judging from the data furnished by MARSHALL (25A), being much less certain in the cases of sexually mature virgins than in parous animals. This point may prove to be of importance, for it suggests that previous fertile coition facilitates sterile coition at a later period, and, if this is so, it may be an indication of the lasting effects of spermatozoal action. The evidence is not sufficient to justify a conclusion, and, so far as the data available go, it must be supposed, for the present, that the ovulation in the rabbit is due to coition, and is brought about either by some nervous influence or by the constituents of the spermatic fluid other than the spermatozoa. It is obvious, bearing in mind the size of the protometra, that such constituents may be fairly abundant.

A survey of facts which fails to secure a definite conclusion is always unsatisfactory, but it must be admitted that the data at present at our disposal are not sufficient to justify a positive statement; whilst, at the same time, they seem to point towards the conclusion that, in animals which ovulate only after coition, something is present which prevents ovulation until it is neutralised by coition, and that it is not present in spontaneously ovulating animals; or conversely, that in spontaneously ovulating animals something is present which favours ovulation, it is absent in animals which only ovulate after coition, and that it is provided by coition; but, in either case, there is no evidence to show what the substance is, or how or where it is formed.

SUMMARY.

In ferrets and ferret-polecat hybrids successive generations of ovarian follicles are formed throughout the whole period of life.

In the interval between two ovulations, whether the period be long or short, successive groups of follicles grow and die, at successively advanced stages, until a group attains to full maturity.

It seems probable that the follicles of one group produce material which favours its own growth and facilitates the further advance of succeeding groups.

The phenomena of the pro-œstrum and the œstrus only appear when a group of follicles has attained a stage of development which may be called pre-inseminal maturity, and the phenomena are due to some secretion produced by the follicles in that phase of their development.

The follicles only become fully mature and only rupture after spermatozoa have entered the caudal third of the oviduct.

The rupture of the follicles is due to the formation of the secondary liquor folliculi which follows successful insemination.

There is no bleeding when rupture occurs, either into the follicles or at the margins of the apertures in their walls, and bleeding only occurs occasionally during the redistension of the follicles.

The greater part of the follicular epithelium remains in the follicles after the rupture and the extrusion of the ovum and the cumulus cells.

After the rupture the follicles redistend, and the redistension is associated with the transformation of the follicle cells into lutein cells.

LIST OF LITERATURE.

This list only contains the communications directly referred to; very complete lists of associated articles will be found in the papers quoted, and especially in No. 40.

(1) Alexando, N., "Contribution à l'histologie normale et pathologique des ovaries de la femme," *Ann. de Gynécologie*, 1891.

(2) Beard, J., *The Span of Gestation*, Jena, 1897.

(3) Benckiser, A., "Zur Entwicklungsgeschichte des Corpus luteum," *Archiv für Gynäkologie*, Bd. xxiii.

(4) Bouin, P., et Ancel, P., "Sur la différenciation d'une membrane propre d'origine épithéliale pendant le développement du corps jaune chez le chienne," *C. R. de la Soc. Biol.*, t. lxv, 1908.

(5) Bouin, P., et Ancel, P., "Sur les homologies et la signification des glandes à sécrétion interne de l'ovaire," *C.R. Soc. Biol. Paris*, t. lxvii, 1909.

(6) Craig, W., "Oviposition induced by the Male in Pigeons," *Journ. of Morph.*, vol. xxii, 1901.

(7) Frankel, L., "Vergleichend histologische Untersuchungen über des Vorkommen drüsiger Formationen im interstitiellen Eierstocks gewebe," *Archiv für Gynäkologie*, Bd. lxxv, 1905.

(8) Heape, W., "The Menstruation of *Semnopithecus entellus*," *Phil. Trans. Roy. Soc.*, vol. B, 1894.

(9) Heape, W., "The Menstruation and Ovulation of *Macacus rhesus*," *Phil. Trans. Roy. Soc.*, vol. B 188, 1897.

(10) Heape, W., "The Menstruation and Ovulation of Monkeys and the Human Female," *Obstetrics Trans.*, vol. xi, 1898.

(11) Heape, W., "Ovulation and Degeneration of Ova in the Rabbit," *Proc. of Roy. Soc.*, vol. B 76, 1905.

(12) Hill, J. P., and O'Donoghue, C. H., "The Reproductive Cycle in the Marsupial *Dasyurus viverrinus*," *Q.J.M.S.*, vol. lix, 1914.

(13) Honoré, C., "Recherches sur l'ovaire du Lapin," *Archiv de Biol.*, t. xvi, 1899–1900.

(14) Janosik, J., "Zur Histologie des Ovariums," *Sitz. d. Kais. Akad. d. Wiss.: Mathem. Naturw. Kl.*, 95–96 Bd., 1887.

(15) Kingery, H. M., "Oogenesis in the White Mouse," *Journ. of Morph.*, vol. xxx, No. 1, 1917.

(16) Lane-Claypon, J. E., "On Ovogenesis and the Formation of the Interstitial Cells of the Ovary," *Journ. of Obstetrics and Gynæcology*, vol. xi, 1907.

(17) Leopold, L. U., and Raveno, A., "Neuer Beitrag zur Lehre von der Menstruation und Ovulation," *Archiv für Gynäk.*, Bd. lxxxiii, 1907.

(18) Limon, M., "Sur l'évolution de la membrane propre des ovisacs au cours de leur atrésie," *Bibl. Anat. Paris, Nancy*, t. xiii, 1904.

(19) Loeb, L., "Der normale und pathologische Zyklus im Ovarium des säugetier," Virchow's *Archiv*, Bd. xx, 1911.

(19a) Loeb, L., "The Cyclic Changes in the Ovary of Guinea-pig," *Journ. of Morph.*, vol. xxii, 1911.

(20) Longley, W. H., "The Maturation of the Egg and Ovulation in the Domestic Cat," *American Journ. Anat.*, vol. xii, 1911–12.

(21) Marshall, F. H. A., "The Œstrus Cycle in the Common Ferret," *Q.J.M.S.*, vol. xlviii, 1904.

(22) Marshall, F. H. A., *The Physiology of Reproduction*, London, 1910.

(23) Marshall, F. H. A., "On the Ovarian Factor concerned in the Recurrence of Œstrus," *Proc. of the Phy. Soc. Jour. of Phys.*, vol. xliii, 1911–12.

(24) Marshall, F. H. A., "The Œstrus Cycle and the Formation of the Corpus luteum of the Sheep," *Phil. Trans. Roy. Soc.*, vol. B 196, 1904.

(25) Marshall, F. H. A., and Jolly, W. A., "The Œstrus Cycle in the Dog," *Phil. Trans. Roy. Soc.*, vol. B 198, 1906.

(25a) Marshall, F. H. A., "The Functional Correlation between the Ovaries, Uterus, and Mammary Glands in the Rabbit; with Observations on the Œstrus Cycle," *Proc. Roy. Soc.*, vol. B 87, 1914.

(26) Miller, G. S., "*Catalogue of Mammals of Western Europe*, p. 423, London, 1913.

(27) Monterosso, B., "Sur la struttura e la funzione della cellule parietali della granulosa nel follicolo ovarico del Maiale," *Atti della Accad. Gioenia di Sc. Nat. Catania*, vol. v, 1912.

(28) Nagel, W., "Das Menschlich Ei," *Archiv f. mikr. Anat.*, Bd. xxxi, 1888.

(29) O'Donoghue, C. H., "On the Corpora lutea, and the Interstitial Tissue of the Ovary in Marsupialia," *Q.J.M.S.*, vol. lxi, 1916.

(30) Paton, D. Noël, *Regulation of Metabolism*, London, 1913.

(31) Raveno, A., "Ueber die Frage nach der Thätigkeit des Eierstocks in der Schwangerschaft," *Arch. f. Gynäk.*, Bd. lxxxiii, 1907.

(32) Robinson, Arthur, "The Position and Peritoneal Relations of the Mammalian Ovary," *Jour. of Anat. and Phys.*, vol. xxi, 1887.

(33) Rubaschkin, W., "Zum Lehre von der Keimbahn bei Säugetieren," *Anat. Hefte*, Bd. xlvi, 1912.

(34) Russo, A., "Sulla cromolisi delle cellule della granulosa durante il digiuno e sul suo significato nella differenaiazione sessuale delle ova dei mammiferi," *Atti della Accad. Gioenia di Sc. Nat. in Catania*, vol. ii, 1909.

(35) Sandes, F. P., "The Corpus luteum of *Dasyurus viverrinus*; with Observations on the Growth and Atrophy of Graafian Follicles," *Proc. of the Linnean Soc. of New South Wales*, 1903.

(36) Schottländer, J., "Ueber den Graaf'schen Follikel seine Entstehung beim Menschen und seine Schicksale bei Menschen und Säugethieren," *Arch. f. mikr. Anat.*, Bd. xli, 1893.

(37) Seitz, L., "Die Follikelatresie während der Schwangerschaft," *Arch. f. Gynäk.*, Bd. lxxvii, 1905–06.

(38) Van Beneden, E., "Contribution à la connaissance de l'ovaire des mammifères," *Arch. de Biol.*, t. i, 1880.

(39) Van der Stricht, O., "La ponte ovarique et l'histogénèse du corps jaune," *Bull. de l'Acad. Roy. de Belgique*, 1901.

(39a) Van der Stricht, O., "Sur le processus de l'excrétion des glandes endocrines. Le corps jaune et la glande interstitielle de l'ovaire," *Arch. de Biol.*, t. xxvii, 1912.

(40) Van der Stricht, R., "Vitellogénèse dans l'ovule de Chatte," *Arch. de Biol.*, t. xxvii, 1912.

(41) Wagener, G., "Bemerkungen über den Eierstock und des gelben Körper," *Arch. f. Anat. u. Physiol.*, 1879.

(42) Waldeyer, *Eierstock und Ei*, Leipzig, 1870.

(43) Winiwarter, H. von, et Sainmont, G., *Nouvelles recherches sur l'ovogénèse de l'ovaire des mammifères, (chat)*, Liége, 1912.

EXPLANATION OF THE LETTERS IN THE TABLES INDICATING THE METHODS OF FIXATION.

Fl.	Strong Flemming's fluid with 2–3 per cent. acetic acid.
Len.	Lenhossek's fluid.
Mann.	Mann's fluid.
M.F.	Mann's fluid with 5 per cent. formol.
Mx.	Maximow's fluid.
Per.	Perenyi's fluid.
P.N.F.	Picro-nitric fluid with 5 per cent. formol.
PO.	Perenyi's fluid with osmic acid.
Z.	Zenker's fluid.

EXPLANATION OF THE LETTERS INDICATING THE STAINS USED IN THE SECTIONS SHOWN IN THE FIGURES.

E.	Eosin.
H.E.	Hæmatoxylin and eosin.
I.H.	Iron-hæmatoxylin.
Mallory.	Mallory's connective-tissue stain.
O.G.	Orange green.

TABLE I.—FERRETS AND FERRET-POLECAT HYBRIDS IN THE ANŒSTRUS PERIOD.

Specimen.	Weight in Ounces.	Date of Death.	Size of Ovary in mm.^{3}	Size of largest Follicle in mm.^{3}	No. of Follicles of largest size, Normal and Degenerate.
1. F.Z.R.A. 4/14	?	18/11/14	18·666 320 000	·036 780 480	13 (4 deg.)
2. F.Fl.L.A. 4/14	,,	,,	22·482 360 000	,,	7 (1 deg.)
3. F.Z.R.A. 1/14	20	,,	19·584 400 000	·008 506 080	9 (3 deg.)
4. F.Fl.L.A. 1/14	,,	,,	27·800 960 000	·002 520 400	7 (3 deg.)
5. F.Z.R.A. 2/14	14½	19/11/14	17·264 855 600	·007 983 360	10 (5 deg.)
6. F.Fl.L.A. 2/14	,,	,,	15·256 512 000	·005 987 520	3 (2 deg.)
7 F.Z.R.A. 3/14	19	21/11/14	9·000 375 000	·025 920 000	9 (5 deg.)
8 F.Fl.L.A. 3/14	,,	,,	9·002 487 500	,,	7 (4 deg.)
9. F.Z.R.A. 5/14	16½	10/12/14	16·905 920 000	·004 608 000	7 (6 deg.)
10. F.Fl.L.A. 5/14	,,	,,	20·841 435 000	,,	6 (4 deg.)
11. F.Z.R.A. 6/14	,,	,,	12·327 900 000	·009 000 000	10 (5 deg.)
12. F.Fl.L.A. 6/14	,,	,,	18·274 291 200	·016 848 000	7 (2 deg.)
13. F.Z.R.A. 7/14	,,	17/12/14	16·086 470 400	·042 768 000	10 (3 deg.)
14. F.Fl.L.A. 7/14	,,	,,	22·522 752 000	,,	12 (4 deg.)
15. P.Z.R.A. 8/14	,,	,,	23·598 800 000	·051 166 080	13 (6 deg.)
16. P.Fl.L.A. 8/14	,,	,,	17·998 848 000	·030 948 000	13 (4 deg.)
17. F.Z.R. B/14	?	?/1/14	15·517 756 800	·027 279 360	9 (5 deg.)
18. F.Z.R. C/14	,,	,,	11·859 187 500	·036 936 000	6 (1 deg.)
19. F.Mx.R.A. 9/15	19	9/1/15	15·993 288 000	·035 251 200	14 (4 deg.)
20. F.Fl.L.A. 9/15	,,	,,	29·298 456 000	·052 941 600	18 (6 deg.)
21. F.Z.R.A. 10/15	26	,,	27·864 000 000	·037 402 560	9 (1 deg.)
22. F.Fl.L.A. 10/15	,,	,,	44·010 000 000	·040 068 000	11 all normal
23. P.Z.R.A. 11/15	24	5/2/15	18·159 336 000	·054 550 080	7 (4 deg.)
24. P.Fl.L.A. 11/15	,,	,,	25·122 636 000	·030 355 200	9 (5 deg.)
25. P.PO.R.A. 12/15	18	,,	27·607 172 000	·005 348 880	3 (1 deg.)
26. P.Z.L.A. 12/15	,,	,,	25·588 440 000	·021 772 800	5 (2 deg.)
27. P.Fl.R.A. 13/15	15½	19/2/15	15·780 992 000	·036 288 000	12 (5 deg.)
28. P.Z.L.A. 13/15	,,	,,	14·826 240 000	·059 940 000	6 (1 deg.)
29. P.Fl.R. 14/15	18½	,,	19·542 124 800	·029 030 400	2 both deg.
30. P.PO.L. 14/15	,,	,,	25·256 448 000	·040 824 000	6 (3 deg.)
31. P.PO.R. A/15	22	18/3/15	21·528 000 000	·156 103 200	7 (3 deg.)
32. P.PO.R. A/16	21	,,	28·392 120 000	·096 782 400	9 (3 deg.)
33. P.Z.L. A/16	,,	,,	18·658 727 600	·101 178 000	12 (3 deg.)
34. F.G.A. 19/15 R.Per.	12¾	5/5/15	34·673 328 000	·125 439 600	6 all normal
35. F.G.A. 19/15 L.Fl.	,,	,,	24·713 640 000	·075 790 080	8 (5 deg.)

Note.—All the measurements used in the calculations of the cubic size of the ovaries, follicles, and ova were made in thousandths of a millimetre, and the full number obtained in the calculations is stated, in the tables, in each case, but the figures after the fourth significant figure have no practical value.

TABLE II.—FERRETS, POST-PARTUM OR POST-ABORTION, NOT IN HEAT.

Specimen.	Weight in Ounces.	Number of Days after attempted Insemination.	Number of Days Post-partum.	Date of Death.	Size of Ovary in mm.^{3}	Size of largest Follicle in mm.^{3}	Number of Follicles of largest size.	Notes.
1. F.G.A. 17/15 R.Fl.	15½	36	..	22/6/15	16·391 280 000	·363 242 880	6 (3 deg.)	Not in heat, but uterine cornua larger than in an ordinary anœstrus ferret. No corpora lutea in right ovary, but one corresponding with date of insemination in left ovary.
2. ,, ,, L.Mx.	,,	,,	..	,,	21·555 072 000	·375 210 000	7 (3 deg.)	
3. F.G.A. 16 A/15 R.Fl.	18½	,,	..	21/6/15	42·620 256 000	·047 090 160	8 (6 deg.)	4 corpora lutea corresponding with date of insemination. 3 old corpora lutea which must have belonged to pregnancy of previous season.
4. ,, ,, L.Mx.	,,	,,	..	,,	24·761 547 200	·045 481 600	2 normal	3 corpora lutea corresponding with date of insemination. 3 old corpora lutea which must have belonged to pregnancy of previous season.
5. F D. Y/16 R.Per.	11½	..	1	6/6/16	34·936 488 000	·138 520 800	5 (4 deg.)	7 corpora lutea.
6. ,, ,, L.M.F.	,,	..	,,	,,	28·317 600 000	·834 960 000	7 (3 deg.)	5 ,, ,,
7 F.D. Z¹/16 R.Per.	13	..	2	7/6/16	17·781 120 000	·076 626 000	6 (4 deg.)	3 ,, ,,
8. ,, ,, L.Fl.	,,	..	,,	,,	13·592 448 000	·043 908 480	8 (4 deg.)	3 ,, ,,
9. F.D. V/16 R.Fl.	17¼	..	6	26/5/16	40·723 200 000	·174 919 080	5 all normal	8 ,, ,,
10. ,, ,, L.Z.	,,	..	,,	,,	18·387 111 600	·275 868 000	10 (2 deg.)	3 ,, ,,
11. F.D. X/16 R.Per.	19	..	12	6/6/16	31·022 160 000	·731 289 600	5 (1 deg.)	10 ,, ,,
12. ,, ,, L.Fl.	,,	..	,,	,,	54·577 152 000	1·165 233 600	7 all normal	6 ,, ,,
13. F.D. Z²/16 R.Fl.	17½	..	26	2/6/16	34·776 000 000	·054 432 000	5 (1 deg.)	8 ,, ,,
14. ,, ,, L.Per.	,,	..	,,	,,	44·906 400 000	·051 324 000	9 (4 deg.)	5 ,, ,,
15. D.A. 42/15 R.Mx.	17	..	28	8/6/15	33·103 980 000	·111 600 000	10 (1 deg.)	3 ,, ,,
16. ,, ,, L.Fl.	,,	..	,,	,,	28·827 452 500	·109 058 400	9 (5 deg.)	5 ,, ,,

TABLE III.—FERRETS AND FERRET-POLECAT HYBRIDS IN ŒSTRUS, NOT INSEMINATED, AND INSEMINATION NOT ATTEMPTED.

Specimen.	Weight in Ounces.	Length of Œstrus.	Date of Death.	Size of Ovary in mm.^{3}	Size of largest Follicle in mm.^{3}	Number of Follicles of largest size.	Notes.
1. P.G.B. 1/15 R.Fl.	18	Pro-œstrum just commencing.	21/4/15	40·197 854 700	·185 241 600	9 (2 deg.)	
2. ,, ,, L.Mx.	,,	,,	,,	35·797 500 000	·198 900 000	8 all normal	
3. G.A./16 R.M.F.	15	Pro-œstrum.	28/4/16	39·522 600 000	·163 244 130	6 ,,	
4. ,, ,, L.Per.	,,	,,	,,	32·418 000 000	·149 572 800	6 ,,	
5. F.Z.R.A./17	16½	Œstrus No. of days ?	17/5/15	37·830 672 000	·199 267 200	8 (5 deg.)	
6. F.Fl.L.A./17	,,	,,	,,	28·813 750 000	·324 124 416	11 (6 deg.)	
7. G.A. 18/15 R.Fl.	17½	32 days.	3/7/15	17·572 464 000	·569 963 520	4 (1 deg.)	
8. ,, ,, L.Mx.	,,	,,	,,	22·353 408 000	·782 127 360	10 (4 deg.)	

TABLE IV.—FERRET AND FERRET-POLECAT HYBRIDS, POST-PARTUM AND IN ŒSTRUS.

Specimen.	Weight in Ounces.	Number of Days post-partum.	Number of Days of 2nd Œstrus.	Date of Death.	Size of Ovary in mm.^{3}	Size of largest Follicle in mm.^{3}	Number of Follicles of largest size.	Notes.
1. P.D.A. 40/15 R.Fl.	19	23	?	1/6/15	23·597 568 000	·513 520 000	6 all normal	Young were cast on May 8, and the animal was in full heat when killed on June 1
2. ,, ,, L.Z.	,,	,,	. ,,	,,	33·412 392 000	·524 422 800	5 ,,	
3. F.D.A. 45/15 R.Mx.	16	43	At least 30	3/7/15	18·501 768 000	·309 236 400	8 all deg.	Young were cast May 21, and the animal was in full heat on June 7, and, judging by the state of the vulva, it must have been in heat for at least four days. It was quite healthy when killed on July 3
4. ,, ,, L.Fl.	,,	,,	,,	,,	25·185 560 000	·266 760 000	5 (4 deg.)	

TABLE V.—FERRETS AND FERRET-POLECAT HYBRIDS IN ŒSTRUS. INSEMINATION ATTEMPTED BUT UNSUCCESSFUL, ALL IN FULL HEAT.

Specimen.	Weight in Ounces.	Number of Days after attempted Insemination.	Date of Death.	Size of Ovary in mm.^{3}	Size of largest Follicles in mm.^{3}	Number of Follicles of largest size.	Notes.
1. F.Z.R. 1/14 .	10½	1	20/5/14	10·222 380 000	·891 692 928	12 (4 deg.)	
2. F.Fl.L. 1/14 .	,,	,,	,,	12·398 226 750	·502 842 060	10 (5 deg.)	
3. F.Mx.R. 1·1/14	9	,,	,,	7·858 900 000	·410 743 872	. .	
4. F.Mann.L. 1·1/14	,,	,,	,,	13·106 537 500	·409 600 800	10 (5 deg.)	
5. P.D. L/16 R.M.F.	15½	2	10/5/16	26·707 968 000	1·241 612 800	6 all normal	
6. ,, ,, L.Per.	,,	,,	,,	22·149 072 000	1·165 847 360	1 ,,	
7. F.Z.R. 1·2/14 .	?	3	14/4/14	34·095 698 840	·162 938 880	8 (2 deg.)	
8. F.Fl.L. 1/14 .	,,	,,	,,	48·906 250 000	·095 800 320	10 (5 deg.)	
9. F.Z.R. 1·1/14 .	,,	,,	,,	?	·751 559 040	6 (2 deg.)	Ovary enlarged, and greater part of it converted into myomatous tumour.
10. F.Fl.L. 1·1/14 .	,,	,,	,,	37·419 932 500	1·373 760 000	4 all normal	
11. G.6. Mann. . .	,,	4	5/4/04	16·288 207 380	·638 820 000	5 (2 deg.)	
12. F.Z.R. 1/14 .	,,	,,	12/4/14	13·834 800 000	1·086 618 240	3 (2 deg.)	
13. F.Fl.L. 1/14 .	,,	,,	,,	25·644 609 375	1·319 760 000	6 all normal	
14. F.Mann.R. 1·2/14	,,	,,	,,	25·414 565 880	·933 660 000	6 (2 deg.)	
15. F.Len.L. 1·2/14	,,	,,	,,	24·329 440 000	·758 939 520	5 (2 deg.)	
16. F.Mx.R. 1·1/14 .	,,	5	26/4/14	24·465 210 000	2·173 500 000	8 all normal	
17. F.Per.L. 1·1/14 .	,,	,,	,,	28·350 000 000	3·353 853 600	7 ,,	
18. F.Z.R. 1/14 .	24	6	1/5/14	20·233 651 200	·835 380 880	5 (3 deg.)	
19. F.Fl.L. 1/14 .	,,	,,	,,	36·661 248 800	·639 133 200	12 (2 deg.)	
20. F.D.A. 10/15 R.Fl.	23½	13	24/4/15	18·906 739 200	·890 265 600	4 (2 deg.)	
21. ,, ,, L.Mx.	,,	,,	,,	23·425 920 000	·849 139 000	10 (4 deg.)	
22. P.D.A. 37/15 R.Mx.	8½	14	10/5/15	17·107 200 000	·616 896 000	5 (4 deg.)	
23. ,, ,, L.Fl.	,,	,,	,,	21·735 000 000	1·273 050 000	7 (2 deg.)	
24. P.D.A. 1/15 R.Z.	21½	15	7/4/15	22·208 472 000	1·206 975 600	7 normal	
25. ,, ,, L.Fl.	,,	,,	,,	28·230 094 000	1·044 505 440	4 normal	

TABLE VI.—FERRETS AND FERRET-POLECAT HYBRIDS INSEMINATED AT FIRST ŒSTRUS OF SEASON. TIME OF DEATH AFTER INSEMINATION NOT MORE THAN 24 HOURS.

Specimen.	Weight in Ounces.	Number of Hours after Insemination.	Date of Death.	Size of Ovary in mm.³	Size of largest Follicle in mm.³	Number of Follicles of largest size.	Notes.
1. F. 3–5/08 Z.	?	19¾	31/5/08	37·582 000 000	2·328 422 400	7 all normal	The side to which each ovary belonged is uncertain. First polar body stage.
2. F. 1–2/08 Mann.	,,	,,	,,	20·657 000 000	1·840 302 000	3 ,,	
3. F.D.A. 41/15 R.Fl.	11½	21	2/6/15	15·886 293 600	·832 032 000	8 (2 deg.)	The ova in the large follicles were in the stage of the first maturation spindle stage.
4. ,, ,, L.Z.	,,	,,	,,	18·389 376 000	1·236 452 400	5 (3 deg.)	
5. P.D.B. 1/16 R.Mx.	24	Under 24	28/4/16	25·991 500 000	·533 360 800	6 all normal	The animal was dispatched from the trader in the same box with a male, but in a separate compartment. The compartment was broken in transit, and the female was killed 23 hours after it left the breeder's premises. Nucleus present. First maturation spindle not formed.
6. ,, ,, L.M.F.	,,	,,	,,	33·205 450 000	1·007 760 240	8 ,,	
7. F.Fl.R. 1·1/14	?	,,	26/5/14	31·835 546 875	1·471 335 936	2 both normal	Between 21 and 24 hours after insemination, but exact time uncertain. Some ova with first maturation spindle, some with first polar body.
8. F.Per.L. 1·1/14	,,	,,	,,	27·799 065 000	·725 760 000	6 all normal	
9. F.Z.R. 1/14	21	,,	,,	29·180 937 500	1·412 775 000	6 all normal	Between 21 and 24 hours after insemination, but exact time uncertain. First maturation spindle stage.
10. F.Fl.L. 1/14	,,	,,	,,	38·322 308 740	2·162 073 600	5 ,,	

TABLE VII.—FERRETS INSEMINATED AT FIRST ŒSTRUS OF SEASON. TIME OF DEATH AFTER INSEMINATION OVER 24 AND UNDER 49 HOURS.

Specimen.	Weight in Ounces.	Number of Hours after Insemination.	Date of Death.	Size of Ovary in mm.³	Size of largest Follicle in mm.³	Number of Follicles of largest size.	Notes.
1. F.D.A. 43/15 R.Mx.	21	26¼	9/6/15	41·343 120 000	1·253 070 000	5 all normal	In first polar body stage in ovary. In the right ovary there were two and in the left ovary three degenerate follicles slightly smaller than the normal follicles.
2. ,, ,, L.Fl.	,,	,,	,,	39·127 762 800	1·581 465 600	9 ,,	
3. F.G.B. 3/15 R.Fl.	16½	27½	23/4/15	34·215 640 625	1·353 081 600	5 ,,	In first polar body stage in ovary.
4. ,, ,, L.Z.	,,	,,	,,	40·381 035 968	1·433 700 000	6 ,,	
5. F.G.A. 1/15 R.Z.	22	,,	,,	38·598 906 250	1·380 744 000	7 ,,	First maturation spindle not yet formed. Nuclei of ova peripheral, but still with distinct nuclear membranes and no signs of mitosis.
6. ,, ,, L.Fl.	,,	,,	,,	21·081 098 750	1·089 262 080	1 normal	
7. F.D. D/16 R.Per.	?	30½	5/5/16	45·622 050 000	3·595 536 000	4 all normal	In first maturation spindle stage in ovary.
8. ,, ,, L.P.N.F.	,,	,,	,,	58·201 200 000	2·967 674 400	7 ,,	

TABLE VII.—*continued.*

Specimen.	Weight in Ounces.	Number of Hours after Insemination.	Date of Death.	Size of Ovary in mm.^{3}	Size of largest Follicle in mm.^{3}	Number of Follicles of largest size.	Notes.
9. P.D. C/16 R.M.F.	17½	31½	5/5/16	40·523 000 000	·947 700 000	4 all normal	Ova in middle third of uterine tube (oviduct) in pronuclear stage. Ruptured follicles plugged but not distended. In right ovary there were two unruptured degenerate follicles of ·251 856 000 mm.^{3}, and in the left ovary two unruptured normal follicles of ·634 752 000 mm.^{3}
10. ,, ,, L.Per.	,,	,,	,,	38·848 300 000	1·045 816 200	2 both normal	
11. P.D.B. 1/15 R.Z.	20	40½	29/4/15	27·446 265 000	3·736 789 200	3 all normal	In first maturation spindle stage in ovary.
12. ,, ,, L.Fl.	,,	,,	,,	41·136 861 600	1·620 259 200	5 ,,	
13. P.D.B. 2/15 R.Fl.	24	,,	29/4/15	23·522 238 000	1·444 752 000	3 ,,	In first maturation spindle stage in ovary.
14. ,, ,, L.Z.	,,	,,	,,	43·275 085 600	1·086 750 000	8 ,,	
15. F.D. F/16 R.Per.	19	40¾	7/5/16	41·908 536 000	·515 782 300	5 ,,	Ova in middle third of the oviduct in pronuclear stage. Ruptured follicles plugged but not distended. In right ovary five unruptured follicles of ·182 019 000 mm.^{3}, of which four were degenerate. In left ovary four unruptured follicles of ·099 792 000 mm.^{3}, all degenerate.
16. ,, ,, L.Mx.	,,	,,	,,	41·105 232 000	·725 760 000	5 ,,	
17. F.D. I/16 R.Per.	20	41	8/5/16	35·358 848 000	·826 096 000	3 ,,	Ova in middle third of the oviduct, some in pronuclear stage, some just fertilised with second spindle and first polar body. In right ovary four unruptured degenerated follicles of ·310 515 840 mm.^{3} In left ovary one unruptured degenerate follicle of ·324 161 520 mm.^{3}
18. ,, ,, L.M.F.	,,	,,	,,	49·956 480 000	1·370 880 000	7 ,,	
19. F.D. J/16 R.M.F.	15¾	41⅓	,,	31·408 128 000	·887 040 000	7 ,,	Ova in middle third of the oviduct in pronuclear stage. In right ovary four unruptured follicles of ·124 416 000 mm.^{3} In left ovary one unruptured follicle of ·140 808 240 mm.^{3} The ruptured follicles in the left ovary beginning to redistend.
20. ,, ,, L.Per.	,,	,,	,,	30·873 600 000	2·304 000 000	2 both normal	
21. F.G.A. 2/15 R.Fl.	16½	41⅓	25/4/15	36·281 250 000	1·940 389 600	12 all normal	In the right ovary some of the ova in the large follicles were in the first maturation spindle stage, others had not reached that stage. In the left ovary the ova of the large follicles were in the first maturation spindle stage or the first polar body stage.
22. ,, ,, L.Z.	,,	,,	,,	56·306 250 000	2·490 912 000	8 ,,	
23. F.G.B. 4/15 R.Per.	13	41½	,,	35·985 600 000	·772 761 600	4 ,,	Ova in middle third of the oviduct in pronuclear stage. In right ovary four unruptured follicles of ·586 872 000 mm.^{3}, all degenerate. In left ovary one unruptured follicle of 1·271 061 000 mm.^{3}, with ovum with first maturation spindle and a second follicle slightly smaller and degenerate.
24. ,, ,, L.Fl.	,,	,,	,,	26·939 808 000	·510 801 200	5 ,,	
25. F.D. G/16 R.M.F.	13½	,,	7/5/16	27·212 050 000	·538 783 200	3 ,,	Ova in middle third of the oviduct in pronuclear stage. In right ovary four unruptured follicles of ·142 128 000 mm.^{3}, of which two were degenerate. In left ovary three unruptured follicles of ·167 961 000 mm.^{3}, of which one was degenerate. The ruptured follicles had not commenced to distend.
26. ,, ,, L.Per.	,,	,,	,,	35·417 088 000	·524 880 000	5 ,,	

TABLE VII.—*continued.*

Specimen.	Weight in Ounces.	Number of Hours after Insemination.	Date of Death.	Size of Ovary in mm.^{3}	Size of largest Follicle in mm.^{3}	Number of Follicles of largest size.	Notes.
27. F.Mx.R. 1·1^2/14 .	?	44½	8/4/14	20·950 200 000	·465 585 120	3 all normal	The first maturation spindle had not yet formed. The spermatozoa in the oviduct and uterus were very few.
28. F.Per.L. 1·1^2/14 .	,,	,,	,,	26·986 500 000	·456 805 400	5 ,,	
29. F.D. K/16 R.Per. .	16	44⅔	10/5/16	51·004 800 000	·938 936 400	3 ,,	The ova were in the middle third of the oviduct in the pronuclear stage. The ruptured follicles were contracted and plugged. In the right ovary there were seven unruptured follicles of ·085 708 800 mm.^{3}, of which one was degenerate. In the left ovary there were six unruptured follicles of ·083 721 600 mm.^{3}, of which one was degenerate.
30. ,, ,, L.M.F. .	,,	,,	,,	44·248 780 000	·912 192 000	6 ,,	
31. F.Z.R. 1^2/14 . .	?	45½	,,	25·519 500 000	·677 784 400	4 ,,	The first maturation spindle had not yet formed. The spermatozoa in the uterus and oviduct were very few.
32. F.Fl.L.1^2/14 . .	,,	,,	,,	24·777 500 000	·534 518 640	4 ,,	
33. F.Mann.R. 1·2^2/14 .	,,	,,	,,	25·624 350 000	·276 236 120	2 both normal	The first maturation spindle had not yet formed. The spermatozoa in the uterus and oviduct were very few.
34. F.Len.L. 1·2^2/14 .	,,	,,	,,	37·691 250 000	·779 188 420	7 all normal	
35. P.G.A. 3/15 R.Fl. .	19¾	47½	26/4/15	37·311 750 000	·880 308 800	3 ,,	The ova were in the middle third of the oviduct. One ovum on the right side was in the 2-cell stage, the other two were in the pronuclear stage. The ova on the left side were in the first polar body stage or the pronuclear stage. The ruptured follicles were beginning to distend. In the right ovary there were two unruptured follicles of ·232 696 800 mm.^{3}, both degenerate. In the left ovary there was one unruptured follicle of 1·741 344 000 mm.^{3}, with the ovum in the first maturation spindle stage, and four unruptured follicles of ·160 923 840 mm.^{3}, all degenerate.
36. ,, ,, L.Z. .	,,	,,	,,	45·941 210 000	·799 200 000	5 ,,	
37. F.G.B. 5/15 R.Z. .	17½	,,	,,	43·273 350 000	·679 680 000	7 ,,	The ova were in the middle third of the oviduct in the stage of fusion of the pronuclei. In the right ovary there were four unruptured follicles of 1·705 017 600 mm.^{3}, one in first maturation spindle stage, one in first polar body stage, others younger, and all showing signs of degeneration. In the left ovary there were four unruptured follicles of ·379 848 000 mm.^{3}, all degenerated.
38. ,, ,, L.Fl. .	,,	,,	,,	35·593 750 000	·612 320 000	4 ,,	
39. F.D.A. 33/15 R.Fl.	16½	,,	12/5/15	17·769 375 000	·760 838 400	2 both normal	The ova were in the middle third of the oviduct in the pronuclear stage. In the right ovary there were two unruptured follicles of ·118 117 400 mm.^{3}, both degenerate. In the left ovary there were three unruptured follicles of ·734 976 000 mm.^{3}, all degenerate. The ruptured follicles in the left ovary were beginning to distend.
40. ,, ,, L.Z.	,,	,,	,,	26·462 592 000	1·143 072 000	4 all normal	

Table VIII.—Ferrets and Ferret-Polecat Hybrids Inseminated at First Œstrus of Season. Time of Death after Insemination over 48 and under 73 hours.

Specimen.	Weight in Ounces.	Number of Hours after Insemination.	Date of Death.	Size of Ovary in mm.^{3}	Size of largest Follicle in mm.^{3}	Number of Follicles of largest size.	Notes.
1. F.D.A. 38/15 R.Fl.	14	51¾	29/5/15	16·798 377 500	·410 400 000	3 all normal	The ova were in the middle third of the oviduct, in the pronuclear stage. In the right ovary there was one unruptured follicle of ·471 744 000 mm.^{3} degenerate. In the left ovary there were two unruptured follicles of ·340 982 000 mm.^{3} degenerate. The ruptured follicles had not begun to distend.
2. „ „ L.Z.	„	„	„	17·392 976 250	·704 418 400	2 both normal	
3. P.D.A. 31/15 R.Z.	21	53½	7/5/15	41·103 036 900	1·945 944 000	7 all normal	The ova were in the lower part of the middle third of the oviduct, some in 1-, some in the 2-cell stage. In the right ovary there were three unruptured follicles of ·544 056 000 mm.^{3}, all degenerate. In the left ovary there were seven unruptured follicles of ·516 096 000 mm.^{3}, all degenerate. The ruptured follicles of the right ovary were partially distended.
4. „ „ L.Fl.	„	„	„	36·956 160 000	·508 034 000	7 „	
5. F.G.A. 4/15 R.Fl.	16½	64	28/4/15	49·723 380 000	·836 352 000	7 „	The ova were in the lower part of the middle half of the oviduct, some in the 4-, some in the 8-cell stage. In the right ovary there were three unruptured follicles of ·241 488 000 mm.^{3}, all degenerate. In the left ovary there were seven unruptured follicles of ·254 826 000 mm.^{3}, all degenerate. Distension was commencing in the ruptured follicles.
6. „ „ L.Z.	„	„	„	49·286 250 000	·816 480 000	5 „	
7. P.G.B. 7/15 R.Z.	12	„	29/4/15	23·589 843 750	2·225 462 400	2 both normal	The ova were in the middle third of the oviduct in the 2-cell stage. In the right ovary there were four unruptured follicles of ·117 661 780 mm.^{3} degenerate. In the left ovary there were four unruptured follicles of ·210 375 000 mm.^{3} degenerate. The ruptured follicles were definitely distended.
8. „ „ L.Fl.	„	„	„	21·936 093 750	1·080 241 920	3 all normal	
9. F.G.A. 5/15 R.Fl.	16½	64½	„	18·207 000 000	1·189 881 000	3 „	The ova were in the lower part of the middle third of the oviduct, some in the 4-, some in the 8-cell stage. In the right ovary there was one unruptured follicle of 1·766 044 800 mm.^{3} degenerate. In the right ovary there were five unruptured follicles of ·187 246 080 mm.^{3} degenerate. In the left ovary there were four unruptured follicles of ·249 687 795 mm.^{3} degenerate. Distension of the ruptured follicles was definite.
10. „ „ L.Z.	„	„	„	29·347 683 750	1·950 342 880	6 „	

TABLE VIII.—*continued.*

Specimen.	Weight in Ounces.	Number of Hours after Insemination.	Date of Death.	Size of Ovary in mm.^{3}	Size of largest Follicle in mm.^{3}	Number of Follicles of largest size.	Notes.
11. F.G.B. 6/15 R.Z.	12	65	28/4/15	26·212 725 200	2·187 360 000	3 all normal	The ova were in the lower part of the middle third of the oviduct in the 4-cell stage. In the right ovary there were five unruptured follicles of ·491 803 200 mm.^{3} degenerate. In the left ovary there were six unruptured follicles of ·703 800 000 mm.^{3} degenerate. The ruptured follicles in the right ovary were definitely distended.
12. ,, ,, L.Fl.	,,	,,	,,	26·068 037 980	·574 560 000	4 ,,	
13. P.G.B. 8/15 R.Z.	17	67	1/5/15	33·468 750 000	2·358 720 000	3 ,,	The ova were in the middle third of the oviduct in the 4-cell stage. In the right ovary there were five unruptured follicles of ·491 803 200 mm.^{3}, all degenerate. In the left ovary there were six unruptured follicles of ·703 800 000 mm.^{3}, all degenerate. Some of the ruptured follicles were almost completely distended.
14. ,, ,, L.Fl.	,,	,,	,,	33·500 000 000	1·506 600 000	7 ,,	
15. F.G.A. 6/15 R.Fl.	18	68	,,	31·706 375 000	1·390 802 400	3 ,,	On the right side two ova were in the middle third of the oviduct, one in the 4-cell and one in the 2-cell stage. One ovum was in the ovarian pouch in the first polar body stage. On the left side the ova were in the middle third of the oviduct, one still undivided, and four in the 4-cell stage. In the right ovary one unruptured normal follicle and five unruptured degenerate follicles of ·774 040 000 mm.^{3} In the left ovary three unruptured follicles of 1·890 029 800 mm.^{3}, with ova in first spindle stages. The ruptured follicles were partly distended.
16. ,, ,, L.Z.	,,	,,	,,	30·345 000 000	1·642 291 200	5 ,,	
17. F. 22–23/08 Mann. .	?	69½*	. .	17·770 462 500	1·151 073 000	3 ,,	The first maturation spindles had not yet formed. There were very few sperms in the lower part of the oviduct. Side to which ovary belonged not known.
18. F. 12–14/08 Z.	,,	,,	5/4/08	61·992 000 000	1·416 600 000	6 ,,	The ova were not yet in the first spindle stage. The sperms in the lower part of the oviduct were not numerous. Side to which each ovary belonged not recorded.
19. G. 25–26/08 Mann.	,,	,,	,,	43·761 000 000	·721 201 400	6 ,,	
20. F. 15–17/08 Mann.	,,	,,	,,	19·068 750 000	·856 517 760	5 ,,	The ova were not yet in the first spindle stage. The sperms in the lower part of the oviduct were few. The side to which each ovary belonged not recorded.
21. F. 24–27/08 Z.	,,	,,	,,	25·110 000 000	1·058 400 000	6 ,,	
22. F.D.A. 21/15 R.Z.	21	69¾	29/4/15	23·931 093 750	1·628 640 000	3 ,,	The ova were in the lower part of the middle third of the oviduct, some in the 4-cell, some in the 8-cell stage. The ruptured follicles were closed and almost fully distended. In the right ovary there were three follicles of ·190 969 920 mm.^{3}, of which two were degenerate. In the left ovary there were numerous follicles of ·024 235 200 mm.^{3}, both normal and degenerate.
23. ,, ,, L.Fl.	,,	,,	,,	27·287 195 040	1·140 480 000	5 ,,	

TABLE VIII.—*continued.*

Specimen.	Weight in Ounces.	Number of Hours after Insemination.	Date of Death.	Size of Ovary in mm.^{3}	Size of largest Follicle in mm.^{3}	Number of Follicles of largest size.	Notes.
24. F.D.A. 22/15 R.Fl.	17	70	29/4/15	22·796 425 000	1·968 320 000	4 all normal	The ova were in the lower part of the middle third of the oviduct, some in the 8-, some in the 10-cell stage. The ruptured follicles were moderately distended. In the right ovary there were seven unruptured follicles of ·072 331 840 mm.^{3}, of which three were degenerate. In the left ovary there were two unruptured follicles of ·127 872 000 mm.^{3}, both degenerate.
25. ,, ,, L.Z.	,,	,,	,,	22·545 056 250	1·221 158 400	6 ,,	
26. F.D.A. 23/15 R.Z.	18½	,,	,,	29·772 343 750	1·544 212 800	3 ,,	The ova were in the lower part of the middle third of the oviduct, some in the 8-, some in the 10-cell stage. The ruptured follicles were distended. In the right ovary were two unruptured follicles of ·147 840 000 mm.^{3} degenerate. In the left ovary were four unruptured follicles of ·126 905 120 mm.^{3} degenerate.
27. ,, ,, L.Fl.	,,	,,	,,	29·949 306 250	1·118 476 800	6 ,,	
28. F.G.A. 10/15 R.Fl.	12½	72	31/5/15	16·731 750 000	1·837 404 000	1 normal	The ova were in the middle third of the oviduct, some in the 4-, some in the 8-cell stage. The ruptured follicles were distended, especially on the left side. In the right ovary were three degenerate unruptured follicles of ·115 394 400 mm.^{3} In the left ovary were two degenerate unruptured follicles of ·346 959 360 mm.^{3}
29. ,, ,, L.Z.	,,	,,	,,	44·261 100 000	2·539 641 600	7 all normal	
30. F.G.B. 9/15 R.Fl.	14¾	,,	4/5/15	18·791 797 000	·623 920 000	2 both normal	The ova were in the middle third of the oviduct, some in the 2-, some in the 4-cell stage. The ruptured follicles had begun to distend. In the right ovary was one degenerate follicle of ·355 924 800 mm.^{3} In the left ovary were six degenerate follicles of ·091 332 000 mm.^{3}
31. ,, ,, L.Z.	,,	,,	,,	31·104 000 000	·844 240 000	3 all normal	

[TABLE IX.

TABLE IX.—FERRETS AND FERRET-POLECAT HYBRIDS INSEMINATED AT THE FIRST ŒSTRUS OF THE SEASON. TIME OF DEATH AFTER INSEMINATION OVER 72 AND UNDER 97 HOURS.

Specimen.	Weight in Ounces.	Number of Hours after Insemination.	Date of Death.	Size of Ovary in mm.^{3}	Size of largest Follicle in mm.^{3}	Number of Follicles of largest size.	Notes.
1. F.D.A. 44/15 R.Fl. .	13½	74	19/6/15	33·239 808 000	2·078 600 000	3 all normal	The ova were in the middle third of the oviduct, some in the 3-, some in the 4-cell stage. The ruptured follicles were distended. In the right ovary were four degenerate follicles of ·315 872 000 mm.^{3} In the left ovary was one follicle of degenerate epithelium, and with an ovum in the first polar body stage. The follicle measured ·886 356 000 mm.^{3}
2. ,, ,, L.Mx. .	,,	,,	,,	20·528 640 000	1·980 576 000	4 ,,	
3. F.G.A. 7/15 R.Z. .	15	76	4/5/15	30·840 328 800	3·036 217 400	8 ,,	The ova were in the uterus, some in the 1-, some in the 2-, and one in the 4-cell stage, and all were degenerate. In the right ovary were three unruptured degenerate follicles of ·173 880 000 mm.^{3} In the left ovary were four unruptured degenerate follicles of ·090 248 000 mm.^{3} The ruptured follicles were distended.
4. ,, ,, L.Fl. .	,,	,,	,,	39·180 625 000	3·045 168 000	8 ,,	
5. P.D.A. 5/15 R.Per. .	20½	76½	22/4/15	21·356 055 000	·607 500 000	3 ,,	The ova were in the middle third of the oviduct in the stage of fusing pronuclei. The ruptured follicles were not distended. In the right ovary was one unruptured degenerate follicle of ·186 263 600 mm.^{3} In the left ovary were four unruptured degenerate follicles of ·077 760 000 mm.^{3}
6. ,, ,, L.Fl. .	,,	,,	,,	29·804 709 375	·665 280 000	7 ,,	
7. F. 1 27–28/08 Z.	?	93½	5/4/08	29·204 331 250	1·451 980 800	3 ,,	The ova were in the lower part of the middle third of the oviduct, some in the 7-, some in the 8-, and some in the 9-cell stage. The ruptured follicles were distended, and there were signs of lutein formation. In the right ovary were four normal unruptured follicles of ·269 892 000 mm.^{3} In the left ovary were three normal unruptured follicles of ·140 616 000 mm.^{3} The sides to which the ovaries belonged is uncertain.
8. F. 1·1 29–30/08 Mann.	,,	,,	,,	16·334 156 250	1·136 851 200	5 ,,	
9. F. 1·2 31–34/08 Mann.	,,	,,	,,	48·129 900 000	1·932 096 000	8 normal 3 degenerate	The follicles were unruptured, and contained ova either in the first spindle stage or the first polar body stage. In addition ovary 31–34 contained three degenerate follicles of ·184 680 000 mm.^{3}, and the ovary 35–37 contained twelve degenerate follicles of ·200 250 000 mm.^{3} The sides to which the ovaries belonged is uncertain.
10. F. 1·3 35–37/08 Z.	,,	,,	,,	56·772 000 000	2·938 328 000	3 all normal	

TABLE IX.—*continued.*

Specimen.	Weight in Ounces.	Number of Hours after Insemination.	Date of Death.	Size of Ovary in mm.^{3}	Size of largest Follicle in mm.^{3}	Number of Follicles of largest size.	Notes.
11. F. 1·4 G. 1–2/08 M. .	?	94½	16/4/08	25·699 850 000	·889 056 000	3 all normal	The ova were in the middle third of the oviduct, some in the pronuclear stage, and some in the stage of the first division. The ruptured follicles were partially or completely distended. In the ovary G 1–2 there were five degenerate follicles of ·154 242 720 mm.^{3} In the ovary G 3–5 there were five degenerate follicles of ·180 633 600 mm.^{3} The sides to which the ovaries belonged is uncertain.
12. F. 1·5 G. 3–5/08 Z. .	,,	,,	,,	56·594 375 000	1·995 022 000	7 ,,	
13. P.D. M/16 R.M.F. .	14½	,,	13/5/16	33·125 760 000	1·933 282 880	3 abnormal 2 normal	Most of the ova were in the lower third of the oviduct in the morula stage, with not less than 14 cells. One ovum on the right side was in the ovarian pouch, and was degenerated. One ovum on the left side was in the lower third of the oviduct in the 1-cell stage, and was abnormal. In the right ovary were six unruptured follicles of ·071 064 000 mm.^{3}, of which one was degenerate. In the left ovary were three normal unruptured follicles of ·200 970 000 mm.^{3} The ruptured follicles were distended.
14. ,, ,, L.Per. .	,,	,,	,,	56·842 560 000	1·640 380 080	5 abnormal 7 normal	
15. F.D. W/16 R.Per. .	17½	95	21/5/16	40·166 784 000	1·651 104 000	6 all normal	The ova were in the lower third of the oviduct in the morula stage (about 12 cells). The ruptured follicles were distended. In the right ovary were four unruptured degenerate follicles of ·764 640 000 mm.^{3} In the left ovary was one unruptured degenerate follicle of 2·000 700 000 mm.^{3}
16. ,, ,, L.Mx. .	,,	,,	,,	35·834 400 000	1·553 378 000	3 ,,	
17. F.Mx.R. 1·1 4^d/14 .	?	95½	12/4/14	36·978 913 125	1·862 784 000	1 abnormal 5 normal	The ova were in the lower third of the oviduct in the morula stage, some of about 12, others of about 20 cells. The ruptured follicles were distended. In the right ovary were two normal unruptured follicles of ·128 520 000 mm.^{3} In the left ovary were three normal unruptured follicles of ·086,788,800 mm.^{3}, and one unruptured degenerate follicle of same size.
18. F.Per. L. 1·1 4^d/14 .	,,	,,	,,	27·221 250 000	·973 477 440	1 abnormal 1 normal	

[TABLE X.

TABLE X.—FERRETS AND FERRET-POLECAT HYBRIDS INSEMINATED AT THE FIRST ŒSTRUS OF THE SEASON. TIME OF DEATH AFTER INSEMINATION OVER 96 AND UNDER 121 HOURS.

Specimen.	Weight in Ounces.	Number of Hours after Insemination.	Date of Death.	Size of Ovary in mm.^{3}	Size of largest Follicle in mm.^{3}	Number of Follicles of largest size.	Notes.
1. F. 1·1/04 G 8 Mann.	?	116½	7/5/04	27·677 672 400	1·355 270 400	4 all normal	The ova were in the middle third of the oviduct in the pronuclear stage. The ruptured follicles were distended. In ovary G 8 there was one unruptured degenerate follicle of 1·336 500 000 mm.^{3} which contained an ovum in the first spindle stage. In the ovary G 10 there were two unruptured degenerate follicles of ·111 825 000 mm.^{3} The side to which each ovary belonged is uncertain.
2. F. 1·2/04 G 10 Z.	,,	,,	,,	33·409 950 000	2·193 408 000	4 ,,	
3. F. 1·3/04 G 12 Mann.	,,	,,	,,	20·235 807 190	3·171 571 200	4 ,,	The ova were in the cranial part of the lower third of the oviduct, some in the 8- and some in the 12-cell stage. The ruptured follicles were distended. In ovary G 12 were three unruptured degenerate follicles of ·115 153 920 mm.^{3} In ovary G 14 was one unruptured degenerate follicle of ·321 235 200 mm.^{3} The side to which each ovary belonged is uncertain.
4. F. 1·4/04 G 14 Z.	,,	,,	,,	30·706 250 000	4·177 958 400	6 ,,	
5. F. 1·5/04 G 17 Mann.	,,	117½	23/4/04	43·499 531 250	2·195 726 400	4 ,,	The ova were in the caudal third of the oviduct in the morula stage of about 20 cells. The ruptured follicles were distended. In ovary G 17 were two unruptured degenerate follicles of ·619 718 400 mm.^{3} In ovary G 19 was one unruptured degenerate follicle of 4·865 112 000 mm.^{3}, containing a degenerate ovary, and with the follicle wall becoming luteal. The side to which each ovary belonged is uncertain.
6. F. 1·6/04 G 19 Z.	,,	,,	,,	34·420 156 250	1·862 784 000	5 ,,	
7. F. 1·7/04 G 21 Mann.	,,	,,	,,	23·326 875 000	2·406 487 200	4 ,,	The ova were in the caudal third of the oviduct in the morula stage with many cells. The ruptured follicles were redistended. In the right ovary was one unruptured degenerate follicle of ·376 992 000 mm.^{3} In the left ovary were six unruptured degenerate follicles of ·049 920 000 mm.^{3} The side to which each ovary belonged is uncertain.
8. F. 1·8/04 G 23 Z.	,,	,,	,,	28·411 175 000	1·693 094 400	6 ,,	
9. P.Z.R. 1/14	,,	119½	26/4/14	30·188 276 250	1·675 696 000	5 ,,	The ova were in the caudal third of the oviduct in the morula stage of about 20 cells. The ruptured follicles were redistended. In the right ovary were four unruptured abnormal follicles of 1·053 360 000 mm.^{3}, with ova in the first spindle or first polar body stage. In the left ovary were five abnormal unruptured follicles of 1·591 200 000 mm.^{3}
10. P.Fl.L. 1/14	,,	,,	,,	43·157 625 000	2·462 140 800	5 ,,	
11. P.Mann.R. 1·2/14	,,	120	,,	21·745 899 000	·656 064 000	8 ,,	The ova were in the caudal third of the oviduct in the morula or commencing blastula stage. The ruptured follicles were redistended. In the right ovary were two unruptured degenerate follicles of ·056 200 000 mm.^{3} In the left ovary were five unruptured degenerate follicles of ·076 608 000 mm.^{3}
12. P.Len.L. 1·2/14	,,	,,	,,	27·522 450 000	·907 200 000	3 ,,	

TABLE XI.—FERRET AND FERRET-POLECAT HYBRIDS INSEMINATED AT THE FIRST ŒSTRUS OF THE SEASON. TIME OF DEATH AFTER INSEMINATION OVER 120 AND UNDER 145 HOURS.

Specimen.	Weight in Ounces.	Number of Hours after Insemination.	Date of Death.	Size of Ovary in mm.^{3}	Size of largest Follicle in mm.^{3}	Number of Follicles of largest size.	Notes.
1. P.D. N/16 R.Per.	14½	120½	17/5/16	47·076 019 200	2·057 745 600	5 normal 5 abnormal	The ova were in the caudal third of the oviduct in the morula stage of about 12 cells. The ruptured follicles were redistended. In the right ovary were two unruptured follicles ·185 724 000 mm.^{3}, one becoming luteal. In the left ovary were four unruptured follicles ·205 128 000 mm.^{3}, all luteal and three degenerate.
2. ,, ,, L.Fl.	,,	,,	,,	48·553 344 000	1·373 888 160	6 normal 7 abnormal	
3. P.G.A. 16 B/15 R.Mx.	17	122½	22/6/15	37·739 520 000	1·417 950 000	8 all normal	The ova were in the middle third of the oviduct, some in the 1-cell and others in the 4-cell stage. Some of the ova in the 1-cell stage were abnormal. The ruptured follicles were redistended. In the right ovary were six unruptured follicles ·271 209 600 mm.^{3}, of which three were degenerate, and one of the three was luteal. In the left ovary were eight unruptured follicles ·534 600 000 mm.^{3}, of which five were degenerate, and of these three were luteal.
4. P.G.A. 16 B/15 L.Fl.	,,	,,	,,	26·578 175 000	1·004 400 000	6 ,,	
5. F.D. T/16 R.Per.	16½	123⅓	20/5/16	24·155 820 000	1·945 866 240	1 normal	The ova were in the caudal third of the oviduct, some in the 8- and some in the 10-cell stage. The ruptured follicles were redistended. In the right ovary were eight unruptured follicles ·157 172 400 mm.^{3}, of which three were degenerate. In the left ovary were five unruptured follicles ·099 290 800 mm.^{3}, of which one was degenerate.
6. ,, ,, L.M.F.	,,	,,	,,	42·021 504 000	1·453 140 000	5 normal 1 abnormal	
7. F. 1·5 H. 8/08 R.Z.	?	139¾	7/5/08	48·785 156 250	1·766 793 600	9 all normal	The ova were in the uterus in the blastula stage. The ruptured follicles were redistended. In No. 7 were seven unruptured follicles ·159 224 000 mm.^{3}, of which three were degenerate. In No. 8 were nine unruptured follicles ·245 674 080 mm.^{3}, of which six were degenerate, and one of these was luteal.
8. F. 1·6 H. 6/08 L.Z.	,,	,,	,,	26·146 601 250	1·422 230 400	7 ,,	
9. F. 1·9 H. 10/08 R.Mann.	,,	140¼	2/5/08	21·535 552 500	1·560 971 520	5 ,,	The ova were in the uterus in the blastula stage. The ruptured follicles were redistended. In No. 9 were three unruptured follicles ·101 361 200 mm.^{3}, of which one was degenerate. In No. 10 were three unruptured follicles ·086 860 800 mm.^{3}, all normal.
10. F. 1·10 H. 1/08 L.Z.	,,	,,	,,	15·184 800 000	1·543 050 000	2 both normal	
11. F. 1·11 H. 3/08 R.Mann.	,,	140½	7/5/08	32·701 016 250	1·551 420 000	2 ,,	One ovum was in the caudal end of the oviduct in the morula stage. The others were in the cranial part of the uterus in the blastula stage. The ruptured follicles were redistended and luteal. In No. 11 were seven unruptured follicles ·128 493 420 mm.^{3}, of which four were degenerate. In No. 12 were three unruptured follicles ·195 854 400 mm.^{3}, all normal.
12. F. 1·8 G. 37/08 L.Z.	,,	,,	,,	15·497 133 750	·817 080 000	2 ,,	

TABLE XI.—*continued.*

Specimen.	Weight in Ounces.	Number of Hours after Insemination.	Date of Death.	Size of Ovary in mm.^{3}	Size of largest Follicle in mm.^{3}	Number of Follicles of largest size.	Notes.
13. F. 1·3 G. 35/08 Mann.	?	$140\frac{3}{4}$	30/4/08	32·922 540 000	1·289 389 200	4 all normal	The ova were in the caudal part of the oviduct in the morula stage. The ruptured follicles were redistended and luteal. The side to which each ovary belonged is uncertain. In No. 13 were four unruptured follicles ·045 158 400 mm.^{3}, of which three were degenerate. In No. 14 were five unruptured follicles ·110 376 000 mm.^{3}, all normal.
14. F. 1·4 G. 31/08 Z.	,,	,,	,,	39·503 750 000	2·287 000 000	5 ,,	
15. P.Mx.R. 1·1^6/14 .	19	144	1/5/14	28·306 026 000	3·122 841 600	1 abnormal 9 normal	Some of the ova were in the caudal part of the oviduct in the morula stage, others were in the cranial part of the uterus, some in the morula stage and some in the early blastula stage. The ruptured follicles were redistended and luteal. In the right ovary were three unruptured follicles of ·103 774 608 mm.^{3}, of which one was degenerate. In the left ovary were four unruptured follicles of ·031 303 920 mm.^{3}, of which one was degenerate.
16. P.Per.L. 1·1^6/14 .	,,	,,	,,	25·909 632 000	1·086 750 000	7 all normal	
17. F.D.A. 28/15 R.Z. .	,,	143	2/5/15	43·223 687 500	1·875 200 000	5 ,,	The ova were in the caudal third of the oviduct in the morula stage. The ruptured follicles were all closed, redistended, and luteal. In the right ovary were twelve unruptured follicles (of which three were degenerate) of ·171 417 600 mm.^{3} In the left ovary were three normal unruptured follicles of ·157 132 800 mm.^{3}
18. ,, ,, L.Fl. .	,,	,,	,,	43·160 386 880	1·632 960 000	5 ,,	
19. F.Mann.R. 1·2^6/15 .	17	$144\frac{1}{6}$	1/5/14	22·297 680 000	1·412 460 000	4 ,,	Some of the ova were in the caudal part of the uterine tube in the morula stage, others were in the cranial part of the uterus in the early blastula stage. The ruptured follicles were redistended and luteal. In the right ovary were two normal unruptured follicles of ·216 940 800 mm.^{3} In the left ovary were two normal unruptured follicles of ·032 125 520 mm.^{3}
20. F.Len.L. 1·2^6/15 .	,,	,,	,,	17·694 720 000	1·176 940 000	4 ,,	
21. F. 1 G. 27/08 Z.	?	144	23/4/08	46·786 162 500	2·467 584 000	6 ,,	The ova were in the cranial part of the uterus in the blastula stage. The ruptured follicles were redistended and luteal. The side to which each ovary belonged is uncertain.
22. F. 1·1 G. 33/08 Mann.	,,	,,	,,	28·622 896 250	1·617 408 000	4 ,,	

TABLE XII.—FERRETS INSEMINATED AT SECOND ŒSTRUS.

Specimen.	Weight in Ounces.	Number of Hours after Insemination.	Number of Days Post-partum or Post-abortion.	Date of Death.	Size of Ovary in mm.^{3}	Size of largest Follicle in mm.^{3}	Number of Follicles of largest size.	Notes.
1. F.D.A. 39/15 R.Z.	16	24	22	30/4/15	21·441 024 000	2·105 064 000	3 all normal	Ova of second pregnancy in first polar body stage. Young of first pregnancy were cast on May 8, 1915. The animal was in full heat on May 29, 1915, and was killed after insemination on May 30, 1915.
2. ,, ,, L.Fl.	,,	,,	,,	,,	36·824 470 000	1·819 584 000	6 ,,	
3. F. 6–9/08 Z.	?	43½	?	23/5/08	24·178 500 000	·720 824 000	4 ,,	The side to which the ovaries belong is uncertain. The ova in both cases were in the middle third of the oviduct in the first polar body stage. Some were fertilised, others were not fertilised. In ovary 3 there were seven old corpora lutea. In ovary 4 there were two old corpora lutea.
4. F. 10–11/08 Mann.	,,	,,	,,	,,	17·227 000 000	·628 560 000	8 ,,	
5. F. 18–19/08 R.Mann.	,,	65⅙	,,	,,	35·709 375 000	2·046 179 200	5 ,,	The ova were in the lower part of the middle third of the oviduct, some in the 7- and others in the 9-cell stage. In the right ovary there were two large unruptured follicles, one of ·894 240 000 mm.^{3}, one of 1·272 290 000 mm.^{3}, both with ova in the first polar body stage. In the left ovary there was one follicle of 1·089 849 600 mm.^{3} with ovum in first spindle stage, and one follicle of ·406 378 000 mm.^{3} with unripe ovum. The ruptured follicles were closed and distended. Four corpora lutea of previous pregnancy were present in each ovary.
6. 20–21/08 L.Z.	,,	,,	,,	,,	25·100 000 000	1·645 712 640	4 ,,	
7. F.G.A. 11/15 R.Z.	13¾	69	,,	31/5/15	27·845 141 060	1·550 016 000	3 ,,	The ova were in the middle third of the oviduct; two of those on the right side were in the 4-cell stage and one in the 3-cell stage. On the left side three were in the 4-cell stage and one in the 2-cell stage. In the right ovary there were four unruptured follicles of ·087 768 000 mm.^{3}, of which three were degenerate. In the left ovary there were five unruptured follicles of ·251 164 800 mm.^{3}, of which four were degenerate. The ruptured follicles were partially distended. In the right ovary four corpora lutea of the previous pregnancy. In the left ovary seven corpora lutea of the previous pregnancy.
8. ,, ,, L.Fl.	,,	,,	,,	,,	34·166 643 600	1·144 044 000	4 ,,	

TABLE XII.—*continued.*

Specimen.	Weight in Ounces.	Number of Hours after Insemination.	Number of Days Post-partum or Post-abortion.	Date of Death.	Size of Ovary in mm.^{3}	Size of largest Follicle in mm.^{3}	Number of Follicles of largest size.	Notes.
9. F.D. Z^3/16 R.Per.	17	17	?	3/7/16	18·576 000 000	·875 427 840	3 all normal	The ova from the ruptured follicles of the second œstrus were in the caudal third of the oviduct in the morula stage of many cells, except one which was degenerate and unfertilised. The ruptured follicles were definitely luteal. In the left ovary there was a large unruptured follicle of 2·574 400 000 mm.^{3}, with walls becoming luteal, and three degenerate unruptured follicles of ·152 182 800 mm.^{3} In the right ovary were three degenerate unruptured follicles of ·062 640 000 mm.^{3}
10. ,, ,, L.Fl.	,,	,,	,,	,,	38·074 176 000	·920 160 000	6 ,,	

EXPLANATION OF FIGURES IN THE PLATES.

A.	Artery.
A.f.	Cavity of ovarian follicle.
A.p.f.	Aperture of ruptured follicle.
B.o.c.	Base of ovarian cumulus.
B.v.	Blood-vessel.
B.vs.	Blood-vessels.
C.	Centrosome.
C.o.	Ovarian cumulus.
C.p.o.	,, capsule.
C.r.	Corona radiata.
C.r.e.	,, ,, epithelium.
C.t.c.	Connective-tissue cell.
C.t.o.	Cortex ovarii.
C.t.t.	Tubule of cortex.
D.f.	Degenerate follicle.
D.fs.	,, follicles.
E.f.	Follicular epithelium.
E.o.	Escaping ovum.
F.a.	Atresic ovarian follicle.
F.g.	Fat granules.
Fl.o.	Ovarian follicle.
Fl.os.	Ovarian follicles.
F.o.	Surface of ovary.
F.s.	Fibrous stroma.
I.c.	Interstitial cell.
I.cs.	,, cells.
L.f.	Liquor folliculi.
L.f.p.	Primary liquor folliculi.
L.f.s.	Secondary ,, ,,
L.f.t.	Tertiary liquor folliculi.
L.v.	Lymph vessel.
M.e.	Membrana externa.
M.i.	,, interna.
Minl.	Nucleus in mitosis.
M.o.	Medula ovarii.
M.s.p. 1.	First maturation spindle.
M.s.p. 2.	Second ,, ,,
N.	Needle in opening of ovarian capsule.
Nl.	Nucleus.
Nll.	Nucleolus.
O.	Ovum.
O.c.	Opening of ovarian capsule.
Od.	Oviduct.
Ol.	Oolemma.
Pl.	Plug in aperture of ruptured follicle.
Pv.s.	Perivitelline space.
R.f.	Ruptured follicle.
S.c.	Stroma cell.
S.cs.	Stroma cells.
Sp.c.st.	Spindle-cell stroma.
St.l.f.p.	Stroma of the primary liquor folliculi.
St.l.f.t.	,, ,, tertiary ,, ,,
St.v.f.	Vascular layer of wall of follicle.
T.a.	Tunica albuginea.
U.c.	Uterine cornu.
V.	Vein.
V.c.	Vitellogenous crescent.
W.b.c.	White blood corpuscles.

PLATE I.

Fig. 1. Surface view of the ovarian capsule and the cranial end of the uterine cornu of a ferret. × 1·8. A needle is placed in the opening through which the cavity of the capsule communicates with the peritoneal cavity. The corresponding aperture is seen in section in fig. 2, together with an ovum which has just escaped through the aperture into the peritoneal cavity.

Fig. 2. Section of the ovary, ovarian capsule, and the cranial end of the uterine cornu of a ferret-polecat hybrid. × 11. The section traverses the opening through which the interior of the ovarian capsule communicates with the peritoneal cavity, and a recently extruded ovum is seen escaping into the peritoneal cavity between the uterine cornu and the apex of one of the fimbriæ of the cranial end of the oviduct. (Specimen P.D. C/16. L.Per. 31½ hours after insemination.) I.H. O.G.

Fig. 3. Section through the cortex of the ovary of a ferret, showing ovarian follicles of various sizes, some normal and some degenerate. Some of the follicles are situated superficially and others deeply in the cortex. × 65. (Specimen F.D. T/16. L.M.F. 123⅓ hours after insemination.) I.H. O.G.

Fig. 4. Section of several primitive ovarian follicles of a ferret. × 800. (Specimen F.G.A. 18/15. L.Mx. 32 days' œstrus.) I.H.

Fig. 5. Section of young ovarian follicles of a ferret. × 540. One of the follicles shows a surface view of the follicular epithelium. The other follicle has been cut obliquely, so that on one side a single layer of cubical epithelium is seen, and on the other side an oblique section through the cubical follicular cells is shown. (Specimen F.D. G/16. L.Per. 41½ hours after insemination.) I.H. O.G.

Fig. 6. Longitudinal section through an ovarian follicle of a ferret, showing the ovoid form of the follicle. × 800. The follicular epithelium is entering on the two-layered stage at one end of the follicle. (Specimen F.D.A. 42/15. R. 28 days post-partum and not in heat.)

Fig. 7. Section through an ovarian follicle of a ferret-polecat hybrid. × 540. The follicular epithelium is in the early part of the two-layered stage. (Specimen P.D. C/16. R.M.F. 31½ hours after insemination.) I.H. O.G.

PLATE II.

Fig. 8. Longitudinal section of an ovarian follicle of a ferret. × 350. Follicle and ovum are both ovoid. The follicular epithelium is in the early part of the three-layered stage. (Specimen F.Z.R.A. 10/15, anœstrus period.) I.H.

Fig. 9. Longitudinal section through an ovarian follicle of a ferret, showing the more rapid increase of the follicular cells at the poles of the follicle. × 540. (Specimen F.D. F/16. L.Mx. 40¾ hours after insemination.) I.H.

Fig. 10. Oblique section through an ovarian follicle of a ferret, showing the commencement of the cavity (antrum folliculi) of the follicle at one pole of the follicle. × 540. (Specimen F.D. G/16. R.M.F. 41½ hours after insemination.) I.H. O.G.

Fig. 11. Longitudinal section through an ovarian follicle of a ferret, showing a more advanced stage in the formation of the cavity of the follicle. × 540. (Specimen F.D. G/16. R.M.F. 41½ hours after insemination.) I.H. O.G.

Fig. 12. Section through an ovarian follicle of a ferret, showing changes in the follicle cells as the cavity of the follicle increases. × 549. (Specimen F.D. G/16. L.Per. 41½ hours after insemination.) I.H. O.G.

Fig. 13. Section through a part of a full-grown ovarian follicle of a ferret which was not inseminated though insemination was attempted, showing the strands of primary stroma which permeate the primary liquor folliculi and which are connected with the follicular epithelium. × 65. (Specimen F.Z.R. 1/14. 6d.) I.H.

PLATE III.

Fig. 14. Section through part of the ovarian follicle depicted in fig. 13. × 310. Showing the relation of the strands of the stroma of the primary liquor folliculi to the follicular epithelium and to the epithelium of ovarian cumulus.

Fig. 15. Section of an ovarian follicle of a ferret almost ready for ripening, showing the stalk of the

ovarian cumulus, and the separation of the cumulus cells into an outer group which will be dispersed, and an inner group which will form the corona radiata. The reticular character of the primary liquor folliculi is also shown. × 65. (Specimen P.D. C/16. 31 hours after insemination.) I.H. O.G.

Fig. 16. The ovarian cumulus and part of the wall of the follicle shown in fig. 15. × 310. Showing more definitely the separation of the cumulus cells into two groups, and the relationship of the reticulum of the primary liquor folliculi to the follicular cells and to the cells of the cumulus.

Fig. 17. Section through an ovarian follicle of a ferret 27½ hours after insemination, showing the commencing dispersion of the more external cumulus cells. × 55. The membrana interna is quite distinct on the inner surface of the follicular epithelium and on the outer surface of the cumulus. (Specimen F.G.A. 1/15. R.Z. 27½ hours.) I.H.

Fig. 18. Section through an ovarian follicle of a ferret 19¾ hours after insemination. × 30. The ovum is in the first maturation spindle stage, but the section does not pass through the spindle. The membrana interna surrounds the primary liquor folliculi. The secondary liquor folliculi is dispersing the outer cells of the ovarian cumulus, and is also beginning to force its way between the membrana interna and the inner surface of the follicular epithelium. (Specimen F. 3–5. Z. 1904.) H.E.

Fig. 19. Section through the ovarian follicle of a ferret 30½ hours after insemination. × 30. Part of the primary liquor folliculi has been coagulated and shrunk by the fixing fluid. The membrana interna has been separated from the follicular epithelium to a greater extent than in the specimen shown in fig. 18, and part of it has been dragged into folds by the contraction of the coagulated primary liquor folliculi. (Specimen F.D. D/16. L.P.N.F. 30½ hours.) I.H. O.G.

Fig. 20. Section through an ovarian follicle of a ferret 26¼ hours after insemination. × 30. The ovum was in the first polar body stage, but the polar body and the second spindle are not in the plane of the section. Although the amount of secondary liquor folliculi in the region of the cumulus is not greater than in the follicle shown in fig. 19, the membrana interna is separated from the follicular epithelium to a greater extent—that is, along the whole of one side and at the superficial part of the follicle. (Specimen F.D.A. 43/15. L.Fl. 26¼ hours.) E.

PLATE IV.

Fig. 21. Section through an ovarian follicle of a ferret 24 hours after insemination. × 30. The ovum was in the first polar body stage, and the polar body is seen as a black dot in the upper and left part of the ovum, close to the oolemma. The dispersion of the cumulus epithelium has proceeded to a greater extent than in the specimens shown in the previous figures; there is also a greater amount of secondary liquor folliculi, and a greater extent of separation of the membrana interna from the follicular epithelium. (Specimen F.D.A. 39/15. R.Z. 24 hours.) I.H.

Fig. 22. Section through an ovarian follicle of a ferret 19¾ hours after insemination. × 30. In this follicle the ovum was situated near the surface of the ovary, and was in the first maturation spindle stage, but the section does not pass through the plane of the spindle. There is greater dispersion of the cumulus epithelium than in the follicles shown in the preceding figures, and the membrana interna is separated from the follicular epithelium over more than a third of the superficial part of the wall of the follicle. (Specimen F. 3–5. Z. 1904. 19¾ hours.) H.E.

Fig. 23. Section through an ovarian follicle of a ferret 21 hours after insemination. × 30. The ovum was in the first maturation spindle stage, but the section does not pass through the plane of the spindle. The follicle is of smaller size than those shown in the preceding figures, and the dispersion of the cumulus epithelium is less advanced than in the follicle depicted in fig. 22, but the separation of the membrana interna from the follicular epithelium is more advanced. (Specimen F.D.A. 41/15. R.Fl. 21 hours.) I.H.

Fig. 24. Section through an ovarian follicle of a ferret 26¼ hours after insemination. × 30. The ovum was in the first polar body stage, but the section does not pass through the plane of the polar body. In the plane through which the section passes the membrana interna has been completely separated from the follicular epithelium by the secondary liquor folliculi. (Specimen F.D.A. 43/15. R.M. 26¼ hours.) I.H.

Fig. 25. Section through an ovarian follicle of a ferret 41⅓ hours after insemination. × 30. The

ovum was in the first polar body stage, but the polar body does not lie in the plane of the section. In the plane of section the membrana interna is separated from the follicular epithelium for some distance on each side of the cumulus, and the secondary liquor folliculi, extending more rapidly in a plane at right angles to the plane of the section, has reached the superficial part of the follicle, and in its progress, along a relatively narrow pathway, it has invaginated the membrana interna towards the centre of the follicle. (Specimen F.G.A. 2/15. R.Fl. 41$\frac{1}{3}$ hours.) E.

Fig. 26. Section through a recently ruptured ovarian follicle of a ferret 41$\frac{1}{2}$ hours after insemination. × 30. The ovum from the follicle is in the middle third of the oviduct in the pronuclear stage. A portion of the membrana interna is still adherent to the follicular epithelium on the lower part of the right-hand wall of the follicle, but the membrana interna has disappeared from the greater part of the area, and the cavity of the follicle is filled with liquor folliculi tertia, which plugs the orifice in the follicle wall. The liquor folliculi tertia consists of fluid interspersed with strands of fibrils which are connected with the follicle cells. (Specimen F.D. G/16. L.Per. 41$\frac{1}{2}$ hours.) I.H. O.G.

Fig. 26A. A portion of the lower and left part of the follicle shown in fig. 26. × 260. Showing the relation of the stroma of the tertiary liquor to the follicle cells. The plane of section is 20μ from that shown in fig. 26.

Fig. 26B. A portion of the floor of the follicle shown in fig. 26, in the same plane as the section shown in fig. 26B. × 260. Showing the characters of the follicular cells and the relation of the cells to the tertiary liquor.

PLATE V.

Fig. 27. Section through a ruptured ovarian follicle of a ferret 41 hours after insemination. × 30. The ovum from the follicle is in the middle third of the oviduct in the stage of fusing pronuclei. As contrasted with the follicle shown in fig. 26, the orifice of rupture is smaller, the wall is more folded, and the blood-vessels round the external periphery of the follicular epithelium are more numerous. (Specimen F.D. I/16. R.Per. 41 hours.) I.H. O.G.

Fig. 27A. Section through the orifice of a follicle in the same stage as that shown in fig. 27. × 260. Showing (*a*) the relation of the plug to the left-hand margin of the orifice, (*b*) white blood corpuscles in the liquor folliculi, (*c*) the relation of the strands of the tertiary liquor and the relation of the blood-vessels to the follicular epithelium. (Specimen F.D. I/16. R.Per. 41 hours.) I.H. O.G.

Fig. 27B. Section through a part of the floor of the same follicle as that represented in fig. 27A. × 260. Showing white blood corpuscles and follicle cells in the tertiary liquor.

Fig. 27C. Section through a portion of a follicle in the same stage as that shown in fig. 27, and from the same ovary. × 260. Showing the relation of the follicle cells in the tertiary liquor to the strands of the stroma.

Fig. 28. Section through two adjacent ruptured ovarian follicles of a ferret 44$\frac{2}{3}$ hours after insemination. × 30. Showing different stages of contraction of ruptured follicles. In the right-hand follicle the orifice is widely open, and few remnants of the liquor folliculi are left in the cavity. In the case of the left-hand follicle the orifice is firmly plugged and a considerable amount of liquor is present in the superficial part of the follicle. (Specimen F.D. K/16. L.M.F. 44$\frac{2}{3}$ hours.) I.H. O.G.

Fig. 29. Section through a ruptured ovarian follicle of a ferret 70 hours after insemination. × 30. The orifice of the follicle is contracted and plugged, but redistension of the cavity has not commenced. The blood-vessels around the periphery of the follicular epithelium are relatively few, but there are numerous small blood-vessels amidst the cells of the follicular epithelium. (F.D.A. 22/15. L.Z.) I.H. Mallory.

Fig. 30. Section through a ruptured ovarian follicle of a ferret 64$\frac{1}{2}$ hours after insemination. × 30. The orifice of the follicle is contracted and firmly plugged. There are remnants of the tertiary liquor folliculi and its stroma in the remains of the cavity of the follicle. There are few blood-vessels around the periphery of the follicular epithelium and amidst the follicle cells, and redistension of the follicle has not commenced. The folding of the follicular epithelium layer and the adjacent connective-tissue stroma of the wall of the follicle is very marked. The ova from the specimen ovary from which the section is taken are in the middle third of the oviduct, one in the 2-cell and others in the 4-cell stage. (Specimen F.G.A. 5/15. L.Z. 64$\frac{1}{2}$ hours.) I.H.

Plate VI.

Fig. 31. Section through the ruptured ovarian follicle of a ferret-polecat hybrid 53½ hours after insemination. The orifice is contracted and firmly plugged, blood-vessels are fairly numerous around the periphery of the follicular epithelium, and the redistension of the cavity of the follicle with tertiary follicular fluid has taken place to a slight extent. × 30. (Specimen P.D.A. 31/15. L.Fl. 53½ hours.) The ova are in the middle of the oviduct in the 2-cell stage. I.H.

Fig. 32. Section through the ruptured ovarian follicle of a ferret 64 hours after insemination. The orifice of the follicle is more contracted than in the specimen represented in fig. 33, and the redistension of the follicle is more advanced. Blood-vessels are numerous in the follicular epithelium. × 30. The ova are in the middle third of the oviduct, some in the 4-cell and some in the 8-cell stage. (Specimen G.A. 4/15. L.Z. 64 hours.) I.H.

Fig. 33. Section through the ruptured ovarian follicle of a ferret 64 hours after insemination. The orifice of the follicle is a little more contracted than in the follicle shown in fig. 34. Blood-vessels are numerous in the follicular epithelium and around its periphery, and the redistension of the follicle has taken place to a slight extent. × 30. The ova are in the middle third of the oviduct, some in the 4- and some in 8-cell stage. (Specimen G.A. 4/15. L.Z. 64 hours.) I.H.

Fig. 33A. Section through a portion of the wall of the follicle represented in fig. 33. × 540. Showing the relation of the blood-vessels to the follicular epithelium.

Fig. 34. Section through the ruptured ovarian follicle of a ferret-polecat hybrid 53½ hours after insemination. The orifice of the follicle is very much reduced, and the cavity of the follicle is considerably redistended. The ova are in the middle third of the oviduct in the 2-cell stage. (Specimen P.D.A. 31/15. L.Fl. 53½ hours.) I.H.

Fig. 35. Section through the ruptured ovarian follicle of a ferret 70 hours after insemination. The orifice of the follicle is closed externally, and the redistension of the cavity is well advanced. (Specimen. The ova are in the middle third of the oviduct in the 8-cell stage. (Specimen F.D.A. 23/15. L.Fl. 70 hours.) E.

Fig. 36. Section through the ruptured ovarian follicle of a ferret 69¾ hours after insemination. The orifice of the follicle is completely closed, and the redistension of the cavity is well advanced. The ova are in the middle third of the oviduct, some in the 6- and some in the 8-cell stage. × 30. (Specimen F.D.A. 21/15. R.Z. 69¾ hours.) I.H.

Fig. 37. Section through the ruptured ovarian follicle of a ferret 74 hours after insemination. The orifice is completely closed, and the redistension of the cavity is practically complete. × 30. The ova are in the middle third of the oviduct, some in the 6- and some in the 8-cell stage. (Specimen F.D.A. 44/15. R.Fl. 74 hours.) E.

Fig. 38. Section through the ovary of a ferret 69¾ hours after insemination, showing a ruptured, closed, and redistended follicle and an unruptured follicle with a ripening ovum. × 30. The ova from the ruptured follicles of the ovary are in the middle third of the oviduct, some in the 6- and some in the 8-cell stage. (Specimen F.D.A. 21/15. R.Z. 69¾ hours.) I.H.

Plate VII.

Fig. 39. Section through part of the ovary of a ferret in the thirty-third day of œstrus, showing part of the wall of a large normal follicle and several degenerate follicles. × 40. The animal was not inseminated, and insemination was not attempted. (Specimen F.G.A. 18/15. R.F. 32 days' œstrus.) E.

Fig. 40. Section through a portion of the ovum and the ovarian cumulus in the ovarian follicle of a ferret-polecat hybrid in the pro-œstrum. The nucleus of the ovum is placed peripherally, close against the oolemma; mitosis is taking place in two of the cells, which would have formed cells of the corona radiata, and the more peripheral cells of the cumulus are beginning to be separated from the more centrally placed cells by fluid-filled spaces. × 470. (Specimen P.G.B. 1/15. L.Mx. Early pro-œstrum, not inseminated.) I.H.

Fig. 41. Section through a part of the ovum, the nucleus, and part of the corona radiata of the follicle ovum of a ferret 19¾ hours after insemination. × 1000. The nuclear membrane is still quite distinct, and chromosomes have not yet formed. The nuclei of most of the corona radiata cells have begun to migrate

peripherally. Mitochondria are visible in the bodies of the cells of the corona radiata. (Specimen F. 1–2/08. 19¾ hours.) H.E.

Fig. 42. Section through the cumulus of an unruptured ovarian follicle of a ferret 27½ hours after insemination. × 240. Showing the peripheral migration of the nuclei of the cells of the corona radiata and the commencing dispersion of the more peripherally situated cumulus cells. The membrana interna is seen on the periphery of the cumulus. (Specimen F.G.A. 1/15. R.Z. 27½ hours.) I.H.

Fig. 43. Section through part of the follicular ovum and the corona radiata of a ferret 41⅓ hours after insemination. × 1000. The peripheral extension of the cells of the corona radiata and the peripheral migration of their nuclei is practically completed. Mitochondria are visible in the cell bodies of the corona radiata cells. The nuclear membrane has almost entirely disappeared, and chromosomes have definitely formed. (Specimen F.G.A. 2/15. L.Z. 41⅓ hours.) I.H.

Fig. 44. Section through the follicle ovum and the corona radiata of a ferret 30½ hours after insemination. × 310. The ovum is in the latter part of the anaphase of mitosis, and the typical arrangement of the cells of the corona radiata and their nuclei is well shown. (Specimen F.D. D/16. L.P.N.F. 30½ hours.) I.H. O G.

Plate VIII.

Fig. 45. A portion of the ovum represented in fig. 47. × 1000. Showing the structure of the corona radiata cells and some of the features of the protoplasm of the ovum.

Fig. 46. Section through the cranial end of the uterine cornu and a terminal fimbria of the oviduct of a ferret-polecat hybrid 31½ hours after insemination, showing an ovum surrounded by its corona and a portion of the contents of the ovarian follicle escaping into the peritoneal cavity. × 19. (Specimen P.D. C/16. L.Per. 31½ hours.) I.H. O.G.

Fig. 47. The ovum shown in fig. 49. × 310. Showing the second maturation spindle in the upper and left part of the body of the ovum and the arrangement of the cells, and nuclei of the corona radiata.

Fig. 48. Section of a portion of the wall of the ovarian follicle of a ferret-polecat hybrid at the commencement of the early pro-œstrum. × 300. The portion of the wall shown in the figure is in the region of the ovarian cumulus. It demonstrates the arrangement of the follicle cells and their commencing dissemination, and shows the relationship of the blood-vessels to the external limiting membrane of the follicle. (Specimen P.G.B. 1/15. L.Mx.) I.H.

Fig. 49. Section of a portion of the wall of a ripe unruptured ovarian follicle of a ferret-polecat hybrid 31½ hours after insemination. × 310. The part of the wall seen in the figure is on the opposite side to the ovarian cumulus. The relation of the follicular cells to the blood-vessels and to the interstitial cells of the sheath of the follicle is seen. (Specimen P.D. C/16. L.Per. 31½ hours.) I.H. O.G.

Fig. 50. Section through a portion of the wall of the unruptured follicle of a ferret 41⅓ hours after insemination. × 300. The ovum in the follicle was ripening. The section shows a stage of the invasion of the follicular epithelium by the blood-vessels. (Specimen F.G.A. 2/15. L.Z. 41⅓ hours.) I.H.

Fig. 51. Section through a portion of the wall of a full-grown normal ovarian follicle of a ferret. × 800. Showing the positions of the fat granules in the follicular cells and in some of the interstitial cells. (Specimen F.G.A. 18/15. R.Fl. 32 days' œstrus.)

Plate IX.

Fig. 52. Section through a portion of the wall of a fully-grown ovarian follicle of a ferret. The animal was in full heat, and was killed six days after insemination had been unsuccessfully attempted. × 310. The section shows an early stage in the formation of the internal limiting membrane, its connection with the follicle cells and with the reticulum of the primary liquor folliculi. It also shows the external limiting membrane and the relation of the latter to the blood-vessels. (Specimens F.Z.R. 1/14. Insemination unsuccessfully attempted.) I.H.

Fig. 53. Section through the ovarian cumulus of a fully-grown ovarian follicle of a ferret in full heat and not inseminated. × 310. Showing the commencing formation of the internal limiting membrane on the surface of the cumulus. (Specimen F.D.A. 40/15. L.Z. 23 days post-partum in full heat.) I.H.

Fig. 54. Section through a portion of the wall of a fully-grown ovarian follicle. × 1000. Showing

the expanded external ends of some of the follicle cells, the positions of the nuclei, and the structure of the cells. (Specimen F.D.A. 40/15. L.Z. 23 days post-partum in full heat.) I.H.

Fig. 55. Section through a portion of the wall of the ovarian follicle which contained the cumulus shown in fig. 53. × 310. The section shows a more advanced stage in the formation of the internal limiting membrane on the wall of the follicle than that seen on the cumulus, and a distinctly more advanced stage than that depicted in fig. 54. (Specimen F.D.A. 40/15. L.Z. 23 days post-partum in full heat.) I.H.

Fig. 56. Section of a portion of the wall of a ripening ovarian follicle of a ferret killed 27½ hours after insemination. × 310. The section shows the arrangement of the follicle cells in the immediate neighbourhood of the ovarian cumulus, and the relationship of the very definite internal limiting membrane to the follicle cells. (Specimen F.G.A. 1/15. R.Z. 27½ hours.) I.H.

Fig. 57. Section of a portion of the wall of a fully-grown ovarian follicle of a ferret. × 1000. Showing the inclusion of degenerating follicular cells in the forming internal limiting membrane. (Specimen F.D.A. 40/15. L.Z. 23 days post-partum in full heat.) I.H.

PLATE X.

Fig. 58. Section through a portion of the wall of a fully-grown normal ovarian follicle of a ferret. × 1000. Showing the structure of the cells and the relation of the external limiting membrane to the follicle cells and to the extra-follicular connective tissue. (Specimen F.Z.R. 1/14. Six days after unsuccessfully attempted insemination in full heat.) I.H.

Fig. 59. Section through a portion of the wall of a fully-grown normal ovarian follicle of a ferret. × 1000. Showing strands of granules (mitochondria?) in the cells, the relation of the external ends of the cells to the external limiting membrane, and the relation of the external limiting membrane to the wall of a blood-vessel. (Specimen F.D.A. 40/15. L.Z. 23 days post-partum in full heat.) I.H.

Fig. 60. Section through a portion of the wall of a fully-grown normal ovarian follicle of a ferret. × 1000. Showing the relation of the external limiting membrane to the outer ends of the follicle cells, to the extra-follicular connective-tissue cells, and to the wall of a blood-vessel. (Specimen F.D.A. 40/15. L.Z. 23 days post-partum and in full heat.) I.H.

Fig. 61. Section through the ovary of an anœstrus ferret. × 24. Showing the relation of the cortex to the medulla, the spindle strands of the cortex, and the ovarian follicles. (Specimen F.Z.R.A. 5/14.) I.H.

Fig. 62. Section through a portion of the cortex of the ovary shown in fig 61. × 340. Showing the superficial epithelium, the tunica albuginea, a young follicle, spindle-cell strands, and interstitial cells. (Specimen F.2, R.A. 5/14.)

Fig. 63. Section of a portion of the cortex of the ovary of a ferret. × 340. Showing spindle-cell strands of the cortex, young follicles, and interstitial cells. Compare with fig. 3, which is a section of an adjacent portion of the same ovary. (Specimen F.D. T/16. L.M.F. 123⅓ hours.) I.H. O.G.

NOTE.

I am indebted to the Carnegie Trust for a grant covering the cost of the plates accompanying this communication, and to the Moray Fund for grants for the purchase of some of the animals and materials used in the research.

A. R.

Professor ARTHUR ROBINSON: "The Formation, Rupture, and Closure of Ovarian Follicles in Ferrets and Ferret-Polecat Hybrids, and some Associated Phenomena."—PLATE I.

FIG. 5.

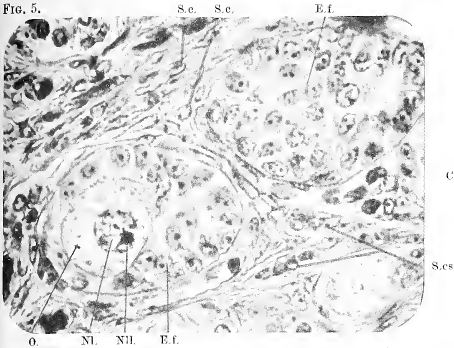


FIG. 1.

FIG. 4.

FIG. 2.

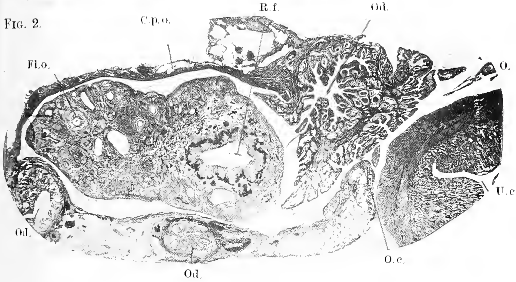


FIG. 4A.

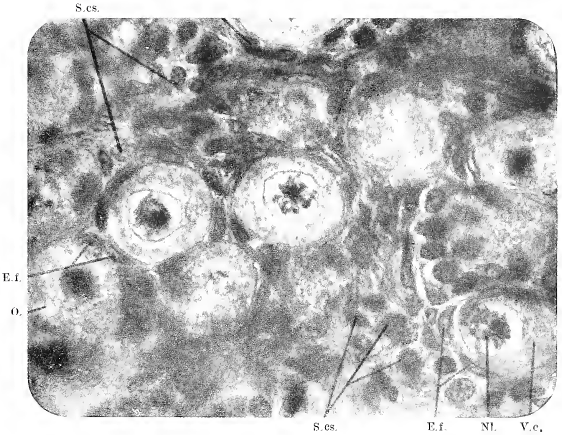


FIG. 3.

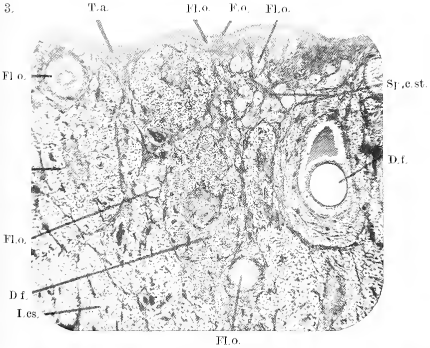
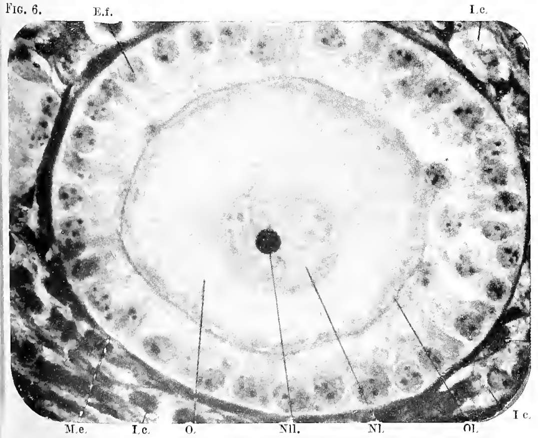
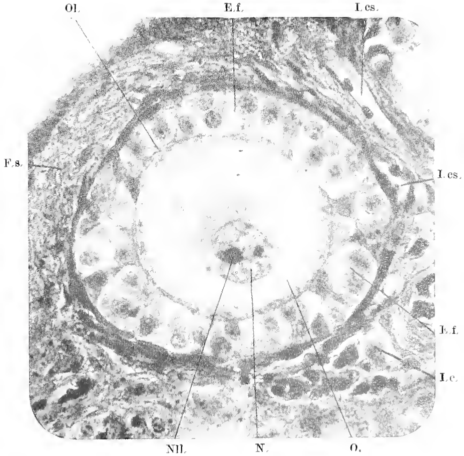


FIG. 7.

FIG. 6.





Professor Arthur Robinson: "The Formation, Rupture, and Closure of Ovarian Follicles in Ferrets and Ferret-Polecat Hybrids, and some Associated Phenomena."—Plate II.

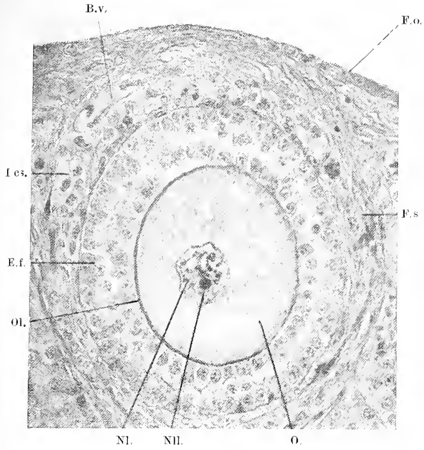
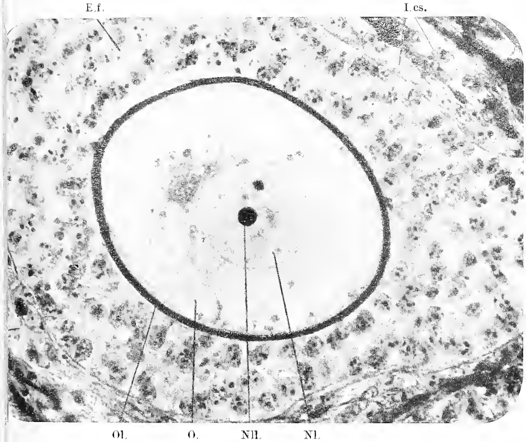


Fig. 8.



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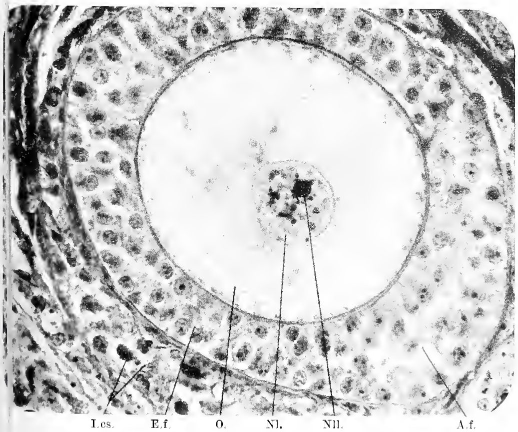

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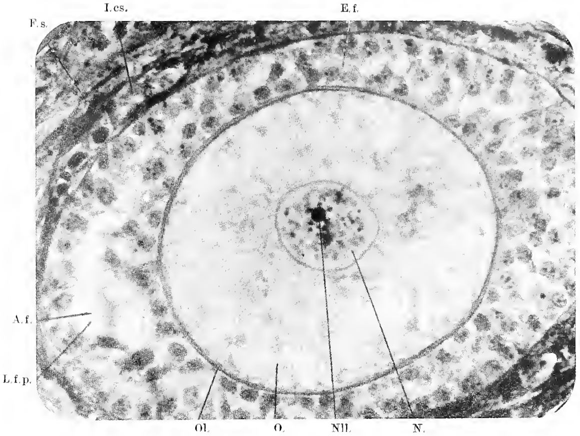

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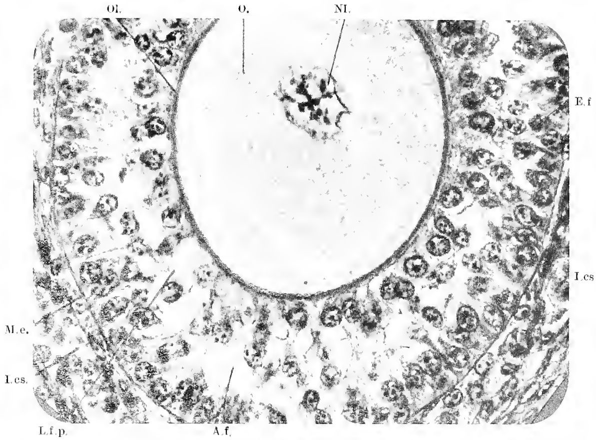

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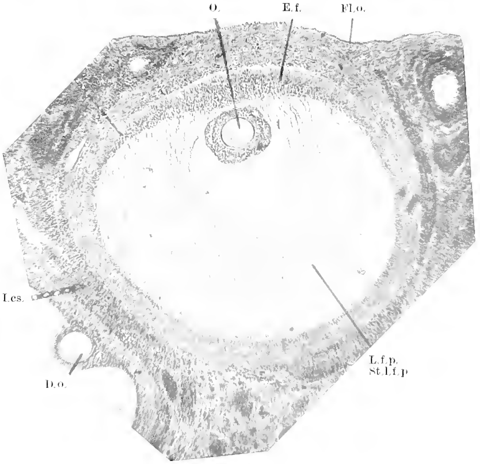


Fig. 13.

Professor ARTHUR ROBINSON: "The Formation, Rupture, and Closure of Ovarian Follicles in Ferrets and Ferret-Polecat Hybrids, and some Associated Phenomena."—PLATE III.

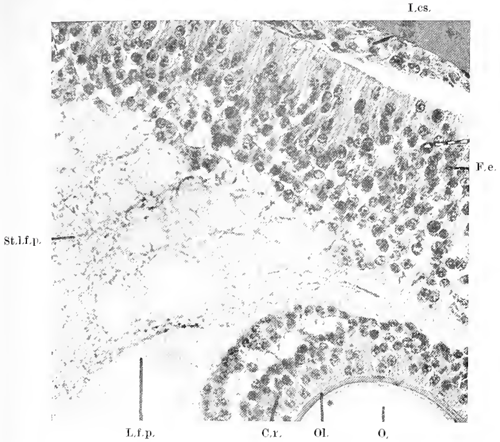
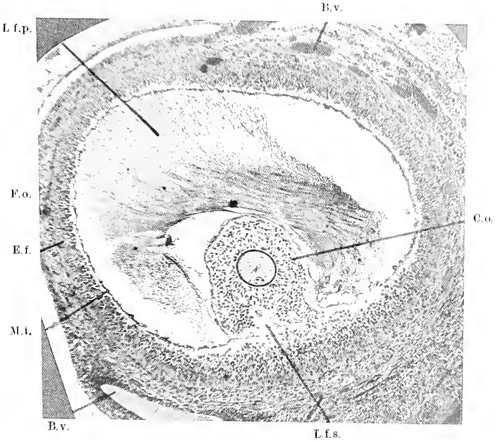


FIG. 14.



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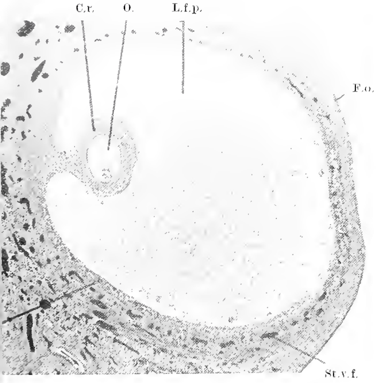

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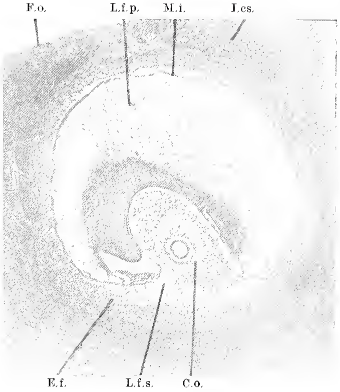

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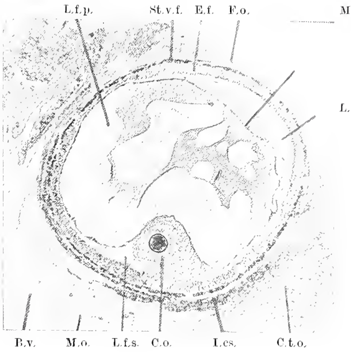


FIG. 20.

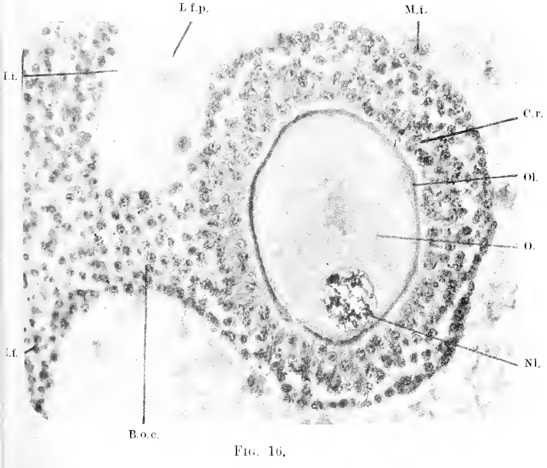


FIG. 16.

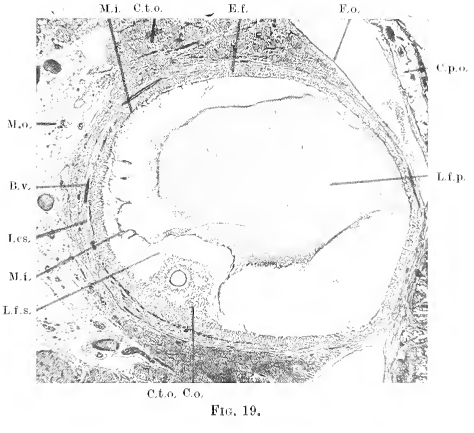


FIG. 19.

Professor Arthur Robinson: "The Formation, Rupture, and Closure of Ovarian Follicles in Ferrets and Ferret-Polecat Hybrids, and some Associated Phenomena."—Plate IV.

Fig. 21.

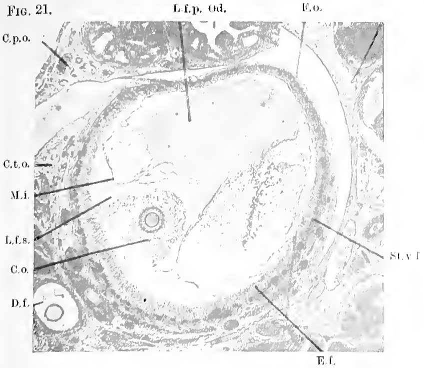
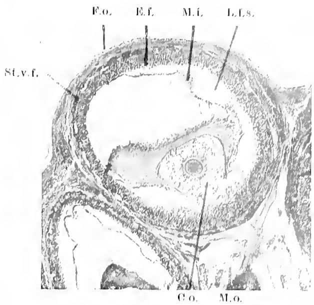


Fig. 23.



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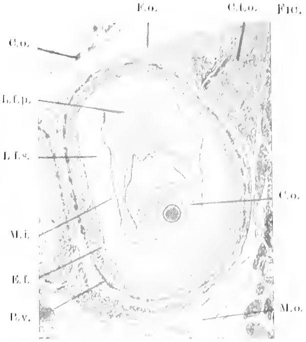

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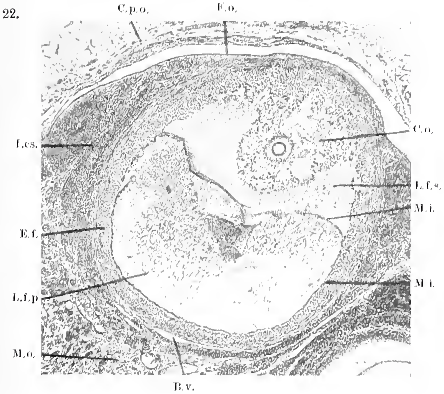

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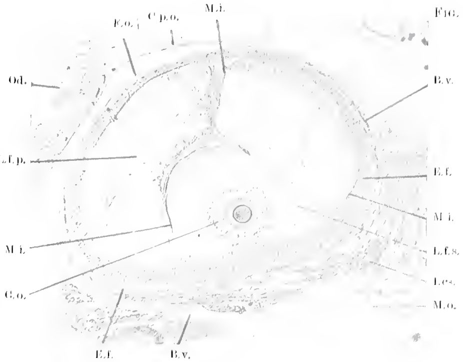

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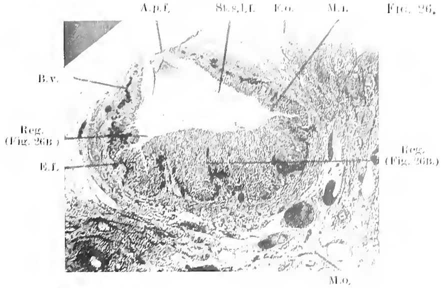

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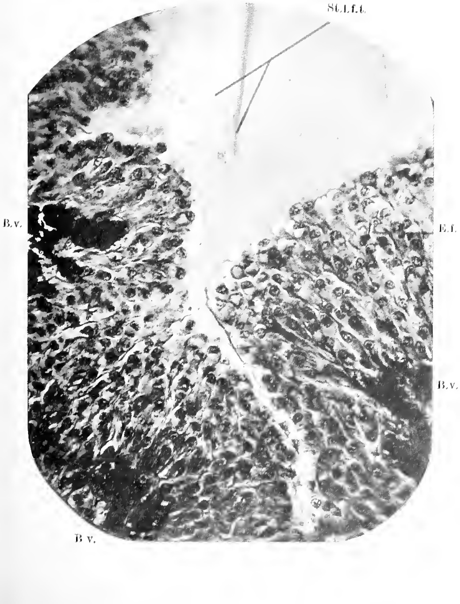


Fig. 26B.

Professor ARTHUR ROBINSON: "The Formation, Rupture, and Closure of Ovarian Follicles in Ferrets and Ferret-Polecat Hybrids, and some Associated Phenomena."—PLATE V.

G. 27.

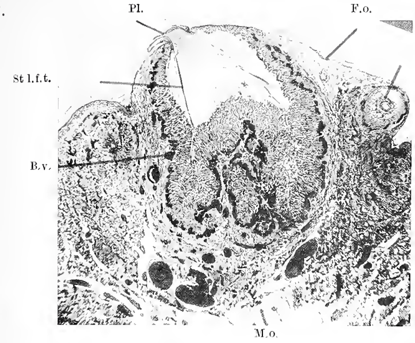
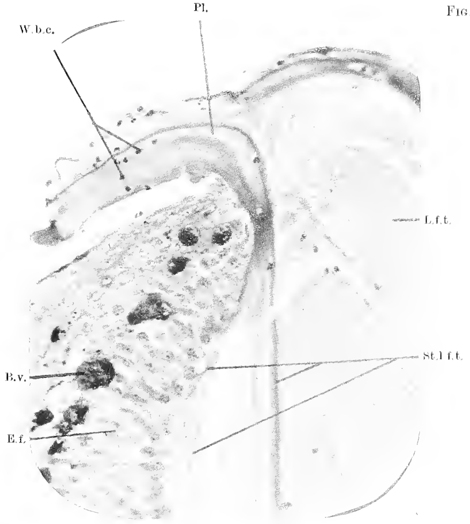


FIG. 27A.



G. 27B.

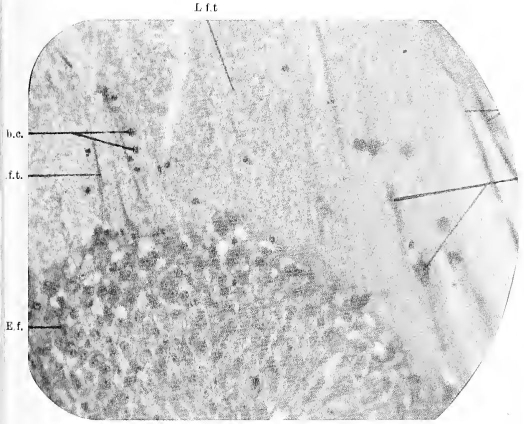
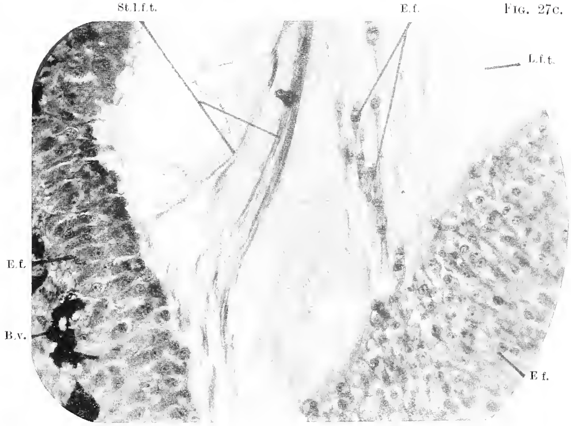


FIG. 27C.



. 28.

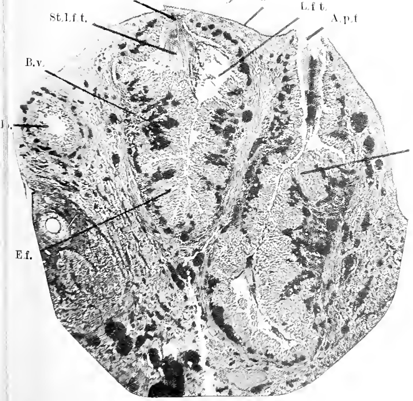
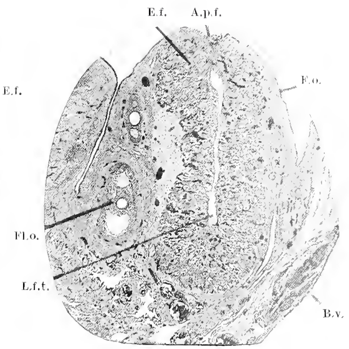


FIG. 29.



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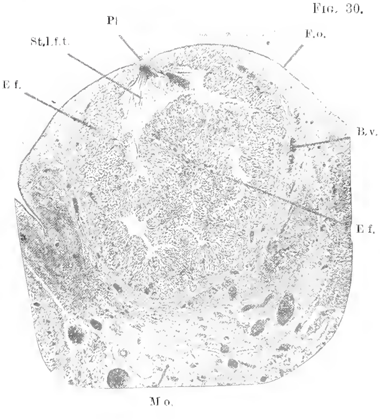
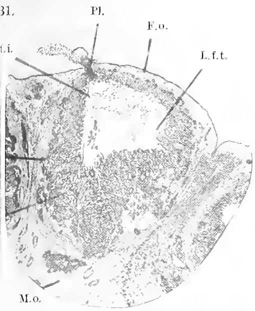


Professor ARTHUR ROBINSON: "The Formation, Rupture, and Closure of Ovarian Follicles in Ferrets and Ferret-Polecat Hybrids, and some Associated Phenomena."—PLATE VI.

Fi31.



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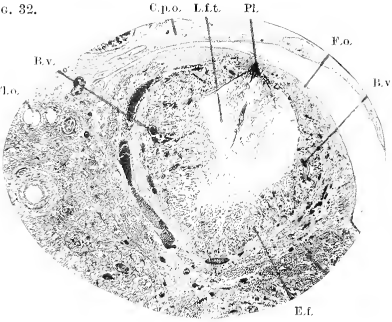
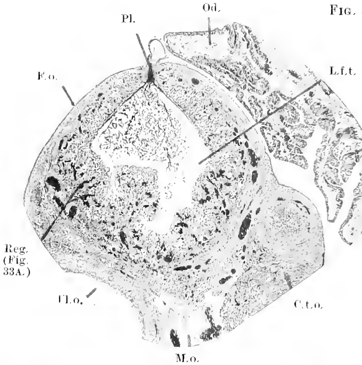
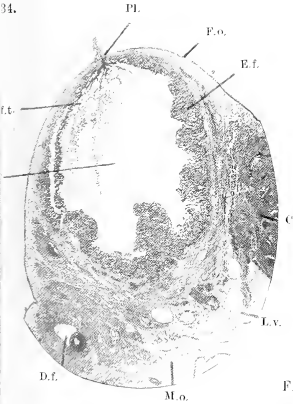


FIG. 33.



Fi34.



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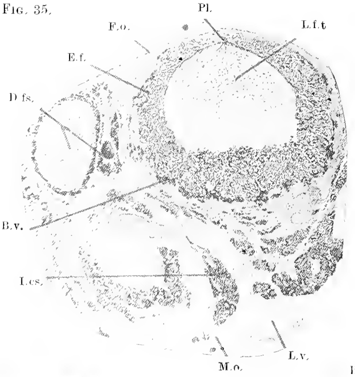
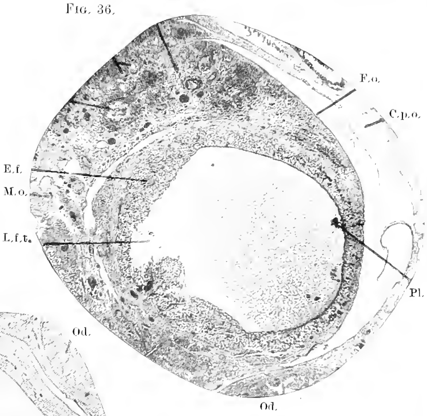


FIG. 33A.

FIG. 36.



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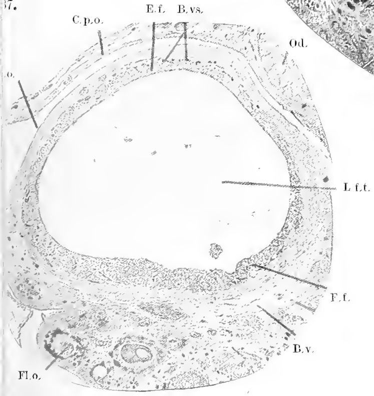
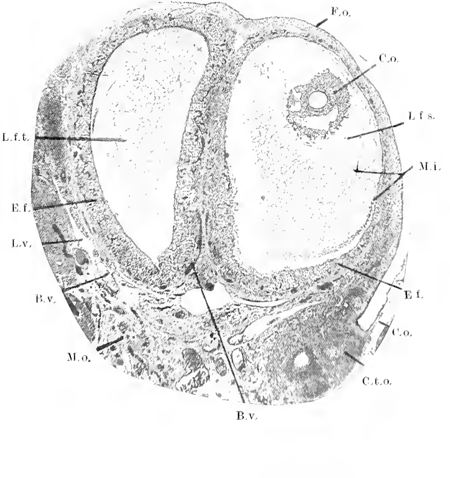


FIG. 38.



Professor ARTHUR ROBINSON: "The Formation, Rupture, and Closure of Ovarian Follicles in Ferrets and Ferret-Polecat Hybrids, and some Associated Phenomena."—PLATE VII.

FIG. 39.

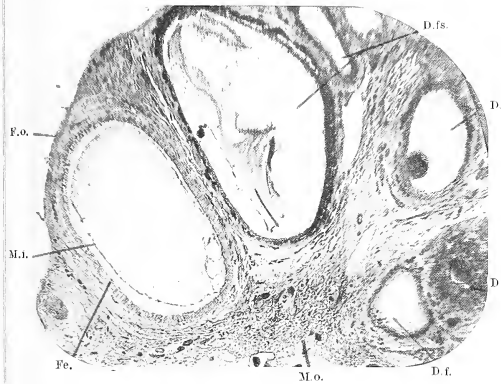
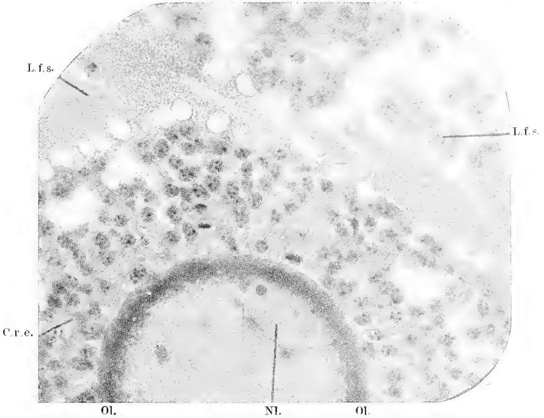


FIG. 40.



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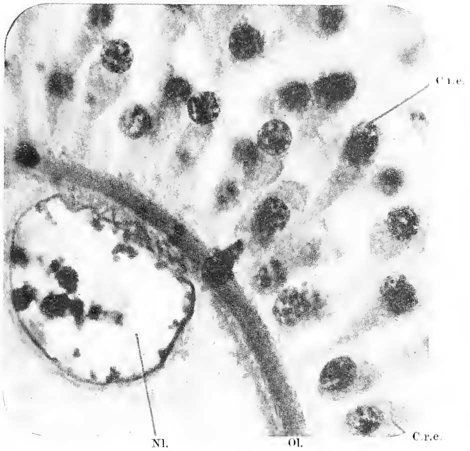
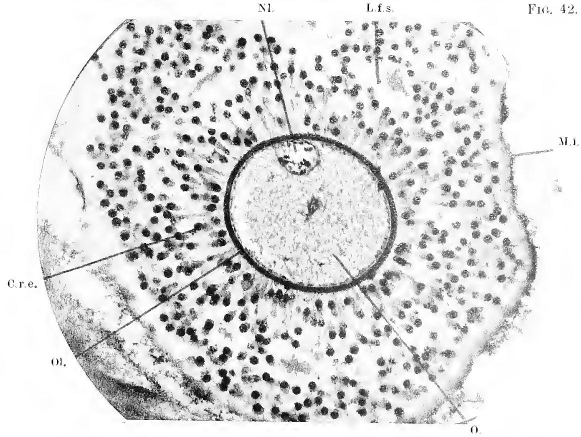


FIG. 42.



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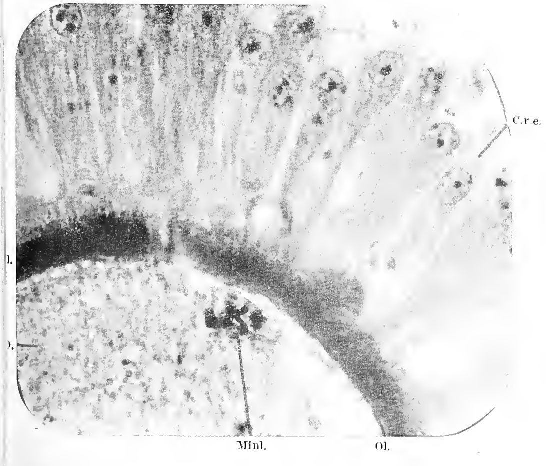
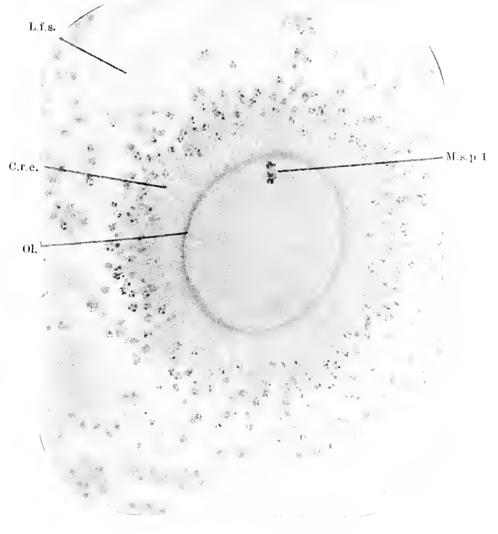


FIG. 44.



Professor ARTHUR ROBINSON: "The Formation, Rupture, and Closure of Ovarian Follicles in Ferrets and Ferret-Polecat Hybrids, and some Associated Phenomena."—PLATE VIII.

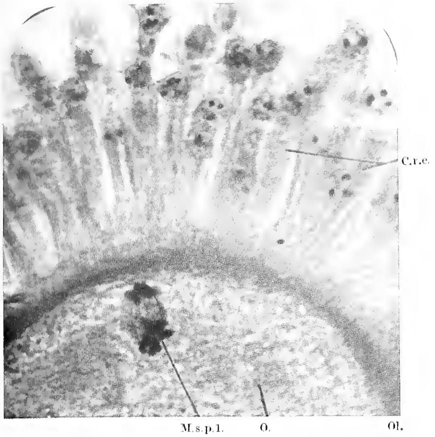


FIG. 45.

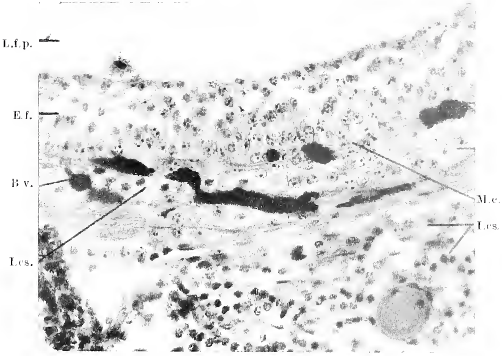
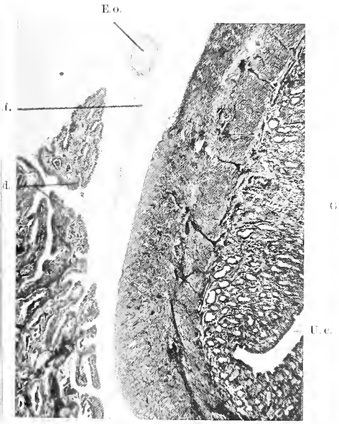


FIG. 49.



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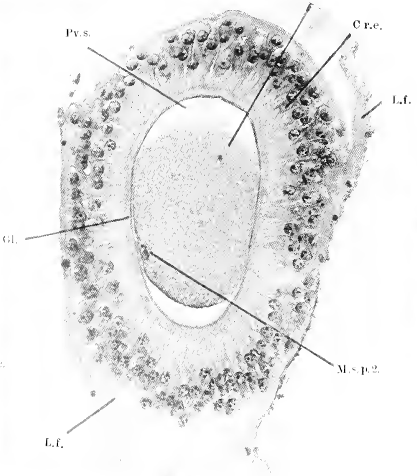


FIG. 47.

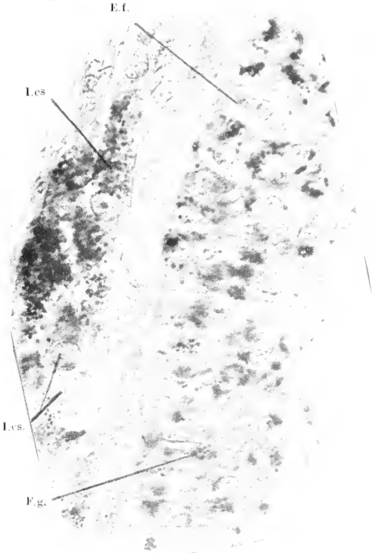


FIG. 51.

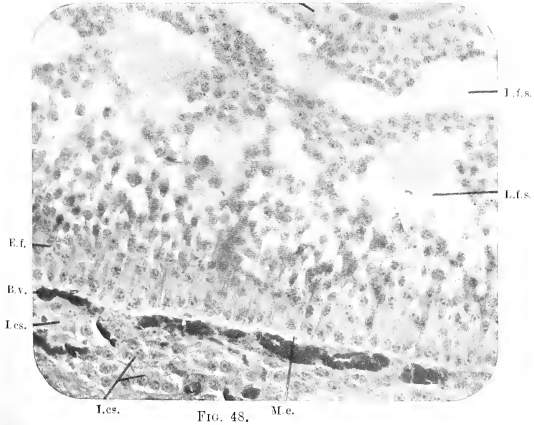


FIG. 48.

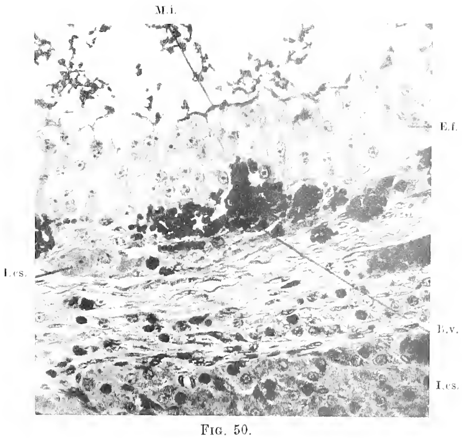


FIG. 50.

Professor Arthur Robinson: "The Formation, Rupture, and Closure of Ovarian Follicles in Ferrets and Ferret-Polecat Hybrids, and some Associated Phenomena."—Plate IX.

Fig. 52.

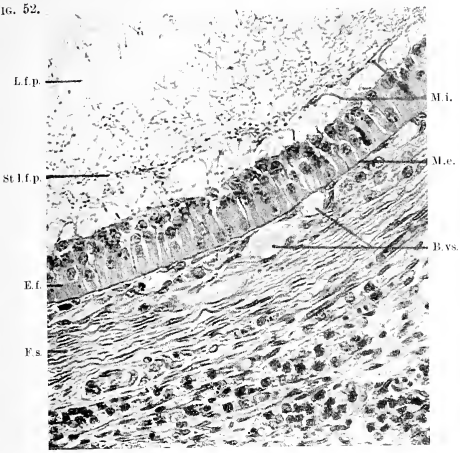


Fig. 55.

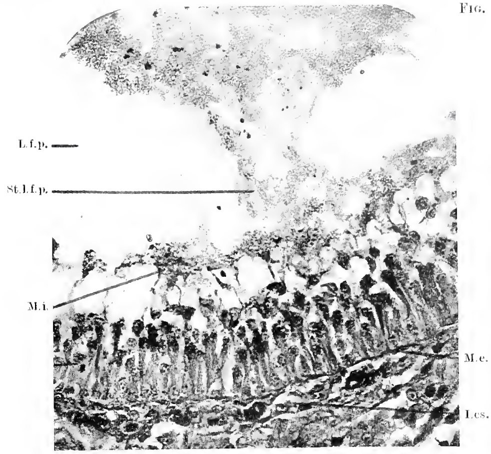


Fig. 53.

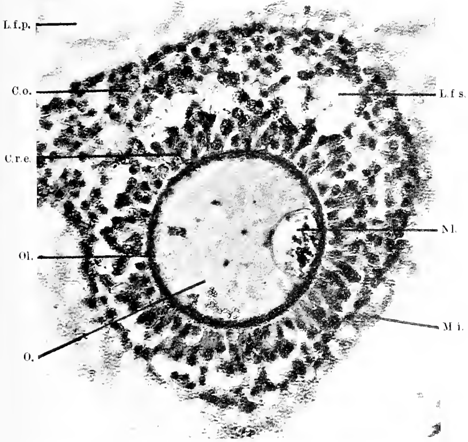
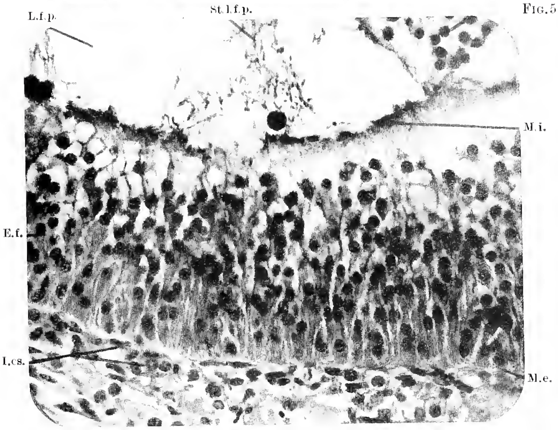


Fig. 56.



IG.54.

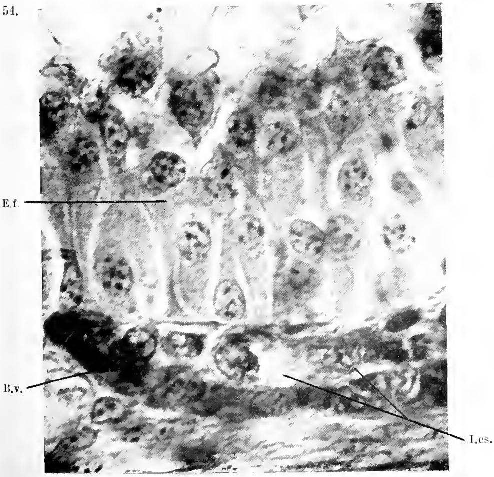
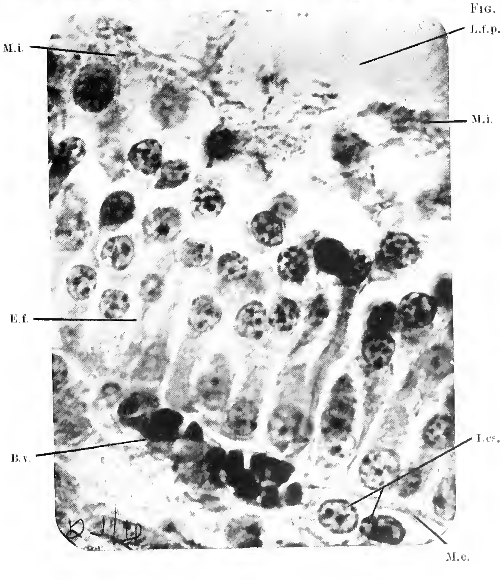


Fig. 57.



Professor ARTHUR ROBINSON: "The Formation, Rupture, and Closure of Ovarian Follicles in Ferrets and Ferret-Polecat Hybrids, and some Associated Phenomena."—PLATE X.

IG. 58.

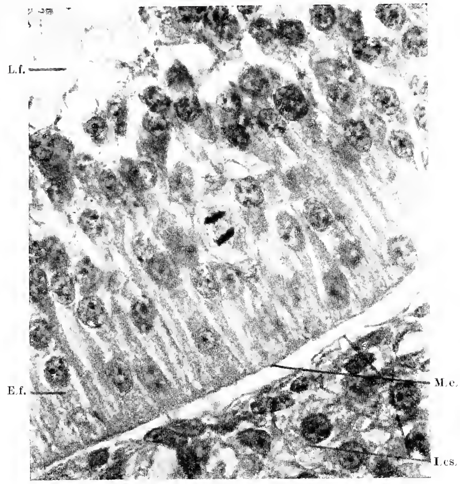
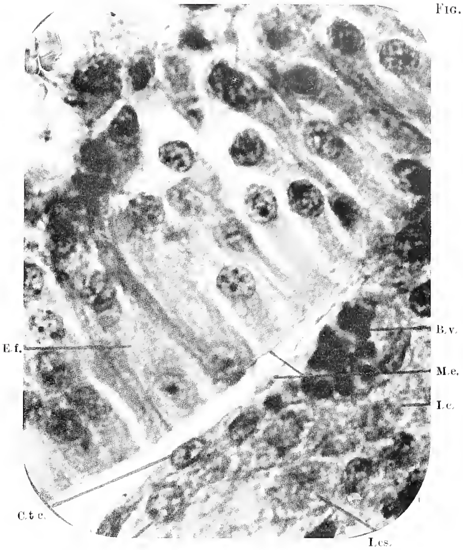
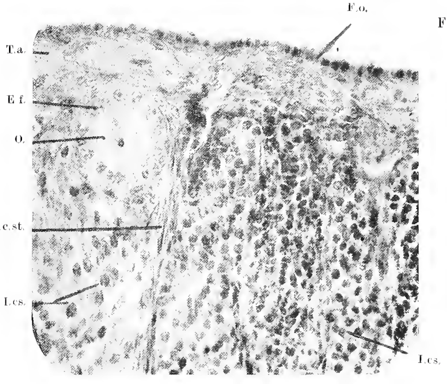


FIG. 60.



IG. 59.

FIG. 62.



G. 61.

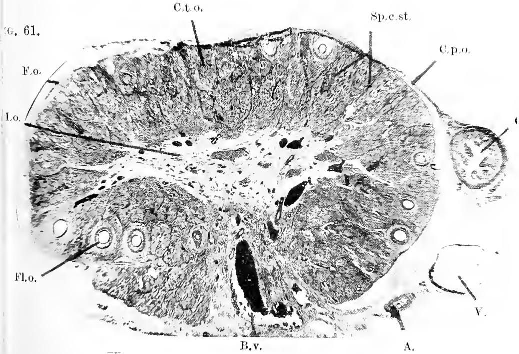
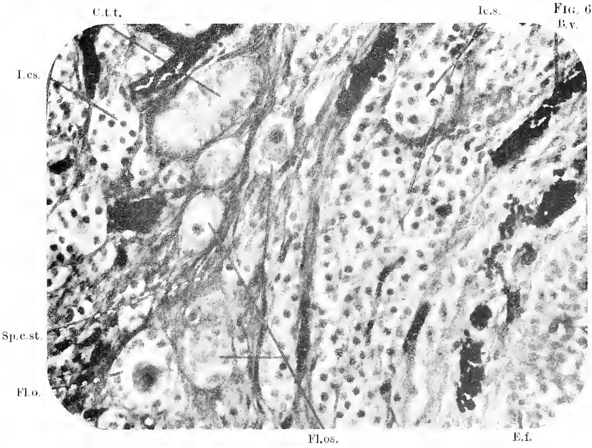


FIG. 63.



XIV.—The Anatomy and Affinity of certain Rare and Primitive Ferns. By John M'Lean Thompson, M.A., D.Sc., Lecturer in Botany, Glasgow University. (With Seven Plates and Thirty Figures in the Text.)

(MS. received February 4, 1918. Read February 4, 1918. Issued separately September 9, 1918.)

A number of rare genera of Ferns of somewhat uncertain affinity had recently come to my hands. As they had by previous writers been referred in some degree to a common relationship it seemed well to embody them together in one memoir. As the work proceeded the justification of this became more apparent, and towards the end of the work the conclusion seemed clear that the suggested affinities were real though not very close.

The genera in question were *Jamesonia*, Hk. Gr., *Llavea*, Lagasca, and *Trismeria*, Fée. Comparisons have also been made with *Gymnogramme*, Desv., *Cryptogramme*, R. Br., *Cheilanthes*, Sw., *Nothochlæna*, R. Br., *Pellæa*, Link., and *Ceratopteris*, Brong., while the facts already known for *Plagiogyria*, Kze., form a further basis for comparison, with a possible reference to a phyletic source in the direction of the *Schizæaceæ*.

Jamesonia, Hk. et Grev.

In the *Icones Filicum* of 1831 Hooker and Greville described a curious Fern discovered by Professor Wm. Jameson, Quito, at an altitude of 12,000 feet, on Mount Cayambe, Peru. The stem was creeping and much branched, the leaves slender and pinnate. The small coriaceous sub-flabellate pinnæ bore a dense covering of tawny hairs. The pinna-margins were incurved as a membranous flap, which was considered an indusium. The sporangia were scattered along the veins on the lower surface of the pinnæ and were concealed by hairs. The sporangial stalk was short, the annulus almost vertical, and the spores tetrahedral. The distal portions of the veins were devoid of sporangia. The sporangial arrangement was considered remarkable and the hairs distinctive. Being then unable to refer this plant satisfactorily to any accepted genus, Hooker and Greville constituted a new one (*Jamesonia*) of it.

In 1840 Kunze (*Farnkr.*) followed the example thus set, and further claimed the existence of six species. In 1856 Mettenius attempted to divide the genus. He accepted as true species some of those already recognised, but referred the remainder to the comprehensive genus *Polypodium*, L., and to *Gymnogramme*, Desv. To Willdenow this plant was a *Pteris*, L.; Desvaux named it *Cheilanthes*, Sw.; and Presl reduced it to *Allosorus*, Berw. In 1864 *Jamesonia* appeared in the *Species Filicum* as the first genus of Hooker's *Grammatidæ*. It was thus associated with a group of non-indusiate Ferns with the majority of which its relationships were not close. In the *Synopsis Filicum* of 1874 the generic rank of *Jamesonia* was upheld. In 1882 KUHN (*Die Gruppe der Chætopterides unter der Polypodiaceen*) renamed *Jamesonia Psilogramme*, and placed it next to *Gymnogramme*. To CHRIST (*Farnkr.*) in 1897 *Jamesonia* was a true genus; in 1897, 1902, DIELS (Engler and Prantl, *Nat. Pfm.*) considered the limits between *Jamesonia* and *Gymnogramme* very conventional; and in 1905 CHRISTENSEN (*Index Filicum*) placed it between *Gymnogramme* and *Coniogramme*, Fée.

No material contribution to the knowledge of the structure of *Jamesonia* has been made. But while opinion has differed regarding species and varieties, the *Jamesonia* of HOOKER and GREVILLE has been widely accepted as a genus allied to *Gymnogramme*. The only references to the anatomical condition of *Jamesonia* are in a paper by DUNZINGER (*Beiträge zur Kenntnis der Morphologie und Anatomie der Genera Hemionitis, Gymnogramme, und Jamesonia*, 1901). This author noted a similarity of hairs and spores as existing between *Jamesonia* and certain species of *Gymnogramme*, and that the slender solenostele of *Jamesonia* is comparable to that of *Gymnogramme angustifrons*, Bak., but that the cortex of the stem of *Jamesonia* possesses a curious spongy tissue. These observations do not seem to form a sufficient basis for DUNZINGER's statement that "only the outward appearance of this xerophytic plant is deceptive, for it is a true *Gymnogramme*. On this point the anatomical state bears convincing evidence."

The facts detailed in the following pages are the result of study of ample preserved materials of *Jamesonia scalaris*, Kze., kindly supplied by Dr WILLIS, Rio de Janeiro, from the Province of São Paulo. An herbarium specimen of the same species, for which I am indebted to Mr A. W. HILL, M.A., F.L.S., Assistant Director, Kew Gardens, has also been examined. This plant was collected in 1903 on boggy ground at an altitude of 15,000 feet in the Urubamba Valley, Pacechac, Peru. As will be seen from Mr HILL's photograph (fig. 2), the plant grows up to the snow-line, and is of a striking appearance. The *Jamesonia* plants are on the left of the photograph and immediately under the rock face. The plants on the right are probably *Lycopods*. JAMESON's statement that this plant grows "in marshy places among *Sphagnum* and at elevations between 8000 and 14,000 feet" is thus demonstrated. The herbarium specimens of *J. verticalis*, Kze., and *J. cinnamomea*, Kze., in Glasgow University have also been examined.

The leaf-habit is admirably suggested in Dr GREVILLE's original drawing (*Ic. Fil.*), and the general habit of the plant is shown well in ENGLER and PRANTL (*Nat. Pfm.*).

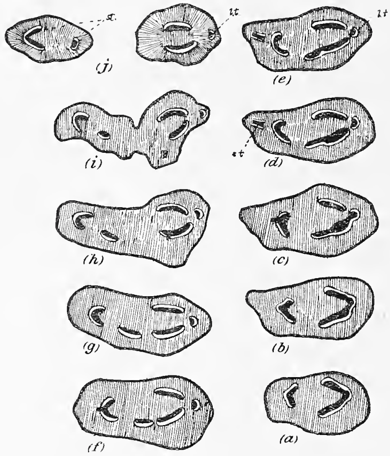
Dermal Appendages.—The dermal appendages of the axis of *J. scalaris* are multicellular mounds and slender, golden-brown hairs. The former are irregular groups of dark sclerotic cells; the latter are multicellular, and terminate in thin-walled glandular cells. The hairs and mounds are commonly combined, either a single hair being seated on a peg, or several hairs being attached to a mound. Examples are given in fig. 1. The dermal appendages of the leaves are tortuous multicellular hairs (fig. 3). Their terminal cells are not glandular. The dermal appendages are for the most part persistent on the mature axis, but the hairs are retained only on the lower surface of the mature pinnæ. The circinate immature rachis and pinnæ are completely hidden by a dense hairy covering. The dermal appendages of the other species examined are similar to those of *J. scalaris*.

The dermal appendages of the species examined are sufficiently distinctive to preclude a close comparison between them and those of any other genus. In questions of affinity the evidence provided by dermal appendages is commonly inconclusive, for while marked differences of form of the dermal appendages may exist within the limits of a single genus, it is common knowledge that similarity of form may characterise the dermal appendages of distinct genera. DUNZINGER'S opinion that the kinship of *Jamesonia* and *Gymnogramme* is demonstrable by a comparison of hairs from *Jamesonia* and *G. elongata*, Hk. et Grev., and *G. myriophylla*, Sw., cannot be upheld.

TEXT-FIG. 1.

Axis.—In a transverse section of the axis above the insertion of the youngest leaf the arrangement of tissues may be as in text-fig. 1 (*a*). The immature stele (*st.*) is lodged in a mass of thin-walled parenchyma (*p.*), and the peripheral band of cortex is sclerotic (*sc.*). Further from the apex the entire medulla (*m.*) becomes sclerotic. A broad neck of sclerenchyma fills the leaf-gap and unites the pith and cortex (text-fig. 1 (*b*)). A crescent of parenchyma is thus isolated between the convex face of the stele and the sclerotic outer cortex. As the point of leaf-insertion is approached a new gap appears in the stele (text-fig. 1 (*c*)), and as the leaf-base merges with the axis a band of sclerotic ground-tissue bridges the moat of thin-walled cells and links the medulla and cortex through the new gap (text-fig. 1 (*d*)). On the adaxial side of the undivided leaf-trace the cortical tissue of the leaf-base is entirely sclerotic, but a crescent of thin-walled parenchyma lies on the abaxial convex face of the trace. This parenchymatous crescent accompanies the leaf-trace through the cortex of the stem, and when the leaf-trace is about to unite with the stele and close the leaf-gap the parenchyma of leaf-base and axis become confluent (text-fig. 1 (*e*), (*f*)). As the first leaf-gap has been closing the second has widened, and the slender bridge of sclerenchyma linking the medulla and cortex has broadened to a thick neck. The sclerenchyma of axis and leaf-base is apparently devoid of intercellular spaces, but the thin-walled parenchyma is well ventilated (fig. 5). The sclerotic cells contain much starch, but the parenchyma is full of granular bodies which are apparently plastids. The pith and outer cortex are uniformly sclerotic, and the parenchyma is maintained in contact with the stele throughout the entire axis. The undivided leaf-trace is inserted on the stele at or near the base of the leaf-gap, and the root-traces originate singly below the leaf-gaps or near their margins (figs. 4, 6, and text-figs. 1, 2).

The anatomical condition described is typical of the axis as a whole, and is in close agreement with that of *J. verticalis*. A reconstruction of the stele based on a long series of sections of the axis is given in fig. 4. The conclusions arrived at from serial sections are, that the vascular system is a slender solenostele, that the undivided leaf-traces depart at or near the base of the gaps, and that the root-traces originate singly on the general stelar surface.

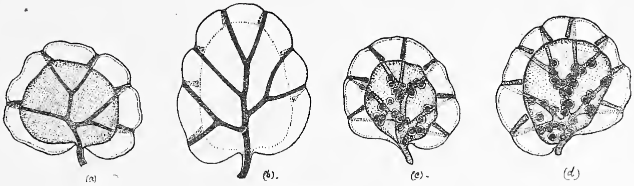


TEXT-FIG. 2.

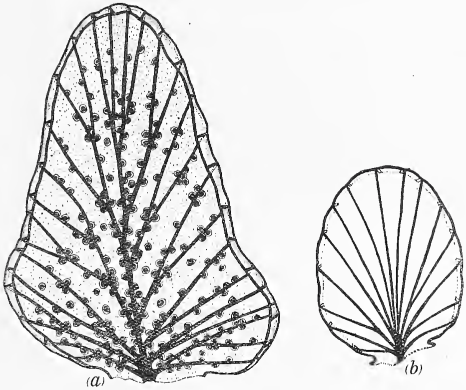
Externally the branching of the axis may appear dichotomous, but the vascular supplies to the branches have never been found to be identical. The stelar reconstruction of a typical branching is shown in fig. 6. It will be seen from this and from the group of diagrams (*a*)–(*j*) composing text-fig. 2, and illustrating steps in this branching, that the products of division of the original solenostele are two dissimilar solenosteles. Of these the right-hand member bears a leaf-trace towards its base, but neither leaf-gap nor leaf-trace is shown on the left-hand branch. That this is the normal condition in stelar-branching follows reasonably from the varying lengths and overlappings of the leaf-gaps in the undivided portion of the axis.

Root.—A transverse section of a root is shown in fig. 8. The stele is small, and the cortical layer external to the endodermis has strongly thickened walls. The general structure is typical of roots of xerophilous Ferns, and supplies no features which can be used in a phyletic discussion.

Leaf.—The typical leaf is about 1 foot long. It is slender, simply-pinnate, and unbranched, and shows a continued apical growth. Reduction forms are not uncommon. In our plants the rachis of these small leaves may not exceed 1½ inches in length; the pinnæ are few and typically malformed, and scattered irregularly along the rachis. The distribution of these small leaves is variable, but the majority of them are formed towards the end of the season's growth and receive their traces from ventral leaf-gaps. The condition thus shown seems similar to that which I have demonstrated in *Platyzoma*, R. Br. (*Trans. Roy. Soc. Edin.*, vol. li, pt. iii, 1916). In both these plants the axis is slow-growing, and the small leaves seem expressive of xerophytic conditions.

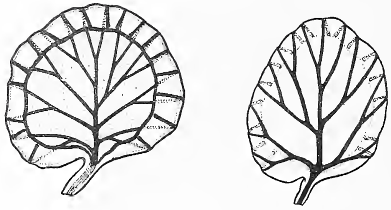


TEXT-FIG. 3.

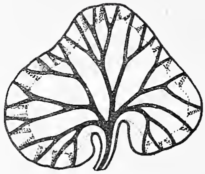


TEXT-FIG. 4.

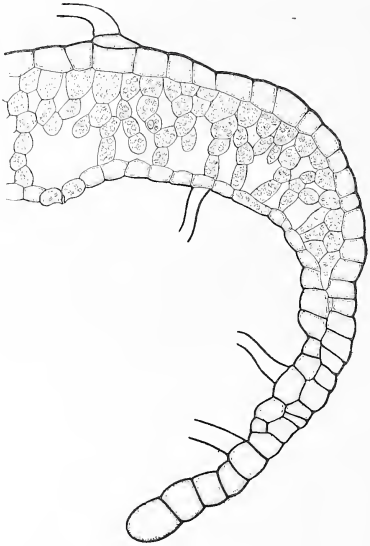
Within the genus there is considerable variation in the details of pinna-form and venation. The smallest pinnæ are found in *J. scalaris* (text-fig. 3), the largest in *J. verticalis* (text-fig. 4). In the latter species the pinnæ are sessile, but in *J. scalaris*, *J. cinnamomea*, and *J. canescens* they are stalked (text-figs. 3, 5, 6). The pinnæ of *J. cinnamomea* and *J. verticalis* are thick and leathery, but those of *J. canescens* and *J. scalaris* are more delicate. The pinna-margin is membranous, and inflexed particularly in the small-pinnate species. In *J. scalaris* the lower surface of the pinna may be almost concealed by the revolute margin. Between the veins the pinna-margin is delicate and devoid of photosynthetic tissue (text-fig. 7), but around the bundle-endings—which run to the very margin of the pinna—the mesophyll is well developed. The venation is a sympodial dichotomy, the simplest arrangement being shown by *J. scalaris*, the most advanced in *J. verticalis*. The details of branching of the sympodium vary considerably in pinnæ from the same leaf. The most marked variations are in *J. verticalis*, in which they are mainly accompaniments of pinna-size. The fertile pinnæ are usually large and have elaborate venation; the small sterile basal pinnæ show a much simpler condition (text-fig. 4).



Text-fig. 5.



Text-fig. 6.



Text-fig. 7.

Fertile pinnæ of *J. scalaris* and *J. verticalis* have been examined. In both species the sporangia are distributed chiefly along the veins, but a few are inserted on the general pinna-surface (text-figs. 3 (*c*), (*d*), 4 (*a*)). There is no definite sorus and no indusium. The general absence of sporangia from the distal portions of the veins is probably a consequence of the membranous condition of the pinna-margin.

The young pinna is completely covered by hairs, but the upper surface of the mature pinna is naked. The upper epidermis is strongly cuticularised, the mesophyll is well ventilated, and the protruding stomata are restricted to the lower surface (text-fig. 7). The general construction is indicative of specialisation under xerophytic conditions.

In passing from stem to leaf-base the undivided trace of a well-developed leaf is accompanied for a short distance by the abaxial strap of parenchyma (fig. 9), but in the base of a reduced leaf the ground-tissue is uniformly sclerotic. The typical leaf-trace appears in transverse section of the leaf-base as in fig. 9. The xylem is a curved strap with marginal protoxylems. The phloem is on its abaxial face. As the petiole is ascended the phloem spreads adaxially until, in the rachis, it has surrounded the xylem (fig. 10). The pinna-traces are of marginal origin. The traces of the reduced leaves are of variable construction; the phloem is ill-defined, and the xylem is on a reduced footing. These points are demonstrated in fig. 7, which shows a reduced trace in section through the leaf-base. The large leaves are of uniform construction, and their tissues are well differentiated, but the occasional small leaves show marked irregularities of form and construction, and their tissues are typically ill-defined. These facts lend support to the belief that the small leaves of *Jamesonia* are reduction forms consequent on mal-nutrition under xerophytic conditions.

Sporangia.—The continued apical growth and slow differentiation of the leaf made it easy to follow the sporangial development in detail. The crowded sporangia are initiated in a "simple" condition astride the veins, and in transverse section of the pinna appear as in fig. 21. Occasional sporangia are inserted on the general surface between the veins, and in the mature pinna the "Acrostichoid" condition is pronounced (text-figs. 3 (*c*), (*d*), 4 (*a*)). The "simple" condition is maintained throughout the early stages of development (fig. 22), but there is a sudden change to a "mixed" condition when the sporangia begin to elongate (fig. 23), and in the later stages of development the "mixed" condition is strongly marked (figs. 24, 25). A "gradate" condition has not been found at any point in the development of the sporangia, but the transition from the "simple" to the "mixed" state is always sudden.

As will be seen from figs. 11, 12, 17, the slender sporangial-stalk consists of three rows of cells. The capsule is lopsided, one cheek being flattened, the other bulging (fig. 13). This lopsidedness seems in no way referable to the position or orientation of the sporangia, and when most prominent is usually accompanied by irregularities of the annulus. As is shown in the side, front, and expanded views of sporangia given in figs. 11, 12, 13, 17, the annulus is vertical and interrupted by the stalk. In the majority of the sporangia examined the annulus is regular, and meets the stalk at the back of the capsule. The main indurated series consists of about twenty cells, and the stomium of from six to twelve. The details of construction of the stomium are very variable; the majority of the cell-walls are unlignified, and there is an absence of uniformity in number and position of those which are thickened. The irregular annulus is typically sinuous, and comprises fewer cells than the regular annulus. These features are demonstrated in figs. 18, 19, 20, which represent opened sporangia. The irregularities may occur at any point in the annulus. In some cases additional indurated cells are in the main series (figs. 18, 19) or in the stomium (fig. 13), in others the continuity of the lignified series is broken (fig. 14), or consecutive cells differ greatly in size and form (figs. 18, 20). The sporangia with irregularities in the annulus give no structural indication of mal-nutrition. They are of average size, and their spores are fully matured. The highest spore-count which has been recorded was made from a sturdy sporangium with an irregular annulus. It seems improbable that these irregularities of the annulus are chance occurrences expressive of irregular nutrition or mechanical interference during development. The frequency of these irregularities may be gauged from the following analysis. 100 sporangia from each of six plants were examined; in 450 the annulus was regular, in 150 irregular. The numbers for the individual plants were :—

	Sporangia with Regular Annulus.	Sporangia with Irregular Annulus.
1st plant	71	29
2nd ,, ...	83	17
3rd	64	36
4th ,, ...	79	21
5th ,, ...	87	13
6th ,, ...	66	34

It is believed that in *Jamesonia*—as in other plants dealt with in these pages—irregularity of form and construction of the annulus is not to be regarded as a chance abnormality, but as a characteristic feature worthy of fuller recognition in a phyletic discussion. The condition may be considered an upgrade one, the sporangia being generally on an upgrade footing as regards form and position of the annulus, but the latter has not yet settled down as a uniform advanced type. The existing irregularities need not be interpreted as reminiscent of the ancestral condition, but they point to changes in construction through which the regular vertical annulus may have arisen.

Spores.—As will be seen from figs. 15, 16, the spores are tetrahedral, and smooth-walled except for certain fine striations on the triangular faces. They are of uniform size. Spore-counts have been made from mature sporangia, and such numbers as 56, 58, 63, 64, 66, 69, 71, and 72 have been recorded. 56 is the smallest number which has been counted, and 72 the largest. 72 is probably the typical spore-number. This number is remarkably high for a genus showing an advanced "mixed" condition of sporangia. The numbers recorded for such plants generally range between 48 and 64. This has been shown by Professor Bower in his "Studies in the Morphology of Spore-producing Members," iv (*Phil. Trans. Roy. Soc.*, 1899), and in *The Origin of a Land Flora*, and much smaller numbers are characteristic of some species of *Nothochlæna*, *Cheilanthes*, and *Pellæa*, and of *Ceratopteris* and *Sadleria*. Among Gradatæ, 64 is the highest number yet recorded for *Cyatheaceæ*, *Dennstædtiinæ*, and *Dicksonieæ*; but in some species of *Hymenophyllum* and *Trichomanes*, and in the Simplices generally, the recorded spore-numbers exceed 128. A general survey of the *Filicales* shows that the transition from 64 to 128 is remarkably sudden. Accordingly, *Jamesonia* is of special interest as possessing a spore-output per sporangium ranging between these numbers. The high spore-output in *Jamesonia* may be considered a primitive character. Its recognition lends added interest to the irregularities of the annulus, and marks the genus as one in which the sporangial characters are not yet of fixed advanced type.

General Conclusion.—It is not proposed to discuss here the value of the specific characters recognised by the systematists, for they refer chiefly to leaf-habit, and lead to the recognition of no features which aid in a question of generic affinity. Attention may, however, be focussed on certain points in the foregoing survey of the structural features of *Jamesonia*.

The dermal appendages are of simple type, but throw no direct light on the phyletic position of *Jamesonia*, and display no special features which would justify detailed comparisons. The same may be said of the stele, for protostely, solenostely, and dictyostely may all exist within the limits of a single group. This is seen, for example, in the *Schizæaceæ*; *Lygodium*, Sw., being protostelic, *Aneimia mexicana*, Kl., solenostelic, and *Mohria*, Sw., dictyostelic. But while the stelar state may not be decisive phyletically, the cortical characters may be used generically. The display of highly ventilated parenchyma immediately outside the stele is peculiar to *Jamesonia*, and may be used as a subsidiary character in generic determinations. The undivided leaf-trace and the marginal pinna-trace supply are simple features, and while they may be matched from modern *Schizæaceæ*, they would not be decisive in a question of affinity. The structure of the pinnæ and roots is expressive only of specialisation under xerophytic conditions. Thus though individually the structural features are indeterminate, collectively they constitute a relatively primitive anatomical state.

The general "Acrostichoid" sporangial arrangement is open to alternative explanations. It may be a primitive arrangement comparable to that typical of modern *Schizæaceæ*, or the result of extension of non-indusiate sori along the veins. The sudden transition from the "simple" to the "mixed" condition during development of the superficially initiated sporangia is, however, a feature of advance. The elongated stalk and vertical annulus are considered features of advance, but the frequent irregularities of the annulus are regarded as accompaniments of a change in the position of the annulus, with, perhaps, a downward spread of induration. In any case the sporangia are held to be of an upgrade type, in which variations of the annulus might naturally be expected to persist.

But the most decisive point which has emerged from the study of this plant is the high spore-count. It gains its value from the rarity of occurrence of numbers in advance of 64 in forms other than those recognised as primitive. It is undoubtedly a primitive feature which in a phyletic treatment enhances the value of simple anatomical characters. In the case under discussion it strengthens the opinion that the dermal appendages, the leaf-trace characters, the "simple" sporangial initiation, and the irregularities of annulus are evidences of a primitive source, and that the stelar state, the "mixed" condition of the mature sporangia, and the regular vertical annulus are features of moderate advance.

The characters described are sufficiently distinctive to fully justify the maintenance of the genus *Jamesonia*, and, in the absence of evidence suggestive of some other ultimate origin, they may indicate for it some Schizæaceous source. This question of ultimate origin will be discussed at length in the conclusion to the memoir.

Llavea, Lagasca.

This second plant appears in the *Synopsis Filicum*, 1874, as *Llavea cordifolia*, Lagasca, the single representative of a genus allied to *Cryptogramme* and *Pellæa*. In 1816 the genus was founded by LAGASCA for the reception of a plant dedicated to M. DE LA LLAVE (*Gen. et Sp.*). In 1827 DESVAUX described it as *Allantodia* (*Journ. de Bot. app.*), and SPRENGEL considered it an *Asplenium* (*Syst.* 4). In 1839 KUNZE sank it in the comprehensive genus *Allosorus* (*Filices*), and it was similarly treated by KEYSERLING in 1873 (*Pol. Cyath. Hb.*). In 1831 Sir WM. HOOKER named it *Ceratodactylis* (*Icones Plantarum*); and in 1839, 1842, J. SMITH maintained this name (*Hk. Gen. Fil.*), remarking that "the sterile portion of the frond agrees with *Osmunda*, and the fertile pinnules with *Ceratopteris*, and the position of the sporangia and form of the sorus with *Cryptogramma*." He accordingly named the species *Ceratodactylis osmundoides*, but found it difficult to suggest what is its nearest affinity. It is the *Botryogramme* of Fée (*Genera*), 1850–52, and a *Cryptogramme* according to PRANTL, 1882. In 1897 CHRIST followed HOOKER in maintaining LAGASCA's foundation (*Farnkr.*), and likewise associated it with *Cryptogramme* and *Pellæa*. In this he has been supported by DIELS (Engler and Prantl, *Nat. Pfm.*), 1897, 1902. And, finally, in 1905 CHRISTENSEN accepted *Llavea* as a monotypic genus (*Index Filicum*), and associated it with *Cheilanthes*, *Nothochlæna*, *Onychium*, and *Cryptogramme*.

This plant has never before been submitted to a detailed examination, and little is known of it beyond its habit features. In the following pages it is shown that the characters of *Llavea* are of transitional type, and it is maintained that LAGASCA's foundation is fully justified by the facts of anatomy and reproduction.

Habit.—The stem is strong, erect, and beset with hairs and scales. The latter are discarded at maturity, leaving the axis straw-coloured. The leaves are long and typically tripinnate. The lower part of the leaf is sterile, and its pinnules are stalked and cordate. The upper pinnules are fertile and linear, with inrolled margins and a general pod-like appearance. At maturity the leaves are virtually naked, the pinnules are delicate but not of filmy texture, and their veins are prominent. According to HOOKER (*Syn. Fil.*), *Llavea* is a Mexican Fern growing up to a level of 7500 feet. The habit is well shown in the *Icones Plantarum*, 1841.

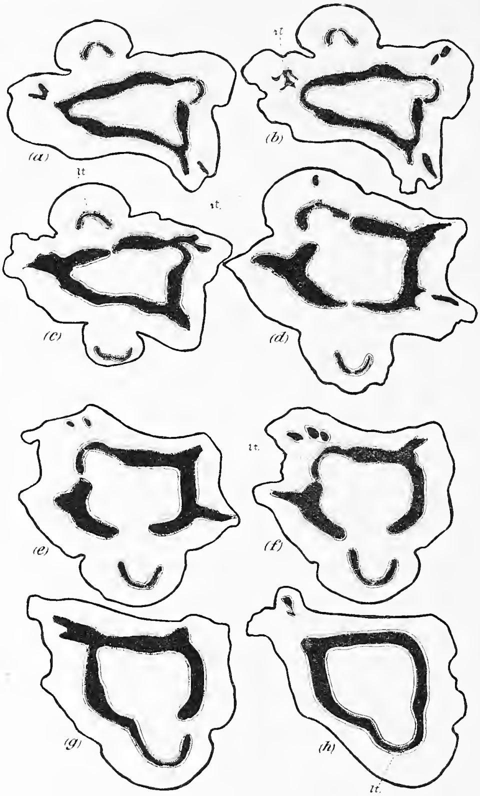
The structural features here described have been investigated in a single specimen, for which I am indebted to Professor BOWER. The plant came originally from Dr GOEBEL, Munich.

Dermal Appendages.—The dermal appendages of the axis are lanceolate scales and unbranched hairs (figs. 28, 29). The scales are sessile, and are massed around the leaf-bases; the hairs are small, non-glandular, and hidden by the broad scale-bases. In our materials the only appendages found on the pinnules are a few hairs distributed along the veins. The scales are of an advanced type, and the simplicity of the hairs may be primitive.

Axis.—The axis is almost erect, and bears the leaves in a loose spiral arrangement. The roots are mainly associated with the leaf-bases, and emerge from the cortex in branched groups. The ground-tissue is mainly storage parenchyma, only a narrow outer margin being sclerotic. The vascular cylinder is a simple solenostele, with short oblique gaps, towards the base of each of which an undivided strap-shaped leaf-trace is obliquely inserted. These points are shown in fig. 31, which represents a stelar reconstruction based on a series of transverse sections of the stem. They are further demonstrated in the series of diagrams comprised in text-fig. 8, and which represents consecutive transverse sections.

Root.—The root-traces are inserted on the stele mainly beneath the leaf-traces, and are frequently branched close to their points of origin (fig. 31). The root-structure shows no features of special interest.

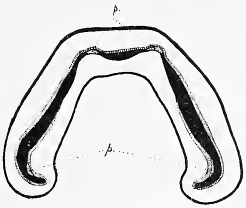
Leaf.—At the point of insertion of the leaf-trace on the stele the leaf-trace xylem has the form of a curved strap, thinner in its middle abaxial region than towards its margins. This is indicated in text-fig. 8 (*f*) and (*h*), *l.t.*, in which the xylem is represented as black, the phloem as a dotted zone completely investing the xylem, and the endodermis as an unbroken line. Further out, the phloem on both sides of the thin zone of xylem is gradually replaced by parenchyma, and a break in the continuity of the tracheides follows. The condition established is represented diagrammatically in text-fig. 8 (*a*)—(*g*) and in fig. 26, which shows the details of construction of the abaxial portion of the trace. The interruption in the phloem is more marked than in the xylem, and in the parenchyma which fills the gap in the latter there are a few small isolated tracheides. Neither the pericycle nor endodermis appear in any way disturbed. There is thus established a potential perforation of the leaf-trace.



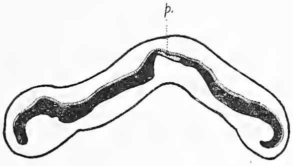
Text-fig. 8.

As the trace is followed outwards the continuity of xylem and phloem are consecutively re-established in the leaf-base, the abaxial xylem is thickened, and there is no sign of the potential break seen in the basal portion of the trace. In the petiole the leaf-trace is enlarged, and in transverse section appears as a wide ∩ (text-fig. 9). There are apparently four protoxylem groups (*p.*), and the phloem —which is hatched in the figure—completely clothes the abaxial face of the xylem, and is continued adaxially around the xylem margins. In the rachis the trace is laterally expanded, the two abaxial protoxylems are replaced by a single group, and phloem is on the abaxial xylem face alone (text-fig. 10). As will be seen from text-figs. 10, 11, the vascular supply to the pinna has a marginal origin. The potential perforation of the leaf-trace described above is a constant feature throughout our specimen, and seems worthy of special note.

The mature sterile pinnules are cordate. Their venation is advanced, with the lateral veins reaching the margins and showing occasional simple reticulations (text-fig. 12). The fertile pinnules are typically long and narrow, and their margins are strongly inrolled and membranous; there are no reticulations, and the lateral vein-endings fall far short of the margins (text-figs. 13, 14, 15). The only dermal appendages which have been found are simple hairs, scattered mainly among the sporangia along the veins (fig. 27) and on the pinnule-margins (text-fig. 15).

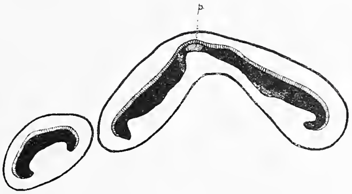


Text-fig. 9.



Text-fig. 10.

Sporangia.—The sporangial distribution is "Acrostichoid." The mature condition is a "mixed" one (fig. 27), and with few exceptions the sporangia are on the veins (text-fig. 14). The sporangial-stalk is slender, and consists of three rows of cells (figs. 27, 30, 37). The capsule is slightly lopsided, and the annulus is variable in both form and position. During development the same sudden transition from the "simple" to the "mixed" condition, recorded for *Jamesonia*, occurs, and in the mature pinnule the developmental range may be as in fig. 27.



Text-fig. 11.

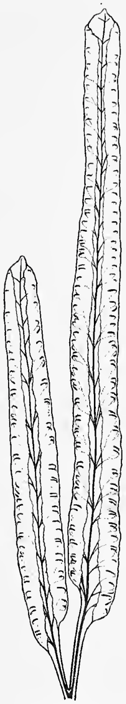
In only a small proportion of the sporangia is the annulus uniseriate and vertical. The most regular condition found is represented in fig. 35, which shows the annulus in extension. It is of an advanced vertical type, with a well-defined stomium. A more common condition is that shown in fig. 33. The back of the annulus is vertical, but the stomium passes obliquely down the cheek of the capsule, so that only the basal indurated cells re-enter the median plane. In some cases the annulus is broken, as in fig. 37. In others lignification is imperfect at the back or top of the annulus (figs. 36, 38), or the number of indurated cells may be increased, so that any condition ranging between a local doubling and a biseriate annulus may be found (figs. 36, 34). In the foregoing types the back of the annulus is vertical and is usually decurrent to the stalk, and a definite, though variably constructed, stomium is always present.

But in some sporangia the condition shown in fig. 30 exists; in others, the arrangement is as in fig. 39. In the former the stomium is well defined. The broken annulus passes obliquely over the capsule, and, instead of descending to the stalk, it terminates on the bulging cheek. In the latter there is no stomium, but the indurated cells form a crescent on the summit of the capsule.

TEXT-FIG. 12.

Spores.—The spores are tetrahedral (fig. 32), and resemble those of *Plagiogyria semicordata*, Kze. The highest spore-count made was 52, the lowest 46. 52 is probably the typical spore-number.

The vertical uniseriate annulus is relatively uncommon in *Llavea*. The capsule form is fairly constant, and suggests no ready explanation of the prevailing irregularities of the annulus. As in *Jamesonia*, the sporangial-stalk is of the uniform advanced type. It may be reasonably suggested that in *Llavea* also upgrade tendencies in sporangial construction are shown, and that the slender three-rowed stalk, the occasional vertical annulus, and the moderate spore-output are features of advance. As in questions of affinity, so also with the study of apparent tendencies an increase in the number of subjects of comparison is of material help towards a balanced conclusion. The sporangial condition in the "Acrostichoid" *Cryptogramme crispa*, R. Br.—with which *Llavea* has been associated by the systematists—is, then, of special interest. The salient features of sporangial-form in his plant are shown in Plates V and VI. The stalk is short and of variable construction. In its simplest condition it is three rowed (figs. 48, 51, 57), but four, five, and six rows have been found (figs. 49, 52, 53). The annulus is typically oblique, and passes close to the stalk (figs. 48, 53, 55). Irregularities are not uncommon (figs. 54, 57). In some cases the annulus does not reach the stalk (fig. 50), in others it both reaches the stalk and is interrupted by it (figs. 51, 52). The spore-counts made are 45, 46, 48, 50, 51, 52. The typical spore-number is 52. I am much indebted to Professor Bower for figures drawn by him from sporangia of *Cryptogramme*. On these my figures are founded.

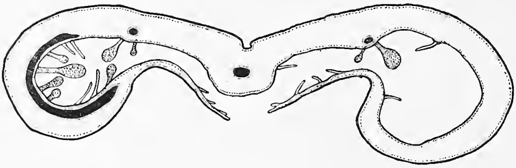


TEXT-FIG. 13.

TEXT-FIG. 14

The figures detailed strengthen the impression that in the genera under discussion variation in sporangial construction is a natural feature, and indicate transitional states from which a uniform sporangial type with regular vertical annulus might emerge. At the same time they suggest that as in stem and leaf, so also in sporangia similar advances may not be made in all features.

General Conclusion.—The anatomical state of *Llavea* is regarded as transitional. It bears no conclusive evidence of the nearer affinities of this plant, though the solenostely is such as to indicate a connection downwards. The dermal appendages show mixed characters, but the scales are distinctly advanced. The stelar anatomy provides no outstanding characters which suggest direct phyletic comparisons. The leaf-trace is simple, but of a more advanced type than is seen in *Jamesonia.* At its base the anatomical state is peculiar, and is open to interpretation as showing a first step towards division of the trace in the median radial plane. This is held to be a feature of advance. As in *Jamesonia*, the pinna-trace supply is of a simple marginal origin. It is open to a Schizæaceous comparison, but carries no decisive weight in a question of affinity.



Text-fig. 15.

With *Cryptogramme* it shares the possession of dimorphic pinnules, but the sporangial characters detailed are sufficiently distinctive to preclude a belief in a close affinity for these plants. The occasional reticulations mark the venation as of a more advanced type than is seen in *Jamesonia.*

Individually the structural features are indeterminate. The most significant is, however, the presence of scales of advanced type. Collectively they constitute a transitional state giving a more advanced condition than is seen in *Jamesonia.*

The "Acrostichoid" sporangial arrangement is open to the same explanations as were advanced in the case of *Jamesonia.* It may be the result of extension of non-indusiate sori along the veins, or a primitive arrangement as in modern *Schizæaceæ.* The sudden transition from the "simple" to the "mixed" condition during development of the superficially initiated sporangia is a feature of advance. The elongated stalk and the occasional vertical uniseriate annulus are upgrade characters, but the frequent irregularities of annulus are considered accompaniments of a change in position of the annulus. The sporangia are held to be of upgrade type, in which variation of the annulus may naturally be expected to persist, and is still pronounced. This constitutes a feature which provides a ready contrast with *Jamesonia.* In the latter, irregularities of the annulus are fairly common, but never dominant.

The anatomical characters of *Llavea* are such as to allow of a reasonable comparison with *Jamesonia*, which the sporangial variations tend to strengthen. But at the same time a *Plagiogyria*, Kze., connection is suggested. This plant has been placed by certain systematists near to *Llavea* and *Cryptogramme*, and this connection is suggested by CHRISTENSEN in his *Index Filicum*, 1905. Professor BOWER has shown that *Plagiogyria* has hairs but no scales, a mixed sorus, an oblique annulus, and a solenostelic or slightly dictyostelic condition ("Studies in Phylogeny of Filicales," No. 1, *Ann. Bot.*, 1910). This suggested connection with *Plagiogyria* is probably a reality.

The spore-output of *Llavea* is on an advanced footing of reduction which forbids a view of close affinity between *Llavea* and *Jamesonia*. It is hardly to be expected that development will be parallel on all lines. Accordingly the view that is taken is, that while in *Jamesonia* the annulus and stalk are in general advanced, the spore-output is primitive; in *Llavea* the spore-output and stalk are advanced, and the annulus generally primitive. In *Cryptogramme*, on the other hand, the sporangia are advanced on the condition seen in *Llavea*, but primitive characters persist in the stalk.

The facts detailed justify the maintenance of *Llavea* as a monotypic "Acrostichoid" genus. As in the case of *Jamesonia*, a suggestion of some Schizæaceous source for *Llavea* seems not unreasonable. The anatomical state will bear it, and, in light of the facts now available regarding *Jamesonia*, the sporangial state may support it. If this view be adopted, *Llavea* may be regarded as a more advanced derivative than *Jamesonia*, which has adopted a relatively small spore-output.

Gymnogramme (*Trismeria*) *trifoliata*, Desv.

There remains to be considered a remarkable Fern of tropical America which is considered by some systematists a species of *Gymnogramme*, and by others a distinct genus *Trismeria*, with one species and several sub-species. Its "Acrostichoid" character was recognised by LINNÆUS in 1753, and he named it *Acrostichum trifoliatum* (*Sp. Pl.*). It was similarly named by SWARTZ in 1806 (*Syn. Fil.*), by SCHKUHR in 1809 (*Fil.*), and by WILLDENOW in 1810 (*Sp. Pl.*). In 1811 DESVAUX (*Berl. Mag.*) held it to be a *Gymnogramme*, and in 1827 he restated his belief in its *Gymnogramme* nature (*Journ. de Bot. appl.*). The opinion of FÉE (*Gen. Fil.*), in 1850–52, was that this plant is neither an *Acrostichum* nor a *Gymnogramme*, but that it merits recognition as a distinct genus. He accordingly renamed it *Trismeria*. The opinion of DESVAUX was upheld by Sir WM. HOOKER in 1862 (*Garden Ferns*), and by BAKER in 1878 (*Jo. B.*). In 1896 KUHN designated it *Ceropteris* (*Engl. Jahrb.*), and in 1897 CHRIST named it *Gymnogramme trifoliata* (L.), Desv. (*Farnkr.*). Both DIELS and CHRISTENSEN have maintained it as a distinct genus *Trismeria*, the former in 1899, 1902 (Engler and Prantl, *Nat. Pfm.*), the latter in 1905 (*Index Filicum*).

The plant is well figured in HOOKER's *Garden Ferns* and in several of the systematic works. It is a tall, erect Fern of striking appearance, with almost erect axis bearing lax scattered brown scales, and stout leaf-stalks arranged almost alternately. The leaves are pinnate, and the pinnæ are numerous. The lower pinnæ are petiolate, and for the most part ternate. Higher up the pinnules are usually in pairs, and in the upper part the pinnæ are usually undivided. The pinnules are linear-lanceolate and of a sub-coriaceous nature. The sterile pinnules are entirely naked, but on the lower surface of the fertile pinnules are glandular hairs and a covering of a characteristic white or yellow wax, similar to that present in *Cheilanthes argentea* (Gmel.), Kze., and in the *Ceropteris* section of *Gymnogramme.*

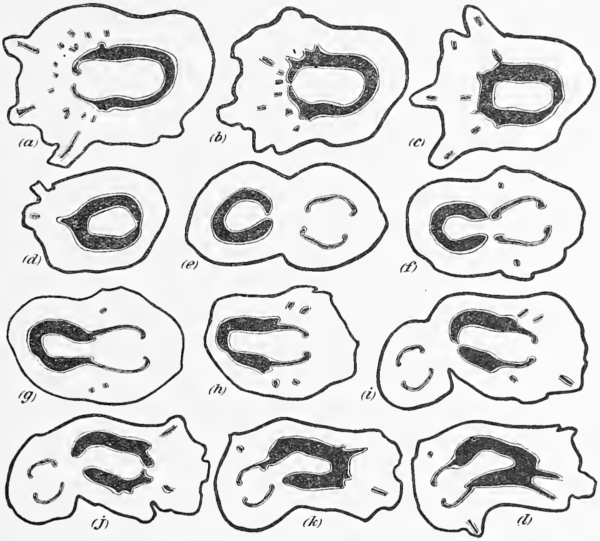
It is a common Fern from Cuba southward to Peru and Brazil. It is well represented in Jamaica and in the West Indian Islands generally. Professor BOWER has found it in streams in Jamaica, with its roots well fixed in the shingle.

The near affinities of this "Acrostichoid" Fern are clearly in doubt, for the opinions held by the systematists have not hitherto been tested against the facts of construction and reproduction. With a view to a full investigation being made Professor BOWER, F.R.S., and Mr J. M. F. DRUMMOND, B.A., F.L.S., collected abundant material in Jamaica, and it is to them that I am indebted for the plants from which the following statement has been constructed.

Dermal Appendages.—The axis-scales are of an advanced lanceolate type, with broad base, slightly serrate margins, and accuminate tip (fig. 40). They are the only dermal appendages which have been found on the stem. The mature petiole and sterile pinnules are entirely naked, but the fertile pinnules bear on their lower surface numerous glandular hairs (fig. 41). Structurally the latter resemble the capitate hairs characteristic of the "golden" and "silver" species of *Gymnogramme*, *Nothochlæna*, and *Cheilanthes.* As has been shown by DE BARY (*Comparative Anatomy of the Phanerogams and Ferns*), 1884, these capitate hairs secrete a resinous substance soluble in alcohol. To this secretion the "golden" and "silver" Ferns owe their dusty appearance. In our materials preserved in alcohol the hairs and general epidermis show no sign of a secreted substance, but in our herbarium specimens a yellow-green deposit of fine rods and granules covers the hairs and the entire epidermis, excepting the raised guard cells (fig. 42). The presence of this secretion is a general guide to the fertility of a pinnule, its absence is an index of sterility. In the *Synopsis Filicum*, 1874, Sir WM. HOOKER placed special reliance in his specific treatment of *Gymnogramme* on the glandular hairs and associated resinous secretions. He considered them indicative of kinship for species possessing them, and included in a section *Ceropteris* all *Gymnogrammes*—including *G.* (*Trismeria*) *trifoliata*—possessing these features. It will be shown in the following pages that on the summation of characters this plant may still be considered a *Gymnogramme.* From this it follows that the basis of HOOKER's grouping of the section *Ceropteris* is justifiable.

Axis.—Storage parenchyma bulks largely in the ground-tissue of the axis, and only a narrow peripheral zone is sclerotic. The vascular system is a solenostele, the only gaps in which are leaf-gaps (fig. 45). As will be seen from this stelar reconstruction, and from the series of diagrams in text-fig. 16, the leaf-trace consists of two similar curved strands. These are inserted laterally towards the base of the leaf-gap. The root-traces are in oblique series outside and beneath the insertions of the leaf-traces, and are commonly branched near their points of origin.

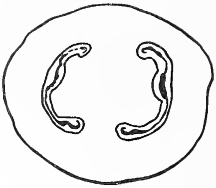
Root.—The root is sturdy, and has a broad, thick-walled cortex (fig. 47). It shows no features which can be used in a discussion of affinity.



TEXT-FIG. 16.

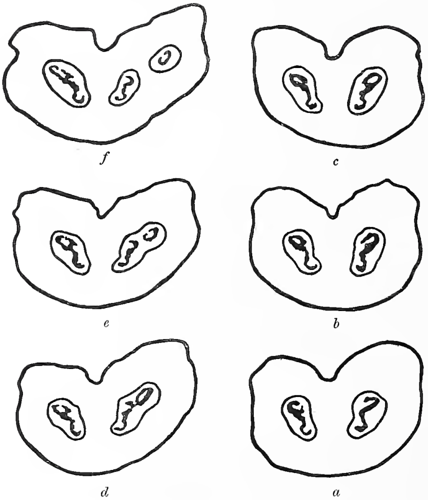
Leaf.—In the base of the petiole the two leaf-trace strands are strongly curved. The xylem-margins are "hooked," and breaks in the continuity of the tracheides are common (text-fig. 17). As the petiole is ascended the strands undergo condensation but retain their relative positions. The chief steps in the supply of the first pair of pinna-traces are represented in text-fig. 18. As will be seen from the series of diagrams (*a*)–(*f*), the margins of the xylem become first united to the main body of tracheides, and the pinna-trace supplies are thus of extra-marginal origin. The second pair of pinna-traces are similarly supplied. A union of the two leaf-trace strands now occurs (text-fig. 19), and the supplies to the third pair of pinnæ are extra-marginal in origin (text-fig. 20 (*a*)–(*f*)). In our plants the supplies to the fourth, fifth, and sixth, and occasionally the seventh, eighth, and ninth, pairs of pinnæ are extra-marginal, though the leaf-trace has become much simplified (text-fig. 21 (*a*)–(*f*)). But to the more distal pinnæ a marginal supply is provided (text-fig. 22 (*a*)–(*c*)).

The divided leaf-trace and the dominant extra-marginal pinna-trace supply in the robust portions of the leaf constitute advanced features, and the undivided trace and marginal pinna-trace supply in the distal parts are the natural accompaniments of vascular reduction.



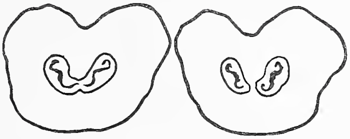
TEXT-FIG. 17.

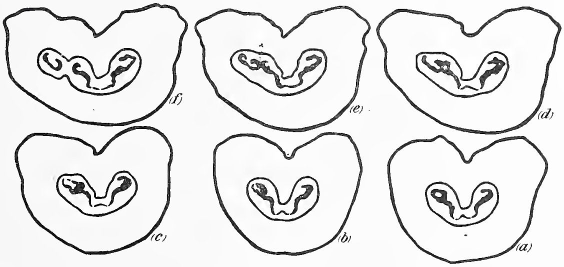
The vascular condition of this plant may be better understood by comparison with an advanced *Gymnogramme* type. For this purpose *Gymnogramme japonica*, Desv., may reasonably be employed. A reconstruction of part of its stele is shown in fig. 56, and a series of diagrams of transverse sections of its stem constitute text-fig. 23. From these it will be seen that the vascular system is a perforated dictyostele. The perforations are confined to the robust portion, and affect both the



TEXT-FIG. 18.

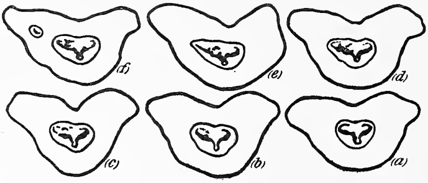
stele proper and the decurrent bases of the leaf-trace strands. The perforations may run outwards for long distances into the leaf-trace bundles, as in the right of the reconstruction. When this occurs the abaxial margin of the leaf-trace strand is reduced to a slender strap decurrent from the leaf-trace strand to the stele. The ontogenetic development of these perforations has been followed. They arise by a local constriction of the endodermis, accompanied by parenchymatous replacement of both phloem and xylem in the constricted area. In the robust portions of the axis they frequently materialise, the endodermis being nipped across as the parenchymatous gap in the phloem and xylem widens (text-fig. 24), but in the base of the leaf-trace and in the slender parts of the stele they commonly remain incipient (fig. 56 and text-fig. 23). It frequently happens, however, that a gap initiated in the stele may not close above in the leaf-trace. In these circumstances the slender marginal strand gradually diminishes, and finally ends blindly in the ground tissue of either axis or leaf-base (fig. 56). From the foregoing it will be seen that in *Gymnogramme japonica* perforation of the stele is a progressive feature which may lead to further division of both stele and leaf-trace with the establishment of blindly-ending strands. This may have a direct bearing on the origin and interpretation of so-called "compensation-strands" commonly developed in certain types of divided leaf-traces. These "compensation-strands" may be in some cases the results of dissection of the vascular system rather than provisions against mechanical or conductive difficulties.


TEXT-FIG. 19.



TEXT-FIG. 20.

In the base of a strong petiole the leaf-trace is progressively reduced as regards actual and potential perforations. Within 3 inches of the leaf-base the changes shown in the diagrams (*a*)–(*q*), text-fig. 25, may take place. In slender leaves, however, the base of the leaf-trace may not be actually on so divided a footing, but may consist initially of two strap-shaped strands. At a point varying between 4 and 7 inches from the leaf-base, the leaf-trace strands unite, as in text-fig. 26. The main pinna-trace supplies are of extra-marginal origin (text-fig. 27), and it is not till the finer distal portion is reached that a marginal supply is encountered. The stele and leaf-trace of *Gymnogramme japonica* are then of an advanced type.

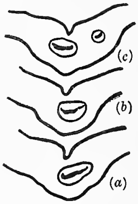


Text-fig. 21.

The stele of *Gymnogramme* (*Trismeria*) *trifoliata* is held to be of an advanced solenostelic type, and the vascular details of the leaf are decidedly advanced and are readily comparable with those of *Gymnogramme japonica.*

The venation of both sterile and fertile pinnæ is of an advanced type, with lateral dichotomies, and no reticulations (text-fig. 28).

Sporangia.—In our materials the sporangia are, with few exceptions, inserted on

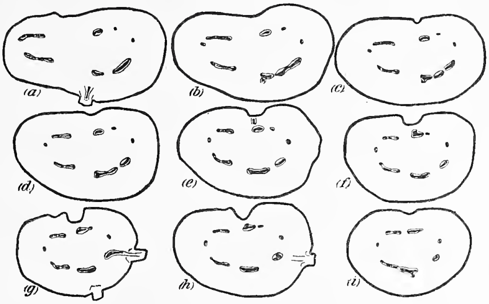


Text-fig. 22.

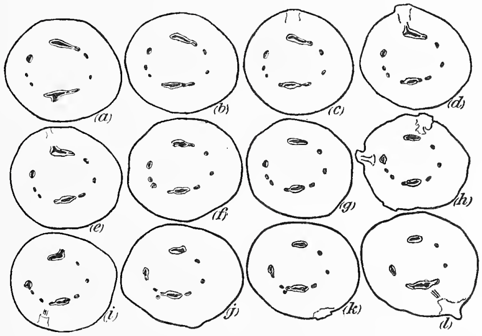
the veins (text-figs. 29, 30). At initiation they show a "simple" condition from which they pass directly to a "mixed" state, in which interpolation of sporangia commonly occurs. The stalk is relatively short, and consists of three rows of cells (figs. 41, 44). The annulus is typically vertical, regular, and interrupted by the stalk. There is a well-defined stomium. Occasional irregularities occur in the annulus, but these do not lead to fundamental disturbances in either the form or position of the annulus (fig. 43).

Spores.—The spores are tetrahedral, and bear on their thin transparent walls irregularly distributed bars of thickening (fig. 46). The spore-counts which have been made from mature sporangia are 49, 48, 46, 44, 43, 39, 35. The full spore-number is probably 52.

General Conclusion.—A general survey of the structural features of this plant reveals no point which militates against a *Gymnogramme* relationship. The advanced dermal appendages and the characteristic capitate hairs and resinous secretions are easily matched from *Gymnogramme* types. With the hairs and secretions, however, matters are different than with the scales. The latter may be reasonably compared with the scales of many plants in no way directly related to *Trismeria.* But glandular hairs and secretions of the type under discussion are uncommon among Ferns, and may be accordingly considered truer indices of affinity. On the grounds of the hairs and secretions, then, a choice of near relationship for this plant is suggested between *Gymnogramme* and *Cheilanthes* or *Nothochlæna.*



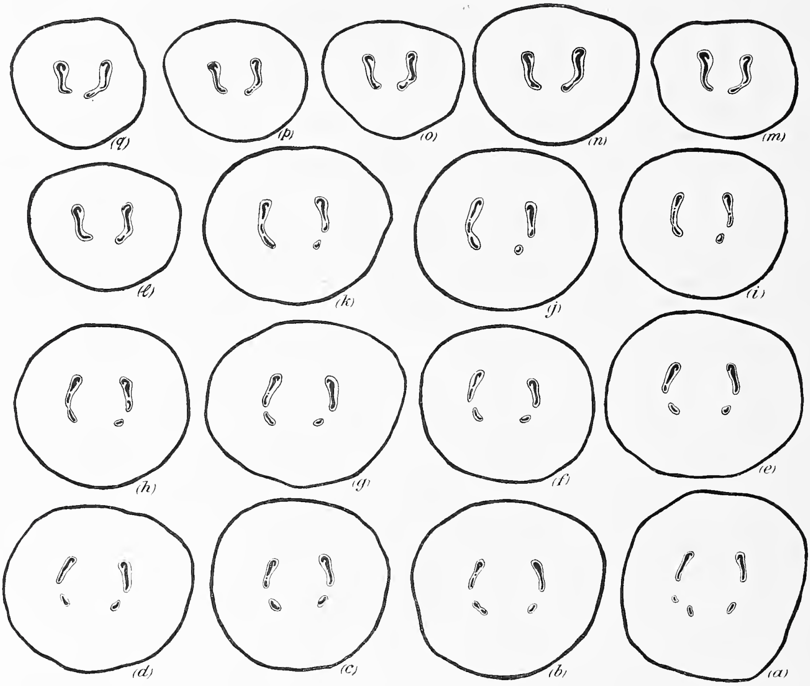
TEXT-FIG. 23.



TEXT-FIG. 24.

The anatomical condition is of an advanced type, not characteristic of this plant alone, but common in the *Gymnogramminæ* in general. The "Acrostichoid" sporangia with typically regular annulus and moderate spore-output would admit of a *Gymnogramme* relationship. On the other hand, the anatomical state would not preclude our plant from the *Cheilanthinæ*, and cannot therefore be relied upon in the final determination of near affinity. The sporangial characters of such genera as *Nothochlæna*, *Cheilanthes*, *Pellæa*, and *Ceratopteris* will then be of special interest as bearing on this point.

In *Nothochlæna affinis* (Mett.), Moore, there is a three-rowed stalk, and a somewhat oblique annulus which is not decurrent to the stalk (figs. 58, 63). The number of indurated cells is relatively small, and irregularities commonly occur (fig. 62). The condition established is certainly not advanced, and the general absence of induration from the lower part of the capsule may be a primitive condition. The spores are of special interest (figs. 59, 60, 61). They vary both in size and number per sporangium. In some cases only small spores are present. When this occurs the spore-output is high. Such numbers as 64, 56, 55, 54 have been counted. In others the spores are few and large, 18, 16, 14, 12 having been frequently found. Between these extremes

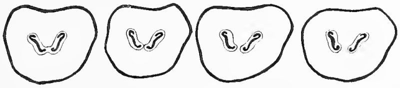


Text-fig. 25.

there is a third condition. In this an admixture of large and small spores, or of large and intermediate spores, or of small and intermediate spores is found. The following are examples of the analysis of spore-numbers in this exceptional type :—

Small Spores.	Intermediate Spores.	Large Spores.	Total Spore-number.
..	..	15	15
8	..	14	22
..	14	10	24
..	20	8	28
6	22	4	32
24	20	2	46
33	27	..	60
58	1	..	59
64	..	..	64

In *N. nivea*, Desv., the sporangial construction resembles that of *N. affinis*, but the obliquity of the annulus and its separation from the stalk are more prominent than in the latter (figs. 66, 67, 68). The spores are of a uniform tetrahedral type and of constant size (fig. 69), and the typical spore-count is 24.



TEXT-FIG. 26.

A more advanced condition is found in *N. distans*, R. Br. (figs. 77, 78, 79). The annulus is usually almost vertical, but the stomium may be directed past the stalk, and irregularities in the lignified series occur. The spores are uniformly large, and number 12.

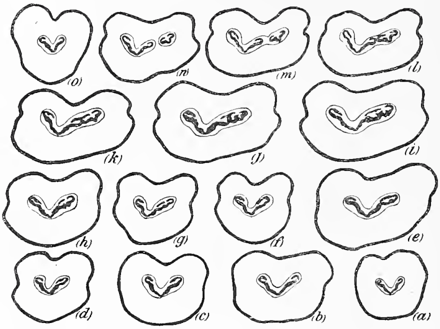
In *N. sinuata* (Lag.), Klf., the annulus is regular and vertical (fig. 64). The spores are of uniform type and size (fig. 65), but their number varies between 32 and 16. This variation appears to be partly referable to differences in sporangial size.

In these species the sporangia are relatively small. The spore-numbers range from 64 to 12, and the annulus is of variable position and form. A general separation of the annulus from the stalk is noticeable throughout, and the form of the unlignified cells does not suggest that the annulus has ever reached the stalk.

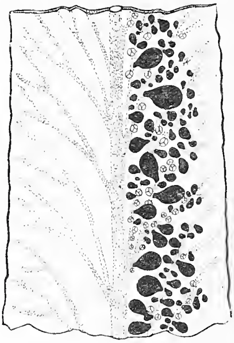
But in *N. trichomanoides* (L.), R. Br., the sporangia are large, and the annulus —though occasionally regular and perfectly vertical—is typically irregular. It reaches the stalk and is interrupted by it (figs. 80, 82, 83, 84). The spores are, as in the other species considered, tetrahedral (fig. 81), and the spore-count appears to be 48.

From the foregoing it is apparent that within the genus *Nothochlæna* the general condition of the sporangial characters is more primitive and irregular than in *Trismeria*, and a view of near affinity may not reasonably be held to exist between them.

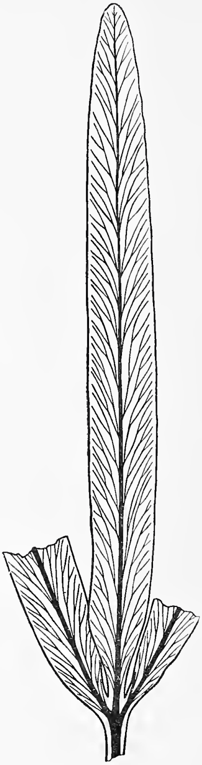
A similar case may be made out with regard to *Cheilanthes*. Throughout the genus the sporangia are typically long-stalked, but the same features which have been noted in the capsule of *Nothochlæna* are recognisable. Irregularities in the annulus are, however, less common in *Cheilanthes* than in *Nothochlæna*, and are marked only in *C. vestita*, Sw. This species and *C. Fendleri*, Hk., as noted by Marsh (*Ann. Bot.*, 1914, "The Anatomy of some Xerophilous Species of Cheilanthes and Pellæa"), shows the highest spore-numbers recorded for the genus.



Text-fig. 27.



Text-fig. 29.



Text-fig. 28.

The spore-counts made are as follows :—

Cheilanthes tenuifolia (Burm.), Sw.	32, 28, 27.	
,, *tomentosa*, Link.	32, 29.	
,, *microphylla*, L.	32, 30.	
,, *hirta*, Sw.	32, 28.	
,, *vestita*, Sw.	54, 52, 48, 47.	
,, *Fendleri*, Hk.	57, 53	spore-counts recorded by MARSH.
,, *gracillima*, Eat.	31, 30	
,, *lanuginosa*, Dav.	32, 30	

With the *Pellæas* examined the matter seems to stand on the same general footing recognised for *Cheilanthes* and *Nothochlæna*. The annulus is almost vertical but does not reach the stalk. Irregularities in the annulus are uncommon. My spore-counts in *P. falcata* (R. Br.), Fée, are 54, 52 ; those of MARSH are 60, 56. In *P. intramarginalis* (Klf.), J. Sm., it is 32 ; and 31, 30 have been noted by MARSH in *P. andromedifolia* (Klf.), Fée. But in *P. hastata* (Thbg.), Prantl, it varies considerably. This is an expression of differences in spore-size, both large and small spores being present. The highest count made was 24, the lowest 16.

TEXT-FIG. 30.

But if the sporangial characters do not indicate a close affinity of *Trismeria* to *Nothochlæna*, *Cheilanthes*, and *Pellæa*, neither will they point a near relationship of *Trismeria* to *Ceratopteris thalictroides* (L.), Brong. The sporangia of *Ceratopteris* are large, and have a short, massive stalk (figs. 70, 71, 75). The stalk is always massive (fig. 74), and the annulus—though typically vertical and interrupted by the stalk—is very variable in construction. In some cases the stomium is well developed, and the annulus almost regular. In others no stomium is recognisable, or, though induration is well developed to the stalk on both sides, the stomium may be ill-defined. The spores are large and of a remarkable, and possibly archaic, type (figs. 72, 73). The spore-count in our material may be anything between 24 and 12.

General Conclusion.—The general conclusion drawn from this study of *Trismeria* is that the plant has no distinctive characters which justify its recognition as a distinct genus. It does not belong to the *Cheilanthinæ*, but falls into line with the *Gymnogramminæ* generally. It may well retain the position assigned to it by Sir WM. HOOKER as *Gymnogramme* (*Trismeria*) *trifoliata*, Desv., an "Acrostichoid" species of Ceropterid type.

A General Survey.

The characters of external form, dermal appendages, and anatomy detailed above do not appear decisive, though they would allow of affinities of these Ferns in a moderately advanced position with references distinctly downwards.

It may be held that *Jamesonia* shows the most primitive vegetative state, with hairs but no scales, a simple solenostele, a simply-pinnate leaf, undivided leaf-trace, marginal pinna-trace supply, and an open venation. A slightly more advanced state is shown by *Llavea.* It has both hairs and scales, a wide solenostele, dimorphic pinnules like those of *Cryptogramme*, a large leaf-trace with an incipient perforation at its base, a marginal pinna-trace supply, and occasional reticulations in the sterile pinnules. Anatomically, *Trismeria* is decidedly the most advanced. Its dominant dermal appendages are massive scales, and the specialised wax-secreting hairs are restricted to the fertile pinnules. The stele is an advanced solenostele, the large pinnate leaf has a divided leaf-trace, and the pinna-trace supplies are of extra-marginal origin.

In all three the sporangial arrangement is "Acrostichoid," the sporangia are initiated *superficially* in a "simple" state, but by interpolation a "mixed" condition is subsequently established. The transition from the "simple" to the "mixed" sorus is sudden, there being no indication of an intermediate "gradate" condition. A state similar to that already demonstrated by Professor Bower for *Plagiogyria* and *Cryptogramme* (with which *Llavea* has been grouped) is thus recognised in the Ferns under discussion (*Ann. Bot.*, 1910).

When attention is turned from this uniformity of soral condition to the details of sporangial construction it is seen that the sporangial states of *Jamesonia*, *Llavea*, and *Trismeria* run more or less parallel to the anatomical conditions already compared. *Jamesonia* is the most primitive, *Trismeria* the most advanced. In all three the sporangial-stalk is slender and three rowed, the annulus is of variable position and construction, and the spores are tetrahedral. In *Jamesonia* the capsule is lopsided, the annulus is frequently irregular and oblique, the stomial construction is variable, and the spore-count is exceptional in being beyond 64, a very rare occurrence in Ferns other than those recognised as definitely primitive. In *Llavea*, as in *Cryptogramme* and *Plagiogyria*, the capsule is lopsided, the annulus is irregular in form and position, the details of stomial construction are variable, but the spore-counts are lower than in *Jamesonia.* The number for *Plagiogyria* is 48, for *Llavea* and *Cryptogramme* it varies below 52. In these Ferns variability of form and position of the annulus and stomium is common, but in *Trismeria* the annulus is typically vertical and regular, and only occasionally irregular. The stomium is of very constant form and construction, and the spore-count varies below 52. The recognition of *Trismeria* as a relatively primitive *Gymnogramme*, in which irregularities of the annulus persist, suggests the possible existence of sporangial irregularities in other *Gymnogramme* types. In the *Cheilanthinæ*, with which *Trismeria* has been associated by some authors, irregularity of sporangial construction is now seen to be widespread. To this is added the remarkable irregularity in spore-size and output per sporangium in *Nothochlæna affinis* and *Pellæa hastata*. These irregularities will strike the reader as particularly significant as generally affecting the Ferns discussed in these pages. Such facts acquire a special value when it is remembered how stereotyped are the sporangia and spores of most advanced types.

The facts appear to indicate that the Ferns now considered are in a transitional position. Taking all their characters into consideration, and noting the suggested connection between *Llavea* and *Plagiogyria*, these Ferns appear to constitute a laxly associated group in which the characters of the "Simplices" are still manifest. They all belong to the "Superficiales," and in the light of our present knowledge their probable origin may now be indicated.

It has recently been suggested by Professor Bower that the distinction between the "Superficiales" and the "Marginales" is based on the relatively early assumption in descent of the superficial position for the sorus in the former and the retention of the marginal position in the latter to the present day (*Ann. Bot.*, 1918). From this it is suggested that on the point of soral position the "Superficiales" generally will group themselves in relation to the relatively primitive *Gleicheniaceæ*, while the "Marginales" may be affiliated to the *Schizæaceæ*. Certain types, however, may be held to take an intermediate position. The underlying hypothesis is that in the ancestry of these Ferns the prevalent or universal position of the sorus was marginal, and that in certain forms for which an intermediate position is claimed indications may still be seen of an original marginal position for the sporangia. These may be viewed as more directly referable to some Schizæoid source. It has been shown by Prantl in 1882 (Engler's *Bot. Jahrb.*, p. 482) that in *Pellæa*, *Cryptogramme*, *Nothochlæna*, and others the first sporangium appears always at some distance from the leaf-margin, but in *Cheilanthes* it is quite close to it, so that as the young sporangia develop at first quicker than the margin the appearance is almost as though (as they actually do in *Schizæa* and *Mohria*) they spring directly from the marginal cells. Sir Wm. Hooker has noted that *Mohria* combines the capsule of the *Schizæaceæ* with the habit of *Cheilanthes* (*Syn. Fil.*, p. 436). When to this similarity of habit between *Cheilanthes* and *Mohria* is added the soral comparison between *Cheilanthes* and the *Schizæaceæ* the suggestion of a phyletic relationship of *Cheilanthes* with the *Schizæaceæ* seems remarkably strong. But it has been noted that *Cheilanthes* shares with *Jamesonia*, *Llavea*, *Trismeria*, *Pellæa*, *Nothochlæna*, *Cryptogramme*, *Plagiogyria*, and *Ceratopteris* an exceptional sporangial variation which may be indicative of kinship. It may be held that although in these latter a close association of the sporangia with the leaf-margin is not seen during development, their relationship to *Cheilanthes*, though not close, is none the less a reality. And further, since *Cheilanthes* is not a Pterid-derivative, but is related more directly on anatomical grounds to *Mohria* and a Schizæoid source than to any other group, a reasonable suggestion as to the ultimate origin of the Ferns discussed in this memoir is that they may similarly have sprung from some Schizæoid source. It is admitted that such a source has not been demonstrated for them, but the evidence available points more clearly to a Schizæoid origin than in any other direction.

In this comparison with the *Schizæaceæ* the most interesting point is the variability of spore-size disclosed in *Nothochlæna* and *Pellæa*. This is also to be noted in relationship to a similar variability which I have demonstrated in *Platyzoma*, R. Br. (*Trans. Roy. Soc. Edin.*, vol. li, 1916; vol. lii, 1917). In this connection the acknowledged Schizæoid affinity of the *Marsiliaceæ* which show marked heterospory is significant (Campbell, *American Naturalist*, 1904; Bower, *Origin of a Land Flora*, 1908; and *Ann. Bot.*, 1918). Such a variability as is now seen in the Ferns for which we contemplate a Schizæoid affinity would give such conditions as suggest the origin of heterospory. But before it can be held as demonstrated that the variability really represents an initial step towards heterospory, the germination of the spores would have to be known and the type of prothallus demonstrated.

The author is indebted to the Carnegie Trust for their assistance in the production of the illustrations of this memoir.

Summary.

I. *Jamesonia.*

1. The dermal appendages are simple hairs and irregular sclerotic mounds.
2. The cortex of the rhizome possesses a peculiar parenchymatous tissue immediately outside the stele. This tissue is well ventilated.
3. The stele is a simple solenostele. The leaf-gaps are long and narrow.
4. The leaf-trace is undivided, and originates from the base of the gap. It is of a simple construction throughout.
5. The pinna-traces are of marginal origin.
6. The typical leaf is unbranched, and its pinnæ are small and leathery. The leaf-apex shows continued apical-growth.
7. Reduced leaves are not uncommon. These show reduced vascular tissues.
8. The leaves and roots are specialised against xerophytic conditions.
9. The venation of the pinnæ is a sympodial dichotomy.
10. Collectively, the anatomical characters constitute a primitive state.
11. The sporangial arrangement is "Acrostichoid," and the sporangia are of an upgrade type, in which irregularities of the annulus still persist.
12. The spore-count is *above* 64. This is considered an important primitive feature.
13. The anatomical state and the sporangial characters are held to indicate for *Jamesonia* an ultimate origin from some Schizæaceous source.

II. *Llavea.*

1. The dermal appendages are simple hairs and large scales of an advanced type.

2. The stele is a wide unperforated solenostele with branched root-traces. The leaf-gaps are short and oblique.

3. The leaf-trace is an undivided strap inserted obliquely towards the base of the gap. There is an incipient perforation in the base of the leaf-trace.

4. The pinna-traces are of marginal origin.

5. The leaf is tripinnate, and has many pinnules.

6. The basal pinnules are typically cordate and sterile. There are occasional reticulations in the lateral veins. The upper pinnules are usually fertile. They are narrow, and have their margins inrolled. There are no vein-reticulations.

7. The sporangial arrangement is "Acrostichoid."

8. The sporangia are of an upgrade type, in which irregularities of the annulus are still common. The spore-output is on an advanced footing of reduction.

9. The sporangia of *Llavea* and *Cryptogramme* have been compared. In the former the sporangial-stalk and spore-output are advanced, in the latter primitive characters persist in the stalk.

10. The anatomical and sporangial characters of *Llavea* are considered such as to justify its recognition as a Schizæoid derivative, which is more advanced than *Jamesonia*, and is distinct from other genera.

III. *Trismeria.*

1. The dermal appendages of the axis are scales of an advanced type. The sterile pinnæ are naked, but the fertile pinnæ possess capitate hairs, with which is associated a secretion of wax.

2. Similar capitate hairs and wax secretions are recorded from certain *Gymnogrammes*, *Nothochlænas*, and *Cheilanthes*.

3. The stele is an advanced solenostele, with long and wide leaf-gaps.

4. The leaf-trace is of an advanced type, being divided in its basal portion into two broad straps.

5. The pinna-trace supply is for the most part of extra-marginal origin. This constitutes an advanced feature.

6. On comparison with the vascular tissue of *Gymnogramme japonica* it is shown that the vascular system of *Trismeria* is of the *Gymnogramme* type, but not so advanced as in *G. japonica.*

7. The sporangia are of an advanced type, with typically regular vertical annulus. Only occasional irregularities are found in the annulus. The sporangial arrangement is "Acrostichoid."

8. The spore-output is small. This is an advanced feature.

9. The anatomical state and the sporangial condition are shown to be of the *Gymnogramme* type.

10. The anatomical state would allow of comparisons with the *Cheilanthinæ*, but the sporangial characters of the latter make a view of near affinity with this group untenable.

11. Certain points which emerge from the discussion of the *Cheilanthinæ* have a bearing on a possible development of heterospory.

12. The general conclusion drawn from the study of *Trismeria* is that it should not be considered a distinct genus, but an "Acrostichoid" *Gymnogramme.*

IV.

From the general survey of the plants discussed it is concluded that these Ferns constitute a laxly associated group which would best find its place phyletically as derivatives from some Schizæaceous source.

DESCRIPTION OF FIGURES IN TEXT.

Figs. 1–7. *Jamesonia*, Hk. et Gr.

Fig. 1. A series of diagrammatic figures showing the distribution of tissues of stem of *J. scalaris*, Kze., cut transversely at levels between stem-apex and second leaf-base. Vascular tissue *black*; sclerotic ground-tissue *hatched*. (× 8.)

Fig. 2. A series of diagrammatic figures of transverse sections of a branched stem of *J. scalaris*, Kze., showing the distribution of tissues at levels below (*a*) to (*i*) and above (*j*) the point of branching. *l.t.* leaf-race; *r.t.* root-trace; *st.* stele. (× 8.)

Fig. 3. Diagrammatic figures of pinnæ of *J. scalaris*, Kze. (*a*) and (*b*) sterile pinnæ seen from below and above, (*c*) and (*d*) fertile pinnæ seen from below, and showing the distribution of the sporangia. (× 8.)

Fig. 4. Diagrammatic figures of pinnæ of *J. verticalis*, Kze. (*a*) large fertile pinna seen from below, and showing the distribution of the sporangia on and between the veins; (*b*) a small basal sterile pinna seen from above. (× 8.)

Fig. 5. Diagrammatic figures of sterile pinnæ of *J. cinnamomea*, Kze., seen from below and above. (× 8.)

Fig. 6. Diagrammatic figure of sterile pinna of *J. canescens*, Kze., seen from above. (× 8.)

Fig. 7. Transverse section of pinna-margin of *J. scalaris*, Kze. (× 60.)

Figs. 8–15. *Llavea cordifolia*, Lagasca.

Fig. 8. A series of diagrammatic figures showing the distribution of tissues of stem cut transversely at consecutive levels. Stele and leaf-trace *black* with a dotted border; root-traces *black* with a plain border. (× 4.)

Fig. 9. Diagram of leaf-trace form as in transverse section towards the base of the petiole: xylem, *black*; phloem, *hatched*; protoxylems, *p.*; endodermis, a continuous line. (× 20.)

Fig. 10. Diagram of leaf-trace form as in transverse section at a point of departure of a pinna-trace: protoxylem, *p.* (× 20.)

Fig. 11. Diagram of leaf-trace form as in transverse section immediately after departure of a pinna-trace: protoxylem, *p.* (× 20.)

Fig. 12. Diagrammatic figures of sterile pinnule. (× 3.)

Fig. 13. Diagrammatic figures of fertile-pinnule to show venation and the inrolled margins. The sporangia are not indicated. (× 4.)

Fig. 14. Diagrammatic figure of portion of a fertile pinnule viewed from below. The sporangia are, with few exceptions, on the veins, and show a "mixed" condition. (× 20.)

Fig. 15. Diagrammatic figure to show the arrangement of parts as seen in transverse section of a fertile pinnule. (× 40.)

Figs. 16–22. *Gymnogramme* (*Trismeria*) *trifoliata*, Desv.

Fig. 16. A series of diagrammatic figures showing the distribution of tissues of stem cut transversely at consecutive levels. (× 4.)

Fig. 17. Diagrammatic figure of transverse section of base of petiole. (× 8.)

Fig. 18. A series of diagrammatic figures showing the distribution of leaf-trace tissues during departure of first pair of pinna-traces. (× 8.)

Fig. 19. Diagrammatic figures of transverse sections of rachis at point of union of the leaf-trace strands. (× 8.)

Fig. 20. A series of diagrammatic figures showing the distribution of leaf-trace tissues during departure of third pair of pinna-traces. (× 8.)

Fig. 21. A series of diagrammatic figures showing the distribution of tissues during departure of sixth pair of pinna-traces. (× 8.)

Fig. 22. Diagrammatic figures showing the departure of a distal pinna-trace. (× 8.)

Figs. 23–27. *Gymnogramme japonica* Desv.

Fig. 23. A series of diagrammatic figures showing the distribution of tissues of stem cut transversely at consecutive levels. (× 8.)

Fig. 24. A series of diagrammatic figures showing the steps in stelar perforation. (× 8.)

Fig. 25. A series of diagrammatic figures showing the steps in condensation of the leaf-trace in the base of the petiole. (× 6.)

Fig. 26. Diagrammatic figures to show steps in reduction of the leaf-trace to a single strand. (× 6.)

Fig. 27. A series of diagrammatic figures showing the distribution of leaf-trace tissues during departure of first pinna-trace. (× 6.)

Figs. 28–30. *Gymnogramme* (*Trismeria*) *trifoliata*, Desv.

Fig. 28. Diagrammatic figure of pinnules. (× 4.)

Fig. 29. Diagrammatic figure of portion of a fertile pinna viewed from below. (× 10.)

Fig. 30 Diagrammatic figure to show the arrangement of parts as seen in transverse section of a fertile pinna. (× 10.)

DESCRIPTION OF FIGURES IN PLATES.

PLATE I.

Jamesonia scalaris, Kze.

Fig. 1. Dermal appendages of axis, consisting of glandular hairs and irregular sclerotic mounds. (× 18.)

Fig. 2. Photograph of a group of plants of *Jamesonia scalaris*, Kze., taken by Mr A. W. HILL, M.A., F.L.S., Assistant Director, Kew Gardens, at an altitude of 15,000 feet in the Andes of Peru.

Fig. 3. Dermal appendages of leaf, consisting entirely of slender tortuous hairs. (× 18.)

Fig. 4. Reconstruction of vascular cylinder of a robust axis. (× 10.)

Fig. 5. Transverse section of axis, showing the typical construction at a level where two leaf-gaps overlap. (× 30.)

Fig. 6. Reconstruction of stele at a forking of the axis. (× 10.)

Fig. 7. Transverse section of leaf-trace in a small leaf inserted towards the under surface of the axis. (× 45.)

Fig. 8. Transverse section of a root. (× 30.)

Plate II.

Jamesonia scalaris, Kze.

Fig. 9. Transverse section of a normal leaf-trace as seen in the leaf-base. (× 45.)

Fig. 10. Transverse section of a normal leaf-trace from which the pinna-trace supply is marginal. (× 45.)

Figs. 11–14. Various sporangia; 11, 12, lateral views; 13, a front view; 14, an apical view. (All × 40.) These serve to show that the annulus is vertical, and interrupted by the stalk; the construction of the stomium is variable, and irregularities exist in the indurated ring.

Figs. 15, 16. Top and bottom views of the tetrahedral spore. (× 40.)

Fig. 17. A sporangium opened. It shows a regular annulus. (× 40.)

Figs. 18–20. Opened sporangia, in each of which the annulus is irregular. Irregularities occur in various positions. (× 40.)

Figs. 21–23. A series of sections of fertile pinnæ, showing a progression from a simple to a "mixed" condition during sporangial development. (All × 45.)

Plate III.

Jamesonia scalaris, Kze. (figs. 24, 25), and *Llavea cordifolia*, Lagasca (figs. 26–31).

Figs. 24, 25. Sections of fertile pinnæ of *Jamesonia scalaris*, Kze., showing later stages of the "mixed" sorus.

Fig. 26. Transverse section of the abaxial portion of the leaf-trace on its passage from the leaf-base to the stele. (× 45.)

Fig. 27. Section of a portion of a fertile pinnule showing the mixed condition of the sporangia. (× 45.)

Fig. 28. Scale from the stem. (× 18.)

Fig. 29. Hair from the stem. (× 40.)

Fig. 30. Front view of a sporangium with an irregular annulus. (× 40.)

Fig. 31. Reconstruction of a portion of the vascular cylinder of the axis. (× 5.)

Plate IV.

Llavea cordifolia, Lagasca (figs. 32–39), and *Gymnogramme* (*Trismeria*) *trifoliata* (L.), Fée (figs. 40, 41).

Fig. 32. Various views of the tetrahedral spores. (× 60.)

Fig. 33. Side view of a sporangium with a regular annulus. (× 40.)

Fig. 34. An irregular annulus showing a double series of indurated cells. (× 40.)

Fig. 35. A regular annulus. (× 40.)

Fig. 36. An irregular annulus showing imperfect lignification of certain cells. (× 40.)

Fig. 37. Back view of a sporangium with a broken annulus. (× 40.)

Fig. 38. Top view of a sporangium with irregular and imperfectly lignified annulus. (× 40.)

Fig. 39. Top view of a sporangium which has no stomium, but in which the indurated cells form an apical crescent. (× 40.)

Fig. 40. Scale from the stem. (× 24.)

Fig. 41. Section of a portion of a fertile pinna. (× 45.)

Plate V.

Gymnogramme (*Trismeria*) *trifoliata* (L.), Fée (figs. 42–47), *Cryptogramme crispa* (L.), R. Br., and *Gymnogramme japonica* (Thnby.), Desv. (figs. 48–54).

Fig. 42. Section of a portion of a sterile pinna. Rods and granules of wax are on the outer wall-surfaces of the lower epidermis. (× 60.)

Fig. 43. Top view of a sporangium with an irregular annulus. (× 40.)

Fig. 44. Side view of a sporangium with a regular annulus. (× 40.)

Fig. 45. Reconstruction of a portion of the vascular cylinder of the axis. (× 8.)

Fig. 46. Various views of the tetrahedral spores. (× 90.)

Fig. 47. Transverse section of a root. (× 30.)

Fig. 48. Side view of a sporangium of *Cryptogramme crispa.* The annulus is regular, but passes the stalk obliquely. (× 60.)

Fig. 49. Transverse sections of the stalks of two sporangia of *Cryptogramme crispa*, the one consisting of six, the other of four rows of cells. (× 60.)

Fig. 50. Oblique posterior view of a sporangium of *Cryptogramme crispa.* The annulus is regular, but the indurated cells do not reach the stalk. (× 60.)

Fig. 51. Portion of the annulus of a sporangium of *Cryptogramme crispa.* The stalk consisted of three rows of cells, the annulus was regular and interrupted by the stalk. (× 60.)

Fig. 52. Portion of the annulus of a sporangium of *Cryptogramme crispa.* The stalk consisted of four rows of cells, the annulus was regular and interrupted by the stalk. (× 60.)

Fig. 53. Portion of a sporangium of *Cryptogramme crispa.* The stalk consisted of five rows of cells, the annulus was irregular and slightly oblique. (× 60.)

Fig. 54. Portion of an irregular annulus of *Cryptogramme crispa.* (× 60.)

PLATE VI.

Cryptogramme crispa (L.), R. Br., *Gymnogramme japonica* (Thnby.), Desv., and *Nothochlæna*, R. Br.

Fig. 55. Back view of a sporangium of *Cryptogramme crispa.* The annulus is regular and oblique. (× 60.)

Fig. 56. Reconstruction of the stele of a portion of axis of *Gymnogramme japonica.* (× 24.)

Fig. 57. Portion of a sporangium of *Cryptogramme crispa*, showing an irregularity at the base of the annulus. (× 60.)

Fig. 58. Front view of a sporangium of *Nothochlæna affinis*, Hk. The stomium is clearly removed from the stalk. (× 45.)

Figs. 59, 60, 61. Spores of large, medium, and small size of *N. affinis*, R. Br. (× 60.)

Fig. 62. The indurated portion of the irregular annulus from a sporangium of *N. affinis*, R. Br. (× 45.)

Fig. 63. Back view of the sporangium of *N. affinis*, R. Br.; depicted in front view in fig. 58. (× 45.)

Fig. 64. Side view of a sporangium of *N. sinuata*, Kaulf. (× 45.)

Fig. 65. Tetrahedral spore of *N. sinuata*, Kaulf. (× 60.)

Figs. 66, 67, 68. Sporangia of *N. nivea*, Desv., 66 and 67 being front views, 68 a back view. (All × 35.)

Fig. 69. Tetrahedral spore of *N. nivea*, Desv. (× 60.)

PLATE VII.

Ceratopteris, R. Br., and *Nothochlæna*, Brong.

Figs. 70, 71. Two side views of sporangia of *Ceratopteris thalictroides*, Brong. In both, the irregular annulus is interrupted by the short, massive stalk. (× 45.)

Figs. 72, 73. Top and side views of a spore of *C. thalictroides*, Brong. (× 60.)

Fig. 74. Portion of a sporangium of *C. thalictroides*, Brong., opened to show the vertical course of the irregular annulus. (× 45.)

Figs. 75, 76. Front and side views respectively of two sporangia of *C. thalictroides*, Brong., with stomium well developed. (× 45.)

Figs. 77, 78. Side views of two sporangia of *N. distans*, R. Br. (× 45.)

Fig. 79. Spore of *N. distans*, R. Br. (× 60.)

Fig. 80. Portion of a sporangium of *N. trichomanoides*, R. Br., opened to show the entire course of the irregular annulus. (× 45.)

Fig. 81. Spore of *N. trichomanoides*, R. Br. (× 60.)

Fig. 82. Portion of a sporangium of *N. trichomanoides*, R. Br., with almost regular vertical annulus. (× 45.)

Figs. 83, 84. Examples of the greatest irregularities in the annulus of *N. trichomanoides*, R. Br. (× 45.)

Dr John M'Lean Thompson on "The Anatomy and Affinity of certain Rare and Primitive Ferns." Part II.—Plate I.

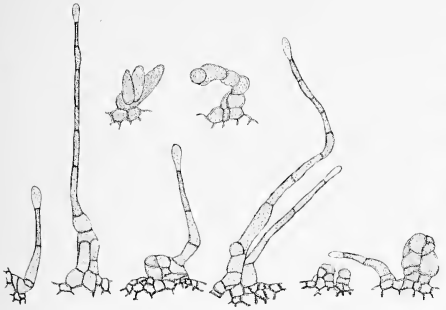

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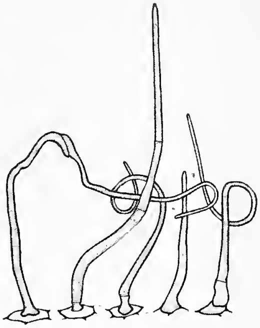
Fig. 2.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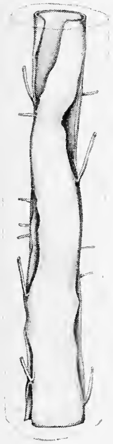
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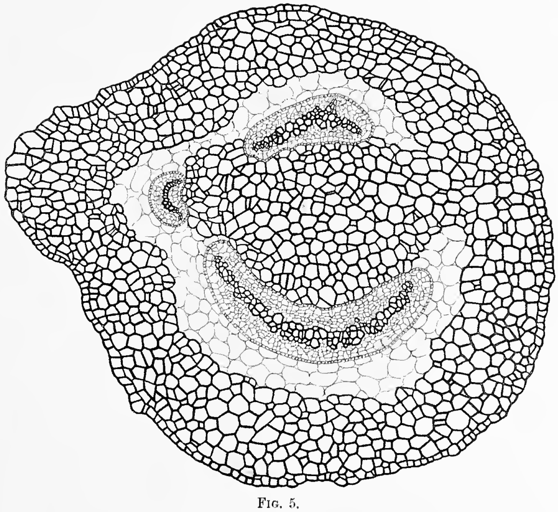
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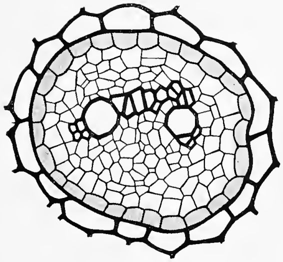
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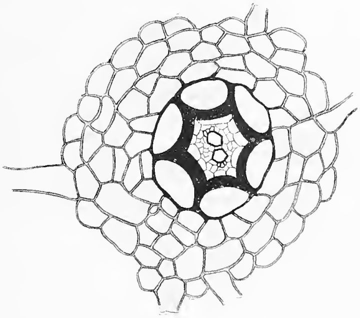
Fig. 8.

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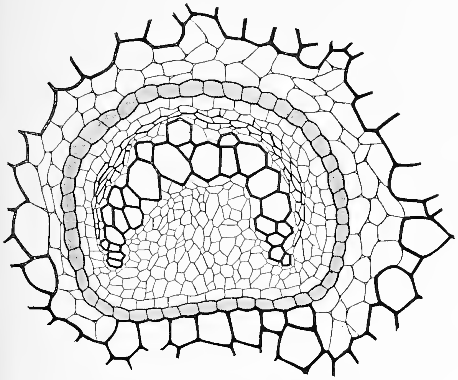

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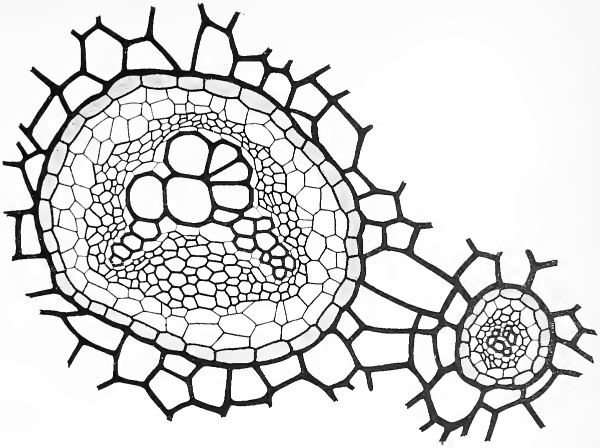

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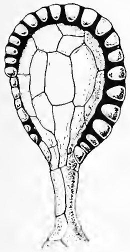

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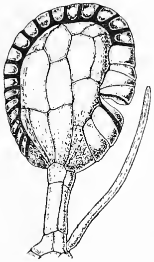

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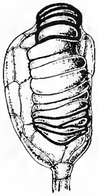

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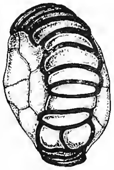

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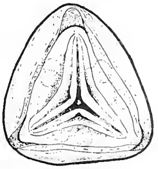

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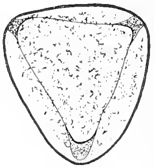

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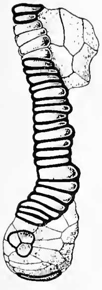

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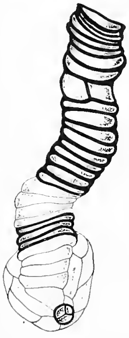

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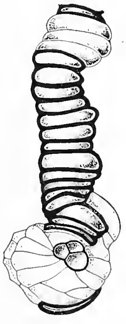

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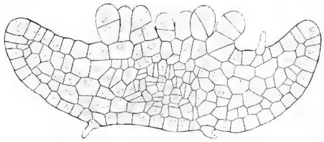

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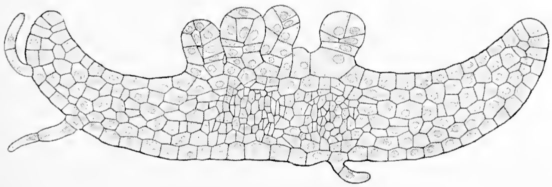

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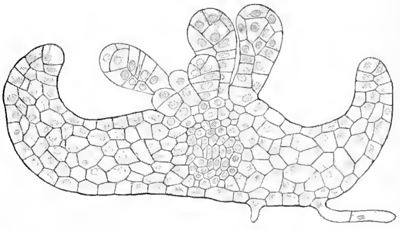

Fig. 23.

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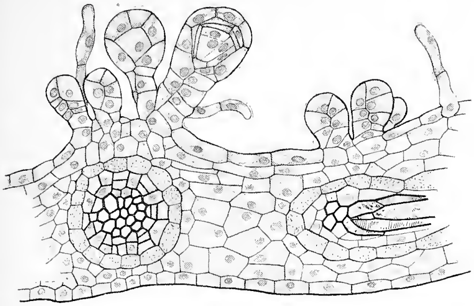
Dr John M'Lean Thompson on "The Anatomy and Affinity of certain Rare and Primitive Ferns." Part II.—Plate III.



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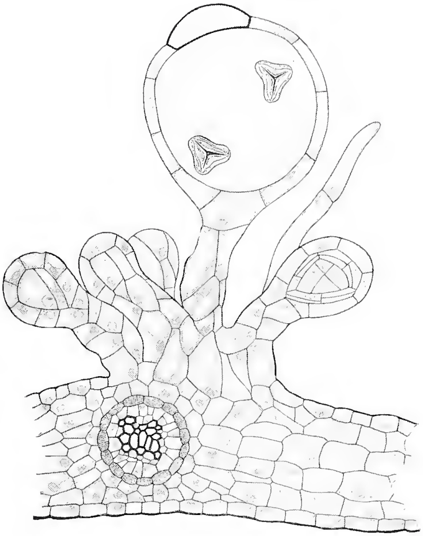

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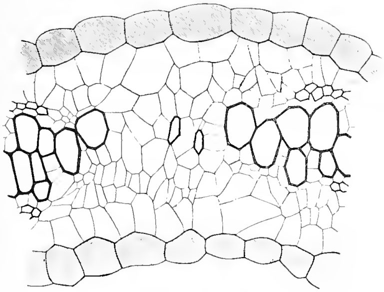

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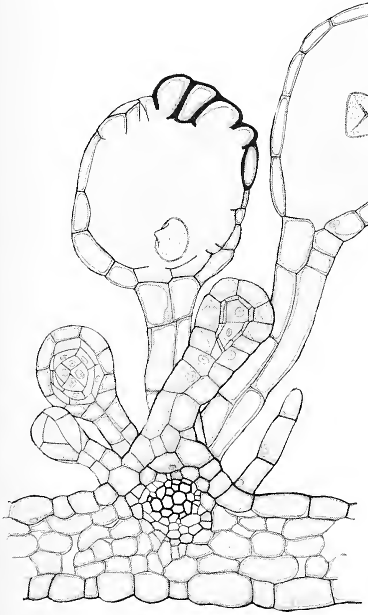

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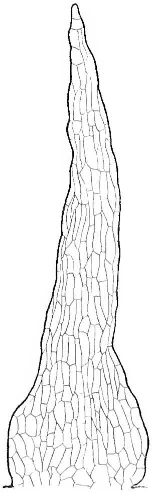

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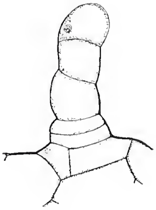

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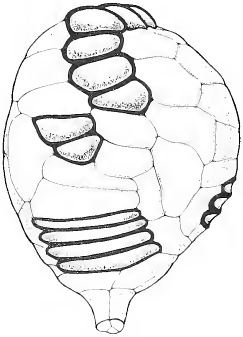

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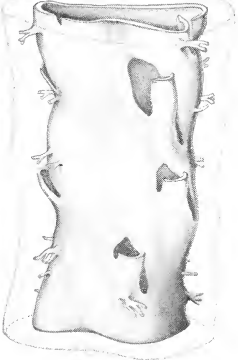

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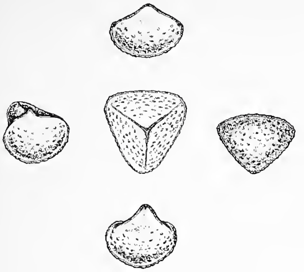

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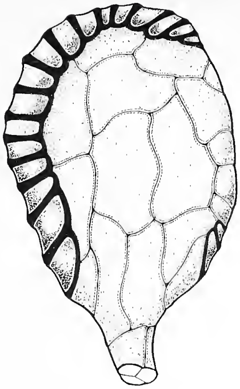

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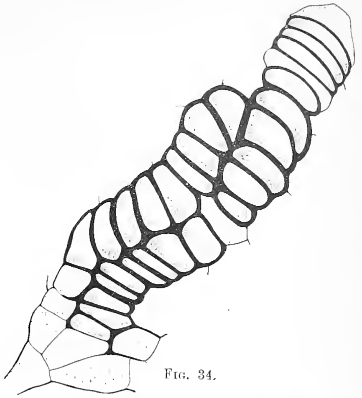
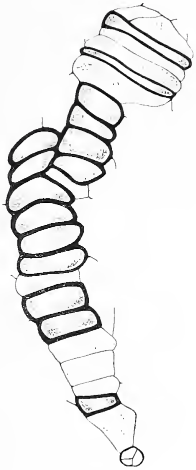


Fig. 34.

Fig. 35.



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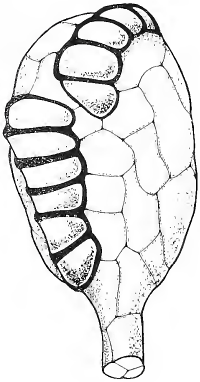

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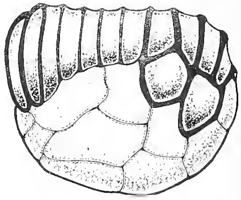

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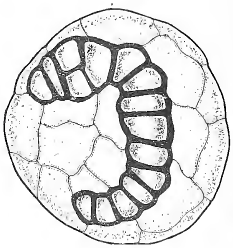

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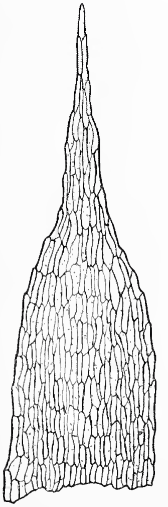

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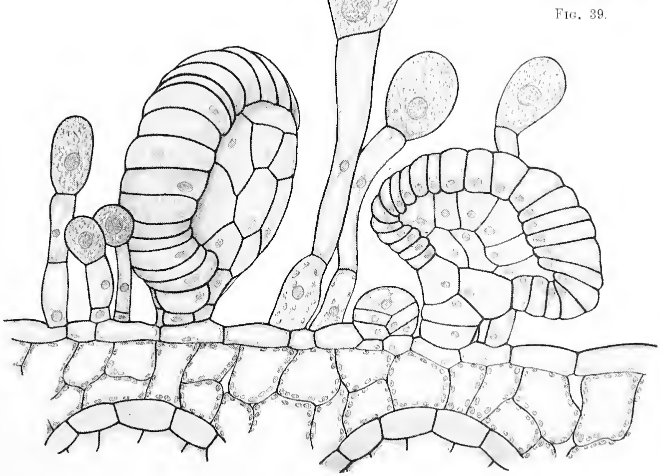

Fig. 41.

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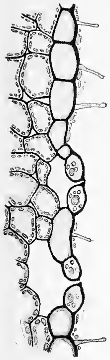
DR JOHN M'LEAN THOMPSON on "The Anatomy and Affinity of certain Rare and Primitive Ferns." Part II.—Plate V.



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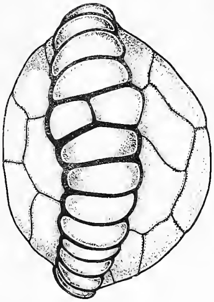

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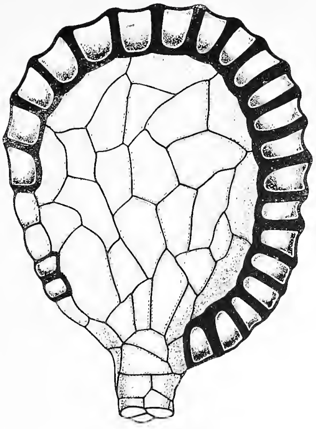

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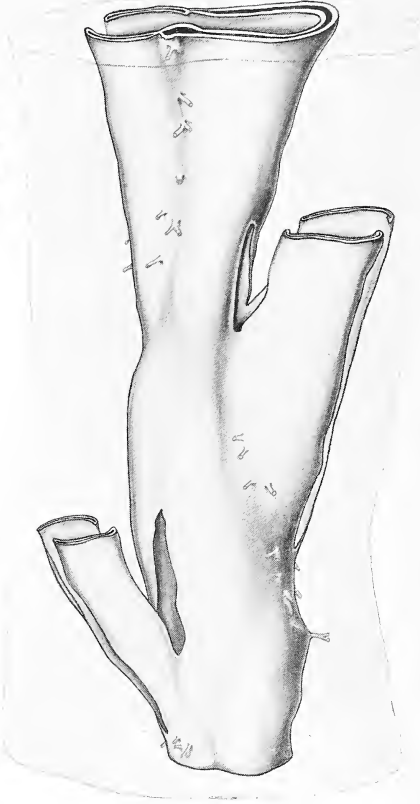

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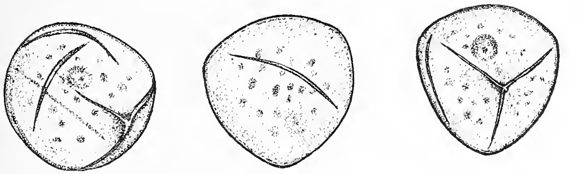

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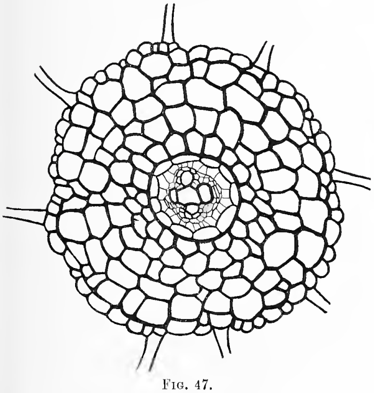

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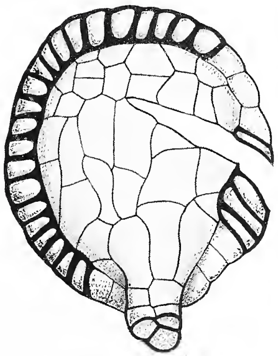

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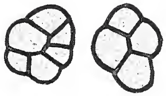
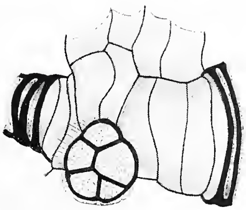


FIG. 49.

FIG. 51.

FIG. 52.



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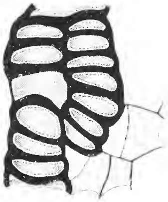

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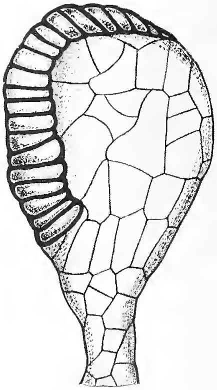

FIG. 50.

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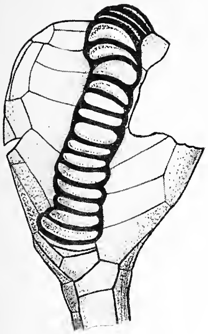
Dr John M'Lean Thompson on "The Anatomy and Affinity of certain Rare and Primitive Ferns." Part II.—Plate VI.



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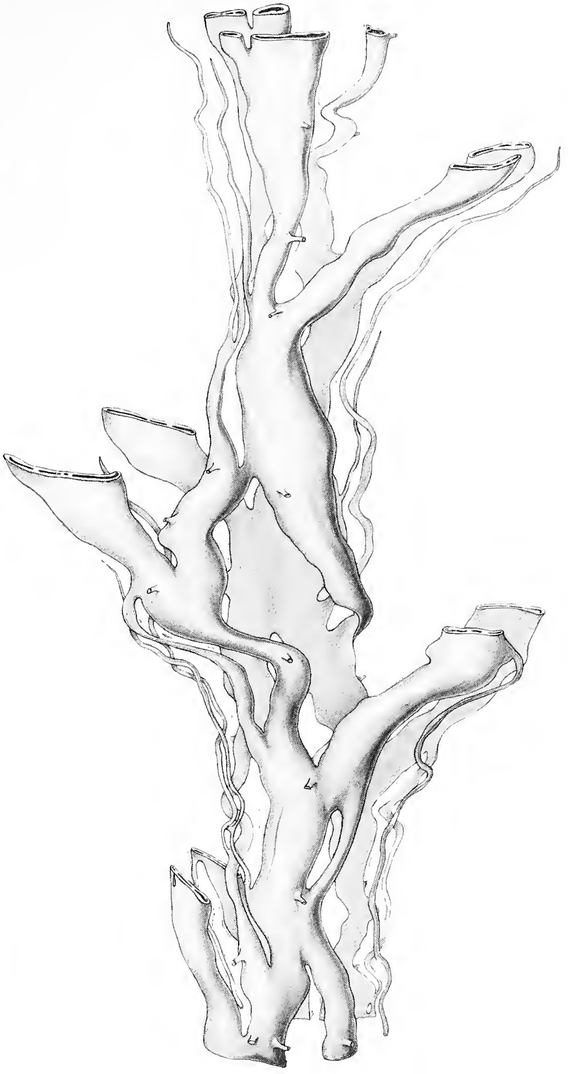

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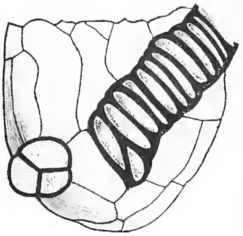

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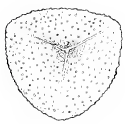

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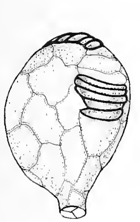

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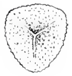
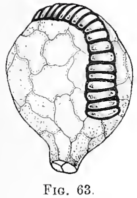


Fig. 60.

Fig. 61.

Fig. 62.



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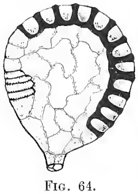

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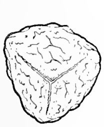

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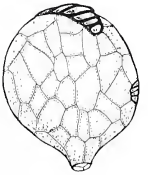

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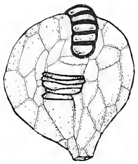

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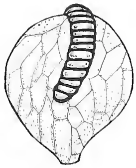


Fig. 68.

Fig. 69.

J. M'L. T. *del.*

Dr John M'Lean Thompson on "The Anatomy and Affinity of certain Rare and Primitive Ferns." Part II.—Plate VII.

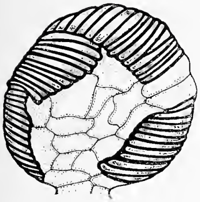


Fig. 70.

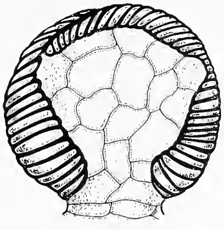


Fig. 71.


Fig. 72.


Fig. 73.


Fig. 74.

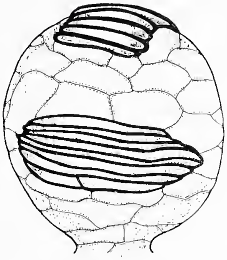


Fig. 75.

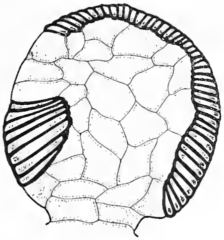


Fig. 76.

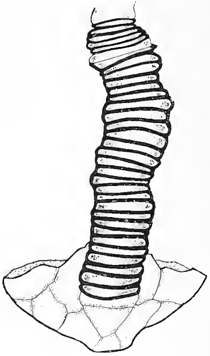


Fig. 82.

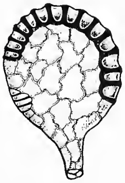


Fig. 77.

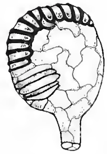
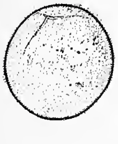


Fig. 78.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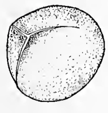
Fig. 81.

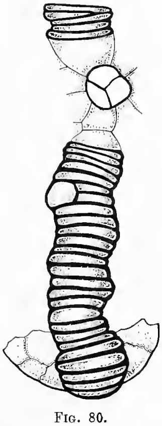
Fig. 80.

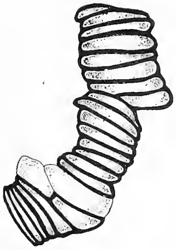
Fig. 83.

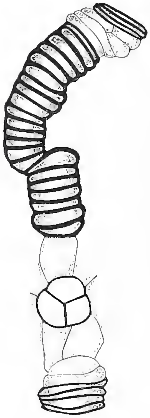
Fig. 84.

J. M'L. T. *del.*

XV.—The Correlation between Relatives on the Supposition of Mendelian Inheritance. By R. A. Fisher, B.A. *Communicated by* Professor J. ARTHUR THOMSON. (With Four Figures in Text.)

(MS. received June 15, 1918. Read July 8, 1918. Issued separately October 1, 1918.)

CONTENTS.

Several attempts have already been made to interpret the well-established results of biometry in accordance with the Mendelian scheme of inheritance. It is here attempted to ascertain the biometrical properties of a population of a more general type than has hitherto been examined, inheritance in which follows this scheme. It is hoped that in this way it will be possible to make a more exact analysis of the causes of human variability. The great body of available statistics show us that the deviations of a human measurement from its mean follow very closely the Normal Law of Errors, and, therefore, that the variability may be uniformly measured by the standard deviation corresponding to the square root of the mean square error. When there are two independent causes of variability capable of producing in an otherwise uniform population distributions with standard deviations σ_1 and σ_2, it is found that the distribution, when both causes act together, has a standard deviation $\sqrt{\sigma_1^2+\sigma_2^2}$. It is therefore desirable in analysing the causes of variability to deal with the square of the standard deviation as the measure of variability. We shall term this quantity the Variance of the normal population to which it refers, and we may now ascribe to the constituent causes fractions or percentages of the total variance which they together produce. It is desirable on the one hand that the elementary ideas at the basis of the calculus of correlations should be clearly understood, and easily expressed in ordinary language, and on the other that loose phrases about the "percentage of causation," which obscure the essential distinction between the individual and the population, should be carefully avoided.

Speaking always of normal populations, when the coefficient of correlation between father and son, in stature let us say, is r, it follows that for the group of sons of fathers of any given height the variance is a fraction, $1-r^2$, of the variance of sons in general. Thus if the correlation is ·5, we have accounted by reference to the height of the father for one quarter of the variance of the sons. For the remaining three quarters we must account by some other cause. If the two parents are independent, a second quarter may be ascribed to the mother. If father and mother, as usually happens, are positively correlated, a less amount must be added to obtain the joint contribution of the two parents, since some of the mother's contribution will in this case have been already included with the father's. In a similar way each of the ancestors makes an independent contribution, but the total amount of variance to be ascribed to the measurements of ancestors, including parents, cannot greatly exceed one half of the total. We may know this by considering the difference between brothers of the same fraternity: of these the whole ancestry is identical, so that we may expect them to resemble one another rather more than persons whose ancestry, identical in respect of height, consists of different persons. For stature the coefficient of correlation between brothers is about ·54, which we may interpret* by saying that 54 per cent. of their variance is accounted for by ancestry alone, and that 46 per cent. must have some other explanation.

It is not sufficient to ascribe this last residue to the effects of environment. Numerous investigations by GALTON and PEARSON have shown that all measurable environment has much less effect on such measurements as stature. Further, the facts collected by GALTON respecting identical twins show that in this case, where the essential nature is the same, the variance is far less. The simplest hypothesis, and the one which we shall examine, is that such features as stature are determined by a large number of Mendelian factors, and that the large variance among children of the same parents is due to the segregation of those factors in respect to which the parents are heterozygous. Upon this hypothesis we will attempt to determine how much more of the variance, in different measurable features, beyond that which is indicated by the fraternal correlation, is due to innate and heritable factors.

In 1903 KARL PEARSON devoted to a first examination of this hypothesis the

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* The correlation is determined from the measurements of n individuals, $x_1, x_2, \ldots x_n$, and of their brothers, $y_1, y_2, \ldots, y_r$; let us suppose that each pair of brothers is a random sample of two from an infinite fraternity, that is to say from all the sons which a pair of parents might conceivably have produced, and that the variance of each such fraternity is V, while that of the sons in general is σ. Then the mean value of $(x-y)^2$ will be 2V, since each brother contributes the variance V. But expanding the expression, we find the mean value of both x^2 and y^2 is σ^2, while that of xy is $r\sigma^2$, where r is the fraternal correlation. Hence $2\text{V}=2\sigma^2(1-r)$, or $\frac{\text{V}}{\sigma^2}=1-r$. Taking the values ·5066 and ·2804 for the parental and marital correlations, we find that the *heights of the parents alone* account for 40·10 per cent. of the variance of the children, whereas the *total effect of ancestry*, deduced from the fraternal correlation, is 54·33 per cent.

twelfth of his Mathematical Contributions to the Theory of Evolution ("On a Generalised Theory of Alternative Inheritance, with special reference to Mendel's Laws," *Phil. Trans.*, vol. cciii, A, pp. 53–87. The subject had been previously opened by UDNY YULE, *New Phytologist*, vol. i). For a population of n equally important Mendelian pairs, the dominant and recessive phases being present in equal numbers, and the different factors combining their effects by simple addition, he found that the correlation coefficients worked out uniformly too low. The parental correlations were $\frac{1}{3}$ and the fraternal $\frac{5}{12}$.*

These low values, as was pointed out by YULE at the Conference on Genetics in 1906 (Horticultural Society's Report), could be satisfactorily explained as due to the assumption of complete dominance. It is true that dominance is a very general Mendelian phenomenon, but it is purely somatic, and if better agreements can be obtained without assuming it in an extreme and rigorous sense, we are justified in testing a wider hypothesis. YULE, although dealing with by no means the most general case, obtained results which are formally almost general. He shows the similarity of the effects of dominance and of environment in reducing the correlations between relatives, but states that they are identical, an assertion to which, as I shall show, there is a remarkable exception, which enables us, as far as existing statistics allow, to separate them and to estimate how much of the total variance is due to dominance and how much to arbitrary outside causes.

In the following investigation we find it unnecessary to assume that the different Mendelian factors are of equal importance, and we allow the different phases of each to occur in any proportions consistent with the conditions of mating. The heterozygote is from the first assumed to have any value between those of the dominant and the recessive, or even outside this range, which terms therefore lose their polarity, and become merely the means of distinguishing one pure phase from the other. In order to proceed from the simple to the complex we assume at first random mating, the independence of the different factors, and that the factors are sufficiently numerous to allow us to neglect certain small quantities.

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* The case of the fraternal correlations has been unfortunately complicated by the belief that the correlation on a Mendelian hypothesis would depend on the number of the fraternity. In a family, for instance, in which four Mendelian types are liable to occur in equal numbers, it was assumed that of a family of four, one would be of each type; in a family of eight, two of each type; and so on. If this were the case, then in such families, one being of the type A would make it less likely, in small families impossible, for a second to be of this type. If, as was Mendel's hypothesis, the different qualities were carried by different gametes, each brother would have an independent and equal chance of each of the four possibilities. Thus the formulæ giving the fraternal correlations in terms of the number of the fraternity give values too small. The right value on Mendel's theory is that for an infinite fraternity. As PEARSON suggested in the same paper, "probably the most correct way of looking at any fraternal correlation table would be to suppose it a random sample of all pairs of brothers which would be obtained by giving a large, or even indefinitely large, fertility to each pair, for what we actually do is to take families of varying size and take as many pairs of brothers as they provide." In spite of this, the same confusing supposition appears in a paper by SNOW "On the Determination of the Chief Correlations between Collaterals in the Case of a Simple Mendelian Population Mating at Random" (E. C. SNOW, B.A., *Proc. Roy. Soc.*, June 1910); and in one by JOHN BROWNLEE, "The Significance of the Correlation Coefficient when applied to Mendelian Distributions" (*Proc. Roy. Soc. Edin.*, Jan. 1910).

1. Let us suppose that the difference caused by a single Mendelian factor is represented in its three phases by the difference of the quantities a, d, $-a$, and that these phases exist in any population with relative frequency P, 2Q, R, where $P+2Q+R=1$.

Then a population in which this factor is the only cause of variability has its mean at

$$m = Pa + 2Qd - Ra,$$

so that

$$P(a-m)+2Q(d-m)-R(a+m)=0.$$

Let now

$$P(a-m)^2+2Q(d-m)^2+R(a+m)^2=\alpha^2 \quad . \quad . \quad . \quad . \quad . \quad . \quad (I)$$

α^2 then is the variance due to this factor, for it is easily seen that when two such factors are combined at random, the mean square deviation from the new mean is equal to the sum of the values of α^2 for the two factors separately. In general the mean square deviation due to a number of such factors associated at random will be written

$$\sigma^2 = \Sigma\alpha^2 \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (II)$$

To justify our statement that α^2 is the contribution which a single factor makes to the total variance, it is only necessary to show that when the number of such factors is large the distributions will take the normal form.

If now we write

$$\mu_3 = P(a-m)^3+2Q(d-m)^3-R(a+m)^3$$
$$\mu_4 = P(a-m)^4+2Q(d-m)^4+R(a+m)^4,$$

and if M_3 and M_4 are the third and fourth moments of the population, the variance of which is due solely to the random combination of such factors, it is easy to see that

$$M_3 = \Sigma\mu_3$$
$$M_4 - 3\sigma^4 = \Sigma(\mu_4 - 3\alpha^4).$$

Now the departure from normality of the population may be measured by means of the two ratios

$$\beta_1 = \frac{M_3^2}{\sigma^6} \quad \text{and} \quad \beta_2 = \frac{M_4}{\sigma^4}.$$

The first of these is

$$(\Sigma\mu_3)^2/(\Sigma\alpha^2)^3,$$

and is of the order $\frac{1}{n}$, where n is the number of factors concerned, while the second differs from its Gaussian value 3 also by a quantity of the order $\frac{1}{n}$.

2. If there are a great number of different factors, so that σ is large compared to every separate α, we may investigate the proportions in which the different phases occur in a selected array of individuals. Since the deviation of an individual is simply due to a random combination of the deviations of separate factors, we must expect a given array of deviation, let us say x, to contain the phases of each factor

in rather different proportions to those in which they exist in the whole population. The latter will be represented now by $\bar{P}, 2\bar{Q}, \bar{R}$, while $P, 2Q, R$ stand for the proportions in some particular array under consideration.

Consider a population which is the same in every respect as the one we are dealing with save that all its members have one particular factor in the heterozygous phase, and let us modify it by choosing of each array a proportion $\bar{P}$ which are to become dominants and to increase by $a-d$, and a proportion $\bar{R}$ which become recessive and diminish by $a+d$: the mean is thereby moved to the extent $m-d$.

Of those which after this modification find themselves in the array with deviation x, the dominants formerly had a deviation $x-a+m$, the heterozygates $x-d+m$, and the recessives $x+a+m$, and since the variance of the original population was $\sigma^2-\alpha^2$, the frequencies of these three types are in the ratio

$$\bar{P}e^{-\frac{(x-a+m)^2}{2(\sigma^2-\alpha^2)}} : 2\bar{Q}e^{-\frac{(x-d+m)^2}{2(\sigma^2-\alpha^2)}} : \bar{R}e^{-\frac{(x+a+m)^2}{2(\sigma^2-\alpha^2)}},$$

or, when σ is great compared to α, so that $\frac{\alpha^2}{\sigma^2}$ may be neglected,

$$\left.\begin{aligned} P &= \bar{P}\left[1+\frac{x}{\sigma^2}(a-m)\right] \\ Q &= \bar{Q}\left[1+\frac{x}{\sigma^2}(d-m)\right] \\ R &= \bar{R}\left[1-\frac{x}{\sigma^2}(a+m)\right] \end{aligned}\right\} \quad . \quad . \quad . \quad . \quad . \quad . \quad \text{(III)}$$

giving the proportions in which the phases occur in the array of deviation x.

3. Hence the members of this array mating at random will have offspring distributed in the three phases in the proportion

$$\bar{P}^2\left[1+\frac{x}{\sigma^2}(a-m)\right]+\bar{P}\bar{Q}\left[2+\frac{x}{\sigma^2}(a-m+d-m)\right]+\bar{Q}^2\left[1+\frac{x}{\sigma^2}(d-m)\right],$$

$$\bar{P}\bar{Q}\left[2+\frac{x}{\sigma^2}(a-m+d-m)\right]+2\bar{Q}^2\left[1+\frac{x}{\sigma^2}(d-m)\right]+\bar{P}\bar{R}\left[2-\frac{x}{\sigma^2}(2m)\right]+\bar{Q}\bar{R}\left[2+\frac{x}{\sigma^2}(d-m\quad a-m)\right],$$

$$\bar{Q}^2\left[1+\frac{x}{\sigma^2}(d-m)\right]+\bar{Q}\bar{R}\left[2+\frac{x}{\sigma^2}(d-m-a-m)\right]+\bar{R}^2\left[1-\frac{x}{\sigma^2}(a+m)\right],$$

and therefore the deviation of the mean of the offspring is

$$2d(\bar{P}\bar{R}-\bar{Q}^2)+\frac{x}{\sigma^2}\left[\bar{P}\bar{Q}(a-d)^2+2\bar{P}\bar{R}(a^2-d^2)+\bar{Q}\bar{R})a+d)^2+(\bar{P}\bar{R}-\bar{Q}^2)d(d-m)\right].$$

Omitting the terms in $(\bar{P}\bar{R}-\bar{Q}^2)$, which for random mating is zero, the regression due to a single factor is

$$\frac{x}{\sigma^2}\left[\bar{P}\bar{Q}(a-d)^2+2\bar{P}\bar{R}(a^2-d^2)+\bar{Q}\bar{R}(a+d)^2\right] \quad . \quad . \quad . \quad . \quad . \quad \text{(IV)}$$

4. To interpret this expression, consider what is involved in taking $a, d, -a$ as representing the three phases of a factor. Genetically the heterozygote is intermediate between the dominant and the recessive, somatically it differs from their

mean by d. The steps from recessive to heterozygote and from heterozygote to dominant are genetically identical, and may change from one to the other in passing from father to son. Somatically the steps are of different importance, and the soma to some extent disguises the true genetic nature. There is in dominance a certain latency. We may say that the somatic effects of identical genetic changes are not additive, and for this reason the genetic similarity of relations is partly obscured in the statistical aggregate. A similar deviation from the addition of superimposed effects may occur between different Mendelian factors. We may use the term Epistacy to describe such deviation, which although potentially more complicated, has similar statistical effects to dominance. If the two sexes are considered as Mendelian alternatives, the fact that other Mendelian factors affect them to different extents may be regarded as an example of epistacy.

The contributions of imperfectly additive genetic factors divide themselves for statistical purposes into two parts: an additive part which reflects the genetic nature without distortion, and gives rise to the correlations which one obtains; and a residue which acts in much the same way as an arbitrary error introduced into the measurements. Thus, if for a, d, $-a$ we substitute the linear series

$$c+b,\ c,\ c-b,$$

and choose b and c in such a way that

$$\mathrm{P}(c+b-a)^2+2\mathrm{Q}(c-d)^2+\mathrm{R}(c-b+a)^2$$

is a minimum, we find for this minimum value δ^2,

$$\delta^2=\frac{4\mathrm{PQR}d^2}{\mathrm{PQ}+2\mathrm{PR}+\mathrm{QR}},$$

which is the contribution to the variance of the irregular behaviour of the soma; and for the contribution of the additive part, β^2, where

$$\beta^2=\mathrm{P}(c+b-m)^2+2\mathrm{Q}(c-m)^2+\mathrm{R}(c-b-m)^2,$$

we obtain

$$\beta^2=2b^2(\mathrm{PQ}+2\mathrm{PR}+\mathrm{QR}),$$

and since

$$b=a+\frac{\mathrm{Q}(\mathrm{P}-\mathrm{R})d}{\mathrm{PQ}+2\mathrm{PR}+\mathrm{QR}},$$

we have

$$\beta^2=2a^2(\mathrm{PQ}+2\mathrm{PR}+\mathrm{QR})-4\mathrm{Q}(\mathrm{P}-\mathrm{R})ad+\frac{2\mathrm{Q}^2(\mathrm{P}-\mathrm{R})^2d^2}{\mathrm{PQ}+2\mathrm{PR}+\mathrm{QR}}.$$

5. These expressions may be much simplified by using the equation

$$\mathrm{Q}^2=\mathrm{PR},$$

for then

$$\delta^2=4\mathrm{Q}^2d^2 \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (\mathrm{V})$$

$$\beta^2=2a^2\mathrm{Q}^2-4\mathrm{Q}(\mathrm{P}-\mathrm{R})ad+2\mathrm{Q}(\mathrm{P}-\mathrm{R})^2d^2 \quad . \quad . \quad . \quad . \quad . \quad (\mathrm{VI})$$

which appears in the regression in Article 3 (IV),
and

$$\alpha^2=2a^2\mathrm{Q}-4\mathrm{Q}(\mathrm{P}-\mathrm{R})ad+2\mathrm{Q}(\mathrm{P}+\mathrm{R})d^2 \quad . \quad . \quad . \quad . \quad (\mathrm{VII})$$

In general

$$\alpha^2 = \beta^2 + \delta^2,$$

and if

$$\sigma^2 = \Sigma\alpha^2 \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (\text{VIII})$$

$$\tau^2 = \Sigma\beta^2 \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (\text{IX})$$

and

$$\epsilon^2 = \Sigma\delta^2 \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (\text{X})$$

then

$$\sigma^2 = \tau^2 + \epsilon^2.$$

The regression due to a single factor of the mean of the offspring of parents of a given array is

$$\frac{x^2}{\sigma^2} \cdot \frac{\beta^2}{2},$$

and adding up the effects of all factors we find

$$\frac{x}{\sigma^2} \frac{\tau^2}{2},$$

so that the parental correlation for a static population mating at random is simply

$$\frac{1}{2} \frac{\tau^2}{\sigma^2} \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (\text{XI})$$

We may regard this formula otherwise. The correlation between the actual somatic measurements such as a, d, $-a$, and the representative linear quantities $c+b$, c, $c-b$ is $\frac{\tau}{\sigma}$. Thus the correlation of parent and child is made up of three factors, two of them representing the relations between the real and the representative measurements, and the third the correlation between the representative measurements of the two relatives. Thus the effect of dominance is simply to reduce certain relationship correlations in the ratio $\frac{\tau^2}{\sigma^2}$.

The values of the correlations between the representative measurements for random mating, which may be called the genetic correlations, are given in the accompanying table :—

Generations.	Half 2nd Cousin.	Half 1st Cousin.	Half Brother.	Ancestral Line.	Brother.	1st Cousin.	2nd Cousin.
Own	$^1/_{64}$	$^1/_{16}$	$^1/_4$	1	$^1/_2$	$^1/_8$	$^1/_{32}$
Father's	$^1/_{128}$	$^1/_{32}$	$^1/_8$	$^1/_2$	$^1/_4$	$^1/_{16}$	$^1/_{64}$
Grandfather's . . .	$^1/_{256}$	$^1/_{64}$	$^1/_{16}$	$^1/_4$	$^1/_8$	$^1/_{32}$	$^1/_{128}$
Great-grandfather's . .	$^1/_{512}$	$^1/_{128}$	$^1/_{32}$	$^1/_8$	$^1/_{16}$	$^1/_{64}$	$^1/_{256}$
Great-great-grandfather's .	$^1/_{1024}$	$^1/_{256}$	$^1/_{64}$	$^1/_{16}$	$^1/_{32}$	$^1/_{128}$	$^1/_{512}$

6. The above reasoning as to the effects of dominance applies without modification to the ancestral line, but in a special class of collaterals requires reconsideration. The reason is that the deviations from linearity are now themselves correlated. In other words, a father who is heterozygote instead of recessive may have offspring

who show a similar variation; but they may also be changed from heterozygote to dominant. In the case of siblings, however, whichever change takes place in one is more likely to occur in the other.

Thus, writing i, j, k for the deviations

$$a-m,\quad d-m,\quad -(a+m),$$

so that

$$i\mathrm{P}+2j\mathrm{Q}+k\mathrm{R}=0 \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad \text{(XII)}$$

and p^2, pq, q^2 for P, Q, R, we can draw up association tables for different pairs of relatives, and readily obtain the correlations between them by substituting the fractions in the nine sections of the table as coefficients of a quadratic function in i, j, k.

Thus the association table between parent and child is

p^3	p^2q	—
p^2q	$pq(p+q)$	pq^2
—	pq^2	q^3

from which we obtain the quadratic

$$p^3i^2+2p^2qij+pq(p+q)j^2+2pq^2jk+q^3k^2,$$

which is equal to

$$\frac{1}{4pq}(p^2i-q^2k)^3=\tfrac{1}{2}\beta^2,$$

while for brother and brother we have the table

$p^2(p+\frac{1}{2}q)^2$	$p^2q(p+\frac{1}{2}q)$	$\frac{1}{4}p^2q^2$
$p^2q(p+\frac{1}{2}q)$	$pq(p^2+3pq+q^2)$	$pq^2(\frac{1}{2}p+q)$
$\frac{1}{4}p^2q^2$	$pq^2(\frac{1}{2}p+q)$	$q^2(\frac{1}{2}p+q)^2$

which gives us a quadratic expression exceeding that for the parental correlation by the terms

$$\frac{p^2q^2}{4}(i^2-2ij+4j^2+2ik-2jk+k^2),$$

which are equal to $\frac{1}{4}\delta^2$, and therefore give for the fraternal correlation

$$\frac{1}{2\sigma^2}(\tau^2+\tfrac{1}{2}\epsilon^2).$$

The effect of dominance is to reduce the fraternal correlation to only half the extent to which the parental correlation is reduced. This allows us to distinguish, as far as the accuracy of the existing figures allows, between the random external effects of environment and those of dominance. This halving of the effect of dominance, it is important to notice, is independent of the relative importance of different factors, of their different degrees of dominance, and of the different proportions in which their phases occur. The correlation between the dominance deviations of siblings is, in all cases, $\frac{1}{4}$.

7. To investigate the cases of uncles and cousins we must deal with all the possible

types of mating down to the second generation. The three Mendelian phases will yield six types of mating, and ordinary cousinships are therefore connected by one of six types of sibship. The especially interesting case of double cousins, in which two members of one sibship mate with two members of another, can occur in twenty-one distinct ways, since any pair of the six types of sibship may be taken. The proportionate numbers of the three Mendelian phases in the children produced by the random matings of such pairs of sibships is given in the accompanying table :—

Type of sibship.	1 . 0 . 0	1 . 1 . 0	0 . 1 . 0	1 . 2 . 1	0 . 1 . 1	0 . 0 . 1
Frequency . .	p^4	$4p^3q$	$2p^2q^2$	$4p^2q^2$	$4pq^3$	q^4
p^4	1 . 0 . 0	3 . 1 . 0	1 . 1 . 0	1 . 1 . 0	1 . 3 . 0	0 . 1 . 0
$4p^3q$	3 . 1 . 0	9 . 6 . 1	3 . 4 . 1	3 . 4 . 1	3 . 10 . 3	0 . 3 . 1
$2p^2q^2$	1 . 1 . 0	3 . 4 . 1	1 . 2 . 1	1 . 2 . 1	1 . 4 . 3	0 . 1 . 1
$4p^2q^2$	1 . 1 . 0	3 . 4 . 1	1 . 2 . 1	1 . 2 . 1	1 . 4 . 3	0 . 1 . 1
$4pq^3$	1 . 3 . 0	3 . 10 . 1	1 . 4 . 3	1 . 4 . 3	1 . 6 . 9	0 . 1 . 3
q^4	0 . 1 . 0	0 . 3 . 1	0 . 1 . 1	0 . 1 . 1	0 . 1 . 3	0 . 0 . 1
	$p \,.\, q \,.\, 0$	$\frac{3p}{4} \,.\, \frac{p+3q}{4} \,.\, \frac{q}{4}$	$\frac{p}{2} \,.\, \frac{1}{2} \,.\, \frac{q}{2}$	$\frac{p}{2} \,.\, \frac{1}{2} \,.\, \frac{q}{2}$	$\frac{p}{4} \,.\, \frac{3p+q}{4} \,.\, \frac{3q}{4}$	$0 \,.\, p \,.\, q$

The lowest line gives the proportions of the phases in the whole cousinship whose connecting sibship is of each of the six types.

If we pick out all possible pairs of uncle (or aunt) and nephew (or niece) we obtain the table

$p^3(p+\frac{1}{2}q)$	$\frac{1}{2}p^2q(3p+q)$	$\frac{1}{2}p^2q^2$
$\frac{1}{2}p^2q(3p+q)$	$\frac{1}{2}pq(p^2+6pq+q^2)$	$\frac{1}{2}pq^2(p+3q)$
$\frac{1}{2}p^2q^2$	$\frac{1}{2}pq^2(p+3q)$	$q^3(\frac{1}{2}p+q)$

the quadratic from which reduces exactly to $\frac{1}{4}\beta^2$, showing that when mating is at random the avuncular correlation is exactly one half of the paternal.

From the twenty-one types of double cousinship pairs may be picked, the proportions of which are shown in the table :—

$p^2(p+\frac{1}{4}q)^2$	$\frac{3}{2}p^2q(p+\frac{1}{4}q)$	$\frac{9}{16}p^2q^2$
$\frac{3}{2}p^2q(p+\frac{1}{4}q)$	$\frac{1}{2}pq(p^2+\frac{13}{2}pq+q^2)$	$\frac{3}{2}pq^2(\frac{1}{4}p+q)$
$\frac{9}{16}p^2q^2$	$\frac{3}{2}pq^2(\frac{1}{4}p+q)$	$q^2(\frac{1}{4}p+q)^2$

which agrees with the table given by SNOW for ordinary first cousins. I cannot explain this divergence, unless it be that SNOW is in error, my values for ordinary first cousins leading to less than half this value for the correlation. Simplifying the quadratic in i, j, k, which is most easily done in this case by comparison with the avuncular table, we find for the correlation of double cousins

$$\frac{1}{4\sigma^2}(\tau^2+\tfrac{1}{4}\epsilon^2),$$

showing that double cousins, like brothers, show some similarity in the distribution of deviations due to dominance, and that with these cousins the correlation will in general be rather higher than it is for uncle and nephew.

For ordinary first cousins I find the following table of the distribution of random pairs drawn from the six types of ordinary cousinship :—

$\frac{1}{4}p^3(4p+q)$	$\frac{1}{4}p^2q^2(7p+q)$	$\frac{3}{4}p^2q^2$
$\frac{1}{4}p^2q(7p+q)$	$\frac{1}{4}pq(p^2+14pq+q^2)$	$\frac{1}{4}pq^2(p+7q)$
$\frac{3}{4}p^2q^2$	$\frac{1}{4}pq^2(p+7q)$	$\frac{1}{4}q^3(p+4q)$

which yields the correlation $\frac{1}{8}\frac{\tau^2}{\sigma^2}$.

In a similar way the more distant kin may be investigated, but since for them reliable data have not yet been published, the table already given of genetic correlations will be a sufficient guide.

8. Before extending the above results to the more difficult conditions of assortative mating, it is desirable to show how our methods may be developed so as to include the statistical feature to which we have applied the term Epistacy. The combination of two Mendelian factors gives rise to nine distinct phases, and there is no biological reason for supposing that nine such distinct measurements should be exactly represented by the nine deviations formed by adding i, j, or k to i', j', or k'. If we suppose that i, j, k, i', j', k' have been so chosen as to represent the nine actual types with the least square error, we have now to deal with additional quantities, which we may term

$$\begin{array}{ccc} e_{11} & e_{12} & e_{13} \\ e_{21} & e_{22} & e_{23} \\ e_{31} & e_{32} & e_{33} \end{array}$$

connected by the six equations, five of which are independent.

$$\begin{array}{ll} p^2e_{11}+2pqe_{21}+q^2e_{31}=0 & p'^2e_{11}+2p'q'e_{12}+q'^2e_{13}=0 \\ p^2e_{12}+2pqe_{22}+q^2e_{32}=0 & p'^2e_{21}+2p'q'e_{22}+q'^2e_{23}=0 \\ p^2e_{13}+2pqe_{23}+q^2e_{33}=0 & p'^2e_{31}+2p'q'e_{32}+q'^2e_{33}=0. \end{array}$$

This is a complete representation of any such deviations from linearity as may exist between two factors. Such dual epistacy, as we may term it, is the only kind of which we shall treat. More complex connections could doubtless exist, but the number of unknowns introduced by dual epistacy alone, four, is more than can be determined by existing data. In addition it is very improbable that any statistical effect, of a nature other than that which we are considering, is actually produced by more complex somatic connections.

The full association table between two relatives, when we are considering two distinct Mendelian factors, consists of eighty-one cells, and the quadratic expression to which it leads now involves the nine epistatic deviations. A remarkable simplification is, however, possible, since each quantity, such as e_{21}, which refers to a partially or wholly heterozygous individual, is related to two other quantities, such as e_{11} and e_{31}, by just the same equation as that by which j is related to i and k, and occurs in the 9×9 table with corresponding coefficients. The elimination of the five deviations e_{21}, e_{12}, e_{32}, e_{23}, e_{22} is therefore effected by rewriting the 9×9 table as a 4×4 table, derived from the quadratic in i and k corresponding to the relationship considered.

Thus the variance, found by squaring the individual variations, is derived from the 3×3 table

p^2	—	—
—	$2pq$	—
—	—	q^2

which yields the 2×2 table

$\frac{p^2}{2q}(p+2q)$	$\frac{1}{2}pq$
$\frac{1}{2}pq$	$\frac{q^2}{2p}(2p+q)$

and the quadratic in e_{11}, e_{13}, e_{31}. e_{33}

$$\frac{1}{4pqp'q'}\Big[(p+2q)(p'+2q')p^3p'^3e_{11}{}^2 + 3 \text{ similar terms} + 2p^2q^2p'^3(p'+2q')e_{11}e_{31} + 3 \text{ similar terms}$$
$$+ 2p^2q^2p'^2q'^2(e_{11}e_{33} + e_{13}e_{31})\Big],$$

which also takes the form

$$\frac{1}{4pqp'q'}\Big[(p^2p'^2e_{11} - p^2q'^2e_{13} - q^2p'^2e_{31} + q^2q'^2e_{33})^2 + 2pqp'^3(pe_{11} + qe_{31})^2 + 3 \text{ similar terms}\Big].$$

The parental table

$p^3/4q$	$-\frac{1}{4}pq$
$-\frac{1}{4}pq$	$q^3/4p$

yields

$$\frac{1}{16pqp'q'}\Big[p^2p'^2e_{11} - p^2q'^2e_{13} - q^2p'^2e_{31} + q^2q'^2e_{33}\Big]^2,$$

and the fraternal table

$p^2/4q$	—
—	$q^2/4p$

leads us to the simple expression

$$\frac{1}{16pqp'q'}\Big[p^3p'^3e_{11}{}^2 + p^3q'^3e_{13}{}^2 + q^3p'^3e_{31}{}^2 + q^3q'^3e_{33}{}^2\Big].$$

For uncles and cousins we obtain respectively $\frac{1}{4}$ and $\frac{1}{16}$ of the parental contribution, while for double cousins the table

$\frac{p^2}{16q}(2p+q)$	$-\frac{1}{16}pq$
$-\frac{1}{16}pq$	$\frac{q^2}{16p}(p+2q)$

and a quadratic similar to that for the variance.

9. With assortative mating all these coefficients will be modified. There will be association between similar phases of different factors, so that they cannot be treated separately. There will also be an increase in the variance.

We must determine the nature of the association between different factors, and ascertain how it is related to the degree of assortative mating necessary to maintain it. Then we shall be able to investigate the statistical effects of this association on the variance of the population and on the correlations.

If μ be the marital correlation, then in a population with variance V the frequency of individuals in the range dx is

$$\frac{1}{\sqrt{2\pi V}}e^{-\frac{x^2}{2V}}dx = M,$$

and the frequency in the range dy is

$$\frac{1}{\sqrt{2\pi V}}e^{-\frac{y^2}{2V}}dy = N\,;$$

but the frequency of matings between these two groups is not simply MN, as would be the case if there were no marital correlation, but

$$\frac{1}{2\pi V\sqrt{1-\mu^2}}e^{-\frac{1}{1-\mu^2}\frac{x^2-2\mu xy+y^2}{2V}}dx\,dy,$$

which is equal to

$$\frac{MN}{\sqrt{1-\mu^2}}e^{-\frac{\mu^2x^2-2\mu xy+\mu^2y^2}{2V(1-\mu^2)}}.$$

In studying the effect of assortative mating we shall require to know the frequency of matings between two groups, each with a variance nearly equal to that of the whole population, but centred about means a and b. The frequencies of such groups in any ranges dx, dy can be written down, and if the chance of any mating depends only on x and y, the frequency of mating between these two groups can be expressed as a double integral. If M and N are the frequencies in the two groups, the frequency of mating between them is found to be

$$MNe^{\frac{\mu ab}{V}}.$$

10. We shall apply this expression first to determine the equilibrium value of the frequencies of the three phases of a single factor. Of the six types of mating which are possible, all save two yield offspring of the same genetic phase as their parents. With the inbreeding of the pure forms D × D and R × R obviously no change is made, and the same is true of the crosses D × H and R × H, for each of these yields the pure form and the heterozygote in equal numbers. On the other hand, in the cross D × R we have a dominant and a recessive replaced in the next generation by two heterozygotes, while in the cross H × H half of the offspring return to the homozygous condition. For equilibrium the second type of mating

must be twice as frequent as the first, and if I, J, and K are the means of the distributions of the three phases,

$$4Q^2 e^{\frac{\mu J^2}{V}} = 4PRe^{\frac{\mu IK}{V}}.$$

Since $\frac{J^2}{V}$ and $\frac{IK}{V}$ are small quantities, we shall neglect their squares, and obtain the equation

$$PR - Q^2 = Q^2 \mu \frac{J^2 - IK}{V} \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad \text{(XIII)}$$

If, as before, the two types of gamete are in the ratio $p:q$, the frequencies of the three phases are expressed by the equations

$$\left.\begin{aligned} P &= p^2 + p^2q^2\mu\frac{J^2 - IK}{V} \\ Q &= pq - p^2q^2\mu\frac{J^2 - IK}{V} \\ R &= q^2 + p^2q^2\mu\frac{J^2 - IK}{V} \end{aligned}\right\} \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad \text{(XIV)}$$

It is evident that

$$PI + 2QJ + RK = 0 \quad . \quad . \quad . \quad . \quad . \quad \text{(XV)}$$

and this enables us, whenever necessary, to eliminate J, and to treat only I and K as unknowns. These can only be found when the system of association between different factors has been ascertained. It will be observed that the changes produced in P, Q, and R are small quantities of the second order: in transforming the quantity

$$p^2q^2\mu\frac{J^2 - IK}{V}$$

we may write $-(p^2\text{I} + q^2\text{K})$ for $2pq\text{J}$, leading to the form

$$\frac{\mu}{4V}(p^2I - q^2K)^2,$$

which will be found more useful than the other.

11. The nine possible combinations of two factors will not now occur in the simple proportions PP′, 2PQ′, etc., as is the case when there is no association; but whatever the nature of the association may be, we shall represent it by introducing new quantities, which by analogy we may expect to be small of the second order, defined so that the frequency of the type

$$DD' \text{ is } PP'(1 + f_{11}),$$

that of

$$DH' \text{ is } 2PQ'(1 + f_{12}),$$

and that of

$$DR' \text{ is } PR'(1 + f_{13}),$$

and so on.

Formally, we have introduced nine such new unknowns for each pair of factors, but since, for instance, the sum of the above three quantities must be P, we have the six equations

$$\left.\begin{aligned} P'f_{11} + 2Q'f_{12} + R'f_{13} &= 0 \qquad & Pf_{11} + 2Qf_{21} + Rf_{31} &= 0 \\ P'f_{21} + 2Q'f_{22} + R'f_{23} &= 0 \qquad & Pf_{12} + 2Qf_{22} + Rf_{32} &= 0 \\ P'f_{31} + 2Q'f_{32} + R'f_{33} &= 0 \qquad & Pf_{13} + 2Qf_{23} + Rf_{33} &= 0 \end{aligned}\right\} \quad . \quad . \quad . \quad . \quad \text{(XVI)}$$

five of which are independent. The unknowns are thus reduced to four, and we shall use $f_{11}, f_{13}, f_{31}, f_{33}$, since any involving a 2 in the suffix can easily be eliminated.

We have further

$$\left.\begin{aligned} \mathrm{I} &= i + \sum(\mathrm{P}'i'f_{11} + 2\mathrm{Q}'j'f_{12} + \mathrm{R}'k'f_{13}) \\ \mathrm{J} &= j + \sum(\mathrm{P}'i'f_{21} + 2\mathrm{Q}'j'f_{22} + \mathrm{R}'k'f_{23}) \\ \mathrm{K} &= k + \sum(\mathrm{P}'i'f_{31} + 2\mathrm{Q}'j'f_{32} + \mathrm{R}'k'f_{33}) \end{aligned}\right\} \quad . \quad . \quad . \quad . \quad . \quad (\mathrm{XVII})$$

in which the summation is extended over all the factors except that one to which i, j, k refer. Since we are assuming the factors to be very numerous, after substituting their values for the f's we may without error extend the summation over all the factors. The variance defined as the mean square deviation may be evaluated in terms of the f's

$$\mathrm{V} = \sum(\mathrm{P}i^2 + 2\mathrm{Q}j^2 + \mathrm{R}k^2) + 2\sum\{\mathrm{PP}'(1 + f_{11})ii' + 8 \text{ other terms}\},$$

which reduces to

$$\sum(\mathrm{P}i^2 + 2\mathrm{Q}j^2 + \mathrm{R}k^2) + 2\sum\{\mathrm{PP}'ii'f_{11} + 8 \text{ other terms}\},$$

so that

$$\mathrm{V} = \sum(\mathrm{P}i\mathrm{I} + 2\mathrm{Q}j\mathrm{J} + \mathrm{R}k\mathrm{K}) \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (\mathrm{XVIII})$$

12. We can only advance beyond these purely formal relations to an actual evaluation of our unknowns by considering the equilibrium of the different phase combinations. There are forty-five possible matings of the nine types, but since we need only consider the equilibrium of the four homozygous conditions, we need only pick out the terms, ten in each case, which give rise to them. The method will be exactly the same as we used for a single factor. Thus the matings DD′ × DD′ have the frequency

$$\mathrm{PP}'\,.\,\mathrm{PP}'\,.\,(1 + f_{11})(1 + f_{11})e^{\frac{\mu(\mathrm{I}+\mathrm{I}')^2}{\mathrm{V}}},$$

which for our purpose is equal to

$$\mathrm{P}^2\mathrm{P}'^2\left[1 + 2f_{11} + \frac{\mu}{\mathrm{V}}(\mathrm{I} + \mathrm{I}')^2\right].$$

Collecting now all the matings which yield DD′, we have for equilibrium

$$\left.\begin{aligned} &\mathrm{P}^2\mathrm{P}'^2\left[1 + 2f_{11} + \frac{\mu}{\mathrm{V}}(1 + \mathrm{I}')^2\right] + 2\mathrm{P}^2\mathrm{P}'\mathrm{Q}'\left[1 + f_{11} + f_{12} + \frac{\mu}{\mathrm{V}}(\mathrm{I} + \mathrm{I}')(\mathrm{I} + \mathrm{J}')\right] \\ &+ 2\mathrm{PQP}^{2\prime}\left[1 + f_{11} + f_{21} + \frac{\mu}{\mathrm{V}}(\mathrm{I} + \mathrm{I}')(\mathrm{J} + \mathrm{I}')\right] + 2\mathrm{PQP}'\mathrm{Q}'\left[1 + f_{11} + f_{22} + \frac{\mu}{\mathrm{V}}(\mathrm{I} + \mathrm{I}')(\mathrm{J} + \mathrm{J}')\right] \\ &+ 2\mathrm{PQP}'\mathrm{Q}'\left[1 + f_{12} + f_{21} + \frac{\mu}{\mathrm{V}}(\mathrm{I} + \mathrm{J}')(\mathrm{J} + \mathrm{I}')\right] + \mathrm{P}^2\mathrm{Q}'^2\left[1 + 2f_{12} + \frac{\mu}{\mathrm{V}}(\mathrm{I} + \mathrm{J}')^2\right] \\ &+ \mathrm{Q}^2\mathrm{P}'^2\left[1 + 2f_{21} + \frac{\mu}{\mathrm{V}}(\mathrm{J} + \mathrm{I}')^2\right] + 2\mathrm{PQQ}'^2\left[1 + f_{12} + f_{22} + \frac{\mu}{\mathrm{V}}(\mathrm{I} + \mathrm{J}')(\mathrm{J} + \mathrm{J}')\right] \\ &+ 2\mathrm{Q}^2\mathrm{P}'\mathrm{Q}'\left[1 + f_{21} + f_{22} + \frac{\mu}{\mathrm{V}}(\mathrm{J} + \mathrm{I}')(\mathrm{J} + \mathrm{J}')\right] + \mathrm{Q}^2\mathrm{Q}'^2\left[1 + 2f_{22} + \frac{\mu}{\mathrm{V}}(\mathrm{J} + \mathrm{J}')^2\right] \\ &= \mathrm{PP}'(1 + f_{11}) \end{aligned}\right\} \quad (\mathrm{XIX})$$

Now since

$$(\mathrm{P} + \mathrm{Q})^2(\mathrm{P}' + \mathrm{Q}')^2 - \mathrm{PP}'(\mathrm{P} + 2\mathrm{Q} + \mathrm{R})(\mathrm{P}' + 2\mathrm{Q}' + \mathrm{R}') = (\mathrm{Q}^2 - \mathrm{PR})\mathrm{P}' + (\mathrm{Q}'^2 - \mathrm{P}'\mathrm{R}')\mathrm{P} + (\mathrm{Q}^2 - \mathrm{PR})(\mathrm{Q}'^2 - \mathrm{P}'\mathrm{R}')$$

the terms involving only P and Q, reduce (XIII) to the second order of small quantities,

$$-\frac{\mu}{V}[P'Q^2(J^2-IK)+PQ'^2(J'^2-I'K')]=-\frac{\mu}{4V}[p'^2(IP-KR)^2+p^2(I'P'-K'R')^2].$$

Also collecting the terms in I and J, we find

$$\frac{\mu}{V}[(P'+Q')(IP+JQ)+(P+Q)(I'P'+J'Q')]^2,$$

which yields on eliminating J,

$$\frac{\mu}{4V}[p'(IP-KR)+p(I'P'-K'R')]^2,$$

while the result of collecting and transforming the terms in f is

$$\tfrac{1}{2}pp'[PP'f_{11}-PR'f_{13}-P'Rf_{31}+RR'f_{33}].$$

Hence, if the frequency of the type DD′ is unchanged

$$\frac{\mu}{2V}pp'(IP-KR)(I'P'-K'R')+\tfrac{1}{2}pp'[PP'f_{11}-PR'f_{13}-P'Rf_{31}+RR'f_{33}]=PP'f_{11} \quad . \quad . \quad . \quad \text{(XIX, } a\text{)}$$

Now the corresponding equations for the types DR′, RD′, R′D′ may be obtained simply by substituting K for I, R for P, and *vice versa*, as required; and each such change merely reverses the sign of the left-hand side, substituting q or q' for p or p' as a factor.

Combining the four equations

$$\frac{\mu}{2V}(IP-KR)(I'P'-K'R')=\tfrac{1}{2}[PP'f_{11}-PR'f_{13}-RP'f_{31}+RR'f_{33}] \quad . \quad . \quad \text{(XX)}$$

so that the set of four equations

$$\frac{\mu}{V}(IP-KR)(I'P'-K'R')=pp'f_{11}=-pq'f_{13}=-qp'f_{31}=qq'f_{33} \quad . \quad . \quad . \quad \text{(XXI)}$$

gives the whole of the conditions of equilibrium.

13. Substituting now in (XVII), which we may rewrite,

$$I=i+\Sigma[P'(i'-j')f_{11}-R'(j'-k')f_{13}]$$
$$K=k+\Sigma[P'(i'-j')f_{31}-R'(j'-k')f_{33}]$$

we have

$$IP-KR=iP-kR+\Sigma\frac{\mu}{V}(IP-KR)(I'P'-K'R')[p'(i'-j')+q'(j'-k')]=iP-kR+A(IP-KR),$$

where

$$A(1-A)=\frac{\mu}{V}\Sigma(i'P'-k'R')[p'(i'-j')+q'(j'-k')]$$

$$=\frac{\mu}{V}\Sigma\beta^2, \text{ since } \beta^2=\frac{(iP-kR)^2}{2Q}.$$

or

$$A(1-A)=\mu\frac{\tau^2}{V} \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad \text{(XXII)}$$

It would seem that there is an ambiguity in the value of A, so that the same amount of assortative mating would suffice to maintain two different degrees of association: we have, however, not yet ascertained the value of V. Since this also depends upon A, the form of the quadratic is changed, and it will be seen that the ambiguity disappears.

Supposing A determinate, we may determine the association coefficients f for

$$\left.\begin{aligned} p^2p'^2f_{11} &= \frac{\mu}{(1-\mathrm{A})^2}\frac{(i\mathrm{P}-k\mathrm{R})(i'\mathrm{P}'-k'\mathrm{R}')}{\mathrm{V}}pp' \\ p^2q'^2f_{13} &= -\frac{\mu}{(1-\mathrm{A})^2}\frac{(i\mathrm{P}-k\mathrm{R})(i'\mathrm{P}'-k'\mathrm{R}')}{\mathrm{V}}pq' \end{aligned}\right\} \quad . \quad . \quad . \quad . \quad . \qquad \text{(XXIII)}$$

Hence

$$\begin{aligned} \mathrm{I} &= i + \frac{\mu}{(1-\mathrm{A})^2}\frac{i\mathrm{P}-k\mathrm{R}}{p\mathrm{V}}\Sigma[p'(i'-j')+q'(j'-k')](i'\mathrm{P}'-k'\mathrm{R}') \\ &= i + \frac{\mu}{(1-\mathrm{A})^2}\frac{i\mathrm{P}-k\mathrm{R}}{p}\cdot\frac{\tau^2}{\mathrm{V}}, \end{aligned}$$

and so

$$\mathrm{I} = i + \frac{\mathrm{A}}{1-\mathrm{A}}\frac{i\mathrm{P}-k\mathrm{R}}{p}$$

Similarly

$$\mathrm{K} = k - \frac{\mathrm{A}}{1-\mathrm{A}}\frac{i\mathrm{P}-k\mathrm{R}}{q} \quad . \quad . \quad . \quad . \quad . \quad . \qquad \text{(XXIV)}$$

and

$$\mathrm{J} = j - \frac{\mathrm{A}}{1-\mathrm{A}}\frac{p-q}{2pq}(i\mathrm{P}-k\mathrm{R})$$

So that the sense in which the mean value of the heterozygote is changed by assortative mating depends only on whether p or q is greater. In spite of perfect dominance, the mean value of the heterozygote will be different from that of the dominant phase.

The value of the variance deduced from the expression

$$\mathrm{V} = \Sigma(\mathrm{P}i\mathrm{I} + 2\mathrm{Q}j\mathrm{J} + \mathrm{R}k\mathrm{K})$$

reduces to a similar form. For evidently

$$\mathrm{V} = \Sigma\alpha^2 + \frac{\mathrm{A}}{1-\mathrm{A}}\cdot\Sigma(i\mathrm{P}-k\mathrm{R})[p(i-j)+q(j-k)].$$

Hence

$$\mathrm{V} = \sigma^2 + \frac{\mathrm{A}}{1-\mathrm{A}}\tau^2 \quad . \quad . \quad . \quad . \quad . \quad . \quad . \qquad \text{(XXV)}$$

Therefore the equation for A finally takes the form

$$\mu\tau^2 = \mathrm{VA}(1-\mathrm{A}) = \mathrm{A}(1-\mathrm{A})\sigma^2 + \mathrm{A}^2\tau^2,$$

and may be otherwise written

$$\mathrm{A}^2\epsilon^2 - \mathrm{A}\sigma^2 + \mu\tau^2 = 0 \quad . \quad . \quad . \quad . \quad . \quad . \quad . \qquad \text{(XXVI)}$$

Now, since the left-hand side is negative when A = 1, there can be only one root less than unity. Since, moreover,

$$(\mu - \mathrm{A}^2)\tau^2 = (\mathrm{A}-\mathrm{A}^2)\sigma^2 \quad . \quad . \quad . \quad . \quad . \quad . \quad . \qquad \text{(XXVI, } a\text{)}$$

it is evident that this root is less than μ, and approaches that value in the limiting case when there is no dominance.

A third form of this equation is of importance, for

$$\frac{\mathrm{A}}{\mu} = \frac{\tau^2}{\sigma^2 - \mathrm{A}\epsilon^2} = \left.\frac{\tau^2 + \frac{\mathrm{A}}{1-\mathrm{A}}\tau^2}{\sigma^2 + \frac{\mathrm{A}}{1-\mathrm{A}}\tau^2}\right\} \quad . \quad . \quad . \quad . \quad . \qquad \text{(XXVI, } b\text{)}$$

which is the ratio of the variance without and with the deviations due to dominance.

14. *Multiple Allelomorphism.*—The possibility that each factor contains more than two allelomorphs makes it necessary to extend our analysis to cover the inheritance of features influenced by such polymorphic factors. In doing this we abandon the strictly Mendelian mode of inheritance, and treat of GALTON'S "particulate inheritance" in almost its full generality. Since, however, well-authenticated cases of multiple allelomorphism have been brought to light by the Mendelian method of research, this generalised conception of inheritance may well be treated as an extension of the classical Mendelism, which we have so far investigated.

If a factor have a large number, n, of allelomorphs, there will be n homozygous phases, each of which is associated with a certain deviation of the measurement under consideration from its mean value. These deviations will be written $i_1, i_2, \ldots i_n$, and the deviations of the heterozygous phases, of which there are $\frac{1}{2}n(n-1)$, will be written j_{12}, j_{13}, j_{23}, and so on. Let the n kinds of gametes exist with frequencies proportional to p, q, r, s, and so on, then when the mating is random the homozygous phases must occur with frequencies proportional to p^2, q^2, r^2, . . . , and the heterozygous phases to $2pq$, $2pr$, $2qr$, . . .

Hence, our measurements being from the mean,

$$p^2i_1+q^2i_2+r^2i_3+\ldots+2pqj_{12}+2prj_{13}+\ldots=0 \quad . \quad . \quad . \qquad \text{(XII*)}$$

As before, we define α^2 by the equation

$$p^2{i_1}^2+q^2{i_2}^2+r^2{i_3}^2+\ldots+2pq{j_{12}}^2+2pr{j_{13}}^2+\ldots=\alpha^2 \quad . \quad . \quad . \quad . \qquad \text{(I*)}$$

and choosing l, m, n, . . . , so that

$$p^2(2l-i_1)^2+q^2(2m-i_2)^2+\ldots\ 2pq(l+m-j_{12})^2+2pr(l+n-j_{13})^2+\ldots$$

is a minimum, we define β^2 by

$$4l^2p^2+4m^2q^2+\ldots\ 2pq(l+m)^2+2pr(l+n)^2\ \ldots=\beta^2,$$

the condition being fulfilled if

$$l=pi_1+qj_{12}+rj_{13}+\ldots,$$
$$m=pj_{12}+qi_2+rj_{23}+\ldots,$$

and so on.

Now

$$\beta^2=\mathrm{S}(4l^2p^2)+\mathrm{S}(2pq\overline{l+m}^2),$$
$$=\mathrm{S}(2p(1+p)l^2)+\mathrm{S}(4pqlm),$$

and since

$$pl+qm+rn+\ldots=0,$$
$$\beta^2=\mathrm{S}(2pl^2),$$

which may now be written as a quadratic in i and j, represented by the typical terms

$$2p^3{i_1}^2+4p^2qi_1j_{12}+2pq(p+q){j_{12}}^2+4pqrj_{12}j_{13}.$$

Now we can construct an association table for parent and child as in Article 6, though it is now more complicated, since the j's cannot be eliminated by equation (XII*), and its true representation lies in four dimensions; the quadratic in i and j derived from it is, however, exactly one half of that obtained above, so that the contribution of a single factor to the parental product moment is $\frac{1}{2}\beta^2$. Hence the parental correlation is

$$\frac{1}{2}\frac{\tau^2}{\sigma^2},$$

where τ and σ retain their previous meanings.

Moreover, from the fraternal table we may obtain a quadratic expression having for its typical terms

$$\tfrac{1}{4}p^2(1+p)^2i_1{}^2+\tfrac{1}{2}p^2q^2i_1i_2+p^2q(1+p)i_1j_{12}+p^2qri_1j_{13}$$
$$\tfrac{1}{2}pq(1+p+q+2pq)j_{12}{}^2+pqr(1+2p)j_{12}j_{13}+2pqrsj_{12}j_{34},$$

which, when simplified by removing one quarter of the square of the expression in (XII*) becomes

$$\tfrac{1}{4}p^2(1+2p)i_1{}^2+p^2qi_1j_{12}+\tfrac{1}{2}pq(1+p+q)j_{12}{}^2+pqrj_{12}j_{13},$$

or, simply,

$$\tfrac{1}{4}(\alpha^2+\beta^2).$$

Here, again, the introduction of multiple allelomorphism does not affect the simplicity of our results; the correlation between the dominance deviations of siblings is still exactly $\frac{1}{4}$, and the fraternal correlation is diminished by dominance to exactly one half the extent suffered by the parental correlation. The dominance ratio plays the same part as it did before, although its interpretation is now more complex. The fraternal correlation may be written, as in Article 6,

$$\frac{1}{2\sigma^2}(\tau^2+\tfrac{1}{2}\epsilon^2).$$

15. *Homogamy and Multiple Allelomorphism.*—The proportions of these different phases which are in equilibrium when mating is assortative must now be determined. As in Article 10, let I_1, I_2, . . . be the mean deviations of the homozygous phases, and J_{12}, J_{13}, . . . those of the heterozygous phases. Let the frequency of the first homozygous phase be written as $p^2(1+f_{11})$, and the others in the same way. Then, since p is the frequency of the first kind of gamete,

$$pf_{11}+qf_{12}+rf_{13}+\ .\ .\ .\ =0,$$

and

$$pf_{12}+qf_{22}+rf_{23}+\ .\ .\ .\ =0,$$

and so on.

Let

$$pI_1+qJ_{12}+rJ_{13}+\ .\ .\ .\ =L,$$
$$pJ_{12}+qI_2+rJ_{23}+\ .\ .\ .\ =M,$$

and so on, then L, M, . . . represent the mean deviations of individuals giving rise to gametes of the different kinds; hence, by Article 9,

$$2pq(1+f_{12})=2pqe^{\frac{\mu}{V}\,.\,LM},$$

that is,

$$f_{12}=\mu/V\,.\,LM\ .\qquad .\qquad .\qquad .\qquad .\qquad .\qquad .\qquad (XIV^*)$$

The association between the phases of two different factors requires for its representation the introduction of association coefficients for each possible pair of phases. Let the homozygous phases of one factor be numbered arbitrarily from 1 to m, and those of the other factor from 1 to n, then, as the phase (12) of the first factor occurs with frequency $2pq(1+\mathrm{f}_{12})$, and of the second factor, with frequency $2p'q'(1+f'_{12})$, we shall write the frequency with which these two phases coincide in one individual as $4pqp'q'(1+f'_{12\,.\,12})$, or as $4pqp'q'(1+f_{12})\,(1+f'_{12})\,(1+f_{12\,.\,12})$, so that

$$f'_{12\,.\,12}=f_{12\,.\,12}+f_{12}+f'_{12}\,.$$

The proportional increase of frequency of the gametic combination (1 . 1) is

$$\begin{aligned}&pp'f'_{11\,.\,11}+pq'f'_{11\,.\,12}+pr'f'_{11\,.\,13}+\;.\;.\;.\\ +\,&qp'f'_{12\,.\,11}+qq'f'_{12\,.\,12}+qr'f'_{12\,.\,13}+\;.\;.\;.\end{aligned}$$

and so on.

By virtue of the equations connecting the f's of a single factor, this expression, which we shall term F_{11}, has the same value, whether written with dashed or undashed f's.

Individuals having the constitution (12 . 12) may be formed by the union either of gametes (1 . 1) and (2 . 2), or of gametes (1 . 2) and (2 . 1); hence the equations of equilibrium are of the form

$$\begin{aligned}2f''_{12\,.\,12}=\mathrm{F}_{11}+\mathrm{F}_{22}+\frac{\mu}{\mathrm{V}}(\mathrm{L}+\mathrm{L}')(\mathrm{M}+\mathrm{M}')\\ +\mathrm{F}_{12}+\mathrm{F}_{21}+\frac{\mu}{\mathrm{V}}(\mathrm{L}+\mathrm{M}')(\mathrm{M}+\mathrm{L}'),\end{aligned}$$

but

$$\begin{aligned}2f_{12\,.\,12}&=2f''_{12\,.\,12}-2f_{12}-2f''_{12}\\ &=2f''_{12\,.\,12}-\frac{2\mu}{\mathrm{V}}(\mathrm{LM}+\mathrm{L}'\mathrm{M}'),\end{aligned}$$

therefore

$$2f_{12\,.\,12}=\mathrm{F}_{11}+\mathrm{F}_{22}+\mathrm{F}_{12}+\mathrm{F}_{21}+\frac{\mu}{\mathrm{V}}(\mathrm{L}+\mathrm{M})(\mathrm{L}'+\mathrm{M}')\quad .\quad .\quad .\qquad \text{(XIX*)}$$

By analogy with Article 12, the solution

$$f_{12\,.\,12}=\frac{\mu}{\mathrm{V}}(\mathrm{L}+\mathrm{M})(\mathrm{L}'+\mathrm{M}')$$

suggests itself, and on trial it leads to

$$\mathrm{F}_{11}=\frac{\mu}{\mathrm{V}}\mathrm{LL}',$$

and is thereby verified.

Hence we may evaluate L, L′, . . . , for

$$\begin{aligned}\mathrm{L}&=p\mathrm{I}_1+q\mathrm{J}_{12}+r\mathrm{J}_{13}+\;.\;.\;.\\ &=l+\Sigma\{p'^2i'(pf_{11\,.\,11}+qf_{12\,.\,11}+\;.\;.\;.)+2p'q'j''_{12}(pf_{11\,.\,12}+qf_{12\,.\,12}+\;.\;.\;.)+\;.\;.\;.\end{aligned}$$

but

$$pf_{11\,.\,11}+qf_{12\,.\,11}+\;.\;.\;.=\frac{\mu}{\mathrm{V}}\mathrm{L}(\mathrm{L}'+\mathrm{M}'),$$

therefore

$$\begin{aligned}\mathrm{L}&=l+\frac{\mu}{\mathrm{V}}\mathrm{L}\Sigma\{p'^2i'(\mathrm{L}'+\mathrm{L}')+2p'q'j''_{12}(\mathrm{L}'+\mathrm{M}')+\;.\;.\;.\}\\ &=l+\frac{\mu}{\mathrm{V}}\mathrm{L}\,\Sigma(2p'l'\mathrm{L}'+2q'm'\mathrm{M}'\;.\;.\;.).\end{aligned}$$

Let

$$\mathrm{L} = l + \mathrm{AL},$$

then

$$\mathrm{L} = \frac{l}{1 - \mathrm{A}},$$

and

$$\mathrm{A} = \frac{\mu}{\mathrm{V}}\Sigma(2p'l'\mathrm{L}' + 2q'm'\mathrm{M}' + \ldots),$$

therefore

$$\mathrm{A}(1 - \mathrm{A}) = \frac{\mu}{\mathrm{V}}\Sigma(2p'l'^2 + 2q'm'^2 + \ldots)$$

$$= \frac{\mu}{\mathrm{V}}\Sigma\beta'^2,$$

therefore

$$\mathrm{A}(1 - \mathrm{A}) = \frac{\mu}{\mathrm{V}}\tau^2 \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad \text{(XXII*)}$$

so that the association constant, A, appearing now in the constant ratio l : L, plays exactly the same part in the generalised analysis as it did in the simpler case.

It may now be easily shown that the mean deviations, I and J, may be calculated from the equations

$$\left.\begin{aligned} \mathrm{I}_1 &= i_1 + \frac{2\mathrm{A}l}{1 - \mathrm{A}} \\ \text{and} \qquad \mathrm{J}_{12} &= j_{12} + \frac{\mathrm{A}}{1 - \mathrm{A}}(l + m), \end{aligned}\right\} \quad . \quad . \quad . \quad . \quad . \quad . \quad \text{(XXIV*)}$$

and that the variance reduces, as before, to

$$\sigma^2 + \frac{\mathrm{A}}{1 - \mathrm{A}}\tau^2 \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad \text{(XXV*)}$$

16. *Coupling.*—In much modern Mendelian work coupling plays an important part, although the results of different investigators do not seem as yet to converge upon any one uniform scheme of coupling. The type found by MORGAN in the American Fruit Fly (*Drosophila*) is, however, of peculiar simplicity, and may be found to be the general type of the phenomenon.

An individual heterozygous in two factors may owe its origin to the union of either of two pairs of gametes, either (1 . 1) × (2 . 2) or (1 . 2) × (2 . 1); when coupling occurs, the gametes given off by such an individual, of all these four types, do not appear in equal numbers, preference being given to the two types from which the individual took its origin. Thus in a typical case these two types might each occur in 28 per cent. of the gametes, and the other two types in 22 per cent. Coupling of this type is reversible, and occurs with equal intensity whichever of the two pairs are supplied by the grandparents. We may have any intensity from zero, when each type of gamete contributes 25 per cent., to complete coupling, when only the two original types of gamete are formed, and the segregation takes place as if only one factor were in action.

The above analysis of polymorphic factors enables us to compare these two extreme cases; for there are 9 phase combinations of a pair of dimorphic factors, or, if we separate the two kinds of double heterozygote, 10, which, apart from inheritance, can be interpreted as the 4 homozygous and the 6 heterozygous phases of a tetramorphic factor. The 4 gametic types of this factor are the 4 gametic combinations (1 . 1), (1 . 2), (2 . 1), (2 . 2).

The mean deviations associated with these 4 gametic types are L + L′, M + M′, . . ., and we therefore write

$$\mathfrak{L} = \mathrm{L}+\mathrm{L}', \quad \mathfrak{M} = \mathrm{L}+\mathrm{M}', \quad \mathfrak{N} = \mathrm{M}+\mathrm{L}', \quad \mathfrak{O} = \mathrm{M}+\mathrm{M}'.$$

Further, if these gametic types occur with frequency,

$$\mathfrak{p} = pp'\left(1+\frac{\mu}{\mathrm{V}}\mathrm{LL}'\right) \quad \mathfrak{q} = pq'\left(1+\frac{\mu}{\mathrm{V}}\mathrm{LM}'\right)$$

$$\mathfrak{r} = qp'\left(1+\frac{\mu}{\mathrm{V}}\mathrm{ML}'\right) \quad \mathfrak{s} = qq'\left(1+\frac{\mu}{\mathrm{V}}\mathrm{MM}'\right),$$

it is clear that the frequencies with which the homozygous phases occur, such as

$$p^2p'^2(1+f''_{11\,.\,11}) = p^2p'^2\left\{1+\frac{\mu}{\mathrm{V}}(\mathrm{L}^2+\mathrm{L}'^2+4\mathrm{LL}')\right\}$$

$$\mathfrak{p}^2\left\{1+\frac{\mu}{\mathrm{V}}(\mathrm{L}+\mathrm{L}')^2\right\} = \mathfrak{p}^2\left(1+\frac{\mu}{\mathrm{V}}\mathfrak{L}^2\right),$$

are exactly those produced, if there really were a single tetramorphic factor.

In the same way the phases heterozygous in one factor also agree, for

$$2p^2p'q'(1+f''_{11\,.\,12}) = 2p^2p'q'\left\{1+\frac{\mu}{\mathrm{V}}\mathrm{L}^2+\mathrm{L}'\mathrm{M}'+2\mathrm{L}(\mathrm{L}'+\mathrm{M}'))\right\}$$

$$= 2\mathfrak{pq}\left\{1+\frac{\mu}{\mathrm{V}}(\mathrm{L}+\mathrm{L}')(\mathrm{L}+\mathrm{M}')\right\} = 2\mathfrak{pq}\left(1+\frac{\mu}{\mathrm{V}}\mathfrak{LM}\right).$$

Finally, taking half the double heterozygotes,

$$2pqp'q'(1+f''_{12\,.\,12}) = 2pqp'q'\left\{1+\frac{\mu}{\mathrm{V}}(\mathrm{LM}+\mathrm{L}'\mathrm{M}'+(\mathrm{L}+\mathrm{M})(\mathrm{L}'+\mathrm{M}'))\right\}$$

$$2\mathfrak{ps}\left\{1+\frac{\mu}{\mathrm{V}}(\mathrm{L}+\mathrm{L}')(\mathrm{M}+\mathrm{M}')\right\} = 2\mathfrak{ps}\left(1+\frac{\mu}{\mathrm{V}}\mathfrak{LO}\right),$$

or, equally,

$$2\mathfrak{qr}\left\{1+\frac{\mu}{\mathrm{V}}(\mathrm{L}+\mathrm{M}')(\mathrm{M}+\mathrm{L}')\right\} = 2\mathfrak{qr}\left(1+\frac{\mu}{\mathrm{V}}\mathfrak{MN}\right).$$

From this it appears that a pair of factors is analytically replaceable by a single factor if the phase frequencies be chosen rightly; but the only difference in the inheritance in these two systems is that in the one case there is no coupling, and in the other coupling is complete. It would appear, therefore, that coupling is without influence upon the statistical properties of the population.

17. The effects both of dominance and of environment may be taken into account in calculating the coefficient of correlation; if we call x the actual height of the individual, y what his height would have been under some standard environment, and z what his height would have been if in addition, without altering the extent to which different factors are associated, each phase is given its representative value of

Article 5. Then, since we are using the term environment formally for arbitrary external causes independent of heredity, the mean x of a group so chosen that $y=t$ for each member will be simply t, but the mean y of a group so chosen that $x=t$ for each member will be c_1t, where c_1 is a constant equal to the ratio of the variance with environment absolutely uniform to that when difference of environment also makes its contribution. Similarly for the group $z=t$, the mean value of y is t, but for the group $y=t$ the mean z is c_2t, where

$$c_2=\frac{\tau^2}{\sigma^2-\mathrm{A}\epsilon^2} \quad . \quad . \quad . \quad . \quad . \quad . \quad . \quad (\mathrm{XXVII})$$

Now, we may find the parental and grandparental correlations from the fact that the mean z of any sibship is the mean z of its parents; but we shall obtain very different results in these as in other cases, according to the interpretation which we put upon the observed correlation between parents. For, in the first place, this correlation may be simply the result of conscious selection. If the correlation for height stood alone this would be the most natural interpretation. But it is found that there is an *independent* association of the length of the forearm [*]: if it is due to selection it must be quite unconscious, and, as Professor PEARSON points out, the facts may be explained if to some extent fertility is dependent upon genetic similarity. Thus there are two possible interpretations of marital correlations. One regards the association of the apparent characteristics as primary: there must, then, be a less intense association of the genotype y, and still less of z. The other regards the association as primarily in y or z, and as appearing somewhat masked by environmental effects in the observed correlation. In the first place, let us suppose the observed correlation in x to be primary.

Then if μ is the correlation for x, $c_1\mu$ will be that for y, and this must be written for μ in the applications of the preceding paragraphs. Hence

$$\mathrm{A}=c_1c_2\mu,$$

and μ, $c_1\mu$ and A are the marital correlations for x, y, and z.

Since the mean z of a sibship is equal to the mean z of its parents, we may calculate the parental and grandparental correlations thus:—For group chosen so that $x=t$: mean y, $\bar{y}=c_1t$; mean z, $\bar{z}=c_1c_2t$; $\bar{x}$ of mate is μt; $\bar{z}$ of mate is $c_1c_2\mu t$. Therefore $\bar{z}$ of children is

$$c_1c_2\frac{1+\mu}{2}.$$

Hence, since there is no association except of z between parents and child, the parental correlation coefficient is

$$c_1c_2\frac{1+\mu}{2}.$$

Now, since we know the mean z of the children to be

$$c_1c_2\frac{1+\mu}{2}t,$$

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[*] PEARSON and LEE, "On the Laws of Inheritance in Man," *Biometrika*, ii, 374.

the mean z of their mates is

$$c_1c_2\frac{1+\mu}{2}At,$$

and the grandparental correlation coefficient will be

$$c_1c_2\frac{1+\mu}{2}\,\frac{1+A}{2}.$$

Similarly, that for the $(n+1)^{\text{th}}$ parent will be

$$c_1c_2\frac{1+\mu}{2}\left(\frac{1+A}{2}\right)^n,$$

giving the Law of Ancestral Heredity as a necessary consequence of the factorial mode of inheritance.

18. If we suppose, on the other hand, that the association is essentially in y, the coefficient of correlation between y of husband and y of wife must be $\frac{\mu}{c_1}$ in order to yield an apparent correlation μ. Also

$$c_2=\frac{\tau^2}{\sigma^2-A\epsilon^2},$$

and

$$A=\frac{\mu}{c_1}c_2.$$

The parental correlation found as before is now

$$\frac{c_1c_2+Ac_1}{2},$$

and the higher ancestors are given by the general form

$$\frac{c_1c_2+Ac_1}{2}\left(\frac{1+A}{2}\right)^n,$$

although A is now differently related to c_1, c_2, and μ.

In the third case, where the essential connection is between z of husband and z of wife—and this is a possible case if the association is wholly due to selective fertility or to the selection of other features affected by the same factors—the equation between the correlations for y and z is changed, for now the marital correlation for y is equal to Ac_2 when we retain the definition

$$c_2=\frac{\tau^2}{\sigma^2-A\epsilon^2}.$$

Hence also

$$\mu=Ac_1c_2,$$

and the correlation coefficients in the ancestral line take the general form

$$c_1c_2\left(\frac{1+A}{2}\right)^{n+1}.$$

19. On the first of these theories a knowledge of the marital and the parental correlations should be sufficient to determine c_1c_2, and thence to deduce the constant ratio of the ancestral coefficients.

Thus for three human measurements :—

	Stature.	Span.	Forearm.
μ	·2804	·1989	·1977
p	·5066	·4541	·4180
c_1c_2	·7913	·7575	·6980
A	·2219	·1507	·1377
$\frac{1}{2}(1+\mathrm{A})$	·6109	·5753	·5689

These figures are deduced from those given by PEARSON and LEE (*loc. cit.*), neglecting sex distinctions, which are there found to be insignificant, and taking the weighted means.

These values for $\frac{1}{2}(1+\mathrm{A})$ agree very satisfactorily with the two ratios of the ancestral correlations which have been obtained, ·6167 for eye colour in man, and ·6602 for coat colour in horses. It is evident that if we also knew the ratio of the ancestral correlations for these features, we could make a direct determination of A and ascertain to what extent it is the cause and to what extent an effect of the observed marital correlation.

20. The correlations for sibs, double cousins, and more distant relations of the same type, in which all the ancestors of a certain degree are common, may be found by considering the variance of the group of collaterals descended from such ancestors. The variance of a sibship, for example, depends, apart from environment, only upon the number of factors in which the parents are heterozygous, and since the proportion of heterozygotes is only diminished by a quantity of the second order, the mean variance of the sibships must be taken for our purposes to have the value appropriate to random mating,

$$\tfrac{1}{2}\tau^2+\tfrac{3}{4}\epsilon^2=\frac{\mathrm{V}}{4}[2c_2(1-\mathrm{A})+3(1-c_2)]$$

plus the quantity $\dfrac{\mathrm{V}}{c_1}-\mathrm{V}$ due to environment. But the variance of the population is V/c_1; and the ratio of the two variances must be $1-f$, where f is the fraternal correlation. Hence

$$f=\frac{c_1}{4}(1+c_2+2c_2\mathrm{A}).$$

In the same way, the variance for a group of double cousins is unaffected by selective mating, and we find the correlation coefficient for double cousins to be

$$\frac{c_1}{16}(1+3c_2+12c_2\mathrm{A}),$$

showing how the effect of selective mating increases for the more distant kin.

On the first hypothesis, then, we must write,

$$\mu=\frac{\mathrm{A}}{c_1c_2},$$

$$p=c_1c_2\frac{1+\mu}{2},$$

and

$$f=\frac{c_1}{4}(1+c_2(1+2\mathrm{A})).$$

21. We shall use this formula for the fraternal correlation to estimate the relative importance of dominance and environment in the data derived from the figures given by Pearson and Lee.

Assuming as the observed correlations

	Stature.	Span.	Cubit.
μ	·2804	·1989	·1977
p	·5066	·4541	·4180
f	·5433	·5351	·4619

we obtain as before

	Stature.	Span.	Cubit.
c_1c_2	·7913	·7575	·6980
A	·2219	·1507	·1377

and calculating c_1 from the formula

$$c_1 = 4f - c_1c_2(1 + 2\mathrm{A}),$$

we obtain the three values

1·031 1·155 ·957

with a standard error of ·072, and a mean of 1·048.

This relatively large standard error, due principally to our comparative ignorance of the fraternal correlations (errors in μ have scarcely any effect, and those in p are relatively unimportant), prevents us from making on a basis of these results a close estimate of the contributions to the total variance of the factors under consideration.

Remembering that c_1 is intrinsically less than unity, the second value is inexplicably high, whilst the first and third are consistent with any value sufficiently near to unity. The mean of these results is materially greater than unity, and therefore gives no support to the supposition that there is any cause of variance in these growth features other than genetic differences. If this is so, we should put $c_1 = 1$, and compare the observed values of f with those calculated from the formula

$$4f = 1 + c_2(1 + 2\mathrm{A}).$$

With their standard errors we obtain

	Stature.	Span.	Cubit.	Standard Error.
Observed	·5433	·5351	·4619	·016
Calculated	·5356	·4964	·4726	·008
Difference	− ·0077	− ·0387	+ ·0107	·018

The exceptional difference in the fraternal correlations for span might, perhaps, be due to the effects of epistacy, or it may be that the terms which we have neglected, which depend upon the finiteness of the number of factors, have some influence. It is more likely, as we shall see, that the assumption of direct sexual selection is not justified for this feature. Accepting the above results for stature, we may ascribe the following percentages of the total variance to their respective causes :—

Ancestry		54 per cent.
Variance of sibship :		
$\frac{1}{2}\tau^2$	31 per cent.	
$\frac{3}{4}\epsilon^2$	15 ,,	
Other causes	...	
		46 ,,
		100 per cent.

Again it may be divided :

Genotypes (σ^2) :		
Essential genotypes (τ^2)	62 per cent.	
Dominance deviations (ϵ^2)	21 ,,	
		83 per cent.
Association of factors by homogamy		17 ,,
Other causes		...
		100 per cent.

These determinations are subject, as we have seen, to considerable errors of random sampling, but our figures are sufficient to show that, on this hypothesis, it is very unlikely that so much as 5 per cent. of the total variance is due to causes not heritable, especially as every irregularity of inheritance would, in the above analysis, appear as such a cause.

It is important to see that the large effect ascribed to dominance can really be produced by ordinary Mendelian factors. The dominance ratio, $\frac{\epsilon^2}{\sigma^2}$, which may be determined from the correlations, has its numerator and denominator composed of elements, δ^2 and α^2, belonging to the individual factors. We may thereby ascertain certain limitations to which our factors must be subject if they are successfully to interpret the existing results. The values of the dominance ratio in these three cases are found to be :

	Stature.	Span.	Cubit.	Standard Error.
Dominance ratio	·253	·274	·336	·045

22. The correlations for uncles and cousins, still assuming that the association of factors is due to a direct selection of the feature x, may be obtained by the methods of Article 14, using the two series already obtained : that for ancestors

$$c_1 c_2 \frac{1+\mu}{2}\left(\frac{1+A}{2}\right)^n,$$

and that for collaterals, like sibs and double cousins, which have all their ancestors of a certain degree in common,

$$\tfrac{1}{4}c_1[1+c_2(1+2A)],$$
$$\tfrac{1}{16}c_1[1+3c_2(1+4A)],$$

and so on.

Thus if a group be chosen so that $x = t$,

$$\begin{aligned} &\bar{y} \text{ of group is } c_1 t, \\ &\bar{z} \text{ of group is } c_1 c_2 t, \\ &\bar{z} \text{ of sibs is } c_1 c_2 \frac{1+\mathrm{A}}{2} t, \end{aligned}$$

also

$$\begin{aligned} &\bar{y} \text{ of sibs is } \tfrac{1}{4} c_1 [1 + c_2 (1 + 2\mathrm{A})] t, \\ &\bar{y} \text{ of sibs mates is } \tfrac{1}{4} c_1 [1 + c_2 (1 + 2\mathrm{A})] c_1 \mu t, \\ &\bar{z} \text{ of sibs mates is } \tfrac{1}{4} c_1 [1 + c_2 (1 + 2\mathrm{A})] \mathrm{A} t. \end{aligned}$$

Hence

$$\bar{z} \text{ of nephews is } \tfrac{1}{8} c_1 [2 c_2 (1 + \mathrm{A}) + \{1 + c_2 (1 + 2\mathrm{A})\} \mathrm{A}] t,$$

giving the correlation

$$c_1 c_2 \left(\frac{1+\mathrm{A}}{2}\right)^2 + \tfrac{1}{8} c_1 \mathrm{A} (1 - c_2).$$

Again for cousins, if a group be chosen so that $x = t$, we have

$$\begin{aligned} &\bar{y} \text{ of uncles is } \left[c_1 c_2 \left(\frac{1+\mathrm{A}}{2}\right)^2 + \tfrac{1}{8} c_1 \mathrm{A} (1 - c_2) \right] t, \\ &\bar{z} \text{ of uncles is } c_1 c_2 \left(\frac{1+\mathrm{A}}{2}\right)^2, \end{aligned}$$

and

$$\bar{z} \text{ of uncles mates is } \left[c_1 c_2 \left(\frac{1+\mathrm{A}}{2}\right)^2 + \tfrac{1}{8} c_1 \mathrm{A} (1 - c_2) \right] \mathrm{A} t,$$

hence

$$\bar{z} \text{ of cousins is } \left[c_1 c_2 \left(\frac{1+\mathrm{A}}{2}\right)^3 + \tfrac{1}{16} c_1 \mathrm{A}^2 (1 - c_2) \right] t,$$

giving the correlation

$$c_1 c_2 \left(\frac{1+\mathrm{A}}{2}\right)^3 + \tfrac{1}{16} c_1 \mathrm{A}^2 (1 - c_2).$$

The formulæ show that these two correlations should differ little from those for grandparent and great-grandparent, using the values already found, and putting $c_1 = 1$ we have

	Stature.	Span.	Cubit.
Grandparent	·3095	·2612	·2378
Great-grandparent . .	·1891	·1503	·1353
Uncle	·3011	·2553	·2311
Cousin	·1809	·1445	·1288

23. On the third supposition, that the marital correlation is due primarily to an association in the essential genotype z, we obtain results in some respects more intelligible and in accordance with our existing knowledge.

From the fundamental equations

$$\begin{aligned} \mu &= c_1 c_2 \mathrm{A}, \\ p &= \tfrac{1}{2}(c_1 c_2 + \mu), \end{aligned}$$

we may deduce

$$\begin{aligned} c_1 c_2 &= 2p - \mu, \\ \mathrm{A} &= \mu/(2p - \mu), \end{aligned}$$

whence the following table is calculated :—

	Stature.	Span.	Cubit.	Standard Error.
μ . .	·2804	·1989	·1977	·0304
p . .	·5066	·4541	·4180	·0115
f . .	·5433	·5351	·4619	·0160
$c_1 c_2$ . .	·7328	·7093	·6383	·038
A . .	·3826	·2804	·3097	·028
$\frac{1}{2}(1+\mathrm{A})$.	·6913	·6402	·6549	·014

and making use of the fraternal correlations to separate c_1 and c_2, by the equations

$$f = \tfrac{1}{4}c_1[1 + c_2(1 + 2A)],$$

or

$$c_1 = 4f - 2p - \mu,$$

we obtain

c_1 . .	·8796	1·0333	·8139	·078
c_2 . .	·8331	·6864	·7842	·077
$\frac{\epsilon^2}{\sigma^2}$ . .	·2450	·3883	·2850	·105

The standard error for the dominance ratio is now very high, since the latter is proportional to the difference $f - p$. If we assume a known value for c_1, and calculate the dominance ratio from p and μ only, the standard error falls nearly to its value in Article 18.

The three values for the ratio of the ancestral correlations ·691, ·640, ·655 are now higher than that obtained from observations of eye colour, and are more similar to the value ·660 obtained for the coat colour of horses. Without knowing the marital correlations in these cases, it is not possible to press the comparison further. It would seem unlikely that the conscious choice of a mate is less influenced by eye colour than by growth features, even by stature. But it is not at all unlikely that eye colour is but slightly correlated with other features, while the growth features we know to be highly correlated, so that a relatively slight selection in a number of the latter might produce a closer correlation in each of them than a relatively intense selection of eye colour.

The value of c_1 for span is still greater than unity, 1·033, but no longer unreasonably so, since the standard error is about ·078. If we were considering span alone the evidence would be strongly in favour of our third hypothesis. A remarkable confirmation of this is that PEARSON and LEE (*loc. cit.*, p. 375), considering organic and marital correlations alone, show that the observed correlations could be accounted for by the following direct selection coefficients :—

Stature.	Span.	Cubit.
·2374	·0053	·1043

Naturally these cannot be taken as final, since there are a large number of other features, which may be connected with these and at the same time may be subject to sexual selection. The correlations of cross assortative mating are in fact smaller than they would be if direct selection to this extent were actually taking place. The influence of other features prevents us from determining what proportion of the observed association is due to direct selection, but if inheritance in these growth features is capable of representation on a Mendelian scheme—and our results have gone far to show that this is likely—it would be possible to distinguish the two parts by comparing the parental and fraternal correlations with those for grandparents and other kindred.

On our present supposition that the association is primarily in z, and for the case of span this seems likely, the correlations for uncle and cousin will be the same as those for grandparent and great-grandparent, being given by the formulæ

$$c_1c_2\left(\frac{1+A}{2}\right)^2 \quad \text{and} \quad c_1c_2\left(\frac{1+A}{2}\right)^3,$$

leading to the numbers

	Stature.	Span.	Cubit.
Grandparent . . .	·3502	·2907	·2737
Great-grandparent . .	·2421	·1861	·1793

24. Neither these nor the similar table for the first hypothesis accord ill with the value obtained for uncle and nephew, ·265, from measurements of eye colour. It may, however, be thought that neither of them give high enough value for cousins. Certainly they do not approach some of the values found by Miss **Elderton** in her memoir on the resemblance of first cousins (*Eugenics Laboratory Memoirs*, iv). Series are there found to give correlations over ·5, and the mean correlation for the measured features is ·336. From special considerations this is reduced to ·270, but if the similarity of first cousins is due to inheritance, it must certainly be less than that between uncle and nephew. No theory of inheritance could make the correlation for cousins larger than or even so large as that for the nearer relationship.

It will be of interest finally to interpret our results on the assumption that the figures quoted (Article 20) represent actual coefficients of selection. Manifestly it would be better to obtain the value of A experimentally from the ratio of the ancestral correlations, using the collateral correlations to determine what are the marital correlations for y. For the present we must neglect the possibility of an independent selection in y; and although we know that the figures are not final, we shall write s, the coefficient of selection, equal to ·2374, ·0053, and ·1043 in our three cases.

Further, let

$$A = c_1c_2s + \frac{\mu - s}{c_1c_2},$$

so that

$$2p = c_1c_2(1+s) + \mu - s,$$

whence we deduce

	Stature.	Span.	Cubit.
c_1c_2	·7841	·7108	·6725
A	·2410	·2761	·2090
$\frac{1}{2}(1+A)$	·6205	·6381	·6045

the values of A being now in much closer agreement for the three features. Further, from the fraternal correlation we have

c_1	1·0112	1·0370	·8940

with a mean at ·9821.

Again, for the dominance ratio

·2763 ·3880 ·2940 ·3194 (mean),

leaving a trifle under 2 per cent. for causes not heritable, but requiring high values about ·32 for the dominance ratio.

25. *The Interpretation of the Statistical Effects of Dominance.*—The results which we have obtained, although subject to large probable errors and to theoretical reservations which render an exact estimate of these errors impossible, suggest that the ratio $\frac{\epsilon^2}{\sigma^2}$, the statistical measure of the extent of dominance, has values of about ·25 to ·38. In his initial memoir on this subject KARL PEARSON has shown that, under the restricted conditions there considered, this ratio should be exactly $\frac{1}{3}$. Subsequently UDNY YULE (Conference on Genetics) pointed out that the parental correlation could be raised from the low values reached in that memoir to values more in accordance with the available figures by the partial or total abandonment of the assumption of dominance. To this view Professor PEARSON subsequently gave his approval; but it does not seem to have been observed that if lower values are required—and our analysis tends to show that they are not—the statistical effects are governed not only by the physical ratio $\frac{d}{a}$, but by the proportions in which the three Mendelian phases are present. This effect is an important one, and very considerably modifies the conclusions which we should draw from any observed value of the dominance ratio.

The fraction $\frac{\delta^2}{a^2}$, of which the numerator and denominator are the contributions of a single factor to ϵ^2 and σ^2, is equal, as we have seen (Article 5, equations V–VII) to

$$\frac{2pqd^2}{(p+q)^2a^2-2(p^2-q^2)ad+(p^2+q^2)d^2},$$

and depends wholly upon the two ratios $\frac{d}{a}$ and $\frac{p}{q}$. We may therefore represent the variations of this function by drawing the curves for which it has a series of constant values upon a plane, each point on which is specified by a pair of particular values for these two ratios. The accompanying diagram (fig. 1, p. 430) shows such a series of curves, using $\frac{d}{a}$ and $\log\frac{p}{q}$ as co-ordinates. The logarithm is chosen as a variable, because equal intensity of selection will affect this quantity to an equal extent, whatever may be its value; it also possesses the great advantage of showing reciprocal values of $\frac{p}{q}$ in symmetrical positions.

It will be seen that ·3 is not by any means the highest value possible: when $d=a$, and when $\frac{p}{q}$ is very great, any value up to unity may appear; but high values are confined to this restricted region. When $\frac{d}{a}$ is less than ·3 the ratio is never greater than ·05, and we cannot get values as high as ·15 unless $\frac{d}{a}$ be as great as ·5. On the other hand, all values down to zero are consistent with complete dominance, provided that the values of $\frac{p}{q}$ are sufficiently small.

We know practically nothing about the frequency distribution of these two ratios. The conditions under which Mendelian factors arise, disappear, or become modified are unknown. It has been suggested that they invariably arise as recessive mutations in a dominant population. In that case $\frac{p}{q}$ would initially be very high, and could only be lowered if by further mutation, and later by selection, the recessive phase became more frequent. These factors would, however, have little individual weight if better balanced factors were present, until $\frac{p}{q}$ had been lowered to about 10. In face of these theories it cannot be taken for granted that the distribution of these ratios is a simple one. It is natural, though possibly not permissible, to think of their distributions as independent. We may profitably consider further the case in which the distribution is symmetrical, in which the factor of known a and d is equally likely to be more frequent in the dominant as in the recessive phase.

For this case we combine the numerators and denominators of the two fractions

$$\frac{2pqd^2}{(p+q)^2a^2-2(p^2-q^2)ad+(p^2+q^2)d^2} \text{ and } \frac{2pqd^2}{(p+q)^2a^2+2(p^2-q^2)ad+(p^2+q^2)d^2},$$

and obtain the joint contribution

$$\frac{2pqd}{(p+q)^2a^2+(p^2+q^2)d^2},$$

the curves for which are shown in fig. 2, representing the combined effect of two similar factors, having their phases in inverse proportions. It will be seen that complete dominance does not preclude the possibility of low value for the dominance ratio: the latter might fall below ·02 if the greater part of the variance were contributed by factors having the ratio between p and q as high as 100 to 1. This ratio is exceedingly high; for such a factor only one individual in 10,000 would be a recessive. We may compare the frequency of deaf mutism with which about one child in 4000 of normal parents is said to be afflicted. It would be surprising if more equal proportions were not more common, and if this were so, they would have by far the greater weight.

The fact that the same intensity of selection affects the logarithm of $\frac{p}{q}$ equally, whatever its value may be, suggests that this function may be distributed approximately according to the law of errors. This is a natural extension of the assumption of symmetry, and is subject to the same reservations. For instance, a factor in which the dominant phase is the commonest would seem less likely to suffer severe selection than one in which the recessive phase outnumbers the other. But if symmetry be granted, our choice of a variable justifies the consideration of a normal distribution.

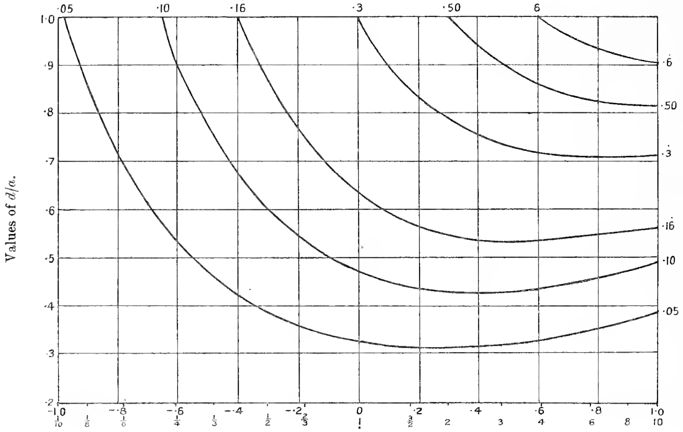

Fig. 1.—Values of $\log_{10}(p/q)$ (upper figures) and of p/q (lower figures).

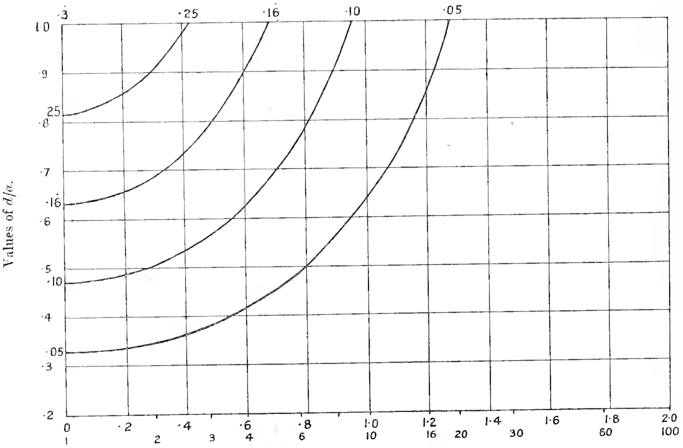

Fig. 2.—Values of $\log_{10}(p/q)$ (upper figures) and of p/q (lower figures).

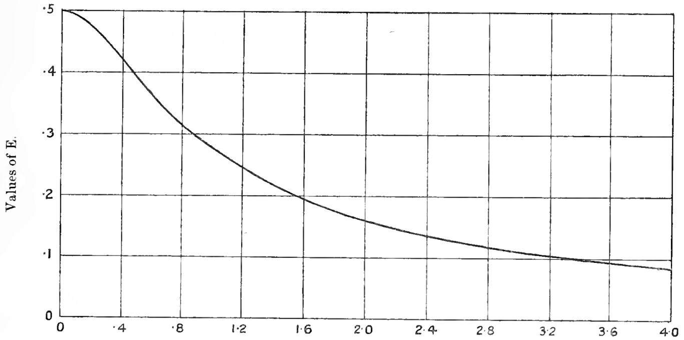

FIG. 3.—Values of $\sigma \log_{10} e = \cdot 4343\sigma$.

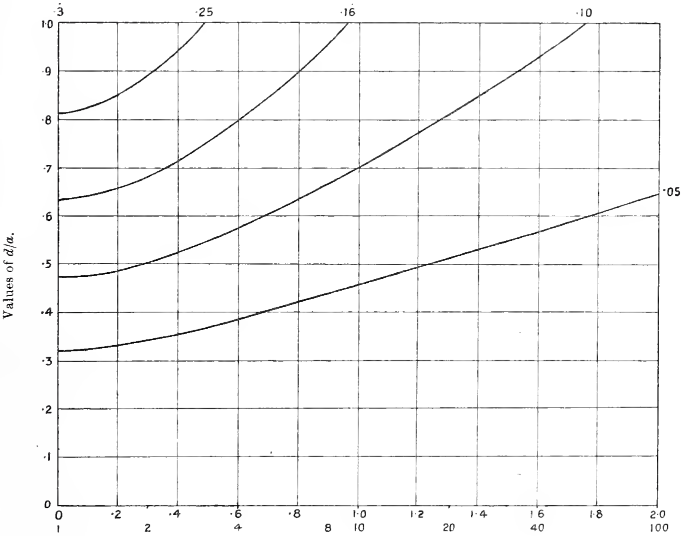

FIG. 4.—Values of $\log_{10}$ of standard ratio (upper figures) and of standard ratio (lower figures).

Writing ξ for $\log_e \frac{p}{q}$ and σ for the standard deviation of ξ, we have

$$p = e^{\frac{1}{2}\xi}/2\cosh\tfrac{1}{2}\xi, \quad q = e^{-\frac{1}{2}\xi}/2\cosh\tfrac{1}{2}\xi, \quad \text{and} \quad 2pq = \tfrac{1}{2}\operatorname{sech}^2\tfrac{1}{2}\xi.$$

Hence we have to evaluate

$$\mathrm{E} = \frac{1}{\sigma\sqrt{2\pi}}\int_{-\infty}^{\infty}\tfrac{1}{2}\operatorname{sech}^2\tfrac{1}{2}\xi\,.\,e^{-\xi^2/2\sigma^2}d\xi = \frac{1}{\sqrt{2\pi}}\int_{-\infty}^{\infty}\tfrac{1}{2}\operatorname{sech}^2\frac{\sigma\xi}{2}e^{-\frac{1}{2}\xi^2}d\xi \quad . \quad . \quad \text{(XXVIII)}$$

and the dominance ratio derived from the whole group is

$$\frac{\mathrm{E}d^2}{a^2+(1-\mathrm{E})d^2}.$$

E is a function of σ only, which decreases steadily from its value $\frac{1}{2}$ when $\sigma = 0$, approaching when σ is large to the function $\frac{2}{\sigma\sqrt{2\pi}}$. The function $\left(16+16\sigma^2+\frac{\pi^2}{4}\sigma^4\right)^{-\frac{1}{4}}$ osculates it at the origin, and appears on trial to represent it effectively to three significant figures. This function has been used for calculating the form of the accompanying curves. Fig. 3 shows the course of the function E. Fig. 4 gives the curves comparable to those of figs. 1 and 2, showing the value of the dominance ratio for different values $\frac{d}{a}$ and σ. If the assumptions upon which this diagram is based are justified, we are now advanced some way towards the interpretation of an observed dominance ratio. A ratio of ·25 gives us a lower limit of about ·8 for $\frac{d}{a}$, and no upper limit. If the possibility of superdominance ($d>a$) is excluded, then the ratio of the phases must be so distributed that the standard ratio e^σ is not greater than about 3 : 1. A greater value of the standard ratio would make the effect of dominance too small; a smaller value could be counteracted by a slight reduction of $\frac{d}{a}$. We have therefore no reason to infer from our dominance ratios that dominance is incomplete. We may speak of it as having at least four-fifths of its full value, but we can set no upper limit to it.

26. Throughout this work it has been necessary not to introduce any avoidable complications, and for this reason the possibilities of Epistacy have only been touched upon, and small quantities of the second order have been steadily ignored. In spite of this, it is believed that the statistical properties of any feature determined by a large number of Mendelian factors have been successfully elucidated. Due allowance has been made for the factors differing in the magnitude of their effects, and in their degree of dominance, for the possibility of Multiple Allelomorphism, and of one important type of Coupling. The effect of the dominance in the individual factors has been seen to express itself in a single Dominance Ratio. Further, the effect of marital correlation has been fully examined, and the relation between this association and the coefficient of marital correlation has been made clear.

By means of the fraternal correlation it is possible to ascertain the dominance ratio and so distinguish dominance from all non-genetic causes, such as environment, which might tend to lower the correlations: this is due to the similarity in siblings of the effects of dominance which causes the fraternal correlation to exceed the parental. The fact that this excess of the fraternal correlation is very generally observed is itself evidence in favour of the hypothesis of cumulative factors. On this hypothesis it is possible to calculate the numerical influence not only of dominance, but of the total genetic and non-genetic causes of variability. An examination of the best available figures for human measurements shows that there is little or no indication of non-genetic causes. The closest scrutiny is invited on this point, not only on account of the practical importance of the predominant influence of natural inheritance, but because the significance of the fraternal correlation in this connection has not previously been realised.

Some ambiguity still remains as to the causes of marital correlations: our numerical conclusions are considerably affected according as this is assumed to be of purely somatic or purely genetic origin. It is striking that the indications of the present analysis are in close agreement with the conclusions of PEARSON and LEE as to the genetic origin of a part of the marital correlation, drawn from the effect of the correlation of one organ with another in causing the selection of one organ to involve the selection of another. This difficulty will, it is hoped, be resolved when accurate determinations are available of the ratio of the grandparental to the parental correlation. From this ratio the degree of genetic association may be immediately obtained, which will make our analysis of the Variance as precise as the probable errors will allow.

In general, the hypothesis of cumulative Mendelian factors seems to fit the facts very accurately. The only marked discrepancy from existing published work lies in the correlation for first cousins. SNOW, owing apparently to an error, would make this as high as the avuncular correlation; in our opinion it should differ by little from that of the great-grandparent. The values found by Miss ELDERTON are certainly extremely high, but until we have a record of complete cousinships measured accurately and without selection, it will not be possible to obtain satisfactory numerical evidence on this question. As with cousins, so we may hope that more extensive measurements will gradually lead to values for the other relationship correlations with smaller standard errors. Especially would more accurate determinations of the fraternal correlation make our conclusions more exact.

Finally, it is a pleasure to acknowledge my indebtedness to Major LEONARD DARWIN, at whose suggestion this inquiry was first undertaken, and to whose kindness and advice it owes its completion.

XVI.—The Prostate Glands of the Earthworms of the Family Megascolecidæ. By **J. Stephenson**, D.Sc., M.B., Lieut.-Col. Indian Medical Service; Professor of Zoology, Government College, Lahore; and **Haru Ram**, M.Sc., Professor of Zoology, Hindu University, Benares; late Demonstrator of Zoology, Government College, Lahore. (With One Plate.)

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CONTENTS.

INTRODUCTION.

The prostates or spermiducal glands form a prominent feature in the anatomy of the large family of the Megascolecidæ. Occurring in the neighbourhood of the termination of the sperm-ducts, they assume one of two forms, the tubular or the lobular. In the first, the gland typically takes the form of a bent, undulating, or coiled tube, cylindrical, with a single central lumen; in the second, it consists of a loosely or tightly packed aggregate of lobules, each with its ductule. The prostatic duct is in the first case a continuation of the glandular tube; in the second, the duct is formed by the union of the ductules; in both cases it is as a rule firm and muscular.

In the original condition, still maintained in certain genera of the sub-family Acanthodrilinæ, the terminations of the vasa deferentia are situated on the eighteenth segment, and two pairs of tubular prostates open in front and behind the male pores, on the seventeenth and nineteenth segments respectively. In the sub-family Megascolecinæ the male pore retains its position, while the prostates are reduced to one pair, which open in common with the vasa deferentia; in the more primitive genera of the sub-family this single pair of prostates have the tubular form, but in the more recently evolved genera the tubular has given way to the lobular form. In all the other sub-families the tubular prostates have been retained, though their number, situation, and relation to the vasa deferentia vary.

We use the term "prostate" in preference to "spermiducal gland" in the present paper, since the glands, as has been said, are not, in this family, primarily connected with the sperm-ducts. There may be glands in other families which are so connected, and all the structures which have been grouped together as "spermiducal glands" may not be homologous; but for the present we confine ourselves to the Megascolecidæ, and express no opinion on these points.

Some time ago, on dissecting a specimen of the common *Pheretima hawayana*, one of us found two small supernumerary prostates, one on each side, a little way behind the normal glands. The larger was loosely attached to septum 21/22 on the right side; the smaller was attached, also loosely, to the posterior part of segment xx. No ducts were to be seen.

The portion of the specimen was immediately fixed in sublimate and acetic acid, and afterwards examined under the dissecting binocular. Before examination, however, the mere changing of the 70 per cent. alcohol used for washing out the sublimate had caused the greater part of the larger gland to become detached, and it lay loose in two pieces in the tube; and on pinning out the specimen the remainder also became detached. On close examination of the fixed specimen no trace whatever of a duct was found on either side, internally or externally.

Since, therefore, there was no connection with the exterior, these supernumerary glands had, it would seem, been developed *in situ*, and hence would be mesodermal and not ectodermal in origin. And if these, then the prostates generally would be mesodermal, and would not—as might be and has been supposed—have originated as invaginations or ingrowths from the surface of the body. We determined, therefore, to investigate the structure and development of both the tubular and lobular forms of the gland from this point of view. The common genus *Pheretima*, which is always to be obtained, was taken as a type of the forms with lobular prostate; for the tubular form we have selected *Eutyphœus*, a representative of a sub-family, the Octochætinæ, in which the histology of the prostate has not, so far as we know, been investigated.

HISTORICAL.

While we are not acquainted with any account of the development of the prostate of the Megascolecidæ—either of the tubular or lobular form,—the histology has been described with more or less fullness by several authors.

According to SPENCER (4), the glandular section of the tubular prostate of *Megascolides australis* consists of an outer and an inner portion. The inner part is composed of a single layer of columnar cells, loosely arranged, radially placed in regard to the lumen, staining deeply, and without visible nuclei; occasionally these cells are very long, and extend into the outer portion. The cells of the peripheral region are much more numerous, and form a layer twice as thick as the former; their necks, in some cases at least, pass between the cells of the inner region; they stain less deeply than these, and a nucleus is visible. Between the two layers a slight development of connective tissue is visible, and a layer of blood vessels. Externally the gland is encased by connective tissue, beneath which masses of yellow-brown pigment spots are sometimes seen.

Beddard, in his monograph (1), gives a short description of the tubular prostate on the above lines, mentioning a peritoneal membrane on the outside.

Miss Sweet, in her study of the prostates of Australian earthworms (7), describes first the macroscopic characters of the male organs in a considerable number of the Megascolecinæ. In the account of the histology of the tubular forms she states that the central lumen is lined by an epithelium of ordinary columnar cells with a nucleus at the inner end of each; sometimes the lining is of cubical cells; outside the lining epithelium is often a small amount of connective tissue with blood vessels. The bulk of the wall is composed of granular gland cells with pear-shaped outer end, and long, narrow, duct-like inner end which opens into the lumen between the cells of the columnar lining, sometimes singly, sometimes in groups. In some forms there are seen a number of cells, staining much more with methylene blue, more granular, and forming a more or less distinct layer at about one-half the depth of the wall; these have a more rounded, club-shaped end than the ordinary form of gland-cell. Fine capillaries are present among the glandular cells. *Acanthodrilus sydneyensis* departs from the type above described.

We may so far anticipate our own conclusions as to say that in *Eutyphœus* the structure of the prostate shows a considerable resemblance to that of *Megascolides australis* as described by Spencer. The inner layer of cells can here, however, scarcely be said to form an epithelium—the cells are much too sparse; nor is there a definite connective tissue or peritoneal covering, as claimed both by Spencer and Beddard. The very well-marked epithelial lining figured by Miss Sweet for the tubular glands of the Megascolecinæ is altogether absent in *Eutyphœus*, certainly so when the gland is fully formed and actively functioning.

Beddard (1), resuming the histological structure of the lobular prostates, states that the ductules are lined by a low columnar epithelium, which does not ever appear to be markedly glandular; attached to these tubes are groups of pear-shaped cells massed into bundles, whose fine processes seem to open into the lumen between the non-glandular cells which line it. The whole is covered by a fine covering of peritoneum. There is no essential difference between this type of gland and the tubular, and there seem to be glands with an intermediate character.

According to Miss Sweet, each lobule has a typically radiate appearance, with sometimes a small lacuna in its centre; this is, however, generally obliterated by the approximation of the inner ends of the cells. In very rare cases a communication can be traced between the lacuna and the terminal branch of the duct; in no instance was any epithelium to be seen around the central lacuna.

Here again, in *Pheretima*, we miss the general peritoneal covering described by

BEDDARD, nor can we find the processes of the gland cells which seem to open into the lumen of the ductule between the lining epithelial cells. The central lacuna, and the typically radiate appearance of the gland cells of the lobule, described by Miss SWEET, are also not present in *Pheretima hawayana*.

It may be added that several authors have described forms of prostate gland intermediate between the tubular and lobular. So Miss SWEET (7) (*Megascolides illawarræ*, *Megascolex dorsalis*, *Perisogaster excavata*); BENHAM (2) in the genus *Tokea* (included by MICHAELSEN in *Megascolides*); MICHAELSEN (3) in *Notoscolex leai*; STEPHENSON (5) in *Megascolides hastatus*.

A large number of structures, both superficially and histologically of very various kinds, have been collected together under the same general head as the prostates of the Megascolecidæ. Such, for example, are the similarly named structures in the Geoscolecidæ, Moniligastridæ, and Tubificidæ; the atrium of various aquatic families of Oligochæta; and the copulatory glands,—also of more than one type—which are widely distributed in the Order. BEDDARD (1), finding reason for supposing that a relation exists between copulatory and spermiducal glands, held that those forms of prostate which are most like the copulatory glands must stand at the base of the series; it seems reasonable, he continues, to suppose that the copulatory glands were originally modified tracts of the body-wall, which became invaginated, and furnished with penial setæ for their greater efficiency; the invagination might or might not involve the muscular layers of the body-wall. According to this view, the prostates would also be invaginated from the surface, and of ectodermal origin.

As will appear from the account here given, this does not seem to be the case in the two forms of gland investigated by us. As to the further questions of relationship between the various structures enumerated above, we express no opinion at present; our aim is to clear a portion of the ground by an elucidation of the forms we have selected for investigation.

MATERIAL AND METHODS.

The example of the lobular form of prostate, *Pheretima hawayana* (Rosa), a member of the sub-family Megascolecinæ, is perhaps the commonest earthworm in Lahore; both adult and young specimens can be obtained at any time of the year. For the adult forms, the portion of the animal containing the prostates was fixed either in 10 per cent. formalin or in sublimate and acetic acid, usually after opening the body-wall by a longitudinal incision. The young specimens, being of small size, were fixed, either whole or the cut-off anterior ends, in the same fixatives. It should perhaps be added that there is no means of distinguishing the immature *P. hawayana* from the two other species of *Pheretima* found in Lahore, and that earthworms of more than one species may be found in the same batch of material; so that the specific identification of the young specimens of *Pheretima* is not absolutely certain.

The specimens of *Eutyphœus waltoni* Michlsn., a common species in the United Provinces, were those prepared and fixed by Professor YOUNGMAN, of Canning College, Lucknow, as mentioned in the following paper. We also used specimens obtained by one of us at Agra, and fixed in Zenker's fluid.

The specimens of *Dichogaster malayana* (Horst) and *D. affinis* (Michlsn.), from Negyatankaray in Travancore, and Anuradhapura in Ceylon respectively, belonged originally to the Indian Museum, and were sectioned in the course of systematic work done on the collections in which they occurred. They were not specially fixed for histological work, and hence have not been described in greater detail than is warranted.

The examples of *Ocnerodrilus* (*Ocnerodrilus*) *occidentalis* Eisen were found near Lahore some time ago, and had been fixed in Zenker's fluid.

For staining, Delafield's hæmatoxylin followed by eosin gave on the whole the most useful results, the granules in the glands being stained differentially; and most of the descriptions are written and drawn from specimens so prepared. Heidenhain's iron-hæmatoxylin in Dobell's modification, brazilin, van Gieson's stain, and borax carmine followed by picroindigocarmine were also used.

PHERETIMA HAWAYANA.

(1) *Structure of the Gland as seen in Dissection.*

On dissection (fig. 1) the gland is seen to take up segments xviii, xix, and xx; it is tripartite, being constricted at the level of septa 18/19 and 19/20, which get an attachment to both inner and outer faces of the gland. Each gland is flattened between intestine and body-wall, and is situated laterally and dorsolaterally, extending dorsalwards to not very far from the mid-dorsal line.

The surface of the gland is marked out into a number of small closely apposed lobules, which, however, are not very distinct; the edges of the gland are slightly indented, in correspondence with this lobulation.

A thin sheet of connective tissue, attached at both ends to the body-wall, and somewhat triangular in shape with its base internal, binds down the antero-internal angle of the gland to the body-wall. The wider end of this sheet of tissue is just underneath the edge of the intestine (as the parts are displayed in dissection) and internal to the termination of the prostatic duct; its narrower apex is at the level of and rather underneath the antero-external corner of the gland. It is interesting to compare this band of tissue with the connective tissue investment of the penial setal bundle in *Eutyphœus* (*cf.* pp. 447, 448); both are attached above not far from the mid-dorsal line, and below internal to the ending of the prostatic duct; both are narrower above than below; and both bind down the gland to the parietes. Though penial setæ are not found in *Pheretima*, they are present in many of the more primitive genera of the sub-family (Megascolecinæ) to which *Pheretima* belongs.

The duct (fig. 1A) is oblique in direction, parallel to and either just underneath or lying alongside of the internal border of the gland in segment xviii. It leaves the gland near its inner border at the constriction occasioned by septum 18/19, and ends in the body-wall at the level of the antero-internal angle of the gland. It is almost straight, moderately stout, and very slightly fusiform; it has the shining appearance which denotes a thick and compact layer of circular muscular fibres.

The vas deferens, coming down from the sperm-sacs some segments in front, lies in segment xviii parallel to and on the outer side of the prostatic duct. It joins the prostatic duct where the latter emerges from the gland. Its further relations will be seen in the microscopical study.

In addition to the septa, strands of connective tissue pass between the gland and the body-wall, and also a number of fine long muscular bands; these latter, longitudinal in direction, pass backwards from the parietes to be attached to the outer surface of the gland near its hinder end.

(2) *Microscopical Structure of the Gland* (fig. 2).

The gland on the whole stains deeply, so that it can be immediately picked out in sections by the naked eye. Under the microscope the lobular constitution is at once seen; the lobules are rounded, and fit fairly close together. It is to be noted, however, that what are henceforward called lobules—small masses with an average diameter of ·12 mm.—are not the lobules seen in the dissection, which are larger, ·3 to ·4 mm. in diameter, and consist of several of the smaller masses.

The lobules are for the most part not composed of cells with distinct outlines; where the word "cell" is used, for convenience, in what follows, it may be taken as denoting a nucleus with the immediately surrounding granular and fibrillar substance.

The glandular mass may be described as generally granular in constitution, with fine fibrillar differentiations running through it; in some specimens this fibrillation is more distinct than in others; nuclei are irregularly scattered throughout. There are numerous more or less empty spaces, giving the gland in some places a vacuolar appearance; in other regions the spaces are partly filled with fluffy or granular matter, and the texture of the mass may be called simply loose, rather than distinctly vacuolated.

The nuclei are of various and rather irregular shape. A few show a definite membrane, and the chromatin mostly aggregated into a central mass; others have a distinct membrane, and the chromatin in scattered granules; the majority are homogeneous or almost so, so that neither membrane nor individual chromatin grains can be distinguished. The largest, with a definite central aggregate of chromatin, average 6 μ in diameter, many being 7 μ long by 5 μ broad; the smallest, of homogeneous constitution, are about 3·5 to 4 μ in diameter; the intermediate type seems to be of intermediate size. These various conditions perhaps represent various stages of functional activity, or correspond to various stages of disintegration of the cell; the nucleus appears to disintegrate by becoming smaller, by solution of the chromatin to form a homogeneous staining mass, and by disappearance of the nuclear membrane.

The most distinct granules stain with eosin; and these occur sometimes in fairly definite aggregates. The rest of the glandular mass—its basis, after the abstraction of the nuclei, eosin-staining granules, and fibrillar differentiations—is indistinctly granular or amorphous.

Neighbouring lobules often fuse indistinguishably in parts of their contour; but often there is a distinct cleft—in sections appearing as a channel—between adjacent lobules. Where capillaries are present between the lobules there may be also a few fine fibrils of connective tissue; but for the most part the channels between the lobules are empty, and the boundary of the lobule is merely the limit of the glandular matter.

A capsule on the outer surface of the gland is seen in places, *e.g.* sometimes bridging the angle between contiguous lobules; it consists of connective tissue with oval nuclei. The capsule may be traceable from such a point over neighbouring cells as a thin membrane, with here and there flattened nuclei. Sometimes the membrane, of extreme tenuity, seems to fuse with the surface of the cells and so to cease to exist. In some places there is no membrane, nor even a sharply limited cell-edge; the granular matter forms the rather indefinite surface of the gland. In some cases where flattened nuclei are present on the surface of the gland they do not belong to a separate membrane, but to the granular matter underneath.

There is thus every gradation between a separate capsule and none. A feasible explanation seems to be that capsule and gland are parts of the same tissue, developed from the same basis, as in the pharyngeal glands (*cf.* STEPHENSON, 6).

Similarly with the strands of connective tissue that attach the gland to the body-wall. There is no definite demarcation between strand and gland; where the strand is attached to the gland it may be, for example, continued on one side over the gland for some distance as a distinct membrane with flattened nuclei; further on these flattened nuclei become the superficial nuclei of the glandular substance; ultimately they cease to be distinguishable from the ordinary nuclei of the mass; on the other side of the attachment of the strand this condition may be attained immediately.

In a few places the margin of the gland stains more deeply; and here discrete cells with well-defined margins are present (fig. 3), the protoplasm of which stains sometimes equably and deeply, obscuring the nucleus, at other times unequally, the cell-body including a mass of deeply staining material—a condition which recalls the "chromophil cells" in the pharyngeal glands (STEPHENSON, 6). The nucleus can usually be made out as relatively large, spherical, with a large central aggregation of chromatin but no scattered granules. The shape and size of these cells are quite irregular; perhaps a length of 11 to 14 μ and a breadth of half that amount would represent the average dimensions; they are separated by spaces and clefts, and so do not form a compact aggregate. There may be a very distinct capsule covering them in; but this capsule may become continuous with the surface of the cells, fusing with them and so ceasing to exist. On following the cells inwards, towards the centre of the gland, they soon become granular, with indistinct margins, and take on the usual structure of the gland. Here and there a lobule is largely composed of such separate cells.

We take such separate cells to be recent formations, indicating growth of the gland, or more probably a regeneration of functional elements after the disintegration of those lying nearer the centre of the mass.

Ducts within the Gland.—Ducts are seen here and there in the sections, both within and between the lobules. In the epithelium of which their wall is composed cell boundaries are not to be made out; if we imagine the layer to be divided up in accordance with the disposition of the nuclei, the elements would be broadly columnar. The ducts stain with a slightly pinker tinge (in Delafield and eosin) than the gland tissue.

The ducts begin within the lobules by the assumption of a regular arrangement of the gland "cells" themselves; the "cells" of the ductule at its origin pass into and are continuous with those of the glandular mass. The height of the epithelial layer is 7–8 μ near the origin within the lobule; the nuclei are relatively large, situated rather basally, and contain scattered grains of chromatin. The diameter of the ductule is 17–20 μ, and the lumen is small. Soon after the ductule has been established, the protoplasm shows a vertical striation, and this appearance continues throughout the larger ducts also.

The larger (interlobular) ducts have a delicate connective tissue coat outside the epithelial layer. The height of the epithelium is 14 μ, and the diameter of the duct 40–45 μ. The large ducts about to unite as they emerge from the gland have a diameter of 60–70 μ.

Relations of Glandular Tissue and Ducts.—We do not think it is possible to suppose that every original cell of the lobule discharges directly, by a narrow neck or otherwise, into the ductule in its centre. The epithelial layer of the ductule certainly is not penetrated by the necks of surrounding cells; and the original cells of the gland are far too numerous to allow us to suppose that they can all cluster round the beginning of the ductule and discharge there. For example, starting from the tip of the gland, there are, in one particular series, five sections (or a thickness of 40 μ) without sign of a ductule; while in one section alone there are more than 100 nuclei—in the very first section there are more than 50; allowing fifteen sections to the whole lobule, and an average of 100 nuclei to each section, the lobule will consist of 1500 cells. The impression received from the disposition of the nuclei also is that the very large majority of "cells" could not ever get near the ductule, and were not even at first connected with it (*cf.* fig. 2).

Where separate cells occur in some places near the periphery of the gland, there are no indications of long necks connecting them with the ductule (fig. 3).

However, in view of the fact that in the adult, separate cells for the most part do not exist, there can be no doubt that the secretion from the peripheral parts of the glandular mass filters through the glandular tissue to the ductule.

The Ducts outside the Gland.—On escaping from the gland the duct—the united ducts of the lobules—acquires its muscular coat. There is no general peritoneal coat over the duct — for the most part the muscular tissue is on the surface.

In a dissection, the vasa deferentia, leading from the two male funnels of each side in segments x and xi respectively, appear to unite in segment xii, and an apparently single duct on each side travels back to the prostate. The two vasa deferentia of each side are, however, though bound up together, still separate up to their junction with the main prostatic duct where this emerges from the gland. Here the vasa deferentia penetrate the muscular coat of the prostatic duct and approach the lumen; but, as was first pointed out to us by Dr Baini Prashad, formerly Assistant Professor in this Department, they can be followed along, still double, in this position throughout the whole length of the prostatic duct, only actually entering the lumen of the latter close to its termination at the surface of the body.

(3) *Structure of Supernumerary Prostates without Ducts* (fig. 4).

These organs were found to be compact masses of closely fitting lobules which were not always distinctly delimited from each other.

On the whole, the cells are here more distinct than in the ordinary gland, and their surface may be defined by a fine deeply staining lamella, or perhaps a fibrillar differentiation; at other times the territories of neighbouring nuclei are not delimited at all. The fibrillar differentiations of the glandular mass appear here to delimit cell territories rather than to wander indiscriminately through the mass.

The cells, where they are distinct, are irregular in shape, and measurements are difficult; they may be about 20 μ in diameter; or an elongated cell may measure 35 by 18 μ. The protoplasmic substance is either evenly granular, or apparently disintegrating, in such a way that there is an area which is only loosely filled with granular matter or is partly empty. Of neighbouring cell territories some may thus appear moderately homogeneous and rather darkly staining; others almost empty, with only a small quantity of granular matter inside. A section has thus a curiously uneven appearance.

The nuclei are large, roundly ovoid, 7 by 5 or 6 μ in diameter, with scattered granules and one larger chromatic grain; the large grain may be absent, but this is exceptional. There are also intracellular fibrillar differentiations, as well as those which appear to mark out cell boundaries.

A marked difference from the ordinary gland is that the above-described is the only type of nucleus present. In the disintegrating cells the nucleus appears to disintegrate by first becoming clearer, keeping, however, the central chromatic grain, and then breaking up by solution of the nuclear membrane.

Ductules are numerous, and are often seen between the lobules as well as in their centres; the smallest have a diameter of 17 μ, the larger of 34 μ. Here also an intralobular ductule, when followed out to its beginning, seems to lose itself amongst the gland cells in the centre of the lobule. And, as before, it seems certain that here also the majority of the cells cannot be in connection with the ductule.

A smaller (and so perhaps younger) gland from the same worm shows a similar structure, except that there is less disintegration of the cells. The whole is more homogeneous, and there are fewer of the comparatively empty cells.

The interesting feature is that previously mentioned in the Introduction—the entire absence of a duct leading to the exterior. The probability, therefore, is that the glandular mass was developed *in situ*, *i.e.* from mesoblastic tissues, and not from an invagination of the epiblast.

(4) *The Prostate in the Young Pheretima* (fig. 5).

In a small worm, in which the male pores were visible but the clitellum had not formed, the prostate was a small mass without distinct lobulation, staining deeply owing to the crowded nuclei in its substance. The nuclei, or "cells," are arranged so as to form—

(*a*) Aggregates in which a lumen is visible in the middle of a dense crowd of nuclei, between which there are no cell-divisions; the protoplasm is hyaline, tending to granular; the chromatin of the nuclei is granular and scattered. These tubes are evidently in process of differentiation in a common mass of nucleated protoplasm; their size varies—some are relatively large.

(*b*) More or less circular aggregates, without lumen. These resemble the last aggregates, except in the absence of a lumen.

(*c*) Small irregular aggregates with no definite arrangement. The nuclei are disproportionately numerous relatively to the amount of protoplasm.

(*d*) A number of nuclei, some staining evenly and densely, with scarcely any protoplasm. These are found in the interspaces between the aggregates of types (*a*), (*b*), and (*c*).

There are no cell outlines in any part of the developing gland; the whole is a continuous mass, with certain definite arrangements of nuclei in certain parts, and a few cavities, or spaces: (i) of regular form, in the centre of the aggregations of nuclei; (ii) or irregular tracts, where the tissue is looser, foreshadowing apparently a division into lobules.

There is no gland capsule—nothing that goes beyond the flattening of the superficial nuclei of the gland substance itself. Where a strand of connective tissue joins the gland, it fuses with it completely and becomes continuous with the substance of the gland.

The cavities in the hollow aggregates of nuclei become continued into the main prostatic duct. The aggregates described under (*b*) are apparently masses which are not yet cavitated, and those of (*c*) may be a still earlier stage. Each aggregate seems destined to become a lobule of the adult gland.

The main duct appears as a thick prolongation of the glandular mass towards the surface. It consists of a large mass of indifferent cells, pierced throughout by a canal which has its own epithelial lining. Where it is continued outwards from the gland, the duct is nearly as thick as the glandular mass itself, but it becomes thinner as it approaches the surface. In the ental portion the lumen with its lining epithelium is about a quarter of the diameter of the whole, but nearer the surface the lumen narrows considerably—more, relatively, than the duct as a whole.

There is no sharp division between the gland and duct—the protoplasm of the gland is continuous with that of the duct; but the nuclei become less dense in the duct-wall. There is as yet no differentiation of muscular tissue in the wall of the duct; the nuclei of the ental portion are ovoid and without definite arrangement; in the ectal portion, however, they are already elongated, and lie transversely to the axis of the tube. There is no connective tissue capsule on the duct.

(5) *The Earliest Stages in the Development of the Prostate* (fig. 6).

Even in a small worm 1·7 mm. in greatest diameter, long before any outward sign of sexuality appears, the vasa deferentia and prostates are present.

On approaching the site of the prostate in the series of sections, the muscular layer of the body-wall is seen to show an infiltration of connective tissue cells—strands of cells passing through the wall more or less vertically to the surface. These cells are in part almost naked nuclei, homogeneous in texture; elongated, spindle-shaped, or irregular in outline; sometimes clothed or accompanied by amorphous matter representing the cell-body. They do not appear to differ from the connective tissue nuclei of the body-wall, into which they shade off. The peritoneal lining of the body-cavity is thickened in this region, and appears as a well-marked layer of connective tissue; the cellular infiltration in the muscular layer is continuous with this thickened peritoneum, and also, as we shall see, with the duct of the gland as it passes through the body-wall. The two vasa deferentia lie close together on the body-wall.

The gland itself makes its first appearance in the series of sections as a dense mass of nuclei, continuous with the thickened connective tissue representing the peritoneal layer. Some of these nuclei almost immediately begin to group themselves into tubes, but the tubes are evidently constituted of the same elements as the general cell proliferation. There is no sign of a capsule over the extremity of the gland, which thus appears to be the freely proliferating tip of a mass of mesoblastic cells.

On passing back the tubes may become distinct from the general mass of cells, or, on the other hand, they may still appear continuous with the general mass. The nuclei are throughout deeply staining and homogeneous.

A number of cells, or rather nuclei, on the surface of the gland are much flattened, and a transformation of the surface of the gland into connective tissue appears to be taking place in parts, especially on the outer side of the gland. Fine strands, continuous with the glandular mass, connect it with the body-wall.

The lower part of the mass, the future muscular duct, shows no elongation or transverse arrangement of the nuclei; continuous with the future gland above, it is continuous in the body-wall with the infiltration of connective tissue cells around it.

The surface epithelium is already canalised to form the pore; the cells around the pore are considerably higher than those over the general surface of the body; the appearances do not point to any ingrowth or invagination of these cells.

The whole prostatic mass, therefore—glandular epithelium, duct epithelium, muscular wall of duct, connective tissue connections of gland to parietes—appears to arise as a proliferation of indifferent, in origin mesoblastic, cells; and the various parts of the adult gland are produced by differentiation of these. The portion of the duct epithelium which arises by invagination from the surface appears to be negligible.

(6) *Other Stages in the Development.*

A number of young specimens of *Pheretima*, and probably one of *Lampito mauritii*, belonging to an allied genus, were sectioned, and help to fill up the interval between the stages already described. Concerning them the following remarks will be sufficient.

The appearances all indicate that the prostate begins as a proliferation of indifferent or connective tissue cells on and in the muscular layer beneath the peritoneum. There is no indication of the place where the mesodermal portion of the duct meets the invaginated epidermal portion, or even if there is any invaginated epidermal portion.

The infiltration of the muscular layer of the parietes with connective tissue cells is seen; in some cases the nuclei are accompanied by delicate fibrils.

Followed to their commencement, the ducts melt away into the substance of the young gland; but at some distance from their origin they become separate and distinct in the middle of the cells which surround them. The main duct inside the gland, in sections where it is cut along its length, appears as a long straight tube with lateral buds.

The young gland has no proper capsule at any place. It is connected to the body-wall by strands which are continuous with the gland substance; one strand in particular, passing from the dorsal end of the gland, extends upwards and becomes continuous with the lining of the body-cavity; this seems to suspend the gland. Another stout strand passes from the lower end also.

(7) *Conclusions from the Study of the Prostate of Pheretima*

The mass of the prostate gland, with its ductules and main duct, is of mesodermal origin.

(*a*) In the young stages the gland is continuous with the peritoneum, of which it appears to be a proliferation.

(*b*) The intraglandular ducts are similarly continuous with the mass of the gland, and appear to arise as a tubular arrangement of some of the nuclei of the mass.

(*c*) A capsule is not to be made out in many places in the young nor even in the adult gland; where present it is a differentiation of the superficial portion of the gland.

(*d*) There is no evidence of invagination or ingrowth of the surface epithelium.

(*e*) Supernumerary prostates may occur, which consist of gland cells and ductules of normal type, but which have no connection with the surface of the body. If these are to be derived from an epithelial ingrowth, it would be necessary to maintain the unlikely supposition that the main duct had totally disappeared.

(*f*) Attention has been drawn to the similarity of the gland cells to the pharyngeal chromophil cells, which have been shown to be of peritoneal origin.

THE PROSTATE OF EUTYPHŒUS.

(1) *The Adult Gland as seen in Dissection.*

The prostate of *Eutyphœus waltoni* occupies segments xvii–xix, and may cause septum 19/20 to bulge backwards. It presents the form of a complicated coil, which is largely covered over on its inner face by a thin membrane (fig. 7).

The glandular portion of the coil is opaquely white. Its commencement—in the example figured at about the middle of the outer (upper in the natural condition of the parts) border—is somewhat narrower than the main portion of the gland. The tube, winding much, first passes backwards; then, curving round, its coils constitute the mesial portion of the hinder half; then, passing forwards, the tube reaches the front end of the mass, and turns back again. Here it narrows very considerably, and soon losing its opaque character, becomes shiny, an indication of the loss of gland cells and development of the thick coat of circular muscular fibres. The duct winds somewhat, but is comparatively short, and pierces the body-wall in line with the inner or lower edge of the gland, in segment xvii.

The bundle of penial setæ in their sacs, bound together by connective tissue, passes across the inner face of the gland in a transverse direction, and in the dissection is seen to be attached to the body-wall above not far from the mid-dorsal line. The membrane previously noted as covering much of the inner face of the gland is continuous with the connective tissue investment of the setal bundle, and appears as an expansion of it.

Many connective tissue strands unite the outer surface of the gland to the body-wall. The septa 17/18 and 18/19, however, seem not to be intimately, or at any rate not strongly, united to the gland—certainly not on its inner surface, which lies against the intestine.

The vas deferens in its backward course (fig. 7A) passes underneath the last portion of the prostatic duct, and then lies posterior to it and on its outer side; then, curving round and being at last directed obliquely forwards, it pierces the body-wall behind and to the inner side of the termination of the prostatic duct. The bundle of penial setæ enters the body-wall to the inner side of both ducts.

(2) *Microscopical Structure of the Gland* (fig. 8).

A section through the glandular portion of the tube shows a thick wall, ·18 to ·20 mm. in thickness, with a narrow lumen of 45 μ, the whole being thus about ·40 to ·45 mm. in diameter.

The cells of which the glandular mass is composed are largely merely masses of pinkish staining (in hæmatoxylin and eosin preparations) granules; indeed, the appearance might be roughly compared to that of bags or tubes of such granules; in some cases the masses of granules have no definite contour—as if the bags had burst. In shape the granular aggregates have a very marked tendency towards elongation in a direction radial to the lumen, and many debouch into the lumen by a narrow neck; in some cases the cell, or tube of granules, can be seen stretching through the greater part—as much as five-sixths—of the glandular wall. It is not difficult to conceive of them all as being radially elongated in this way, and as discharging into the lumen, other shapes, when found, being due to the way in which particular cells have been cut.

For the most part these cells, if they can still be called such, are fairly distinct from each other, and are often separated from each other by clefts, or even by wider spaces. In cells such as have just been described a nucleus is absent. Some have, with or without the pinkish granules, a quantity of bluish staining matter in their interior; pinkish and bluish matter are, however, not very sharply distinct.

Other cells have a homogeneous or finely granular body, also staining of a pinkish or violet colour; and of these many possess nuclei. These nuclei, which are small—3 to 4 μ in diameter—spherical, and possessing a central chromatic granule, do not stand out very sharply, and are perhaps already beginning to undergo degeneration.

The two kinds of cells described above make up the main bulk of the gland. The layer which surrounds the central lumen consists of—

(*a*) Bottle-shaped cells, fairly short, compared with the elongated cells just described, debouching into the lumen by a neck. These are in length equal to one-third the thickness of the glandular walls or less. They are blue in colour in hæmatoxylin and eosin preparations, the blue colour being due to a mass of deep blue staining granules; indeed, the cells consist of these granules, as those described above consist of pinkish granules. No nucleus is discoverable.

(*b*) The necks of the long pink-staining cells, often appearing merely as streams of light pink granules making their way towards the lumen.

(*c*) Similar long necks or streams of blue granules, belonging apparently to those cells, deep in the gland, the contents of which stain bluish.

There is thus no separate epithelium lining the lumen.

In places there is a layer of muscular fibres within the glandular wall, at about one-third of the thickness from the lumen.

There is a thin connective tissue capsule in many places on the surface of the gland, with occasional flattened nuclei; in this capsule muscle fibres and small blood-vessels may occur. Connective tissue strands may join and become continuous with the glandular mass.

In an apparently more advanced condition there are for the most part no cell boundaries; the general substance of the gland stains partly pinkish and partly bluish, is amorphous, and of varying texture. The most obvious constituent of the glandular mass is the very deeply staining granules, almost black in hæmatoxylin preparations; these are very numerous, spherical, and comparatively large: the largest, which are relatively few, are 4 μ in diameter, the smallest 1 μ; intermediate sizes of 2 to 2·5 μ are commonest—one of 3 μ is a fairly large one. These granules occur throughout the mass, in general irregularly scattered, but near the lumen in bands. The appearance is that of dense streams of granules collecting from all parts of the gland, and discharging into the lumen. After discharge the granules appear rapidly to melt away into a pinkish staining substance (eosin staining), which forms a coagulum in the lumen.

The mass is (in this more advanced condition) extensively vacuolated, but less so in the neighbourhood of the lumen than elsewhere; the vacuoles are sometimes almost empty, and sometimes contain numerous granules. Nuclei are not visible, and cannot be made out with certainty even with the oil immersion lens. Here and there a granule appears to be surrounded at some little distance by a spherical membrane, and so simulates a nucleolus within a spherical nucleus.

(3) *The Ducts* (*Prostatic Ducts and Vasa Deferentia*).

On passing along the glandular tube to the duct, the gland becomes narrower. A few elongated, almost rodlike, nuclei appear in the layer nearest the lumen. Muscular fibres begin to surround the whole.

The nuclei near the lumen become more numerous, and of an ovoid form; strings of granules are seen pushing their way through this layer. The outer investment of muscular fibres penetrates the gland substance. Finally, the gland substance disappears, leaving only an epithelial layer and a muscular coat.

After the disappearance of the glandular substance the lumen of the tube is wide, and the wall thin; the muscular fibres have a circular disposition. The lumen becomes smaller, and the muscular coat thicker, while the epithelial lining is lower than at first. This is the constitution of the main portion of the duct. Ultimately the lumen of the duct becomes minute, and joins the sac of a penial seta.

The terminal portion of the vas deferens has no visible epithelial lining, except just at its end, where it becomes dilated; it has a double muscular coat, the inner layer of longitudinal, the outer of circular, fibres. It opens close to but separately from the prostatic duct, on a papilla which is sunk in a depression of the ventral surface.

(4) *Regeneration of Glandular Tissue, and Summary.*

It would appear, from what has preceded, that in the young and non-functioning gland the glandular tissue consists of separate cells, a number or all of which abut on to the central lumen by narrow necks. Later, the cells largely break up to form the secretion, which, in the form of granules, travels along the narrow necks to reach the lumen. Finally, the cellular structure disappears altogether, the granules finding their way along channels established in the situation of the necks of the former cells.

The gland apparently regenerates from the periphery. In one specimen the peripheral region of the gland was largely made up of distinct cells, of various shapes, separated from each other by clefts and spaces; in many of these cells the formation of discrete spherical granules had not begun. Such showed a homogeneous finely granular cytoplasm which stained deeply; they almost certainly did not send prolongations, as yet, to the lumen of the canal, and all contained a nucleus. The size of the nucleus varied from 2·5 to 5 μ in diameter; the form was sometimes irregular; there was a distinct nuclear membrane, granular contents, and a conspicuous central chromatic body. The more central portion of the gland consisted of the usual masses of spherical granules, as previously described.

The tubular prostate of *Eutyphœus*, therefore, consists essentially of elongated cells of varying height, which probably all debouch into the lumen of the tube. These cells are not arranged in definite layers. The secretion is produced in the form of granules, which are discharged as such. The cells appear to disintegrate during the process, and to be regenerated from the periphery of the gland.

THE PROSTATE OF DICHOGASTER.

We have seen that in *Pheretima* the lobate prostate is mesodermal in origin, and is formed as a proliferation of the connective tissue of the lining of the cœlom and of the body-wall. The tubular form, from which the lobate has been derived, will hardly own a different origin, though we have not been able to establish this by following the development, having had no young specimens of *Eutyphœus* at our disposal.

But the adult form of another genus has, it seems to us, provided us with an unmistakable indication of the mesodermal origin of the tubular prostate.

The tubular prostate occurs throughout the Megascolecid sub-family Trigastrinæ, to which the genus *Dichogaster* belongs. In two small specimens belonging to this genus, sectioned by one of us in the course of systematic work (one belonging to *D. malayana*, from Negyatankaray in Southern India, and one to *D. affinis*, from Ceylon), the prostates appear as small, almost straight, tubular structures, each confined to a single segment, and attached to the posterior septum of the segment in which they occur (xvii and xix). The condition is illustrated in fig. 9. There seems no reason whatever for assuming a secondary attachment of the prostates to the septa, and the appearance constrains us to suppose that the gland was derived by proliferation from the septum—from the peritoneal covering, that is, or from the connective tissue.

The Prostate in the Young Ocnerodrilus.

Though not in *Eutyphœus*, we have been successful in obtaining an early stage in the development of the tubular prostate—from some small non-sexual specimens of *Ocnerodrilus occidentalis*. The tubular prostate is found throughout the Ocnerodriline sub-family of Megascolecidæ, and we sectioned some of the above material in the hope that an early stage in the development might possibly be obtained. We were successful in one case. The first rudiment of the gland was present, in a very early stage; the whole only takes up three to four sections.

The gland (fig. 10) consists of deeply staining nuclei in a small amount of protoplasm, which also stains rather deeply. The mass is already hollow, and around the small central cavity the nuclei are arranged in two series, one bounding the lumen, and the other, less regular, outside these. The layer bounding the lumen is continued outwards to the base of the surface epithelium; the outer cells shade off into a looser aggregate, the elements of which are apparently similar to those of the peritoneum and intramuscular connective tissue. On one side of the specimen the epidermis is already indistinctly canalised; on the other there is only a slight dimpling of the surface.

There is no evidence of proliferation of the surface epithelium. The newly forming duct joins the surface cells, but the two can be distinguished by their nuclei—homogeneous and elliptical in the one case (the embryonic cells of the duct), spherical, almost clear, with central chromatic granule in the other. The height of the surface epithelium is four times the greatest measurement of the prostatic cells.

The condition, therefore, is very similar to that of the young *Pheretima*; and the same conclusion may be drawn from it regarding the origin of the gland.

CONCLUSION.

Typical examples of the lobate and tubular prostates of the Megascolecidæ have been studied in detail.

In both, the cells of the gland disintegrate to form the secretion, which takes the form of granules; in the functioning gland, therefore, cell outlines are largely lost. Regeneration takes place in both by the formation of discrete cells at the periphery of the gland.

In the tubular form all the cells probably reach the lumen of the gland, and discharge directly into it. In the lobate form it appears that a large number of cells never reach the lumen of the intralobular ductule.

The glandular mass is in neither case an invagination from the surface, but is derived from tissues of mesoblastic origin. This is shown, in the adult, by the relations of the glandular cells to the capsule and the connective tissue strands which attach it to the parietes; by the occasional occurrence of supernumerary prostates in *Pheretima*, which are without connection with the exterior; by the similarity of the young and still discrete gland cells at the periphery of the gland to the chromophil cells of the pharyngeal mass, which are of peritoneal origin; and, lastly, by the development.

REFERENCES TO LITERATURE.

(1) BEDDARD, F. E., *A Monograph of the Order of Oligochæta*, Oxford, 1895.

(2) BENHAM, W. B., "On some Edible and other new Species of Earthworms from the North Island of New Zealand," *Proc. Zool. Soc. Lond.*, 1904.

(3) MICHAELSEN, W., "Oligochäten von verschiedenen Gebieten," *Mt. Mus. Hamburg*, vol. xxvii, 1910.

(4) SPENCER, W. B., "The Anatomy of *Megascolides australis*," *Trans. Roy. Soc. Victoria*, vol. i, 1888.

(5) STEPHENSON, J., "On some Indian Oligochæta, mainly from Southern India and Ceylon," *Mem. Ind. Mus.*, vol. vi, 1915.

(6) STEPHENSON, J., "On the so-called Pharyngeal Gland-cells of Earthworms," *Quart. Journ. Micr. Sci.*, n.s., vol. lxii, 1917.

(7) SWEET, G., "On the Structure of the Spermiducal Glands and Associated Parts in Australian Earthworms," *Journ. Linn. Soc. Lond.*, vol. xxviii, 1900.

EXPLANATION OF FIGURES.

Fig. 1. Prostate of *Pheretima hawayana*, right side, as seen in dissection. × 10.

a, *b*, *c*, the three lobes of the gland, in segments xviii, xix, xx, separated by septa 18/19 and 19/20; *c.t.*, band of connective tissue binding down antero-internal corner of gland; *int.*, intestine.

Fig. 1A. Prostatic duct and terminal portion of vas deferens of the same; these are normally covered over by the gland, the outline of which is indicated. × 14.

pr. d., prostatic duct; *v.d.*, vas deferens.

Fig. 2. Portion of a lobule of prostate of *P. hawayana* in section. This part of the section is near the margin of the gland, where it is only one lobule thick. There is no distinct capsule anywhere; where the surface of the lobule is shown as a definite line, as at *x*, it indicates only that the superficial margin of the "cells" is clearly defined, and appears as a definite line. × 400.

d., ductule; *fib.*, fibrillar differentiations in gland substance; *gran.*, aggregates of granules; *vac.*, vacuole-like spaces.

Fig. 3. *P. hawayana*; edge of two adjacent lobules in section, showing separate cells. A transition zone is to be seen at the right-hand side of the figure, where the cells are passing into the ordinary structure of the gland substance. There is a distinct capsule separate from the cells. × 700.

caps., capsule; *gran.*, granules; *x*, cells showing darkly staining masses in their interior; these are very similar to the chromophil cells of the pharyngeal glands.

Fig. 4. Supernumerary prostate of *P. hawayana*; central part of a lobule in section. The uneven character of the constituent portions is obvious. × 370.

b.v., capillaries; *d.*, ductule; *fib.*, fibrillar differentiations, often appearing to mark out cell territories.

Fig. 5. Tip of developing prostate of *P. hawayana* (probably). Two sides of the cell-mass are on the surface of the gland; there is, however, no peritoneal covering. × 730.

a, aggregate of cells arranged round a lumen; *b*, more or less spherical aggregates in which no lumen is present; *c*, irregular aggregates; *d*, nuclei in the spaces between the cell aggregates.

Fig. 6. An early stage in the development of the prostate of *P. hawayana* (probably). × 350.

c.t., connective tissue—the thickened peritoneum; *long.*, longitudinal muscle layer of the body-wall; *m.*, muscular fibres coming into relation with the developing gland; *pr.*, developing prostate.

Fig. 7. Prostate of *Eutyphœus waltoni*, left side, as seen in dissection; successive portions of the coil are numbered consecutively. × 8.

a, beginning of coil; *c.t.*, band of connective tissue, in which are contained penial setæ in their sheaths; *int.*, intestine; *pr. d.*, prostatic duct; *v. def.*, vas deferens.

Fig. 7A. Terminal portions of prostatic duct and vas deferens of the above, with the end of the bundle of penial setæ. × 15.

Fig. 8. Section through portion of wall of prostate gland of *E. waltoni*. The section passes longitudinally along a part of the glandular tube, and one-half of the thickness is shown, *i.e.* the whole depth of the wall on one side of the lumen; the lumen is upwards in the figure. The deeply staining (blue with hæmatoxylin) granules are represented darker than the more lightly staining (with eosin) granules. × 400.

a, deeply staining gland cells of inner layer; *b*, cells of outer layer; *b.v.*, capillaries; *caps.*, delicate capsule on outer surface of gland; *m.*, muscle fibres.

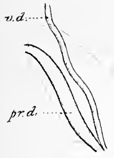
Fig. 9. *Dichogaster malayana*; part of a longitudinal section of the anterior end of the worm, passing through a portion of a prostate gland. There is no hint of a capsule, except at *x*, *y*, and possibly *z*. The attachment of the gland to the septum is such, that, where this occurs, at *a*, the gland cells actually constitute the septum: there are no other constituents. × 160.

d.w., the peritoneum of the dorsal body-wall; *sept.*, the septum, from which the gland has apparently proliferated.

Fig. 10. *Ocnerodrilus occidentalis*; an early stage in the development of the prostate. × 500.

c.m., circular muscular layer of the body-wall; *c.t.*, connective tissue cells; *ep.*, surface epithelium; *l.m.*, longitudinal muscular layer of body-wall; *pr.*, the young prostate.

J. STEPHENSON AND HARU RAM: PROSTATE GLANDS OF EARTHWORMS.



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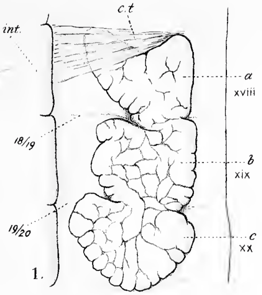

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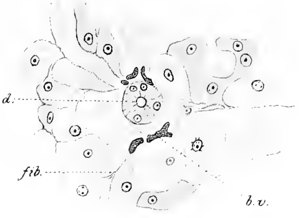

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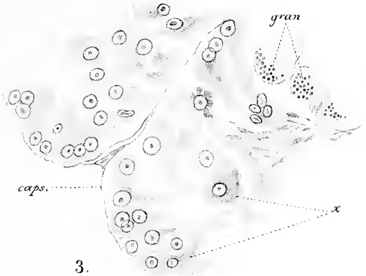

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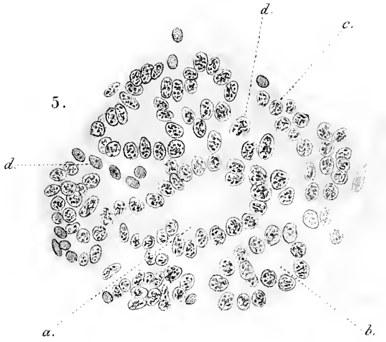

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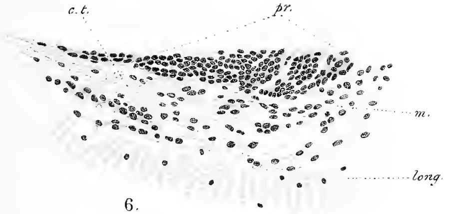

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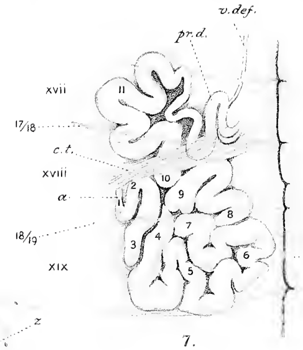

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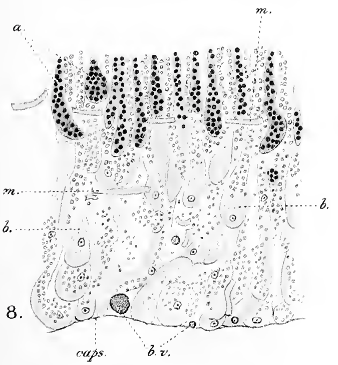

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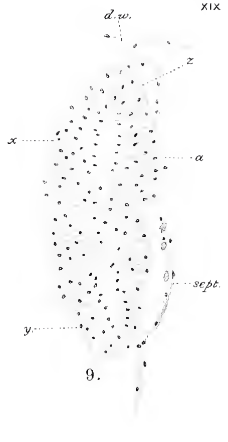

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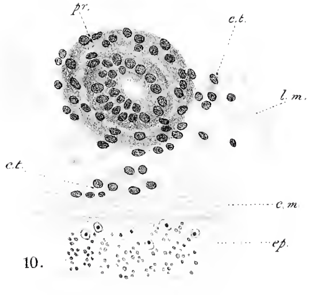

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XVII.—The Calciferous Glands of Earthworms.

By **J. Stephenson**, D.Sc., M.B., Lieutenant-Colonel, Indian Medical Service; Professor of Zoology, Government College, Lahore; and **Baini Prashad**, D.Sc., Assistant Director of Fisheries, Bengal and Bihar and Orissa; late Assistant Professor of Zoology, Government College, Lahore. (With One Plate and One Text-figure.)

(MS. received September 17, 1918. Read December 2, 1918. Issued separately April 15, 1919.)

CONTENTS.

Introduction.

The calciferous glands of earthworms are well-known structures, which occur under a variety of forms, and have been the subject of a considerable amount of research. They are appendages of the œsophagus which occur in different segments in different genera and species; and the usual view of their morphological nature, put forward by Beddard (1) in 1895, and for long generally adopted, is that their epithelium is the œsophageal epithelium thrown into various degrees of folding. Beddard describes these different degrees in a number of different forms.

Since the appearance of Beddard's Monograph, the most noteworthy papers dealing with the morphology of the glands are those of Harrington (12) and Combault (6, 7, 8), to which may be added Ribaucourt (21); all these deal with the Lumbricidæ only. The last-mentioned author considers the glands in the course of a general study of the Lumbricidæ of Northern France; Harrington and Combault are both largely concerned with the physiology of the glands. But it is with the morphological views put forward by these latter authors that we have to do in the present communication.

Briefly, Harrington, to use his own words, holds the secretory epithelium to be a greatly hypertrophied vascular wall, representing both the intima and the endothelium; the glandular cells belong, in other words, to the vascular system. Combault says the same—the histology of the adult and of the embryo seems to show that the tissue of the glands is mesodermal and vascular in its origin; later, he modifies this so far as to say "it is very difficult to state precisely from which embryonic layer the organs are formed."

That the view of the mesodermal origin of the glandular epithelium has gained some adherents is shown by the following quotation from a recent elementary textbook: "These glands are not true glandular diverticula of the œsophagus, but are mesodermal in origin and are merely the walls of the blood-vessels." Since we believe this view to be entirely erroneous, and since one or other species of earthworm is a universally adopted subject of study in all elementary courses of zoology, it seems advisable to combat it, and to advocate a return to the, as we believe, correcter and simpler conception of the older authors.

We imagine that the mistakes of the writers we have mentioned arise in part from their having confined their studies to the Lumbricidæ, in which group the glands reach the highest degree of complexity. What we attempt in the present communication is therefore, firstly, to give an account of the simpler conditions met with in several forms which we have ourselves investigated, with a few notes on forms described by other authors. Secondly, to describe the glands, including their histological structure, in the common Indian genus *Eutyphœus*, in which they have not so far been the subject of investigation; the glands here are of a peculiar type, which is both interesting in itself, and capable of throwing light on the morphology of these organs in general. Thirdly, we deal with the Lumbricidæ; the condition in them is described at some length, because the earlier descriptions are short and, from a modern standpoint, inadequate; while the later, besides being, as we have already said, permeated by false morphological views, are, as regards their purely descriptive part, not at all easy to follow; a lucid account, giving even a moderate amount of detail, of the glands of the common Lumbricidæ does not exist. From these descriptions, and the considerations which attach to them, it will appear, we believe, that the glands are throughout the series what BEDDARD and the earlier authors always supposed them to be—foldings, which attain varying degrees of complexity, of the epithelial lining of the œsophagus.

The literature of the subject is very large, and may be divided under four heads:—

(1) Descriptions of the calciferous glands, from the morphological point of view, in a considerable number of worms.

(2) Descriptions of structures which may be homologous, or of a similar nature, though they differ considerably from the organs generally known as calciferous glands; such are the diverticula from the anterior part of the gut in the genus *Henlea* (Enchytræidæ), certain structures in *Buchholzia* (Enchytræidæ) and in *Limnodriloides winckelmanni* (Tubificidæ; MICHAELSEN, 18), the so-called Chylustaschen in certain genera of Ocnerodrilinæ, and the unpaired diverticula of *Eudriloides* and *Stuhlmannia* (Eudrilinæ).

(3) Descriptions of the form and situation, and sometimes of the disposition of the lamellæ, of the glands in various genera and species, in systematic papers; these occur in abundance, since the organs are of importance from a systematic standpoint, but they do not give any histological detail.

(4) Papers on the physiology of the glands.

Of these, the last three do not concern us, and even of the first group it is scarcely possible to give an adequate account here. All that will be attempted is to give a short *résumé* of the work of previous investigators on forms which are either those or allied to those which we have ourselves examined. This will be most suitably done in the body of the paper, as we take up the various types of structure.

Material and Methods.

We have investigated the following:—(1) *Pheretima hawayana* (Rosa), a widely distributed species of the Megascolecine branch of the Megascolecidæ; it is perhaps the commonest earthworm in Lahore, and the genus is the one which is studied as a type in the colleges of Northern India. (2) *Ocnerodrilus* (*Ocnerodrilus*) *occidentalis* Eisen, found sporadically in India; it belongs to the Ocnerodriline branch of the same family; it was not known to occur in the neighbourhood of Lahore till the course of the present inquiry, when some small worms, supposed to be immature *Helodrilus parvus*, were subjected to examination; these proved to be *O. occidentalis*. (3) *Octochætus barkudensis* Stephenson (Octochætinæ, a sub-family of the Megascolecidæ) has been described by one of us from the Chilka Lake, on the east coast of India. It is a small worm, and had to be investigated by means of sections; these, prepared for the purpose of the systematic description of the worm, have been used for the present paper. (4) *Eutyphœus waltoni* Michaelsen, also belonging to the Octochætinæ; it is common in the United Provinces, and the genus occurs here and there in the Punjab, but it is not known from near Lahore. We owe our specimens to the kindness of Professor Youngman, of the Department of Biology, Canning College, Lucknow. (5) Two species of *Helodrilus* which we have examined, *H.* (*Bimastus*) *parvus* (Eisen) and *H.* (*Allobophora*) *caliginosus* (Savigny), are common in Lahore. (6) *Lumbricus* sp., kindly sent us by Dr J. H. Ashworth, F.R.S., from Edinburgh; the worms were not fully mature, and the species was therefore not determinable.

Previous workers have recommended the avoidance of acid fixatives, as these destroy the calcareous concretions both before and after their discharge from the cells; the precaution as to acid fixatives has most force in work done with a physiological end in view, and it seems rather fanciful to say, as Combault does, that treatment with such an agent causes the epithelium of the glands to take on the appearance of a vascular endothelium. We have, however, used formalin mainly as a fixative for the worms that we have ourselves preserved; but in a few cases where we have used sublimate and acetic acid we cannot point to any marked differences in the gland-cells that could be put down to the difference of treatment. In none of the specimens examined, with the exception of the *Lumbricus*, were there any such accumulations of calcareous particles as to interfere with section-cutting; we have thus been spared a source of trouble which has been felt by some previous workers.

The *Ocnerodrilus* were fixed whole in Zenker's fluid. The *Octochætus*, which came from the collection of the Indian Museum, was not specially fixed for histological work, but we have no reason to complain of the results of fixation as shown in the actual sections; we have, however, been careful not to describe the histological appearances in greater detail than is warranted.

We have to thank Professor Youngman for the careful preparation and fixation of the specimens of *Eutyphœus*. Some worms that he sent us to Lahore alive were unfortunately dead or not in a suitable condition on their arrival, and he kindly then sent us a number of specimens opened under salt solution and fixed in formalin; others were fixed in sublimate-acetic; the alimentary canal had been freed of extraneous matter by feeding for twenty-four hours on damp blotting-paper, or by syringing out at the time of opening of the worm. Our thanks are also due to Dr Ashworth for a similar careful fixation of the specimens of *Lumbricus*.

The two staining methods that we have principally employed have been Delafield's hæmatoxylin followed by eosin as a counter-stain, and Dobell's modification of Heidenhain's iron-hæmatoxylin.

The Alimentary Blood Sinus.

A true conception of the morphology of the calciferous glands depends in the first place on an accurate apprehension of the relations of the vascular channels in the alimentary wall. The subject was exhaustively discussed, on the basis of the results obtained up to that date by the numerous investigators who had, specially or incidentally, worked at the problem, by Lang (14)—it occupies indeed a fundamental place in his *Trophocöltheorie*—and has since that time engaged the attention of a number of his school, as well as of Vejdovsky.

The vascular layer of the alimentary wall in the Annelida, which intervenes between the epithelium and the muscular coats, consists not of definite blood-vessels, but is of the nature of a sinus—rarely continuous all round the gut, mostly divided up into a number of anastomosing channels by adhesions between the epithelial layer on the one side and the muscular coat on the other; the usual condition is that of a copious network. According to Lang and his followers, this network has no proper walls; the blood bathes the epithelial cells on the one hand and the muscular fibres on the other. That flattened nuclei, of unknown origin, are to be seen in many cases on the walls of the sinus is undeniable; but they do not form an endothelial lining, and the peri-intestinal sinus, or network, remains essentially a space between the epithelium and the muscular layer.

This conclusion of LANG's is supported by FREUDWEILER's subsequent work in Enchytræids (10), by SCHILLER's on *Arenicola* (24), and by STERLING's on *Eisenia* and *Pheretima* (28). It is challenged by VEJDOVSKY (30, 31), who goes to the extreme of viewing the sinus as contained within the entoderm. "Choosing the Enchytræidæ as a starting-point, VEJDOVSKY shows that the peri-enteric sinus is crossed by thin protoplasmic strands passing between certain basal replacing cells of the intestinal epithelium, which bounds the sinus on its inner side, and a connective-tissue-like membrane which limits it externally; intimately associated with this membrane are a number of flattened, hemispherical, or sometimes stalked cells, which project into the sinus. External to the membrane are the muscular coats of the intestine and the chloragogen layer. The membrane (vasothel) is interpreted as having been separated from the intestinal epithelium; the cells in connection with the vasothel as having migrated outwards from the layer of replacing cells; and the strands which cross the cavity of the sinus as constituting evidence of the original unity of the outer with the inner wall of the sinus. The sinus is therefore contained within the entoderm." (The quotation is from a former paper by one of us, 26.)

Thus LANG and VEJDOVSKY (to quote again from the same paper) "agree that the origin of the vascular system is to be sought in the accumulation of fluid at the base of the layer of intestinal epithelium, but thereafter they part company. LANG holds that the original position of the fluid is between epithelium and surrounding muscular layer; VEJDOVSKY, that it is within the epithelial layer itself, since it is limited externally by the basement membrane of the epithelial cells and by certain, originally amœboid, replacing entodermal cells which associate themselves closely with the membrane." Whether or not, therefore, we consider the occasional nuclei on the outer side of the sinus as entodermal, and detached from the alimentary epithelium, there can be no doubt that the blood in the sinus directly bathes the base of the lining cell layer of the tube.

The investigations on the alimentary sinus in the Annelida have naturally been carried out mainly or altogether in reference to the intestinal region, and we do not know of any definite statement as to how far forwards the sinus extends with the relations that have been described. According to our preparations, that portion of the alimentary tube with which the calciferous glands are associated possesses in all cases a sinus with the relations described for the more posterior portion of the canal.

ON RODLET EPITHELIUM.

The cells of the calciferous glands and of the neighbouring part of the alimentary tube have often been described as ciliated, and in some cases they undoubtedly are so. In other cases, however, there occurs on their free surface a layer of rodlets, which has apparently hitherto escaped recognition, or has been mistaken for cilia. We place here, therefore, a short general account of rodlet epithelium.

The layer of rodlets (Stäbchen) is well known to occur not uncommonly on columnar epithelium, but its significance is apparently not very clear. SCHAFER (23) says: "Their free surface (the description is of columnar epithelium in general) is covered by a thick striated border, which may sometimes become detached in teased preparations." GURWITSCH (11): "A general occurrence in absorptive cells and excretory cells is the possession of a fringe of bristles,—*e.g.* in the epithelial cells of the gut which take up fat,—but not in secretory cells; it may be inferred that the object is to increase the surface, though this is not at present demonstrated." SCHNEIDER (25) in the section entitled "Nährzelle (Nutrocyte)," which he defines as epithelial cells, mostly pertaining to the enteroderm, always with extracytal differentiations (cilia, flagella, rodlets), seldom with intracytal (muscular fibrillæ), function nutritive: "The rodlets are short stiff structures, held together by a homogeneous substance, in which clear pore-like intervals are often seen"; in the figures they appear as fine lines between rectangular blocks of clear intervening substance; and it would seem that what we have called rodlets in the description of the epithelium of *Eutyphœus* corresponds rather to these blocks—at any rate we have been unable to see the fine bristles between these blocks of lightly-staining substance. He adds: "In many cases it seems as if the cementing mass between the rodlets were itself of importance for absorption."

HEIDENHAIN (13) states that the "brush-border" (Bürstensaum, also called the Stäbchenorgan) is present, as is well known, both in absorptive and secreting cells (thus differing from GURWITSCH); its typical representative being the intestinal epithelium of Vertebrates, the best investigated epithelium of this type; the border of the kidney cells has also been much discussed; numerous other objects possess the border, but have only occasionally been described and figured; it is found, for example, in the polynuclear cells of the decidua epithelium of the rabbit, and in the mantle epithelium of snails beneath the shell. The rodlets possess in general, like the cilia, basal corpuscles, by means of which they are implanted in the surface of the cell; they have been compared by FRENZEL to the basal non-mobile somewhat thicker portions of cilia (Fussstäbe)—which however do not occur in Vertebrates, and are especially seen in the intestinal tract of Worms and Molluscs; JOSEPH is said to have shown that in the intestine of the earthworm the epithelium is ciliated ventrally, while dorsally, on the typhlosole, it has the brush-border; in the transition zone the series of "Fussstäben" pass into the brush-border without break—and one may conclude therefore that in the ciliated part of the tract the immovable basal part of the cilia replaces functionally the rodlets, and has the same relation to absorption as these (what this is is not stated); HEIDENHAIN, however, does not admit a morphological homology. Between the Fussstäben there is sometimes a thin material, stainable and sometimes simulating a pore-cuticle; this may also be the case in the brush-order, in the intestine and kidney.

The figures of the rodlets in HEIDENHAIN show (1) a layer of very numerous lightly-staining threads, not all the same length, resembling cilia, with very marked basal corpuscles; or (2) apparently thicker rods, strictly parallel, and all the same size, with small intervals between them (the condition in *Eutyphœus*, as described below); or (3) relatively shorter rods, very close together. There is no figure like that in GURWITSCH—fine needle-like rods with a relatively large amount of cementing substance staining much more lightly in between them; but the figures of the basal portions or Fussstäben of cilia do show that condition—the spaces being filled up with an almost clear, slightly granular matter.

THE ŒSOPHAGUS IN THE GENUS PHERETIMA (Figs. 1, 2).

In the widely distributed *P. hawayana* the œsophagus is swollen segmentally in segments x–xiii, and constricted intersegmentally. The swellings are approximately globular; in horizontal longitudinal section the anterior may be seen to bulge slightly forwards, and the hindmost slightly backwards.

In these segments the epithelium (fig. 1) is thrown into prominent transverse folds, which may take up almost half the diameter of the tube, leaving only a narrow free channel in the middle; of these folds there may be about a dozen on each side in each segment. Neighbouring folds sometimes join and fuse at or near their free edges, at any rate on the dorsal and ventral regions of the œsophageal wall. Horizontal sections give evidence also of a ventral and of a less marked dorsal fold running longitudinally, the ventral being continuous from segment to segment; but these are not so conspicuous in transverse sections as might have been expected. Alternate transverse folds are sometimes regularly smaller; they might be called ridges, in distinction from the lamellæ, with which they alternate.

In these segments—especially well marked in xii and xiii—is to be seen a very striking system of transverse channels in the œsophageal wall; these vessels are about twelve per segment, are broad—equal in breadth, where they are best seen, to the interval between successive channels—and are not united by longitudinal connections. Above they join the supra-intestinal—a specialisation of the gut plexus (or sinus); below there is no median vessel, and the transverse channels are therefore continuous across the middle line.

The epithelium of this portion of the œsophagus (fig. 2) consists of cells which are shortly to markedly columnar, their average height being about 25 μ, and the extremes about 14 to 35 μ. The protoplasm has a fibrillar structure, the fibrillæ passing in a generally vertical direction (vertical to the surface of the cell); they frequently form a reticulum, especially near the surface, where they are more numerous than in the deeper parts of the cell. There are no rodlets or cilia; the surface of the cell consists of a deeper staining layer, homogeneous and compact, which receives and is continuous with the fibrillæ in the interior of the cell.

Cell partitions are apparently formed by vertical walls of the same nature as the intracellular fibrillæ; where the cells are cut tangentially to the surface of the layer the partitions are seen to constitute a honeycomb-like arrangement. These partitions are also continuous at the surface of the cells with the homogeneous surface layer. The rest of the cell is quite clear—as if it were merely empty spaces. The nucleus, often near the middle of the height of the cell, sometimes nearer the base, is round to roundly ovoid; the chromatin is in the form of scattered grains, with one large particle which is apparently constant.

In the middle of each lamella is an axis, also fibrillar in structure (fig. 2), and continuous with the fibrillæ of the cells and with the partitions between the cells. This axis is mostly, in our preparations, not divided by a blood film in its centre, owing to the fact that this portion of the alimentary canal does not retain its blood supply after fixation; in places, however, a satisfactory demonstration of the basal sinus between the epithelial and muscular coats of the œsophagus and of its extensions into the axis of the lamellæ is obtained. Flattened nuclei may be present in the axis. The circular and longitudinal muscular coats are both well marked.

Owing to the emptying of the blood spaces post-mortem in this portion of the tube our sections do not actually demonstrate the regular series of the transverse channels which are such a prominent feature of this portion of the œsophagus on opening the narcotised or just killed worm. There can be no doubt, however, that the channels are represented by the spaces at the base of the lamellæ, with which they correspond entirely in number and direction.

Other Simple Forms of Glands.

Of the same simple type, or only slightly more complicated, are the œsophageal swellings in a number of other Megascolecinæ. Thus Bourne (4) describes in *Megascolex cæruleus* a series of swellings of the œsophagus occupying segments x–xv; the inner wall is much plicated, raised into ridges and papillæ, and excessively vascular; smaller and larger concretions of calcium carbonate are usually to be found in this portion of the tube.

Miss Raff has studied the alimentary canal in a number of Australian worms (20); she distinguishes simple swellings, sacculated swellings, and diverticula; these portions of the œsophagus have a folded internal lining; the folds are very long and thin, and in the "calcareous glands" they have a very large blood supply. Thus in *Megascolex dorsalis* the swelling is of the simple type; in *Fletcherodrilus* the second stage occurs—there are lateral saccular swellings, but no duct separates them off from the central lumen. In *Cryptodrilus saccarius* (*Notoscolex saccarius*) there are five pairs of glands, separated off from the œsophagus by a distinct duct, each bean-shaped, with a large vessel running along its length on the dorsal side; microscopically, the very long folds of the lining stretch right across the lumen and are richly supplied with blood; the lining cells are ciliated, the cilia being visible with the low power.

A simple form of gland is described by Benham in *Plagiochæta punctata* (3). The folds of the œsophageal lining, present in segments x–xiii, become more marked in segment xiv, where they give rise to calcareous glands. Each gland is a large sac at the side of the alimentary tube, but extending ventrally and dorsally so as almost to surround the tube along with its fellow. The whole region is very vascular.

The Glands in the Genus Ocnerodrilus (Figs. 3, 4).

In the genus *Ocnerodrilus* there are present in segment ix, below and at the sides of the alimentary tube, a pair of ovoid sacs opening ventro-laterally into the œsophagus towards the hinder part of the segment, and lying with their blind ends directed forwards. These have been described by Beddard in *O. eiseni* (2), and by Eisen in *O. beddardi* (9). Beddard found the lumen of the sacs divided up by a network of anastomosing folds of epithelium, the subdivision being more complete towards the blind end of the gland. "The epithelium of the gland appears to be everywhere ciliated, and the alimentary tract from the orifice of the glands becomes ciliated. The structure of the glands is much like that of the calciferous glands of many earthworms, which are in some cases, at any rate, ciliated." **Beddard** here adds a note, "In *Acanthodrilus antarcticus* and in the young of *A. multiporus*. I do not know how far this ciliation is prevalent among earthworms."

Eisen is largely concerned with the vascular supply. The blood-vessel supplying the sac is single at its origin, where the sac originates from the œsophagus; it then breaks up into branches, which are grouped in bunches; the vessels unite again at the distal end of the sac, and in their course are parallel, and do not anastomose. The vessels cause the longitudinal ridges of the inner surface of the sac-wall, which are prominent, and sometimes so large as almost to divide the pouch into several parallel chambers; the inner lining of the pouch is ciliated.

Michaelsen, in the course of systematic studies (16, 17), has examined the glands of *O.* (*Ilyogenia*) *calwoodi* and *O.* (*I.*) *africanus*, which he prefers to call "chylesacs" (Chylustaschen). In the former species the broad lumen is partly narrowed by septa, and contains considerable calcareous masses; the blood-vessels of the sac unite at the free end to form a vessel which then runs freely. In the latter species the lumen is divided by a number of septa, longitudinal in direction, which spring from the wall and meet in the axis of the sac so as to give a wheel-like appearance to a transverse section; the number of radiating septa may be as many as seven; the external wall as well as the septa are rather thick, and are provided with a system of very narrow canals (Chylusgefässe).

Beddard gives no figure, and **Eisen**'s figure of a longitudinal section scarcely affords a good conception of the essential structure. We therefore give a reproduction of a transverse section through the sac of one side of *O.* (*Ocnerodrilus*) *occidentalis* (fig. 3), showing the ridges of the interior, and the relations of the blood sinus—an extension over the sac of the general gut sinus. The muscular layer over the sac is extremely thin, or in places absent; the sinus is then bounded on its outer side by the peritoneal coat, together with a distinct basement membrane.

We cannot discover cilia within the sacs; the cells may be covered by a fluffy secretion, beneath which the surface of the cells is as a rule, though not always, quite sharply defined; or the cells may show on their surface a fine thready raggedness; or the surface of the cells may be quite clear of any appendages or adventitious matter.

The neighbouring portion of the œsophagus shows an interesting condition of the epithelium (fig. 4). In segment ix, in the part adjacent to the opening of the sacs into the œsophageal lumen, and in segments x and xi, the epithelium bears a layer of rodlets, 7 μ in height, with the usual palisade-like arrangement, practically non-staining; the free border of the layer appears crenulated in the sections. The surface of the cells beneath the rodlets stains more deeply than the rest of the cell; in the deeper half of the epithelial layer is a series of oval vacuole-like spaces; the nuclei are round, at the middle of the height of the cells, just superficial to the layer of vacuoles. Cell outlines are not distinguishable; the protoplasm of the superficial half of the layer is close and granular, of the deeper half is rather clearer. Outside the epithelium is an almost continuous blood sinus; the muscular layer is very thin.

In three specimens of this species from the Ross Andamans, sectioned by one of us some time ago in the course of systematic work, the rodlets in segment x appear as if beginning to be transformed into cilia; they slope backwards, and have no longer the regular palisade arrangement. In xi they become typical cilia—thin wavy filaments, 20 μ or perhaps much more in length; they are especially marked at the place where the narrow œsophagus widens to form the intestine, at septum 11/12; here they form a tuft which projects backwards from the narrow neck into the following wider portion. Further back, in the intestine, the epithelium is covered by a thin cuticle-like layer, which, however, is not homogeneous, since it stains in its basal half, though the superficial part is colourless.

The Glands in the Genus Octochætus (Figs. 5, 6).

Beddard in his Monograph (1) gives a short description of the condition in the young *O. multiporus*. The gland is single, and projects forwards in the mid-dorsal line on the œsophagus; where it joins and opens into the œsophagus it begins to extend laterally as well, coming to cover the whole surface of the gut except in the mid-ventral line. The lining epithelium is arranged in numerous folds, some penetrating further towards the lumen than others. The gland epithelium is in general cubical, and therefore lower than the columnar epithelium of the œsophageal tube; but the free edges of the folds are thicker than the rest, since the cells are here more columnar; in the peripheral portions of the gland the cells are ciliated.

We have examined *O. barkudensis* (27) in transverse sections. Here the glands are paired, large, lobed and asymmetrical, occupying segments xv and xvi; but the openings of the two glands are at the same level. The glands are essentially diverticula of the œsophagus, containing a great number of thin lamellæ arising from the wall and projecting into the interior, ending in a free edge near where the lumen of the gland debouches by a narrow duct into the œsophagus (fig. 5).

In the peripheral parts of the glands there are numerous "bridges" between neighbouring lamellæ; and, though the specimen is not injected, and for the most part the enveloping sinus is not marked, some of the lamellæ are distended with blood—a sheet of blood between two layers of epithelium.

The cells of the epithelium of the lamellæ are for the most part much flattened, and the lamellæ extremely thin; in the periphery of the gland the cells are more cubical, transparent, sometimes filling up the peripheral end of the crypt between two adjacent lamellæ. In the crypts are small transparent crystalline-looking particles, probably calcium carbonate, which appear to have been formed within the cells of the peripheral portions of the lamellæ; these cells are often much vacuolated, and sometimes throughout a relatively large region entirely disintegrated. A certain number of the cells are ciliated, especially those towards or at the free edge of the lamellæ (fig. 6).

The duct by which the interior of the gland communicates with the œsophageal lumen is narrow and short, lined with low columnar epithelium which is heavily ciliated. Rodlets, but not distinct cilia, appear as a layer on the lining epithelium of the œsophageal lumen for a short distance on each side of the entry of the ducts.

The Glands in the Genus Eutyphœus (Figs. 7–10).

The Glands as seen in Dissection.

If a large species of *Eutyphœus*, such as *E. gigas*, be taken for dissection, it will be seen that the region of the alimentary canal corresponding to segment xii is slightly swollen, but not sharply delimited from the rest of the tube. On opening this portion by a median longitudinal incision a number of transverse lamellæ will come into view on each side (fig. 7) in such a way as to leave a median vertical channel in the middle; their dorsal edges are not attached to the inner face of the œsophagus, so that a T-shaped lumen is visible in a transverse section of the tube. The lamellæ of either side may be spoken of as constituting a gland; the pair of glands are thus contained within the gut—not appendages which project outwards from the gut.

The individual lamellæ cannot be freely separated from each other, since they are attached to and held together by a vertical wall along their inner borders; this wall partitions off the interlamellar clefts from the central lumen of the œsophagus, which thus forms a median corridor; the interlamellar clefts are, however, open above. In addition, a large blood-vessel may be seen running longitudinally along the upper edge of the vertical wall, or, in other words, along the upper and inner edge of the gland on each side.

Structure of the Glands as studied in Sections.

Sections taken in various directions confirm the above description of the glands as consisting of a large number of vertical transverse lamellæ on each side of a central lumen, a vertical longitudinal wall on each side separating off the lamellæ from the central lumen, and a system of included interlamellar spaces open above (*cf.* fig. 8). In addition, it is seen that a number of the lamellæ are incomplete, attached to the vertical partition and not reaching outwards as far as the lateral wall of the gut; or attached to the lateral wall and not reaching the vertical partition. Neighbouring lamellæ may sometimes be united by synapticula; or a lamella may split into two, the two reuniting at some distance and thus enclosing a long slit-like space. The lamellæ and vertical wall consist of a double layer of epithelium; the muscular coat of the œsophageal wall surrounds the whole, and sends no extensions into the lamellæ or vertical wall.

Vascular Supply of the Glands.

The large vessel in the dorsal edge of the vertical wall (fig. 10) has already been mentioned; it is continued back behind the level of the glands for some distance in the œsophageal wall before it disappears in the general gut sinus.

There is also a sinus in the vertical partition (not visible in fig. 10), which communicates on the one hand with the vessel just mentioned, and on the other is continuous with the sinuses in the lamellæ. These latter are potential or actual, according as the part of the gland is engorged or empty of blood (fig. 9); they separate the two layers of epithelium of which the lamellæ are composed. These lamellar sinuses become, at their peripheral margins, a series of circular sinuses in the œsophageal wall. Leading off from the front end of the glands is a vessel on each side which lies in the lateral wall of the œsophagus. The whole organ is thus permeated throughout with blood.

The Epithelium of the Glands.

(*a*) *On the Lamellæ.*—In the average condition the cells are approximately cubical, about 10 μ in height, and each projects as a low rounded, dome-shaped swelling into the interlamellar space. The nucleus is rather superficial, usually in the dome-shaped swelling; it is roundly ovoid, 5–6 μ in long diameter, with scattered granules of chromatin, and one larger darkly-staining particle.

The surface of the cell is often seen to be disintegrating, and then may best be described as shreddy; here and there long cilia-like threads are given off from the surface; the resemblance to cilia may be very close (some acid-fixed preparations). The epithelium appears for the most part as a single layer; but in places a number of superficial cells are seen, which appear to be disintegrating *in toto*—staining only very lightly, and being thrown off along with their nuclei. In addition, small solid crystal-like particles are being produced and thrown off in certain regions, or in certain preparations (fig. 9).

The epithelium of neighbouring lamellæ is continuous round both the external and internal ends of the interlamellar spaces.

In well-fixed preparations a basement membrane is often not to be made out; it is best seen in badly-fixed specimens (fixed without opening the worm) where acid fixatives have been used (Zenker's fluid). Here the glands are in places skeletonised; the epithelial cells have become detached, and the basement membrane is left to indicate the position of the lamellæ; the membrane may appear as a single or double layer in each lamella—potentially double, no doubt, throughout, and corresponding to the two layers of epithelium which compose the lamella.

Between the two layers of cells there are seen numerous nuclei, much flattened or of an elongated ovoid shape. A number of ovoid or rounded nuclei are also contained in the deeper portions of the epithelial cells themselves.

(*b*) *On the Vertical Partition.*—The vertical partition consists of a double cell layer enclosing a blood sinus (fig. 10); the cells on the lateral face of the partition are continuous with and similar to those of the lamellæ; those on the median face are of the nature of columnar œsophageal epithelium. The basement membrane of the layer on the median face is extremely stout—3 μ in thickness; it forms the median boundary of the partition sinus. The basement membrane of the outwardly facing layer of epithelium is much thinner, and is continuous with that of the lamellæ. The vessel (more correctly sinus) in the upper edge of the partition is covered by columnar cells similar to those on the median face of the partition.

No muscular layer intrudes between the epithelial layers of the vertical partition.

(*c*) *The Occurrence of Rodlets on the Œsophageal Epithelium.*—If a transverse section of any but the most anterior part of the glands be examined the columnar epithelium on the median face of the vertical wall will be seen to bear a layer of short rodlets, perpendicular to the surface of the cells; these are stiff and straight, staining only lightly, of appreciable thickness, and 7·5 μ in height; they are placed close together, and about six placed side by side in one plane take up a space of 10 μ (fig. 10). The remarkable thing in their appearance is that they form a regular palisade, are exactly parallel to each other, and of exactly the same height. The free edge of the cell below the rodlets stains deeply.

It has been said that the rodlets are not present on the vertical partition in the most anterior part of the gland region. They are present on the dorsal wall of the œsophagus, beginning rather behind the level at which they appear on the vertical partition; they disappear towards the dorso-lateral region of the gut wall.

In following a series of transverse sections from the anterior end of the glands backwards there will be seen, in the region in front of the rodlets, a thinner, more homogeneous layer on the columnar cells, in which distinct rodlets are not visible. This may, on the dorsal wall, simulate a cuticle, 2·5 μ thick; and it becomes transformed into the layer of rodlets as we pass backwards in the series. The same passage of a homogeneous cuticle-like layer into rodlets may be seen in the body of the glands, on the free edge of the vertical partition; on following the epithelial layer over this edge the rodlets of the inwardly-looking face of the partition change gradually into such a layer, rather more than 2 μ thick. (Compare also the replacement of the rodlets in *Helodrilus parvus* by a homogeneous cuticle-like layer behind the region of the glands, as described later.)

The rodlets are continued backwards for some segments behind the glands, as a layer 7 μ high on the œsophageal epithelium. The palisade arrangement may be less regular, but the structures are rod-like, not hair-like.

Rodlets are not seen on the cells of the lower portions of the lamellæ of the glands; but they are present on the upper halves, more or less, and on the free upper borders of the lamellæ; here they may have a remarkable resemblance to cilia, and are less regular and appear thinner than the typical rodlets. They are directed obliquely upwards, towards the free upper edge of the lamella, and being more or less separated from each other do not form a regular palisade (fig. 9). They seem to be intermediate between typical rodlets and typical cilia, and again have some resemblance to the ragged hair-like appendages of the cells lower down on the lamellæ.

General Remarks on the foregoing Genera.

So far there can be no doubt that the calciferous glands are to be considered as foldings of the œsophageal wall, and their epithelium as a continuation of the œsophageal epithelium. The condition described in *Eutyphœus* is the most complicated; the genus is to be derived from *Octochætus* (though not directly—the intermediate stages having been lost, or not yet discovered); and the calciferous glands of *Octochætus* have therefore been withdrawn, in *Eutyphœus*, within the œsophagus instead of projecting as considerable diverticula at the sides. Looked at from another point of view, the glands of *Eutyphœus* show us the extreme term attainable by a series of transverse lamellæ; their internal borders have fused together, so forming the vertical partition which separates off the interlamellar spaces from the general cavity of the œsophagus, and the communication of the interlamellar spaces with the œsophagus takes place only by means of their slit-like upper ends.

The Calciferous Glands in the Lumbricidæ (Figs. 11–13).

Historical.

It is in the Lumbricidæ that the glands have been most fully investigated by previous workers. Lankester was the first to examine them in any detail (15), though Morren had given a rough figure without any accurate description. Lankester calls them œsophageal glands, and places them in segments xii and xiii (corresponding to xi and xii in our present nomenclature). The first pair, in the first of the two segments, are round and full, very vascular, and firmly attached to the wall of the œsophagus, but do not appear to have any communication with the interior; their wall is thin, and they contain each a single hard crystalline mass, or numerous smaller bodies; the crystalline substance effervesces on the addition of acid. "I have frequently found the crystalline bodies passed into the œsophagus and lodged in the capacious crop." The second and third pairs of glands are both placed in the next segment, and are a little smaller than the first pair; their walls are much thicker, but no less vascular; they contain a milky secretion. In section, there are seen an inner epithelial coat, a vascular region, and an outer more delicate membrane forming the sheath of the organ, on which the externally visible vessels extend; these vessels are shown in the figure as running longitudinally, parallel and numerous on all three pairs of glands.

Claparède (5) identified three pairs of lateral pouches, the first two pairs in segment xi, the third in segment xii. He describes the glands as consisting of many gland follicles, the follicular cavities being the spaces between a number of lamellæ which are placed perpendicular to the axis of the œsophagus; each follicle occupies the interval between the epithelial layer and the muscular coat. The lamellæ consist of a double layer of cells, with vessels and connective tissue in their centre. These vessels are radially-directed branches of a series of longitudinal vessels in the thickness of the wall, and empty themselves peripherally into the vessels of the outer layer of the œsophagus. At first it was thought that the follicle could discharge the secretion into the œsophageal lumen by the separation of the epithelial cells of the œsophageal lining, but this appears not to be the case; "an gelungenen Durchschnitten finde ich einzelne Spalten des Epithels, welche die Mündungen der Follikel offenbar darstellen. Ob aber jeder Plattenfollikel eine einzige solche Mündung oder deren mehrere besitzt, ist nicht ausgemacht."

Perrier (19) gives an abstract of Claparède's account, but in saying "ces feuillets sont placés entre la couche vasculaire et les couches musculeuses de la paroi œsophagienne," he gets further from the mark than his original.

Beddard, in his Monograph (1), does not give a separate description, but after giving a general account of the glands in their other and less complicated forms, adds that in *Lumbricus* only the most anterior gland on each side opens into the œsophagus, the hinder glands opening into each other and into the first pair.

The textbooks, even when treating *Lumbricus* in detail as a type for study, are scanty or sometimes misleading. Vogt and Yung mention three pairs of thickenings, symmetrically situated in segments xi and xii—follicular glands intercalated between the vascular and muscular layers of the œsophageal wall, supplied with numerous blood-vessels. Marshall and Hurst were apparently the first to give the situation of the glands correctly; the œsophageal pouches are a pair of short lateral diverticula of the œsophagus in segment x; the œsophageal glands are two pairs of lateral protuberances on the sides of the œsophagus in segments xi and xii; they are hollow, and their cavities, which are subdivided by a large number of horizontal lamellæ, contain a milky calcareous fluid; they are local thickenings of the glandular walls of the œsophagus, and their numerous cavities open into the œsophageal pouches. Sedgwick mentions the name, but nothing more. Parker and Haswell present a paraphrase of Marshall and Hurst, adding that the milky appearance of the fluid is due to its containing numerous particles of carbonate of lime. Shipley and MacBride are short, and not quite accurate; the œsophagus "has three pairs of lateral pouches developed on its walls. These pouches secrete calcareous particles, and hence are termed calciferous glands." We do not think that a student would arrive at an adequate conception of the glands from any of these descriptions.

We have previously given the outstanding points in the conceptions of the more recent writers, and shall criticise these more in detail after describing the glands themselves.

General Outline of the Structure of the Glands in Helodrilus.

In segment x the œsophagus suddenly widens to form a pair of pouches (œsophageal pouches); the tube also dilates, though less and less in successive segments, for a short distance behind this, and is constricted at the situation of the insertion of the septa into its walls.

The following measurements will give an indication of the outline of the tube in this region; they are taken from a young specimen of *H. caliginosus*:—

In segment ix, diameter of œsophagus ·22–·24 mm.

In segment x, transverse diameter of whole, including the pouches, ·61 mm. Vertical height of central part of œsophagus ·24 mm., of pouches ·37 mm.

At septum 10/11 the tube is ·35 mm. high, ·28 mm. broad.

In segment xi, ·37 mm. high, ·4 mm. broad.

In segment xii, ·37 mm. high, ·33 mm. broad.

At septum 12/13, ·37 mm. high, ·28 mm. broad.

In segment xiii, ·37 mm. high, ·35 mm. broad.

At septum 13/14, ·37 mm. high, ·28 mm. broad.

In segment xiv, ·35 mm. high, ·28 mm. broad.

A series of transverse sections shows that the pouches in segment x are lateral diverticula of the gut, with widely-open mouths, and longitudinally-ridged internal lining (fig. 11). On following the series of sections backwards the distal portions (the centrally directed ends) of the ridges are seen to fuse with those of their neighbours, and in this way, when the fusion of all is complete, a series of longitudinal tunnels is formed. These extend backwards through segments xi–xiv; the lumina of the tunnels are lined by an epithelium which is continuous at their anterior ends with that of the œsophageal pouches, and so with that of the œsophagus. As in *Eutyphœus*, the muscular coat is entirely outside the glands, which are differentiations of, and included entirely within, the epithelial layer.

The more detailed description will be most conveniently made by following out a series of sections through the successive segments; for this purpose we select a young specimen of *Helodrilus caliginosus* fixed in formalin. The slight differences observed in an adult of the same species, and in *H. parvus*, will be briefly described afterwards.

The Young Helodrilus caliginosus.

The Alimentary Canal in segment x.—In the region immediately in front of the calciferous glands the epithelium of the œsophagus is thrown into about a dozen longitudinal ridges; there is no layer of rodlets, and no cilia; the muscular coat is thin, 4·5 μ in thickness.

At the level of the anterior part of the œsophageal pouches the epithelium of the œsophagus proper (the dorsal and ventral walls) is columnar—the cells extremely elongated, with almost rod-like nuclei. The wall of the anterior part of the pouches is but little ridged, and the lumen of the pouch is a large open cavity; the epithelium of the proximal part of the pouch, near its opening into the œsophagus, consists of cells which are relatively broader than those of the neighbouring part of the œsophagus proper, with more oval nuclei; the height of the cells diminishes further towards the lateral wall of the pouch, where they are shortly columnar or even cubical, and the nuclei may be spherical; there are no rodlets or cilia. The free margin of the cells of the pouches is very definite, as if each cell were bounded at its surface by a membrane. The blood sinus lies outside the epithelial layer of the pouch, and the muscular coat is very thin, hardly definitely measurable.

In the posterior half of the pouch prominent ridges begin—better perhaps called lamellæ. Each lamella consists of a double layer of cells, approximately cubical in shape; the texture of the cells of the central portions of the lamellæ appears loose (in the particular specimens described; but not in the *H. parvus* of fig. 11), as if the cells were disintegrating, and the cells enclose empty spaces of ragged outline. The cells have no rodlets or cilia; nor have they at any place in the tunnels to be described.

Some of these lamellæ immediately unite at their free ends with their neighbours to form tunnels (fig. 11); these are at first irregular in form, but elongated in a direction radial to the centre of the pouch. In a short time the lamellæ have all fused at their margins, and the series of tunnels is complete. From the first appearance of prominent lamellæ to their complete fusion to form tunnels there is a distance represented by only ten sections (·08 mm.).

When the tunnels are well established, the central lumen of the pouch is much diminished. Each layer of a lamella has a basement membrane, and sometimes the blood sinus can be seen extending up between the two layers of a lamella from where it lies, contained externally by the muscular coat. Occasionally, flattened nuclei may be seen in the sinus in the lamella, lying on the basement membrane bounding the sinus on one or other side, or between the two cell layers of a lamella if the sinus does not exist or is only potential there. When first established there are about 14 tunnels on each side, 28 in all.

Each lamella is now the partition between neighbouring tunnels; it contains in its axis, potentially at any rate, an extension of the gut sinus, which lies primarily internal to the muscular layer of the alimentary tube; and by the fusion of the central ends of the lamellæ a layer of epithelium lining the lumen of the œsophagus has been established, which is no longer directly continuous with the epithelium of the lamellæ.

Meanwhile the tunnels have been encroaching on the dorsal and ventral portions of the œsophageal wall, more rapidly on the dorsal than on the ventral wall; or, in other words, what was called above the œsophagus proper—the portion of the alimentary tube between the lateral pouches—has almost disappeared. Where the œsophagus passes through septum 10/11 tunnels surround the whole except in the mid-ventral line; they are now restricted in height, their section being shortly oval.

The Alimentary Canal in segment xi.—In the next segment after the œsophageal pouches (fig. 12) the œsophageal epithelium has been reconstituted as a definite layer, independent of the tunnels which have been separated off below it. It shows only a slight degree of ridging, and consists of elongated cells, broader at their free surface; their narrower, deeper ends are consequently separated (fig. 13). These deeper ends become divided up, and form, or become part of, a spongy reticulum, with large free spaces, which intervenes between the regular œsophageal cell-layer and the tunnels below. On this œsophageal epithelium rodlets now make their appearance; these constitute a layer of equable thickness, staining only very slightly, and are similar to those described in *Eutyphœus*; they become more distinct in subsequent segments; they never show any transition to cilia, as far as we have observed. The cells have a more deeply staining free border beneath the rodlets; the nucleus appears homogeneous, and not very sharply distinct from the cell-body.

The tunnels have a beautifully regular arrangement (fig. 12), and are in general much elongated—four to five times as high as broad—but shorter in the mid-dorsal and mid-ventral lines, especially the latter. Occasionally small lamellæ arise within the tunnels, and these, on being followed back, are seen to unite with one of their neighbours, thus splitting into two a previously existing tunnel, and increasing the number of tunnels. In this way a considerable increase in the number is to be accounted for; when first established, in segment x, the number was seen to be about 28, while in front of septum 11/12 it has risen to between 60 and 70 (69 lamellæ, including one or two incomplete ones); this number is maintained approximately (64 lamellæ in segments xii and xiii) throughout the rest of the gland.

The cells of the tunnels are more or less cubical; the protoplasm is homogeneous, and stains more lightly than that of the cells lining the œsophageal lumen; the nuclei are ovoid; and there is a very evident basement membrane to the layer. The end of the tunnel, which is towards the œsophageal lumen—which may be called its roof—is sometimes closed by a flattish cell (fig. 13, *y*); but often the roof is indefinite, and the cavity of the tunnel appears to be in communication with the loose spongy space which intervenes between the layer of tunnels and the layer of œsophageal epithelial cells (as at *x*). This space is merely crossed by fine trabeculæ with occasional nuclei.

In each lamella is a blood sinus—an extension from the general gut sinus which lies within the muscular coat external to the tunnels; the lamellar sinuses, which may be potential only, are bounded by the basement membrane of the cell-layers, and are dilated at the central ends (towards the œsophageal lumen) (*int.*, fig. 13). The basement membrane is always complete round the inner ends of the sinuses, though the protoplasmic layer may be thin—merely an extension from the central ends of the cell-layers of the lamellæ, or even only a portion of the spongy reticulum beneath the epithelial layer of the œsophagus. These internal dilatations are oval in section; the junctions of the sinuses in the lamellæ with the outer, or general gut sinus, are triangular (*per. sin.*, fig. 13).

Nuclei are occasionally seen in the sinuses of the lamellæ—flattened against the basement membrane of the epithelial layers, and almost unaccompanied by protoplasm (*n.*, fig. 13); or, it may be, more ovoid in shape and accompanied by a certain amount of protoplasm. Much flattened nuclei may be seen, without any protoplasm, between the two layers of basement membrane in the axis of a lamella, where the sinus is only potential. Nuclei, flattened or rounded, and without or with accompanying protoplasm, are to be seen in numerous places on the wall of the general gut sinus between the layer of tunnels and the muscular coat of the œsophagus; but these are very far from forming a continuous investment.

The Posterior Portion of the Gland.—The tunnels become lower in the next segments (xii and xiii), and lower still in xiv; they disappear altogether in front of septum 14/15. In the hinder part of the gland the epithelial lining of the œsophagus becomes regularly ridged longitudinally once again.

The lumina of the tunnels are small, and their roofs (toward the œsophageal cavity) are more often definitely closed by the opposition of the cells constituting their sides. The nuclei between the two layers of a lamella are few.

There is no evident communication between the cavities of the tunnels and that of the œsophagus in the posterior part of the gland; we cannot definitely state that there is no possible passage from the one to the other, as a few sections are damaged. The point is again referred to further on.

The Adult Helodrilus caliginosus.

A series of transverse sections of a specimen fixed in sublimate and acetic acid, and stained in Delafield's hæmatoxylin and eosin, was compared with the above. The structure is identical with what has been described already, except in a few details.

The epithelium in the anterior half of the œsophageal pouches is more ridged than in the young example; and the cells here are more markedly columnar—more like those of the œsophagus proper, the nuclei being oval to rod-like. The nuclei of the cells, however, stain less deeply, and so are not so sharply differentiated from the cell-body, compared with those of the proper œsophagus.

The roofs of the tunnels are closed by a cell; or by extensions of the cells at the sides of the tunnels which fuse together over the roof; or by an indefinite fibrous or granular extension of the sponge-work of the deeper layers of the œsophageal lining; or, finally, the roof may not be completely closed, and the cavity of the tunnel may apparently communicate with the spaces of the loose sponge-work just mentioned.

The central ends of the sinuses in the lamellæ are dilated, as in the young example; but here the dilatation is triangular in shape, not oval; the base of the triangle, which is towards the œsophageal lumen, is broad, and the angles of neighbouring triangles may almost meet; so that, under the low power, the straight and almost continuous bases of the triangles simulate, all taken together, a continuous basement membrane of the œsophageal epithelium.

Towards the hinder end of the gland, where the œsophageal epithelium has again become regularly ridged, the loose reticulum beneath it disappears, so that the whole epithelial layer becomes denser in its texture; the intervals between the neighbouring angles of the triangular dilatations of successive sinuses are necks through which the epithelium of the œsophageal lumen is continuous with the epithelium of the tunnels. The whole extends to the hinder end of segment xiv.

There are no definite openings of the tunnels into the œsophageal lumen; there are, perhaps, very occasionally in segments xi and xii indications of the possibility of a communication; but these passages resemble, and may actually be, accidental breaks in the continuity of the œsophageal epithelium, and appear to us to be of no morphological importance whatever. They quite obviously do not occur in connection with all or the majority of the tunnels, and the tunnels are continued back beyond these breaks.

The number of lamellæ, at one place 62 or 63, become further back 68–72.

Helodrilus parvus.

The anterior part of the œsophageal pouches, in segment x, is almost smooth. Further back, the epithelium of the œsophageal lumen bears very marked rodlets, which come out with extreme distinctness in a chrome-hæmatoxylin stained preparation. These persist to the end of segment xiv; here the canal widens, and the layer of rodlets is replaced by a homogeneous, lightly staining, cuticle-like layer.

The texture of the deeper portion of the œsophageal epithelium is even looser than in the foregoing species; there are large clear spaces, unoccupied even by trabeculæ or strands.

In segment xi there are 27 tunnels, and 30–32 further back; in another specimen 38–44 were counted. The tunnels were not, in any of our specimens, much elongated in a direction radial to the axis of the œsophagus—they were never more than twice as long as broad. The nuclei of the cells of the lamellæ may often be on the free edge of the cell, even forming projections on the surface; a few nuclei are placed deeply in the cell. The roofs of the tunnels are often open, the cavity of the tunnel being thus in communication with the loose space beneath the epithelial lining of the œsophagus; or a wide opening at the top of a tunnel may be spanned by a delicate fluff with nuclei in it. The tunnels are very low in segment xiv, and disappear before the end of the segment; they die away by merging into the loose cells below the layer of œsophageal epithelium.

The inner ends of the sinuses in the lamellæ are always oval in section, not triangular as in the adult *H. caliginosus*, and are always sharply bounded by a basement membrane.

Towards the end of segment xiii there are appearances suggesting the opening of one or a few tunnels into the crypts between the folds of the œsophageal epithelium; but no actual opening could be demonstrated satisfactorily.

The Glands in the Genus Lumbricus.

It has happened that the structure of the glands was by no means so easy to make out in the specimens of *Lumbricus* at our disposal as in those of *Helodrilus caliginosus* and *H. parvus*. This is partly due to the damage caused by calcareous concretions in the case of *Lumbricus*; the glands seem to have been functioning actively, and the œsophageal pouches in particular were much torn in the sections of *Lumbricus* when they came to be examined. The swellings of the œsophagus were more marked in *Lumbricus*, and consequently overlapped from segment to segment, rendering the appearances at first sight rather confusing. The diagrammatic clearness with which the structures were displayed in the case of many or most of our specimens of *Helodrilus*, and the freedom from damage by calcareous particles, has rendered our description of them easy, and it is hoped satisfactory.

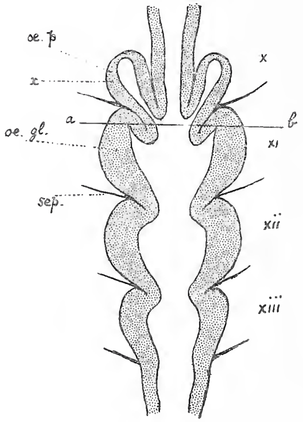
In *Lumbricus* the condition is essentially the same as in *Helodrilus*. In segment x are a pair of subspherical sacs, the œsophageal pouches; in xi are seen a pair of lateral swellings, with somewhat the appearance of stout sausages, applied by their inner curved surfaces to the sides of the alimentary tube; in xii are a similar pair of swellings, of equal size with those in xi; the section of the tube in xiii is somewhat dilated, and subspherical in form, the swelling being general; in xiv the œsophagus is narrower, but at the hinder end of the segment it may widen to form the beginning of the crop. The wall of the œsophagus is longitudinally striated by blood channels in segments xi–xiii.

Microscopically, the epithelial lining of the œsophagus is irregularly ridged and folded in segment ix, in front of the pouches; the ridges become regular and longitudinal in direction as the tube passes through septum 9/10. There is one considerable difference between the pouches of segment x in *Helodrilus* and *Lumbricus*;—the openings of the pouches into the œsophageal tube are at a much more posterior level in *Lumbricus*; instead of opening into the œsophagus by a wide mouth in segment x, the pouches communicate with the œsophageal lumen in the anterior part of segment xi (text-fig. 1), and hence throughout segment x they appear in sections on each side as separate sacs.

Longitudinal lamellæ are present within the pouches over their whole circumference; they are larger on the mesial wall of the pouch, where they extend into its interior so as to take up more than half the transverse diameter of the pouch. The union of the lamellæ to form tunnels takes place, however, only on the outer wall. When this happens, the lamellæ unite, each with its neighbours, at about half their height; and there thus extends for some distance a series of ridges, coexistent with and internal to the series of tunnels, the ridges representing the central halves of the lamellæ and the tunnels being situated between their peripheral portions.

The epithelium of the pouches resembles that of the œsophageal tube; on the surface of the cells in both situations is a fine, completely colourless and non-staining border.

Towards the hinder end of segment x the epithelium of the tunnels changes its character; it becomes cubical, and shows a number of hair-like tags, which soon appear as definite long cilia. In some places the surface of the epithelium is merely shreddy. The tunnels begin to elongate; they may now be 18 in number in each pouch.



Text-fig. 1.

The anterior part of the dilatation in segment xi bulges forwards so as to overlap the hinder part of the sac in x, and therefore both are cut in a number of sections (text-fig. 1).

The lateral dilatations in segment xi show about 35 tunnels on each side, including those which are incompletely divided by lamellæ which, springing from the periphery, do not reach the œsophageal lining. The mid-ventral lining is free from tunnels. The tunnels are in general much elongated in a radial direction. The cells clothing the lamellæ are in these specimens entirely disintegrated, and have thrown off very numerous globular granules which stain deeply with hæmatoxylin. The fine structureless border of the œsophageal epithelium changes into an irregular layer of rodlets in the hinder part of segment xi.

In segment xii the whole circumference of the œsophagus becomes surrounded by tunnels, which are, however, lower in the dorsal and ventral regions than elsewhere; there are about 50 in the half circumference. The disintegration of the epithelium is, in one of the specimens here described, though not in another, much less than in the preceding segment; the epithelium is approximately cubical, and there are no cilia, and no granules are being discharged.

The tunnels continue through segment xiii, where they are lower. Their epithelium is low, and not disintegrating. The œsophageal epithelium is now longitudinally folded again in a regular manner. Rodlets are present as far as xiii, but are absent in xiv. The tunnels die away in xiv.

The vascular relations of the gland are similar to those in *Helodrilus*.

A notable feature was the occurrence of numerous groups of "chromophil cells," of the same kind as those of the pharyngeal glands, on the œsophagus throughout segments ix and x.

Criticisms of Previous Work.

The papers which will be referred to in what follows are those by Harrington (12), Ribaucourt (21), and Combault (6, 7, 8). The latter author has a number of other papers, which, however, are largely physiological, and in part concerned with the circulation through the glands; his paper of 1909 (8) is to some extent a summing up of his results, and repeats much of his earlier communications.

A word on the position of the glands to begin with: Ribaucourt nowhere mentions their situation; Combault invariably places them one segment behind their proper position—the first pair of swellings, the œsophageal pouches, in xi, whereas they are in x.

It has been shown above that the glands (*i.e.* the tunnels) and the œsophageal lining membrane together constitute the epithelial layer, and (except the blood, which bathes the bases of the cells) no other constituent of the wall is present from the lumen of the gut outwards as far as the so-called external sinus. Combault therefore mistakes the constitution of this part of the tube when he writes of the glands as "un véritable manchon œsophagien . . . creusé dans le tissu conjonctif qui sépare l'épithélium œsophagien de la couche musculaire," or of "une couche de tissu conjonctif fasciculé où sont logés les sinus internes" (*i.e.* the dilated inner ends of the sinuses in the lamellæ); in this tissue one is supposed frequently to meet with muscular fibres. On what we believe to be the true view of the morphology of the glands there is no place for either muscular or fibrous tissue in this situation.

Before mentioning Harrington's view of the origin of the glandular epithelium, it is necessary to allude to the process of secretion as described by him. The cells of the glandular layer are irregular, and give an irregular appearance to the layer. After an active wave of secretion the cell projections may almost entirely disappear, being levelled by disintegration to the general surface. The cells form a syncytium, being fused at their bases; in a secretory cycle the protoplasm at first increases, so that the cells project as club-like processes; lime granules appear in the interior, the cytoplasm degenerates and the granules are thrown out; the cytoplasm in the cell projections is nearly all used up, and if there has been over-secretion the cytoplasm disappears almost down to the blood sinus;—"in its lowest terms . . . the secreting layer is very thin, and may be reduced . . . to the thickness of an ordinary blood-vessel scarcely the width of the nuclei which are embedded in it" (the meaning is not very clear). The nuclei also collapse or become cast out into the gland cavity during active secretion, exhaustion of the nucleus running parallel to exhaustion of the cytoplasm; indeed nuclei may be scarcely visible through loss of staining power, and may be distinguishable only by the inconspicuous nuclear membrane.

Now comes the peculiarity of HARRINGTON'S position. The nuclei are replaced by others which migrate from the blood sinus into the glandular layer; nuclei are seen in every possible position between partial and complete embedding in the glandular syncytium; "repeated observations have demonstrated beyond a doubt that these wandering cells or migratory nuclei are constantly and normally making their entrance into the gland cells at certain periods of the gland's activity." These migratory nuclei are attended by a thin protoplasmic film; they may be of the most extraordinarily elongated forms; the cytoplasm which is brought in fuses with the general syncytium, and the nuclei then become the typical nuclei of the glandular layer. Thus what happens is that "wandering cells migrate into an enlarged blood-vessel wall and undergo degeneration, during which the accompanying cytoplasm expands and is finally transformed into lime crystals."

And again: "The cells, which here replace the waste caused by secretion, are derived from the walls of the blood-vascular system. The unusual relations between the glandular and circulatory systems can be interpreted only by regarding the one-layered secretory lamellæ bounding the blood spaces as greatly hypertrophied vascular walls representing both the intima and endothelium."

The follicles are therefore an enlarged blood-vessel wall. It is true that the germ-layer theory seems to stand in the way; but according to HARRINGTON'S observations, the earliest blood corpuscles in the embryo, as well as the follicles themselves, are derived from the mass of yolk cells surrounding the cavity of the gut, and hence corpuscles and follicle cells have the same ultimate origin.

Such is HARRINGTON'S conception of the glands. In criticism it must be remarked that unless "an enlarged blood-vessel wall" is used in a sense very different from the usual one, the expression is wrongly applied to the follicular epithelium. In cases where a vascular endothelium has been described, it is a layer of naked cells lying on a basement membrane, outside which again is the muscular (or muscular and connective) coat of the vessel; here the basement membrane would be the innermost layer, and the endothelium would be outside this. But that the follicular epithelium cannot be anything to which the term blood-vessel can properly be applied is evident from the fact that it is absolutely continuous with the epithelium of the œsophageal pouches, and so with the œsophageal epithelium itself. If it were necessary to go further, the constitution of the glands in other families would be sufficient as proof of the identity of the epithelium of the follicles and of the œsophageal lining.

We entirely disagree, therefore, with Harrington when he says: "It must be repeated that the first pair of glands are entirely different morphologically from the two posterior pairs, and are the only portions of the glandular œsophagus which are true epithelial diverticula." The difference is one of detail only; the ridges of the œsophageal pouches are, in the anterior part of their extent at least, parallel to and independent of each other; further back they fuse at their free edges and so form a series of tunnels, the so-called follicles of the œsophageal glands of segments xi–xiv;—that is all.

The same idea runs through the work of Combault: "L'histologie de l'adulte et de l'embryon me semble montrer que le tissu des glandes de Morren est d'origine mésodermique vasculaire." The difference between the glandular cells and a vascular endothelium is due "avant tout" to a difference of technique; if one fixes by acid reagents (Bouin's solution) the cells, where not destroyed, "presentent assez bien l'aspect de l'endothélium vasculaire avec lequel elles semblent se continuer"; and in *Phœnicodrilus taste*, as described by Eisen, we actually do find the glandular cells represented by "un endothélium aplati très mince rapellant bien l'endothélium vasculaire." There is nothing here that requires further comment however.

Combault's views appear to have undergone some change during the progress of his series of papers; thus in a later paper he says that "chaque feuillet est lui-même constitué de deux assises—l'endothélium vasculaire et l'épithélium branchial." He is speaking of the lamellæ of the gland, which he looks on as a respiratory organ, and here states that in addition to the respiratory (*i.e.* glandular) epithelium there is beneath it a vascular endothelium; the glandular epithelium is not therefore a vascular endothelium. This view is, however, no more admissible than the first; it predicates two cellular layers on each side of the blood film in the lamellæ, whereas, as we have seen, there is universally only a single layer bounding the gut sinus on its inner side—the layer of the alimentary epithelium. That there are nuclei on the basement membrane, bathed by the blood stream, is undeniable, but they do not form an endothelial layer, and are in no sense a vascular endothelium. Combault also begins to have doubts as to the mesodermic origin of the glandular epithelium: "Il est d'ailleurs très difficile d'affirmer d'une façon précise de quel feuillet embryonnaire dérive l'organe de Morren." It is, however, his first view—that the glands are mesodermic—that has been laid hold of by the author of the elementary textbook quoted in the Introduction, and that, more than anything else, we wish to oppose.

One of Combault's statements deserves a word of notice; he says: "Déjà

Beddard, au cours d'une étude sur les Eudrilides, s'etait refusé d'admettre la nature épithéliale des glandes de Morren, et voulait y voir des 'glandes vasculaires sanguines.' . . ." This is misleading. BEDDARD (1) speaks of the glands of the Eudrilidæ as being homologous with the ordinary calciferous glands, and as consisting of a mass of cells in which is a small lumen communicating with the œsophagus; the mass of cells is probably peritoneal in origin, and has increased in amount *pari passu* with the reduction of the glandular secreting surface. These glands must "be referred to the same category as the calciferous glands of other Oligochæta"; though their structure "seems to be irreconcilable with any other theory than that the glands in question have some secreting function in relation to the blood or eliminate effete matters from the blood; we have in fact a gland originally performing a function connected with alimentation converted into a quite different physiological path, and one which must bear some relation to the vascular system." BEDDARD had no doubt whatever of the origin of Morren's glands (the calciferous glands of the Lumbricidæ) or of any other calciferous glands from the œsophageal epithelium; though with overgrowth of the peritoneal covering the glands of the Eudrilidæ have now, apparently, taken on a different function from the original one.

HARRINGTON's statement that the disintegrated cells are replaced by nuclei with a thin protoplasmic film, which make their way into the epithelial layer from the blood sinus, is rejected by COMBAULT. The latter author never found, in "quelques milliers de préparations," appearances recalling those figured by HARRINGTON, though he did observe diapedesis, due to irritation resulting from a too acid diet. (HARRINGTON had fed some of his worms on acid starch, or had kept them in water acidulated with lemon juice.) The definiteness of HARRINGTON's statements, the number of his figures, and the evident care with which they have been drawn, are such that we do not think we are entitled to reject his account of the replacement of the cells forthwith. Somewhat similar cases of wandering nuclei are not unknown. ROHDE (22) finds nuclei of neuroglial origin within the ganglion cells of a number of Invertebrates, and refers to their having been recognised also in Vertebrates (*Delphinus delphis*); many cases of the fusion of follicle cells with growing ova are known—though here it is whole cells rather than nuclei that enter and fuse; the entry of supernumerary spermatozoa with, in many cases, the persistence of the additional male pronuclei, and the exchange of nuclei in the conjugation of Infusoria, are interesting analogies. ROHDE concludes: "Wahrscheinlich kommen in Tierreich gleich selbständig sich bewegende und wirkende Kerne, wie es die von mir beschriebenen Kerne der grossen Neurogliasyncytien sind, viel häufiger vor, als allgemein angenommen wird. Bekannt ist, dass junge Leucocyten selbst bei starker Vergrösserung einen Protoplasmaleib nicht erkennen lassen." Though HARRINGTON speaks of a thin protoplasmic film in these wandering cells, he usually calls them migratory nuclei; in the figures they are designated as such, and the protoplasmic film is absent or at least extremely delicate.

The supposed Posterior Openings of the Glands.

According to HARRINGTON, some of the secreted calcareous particles pass backwards in the tunnels, and break through the œsophageal epithelium into the digestive tract in segment xiv; this second outlet for the escape of the secretion has, he adds, not attracted the notice of previous workers. If the œsophagus be carefully opened along the mid-dorsal line, the milky fluid containing the calcareous particles may be seen issuing into the digestive tract from pit-like indentations in the side walls of the œsophagus just in front of the crop. According to COMBAULT, the second pair of orifices, discovered by HARRINGTON, are invisible to the eye and to a lens: "nous ajoutons que nous n'avons pu la délimiter nettement que sur les coupes en serie; on ne peut la voir qu'au microscope à dissection, mais sur une simple vivisection on se rend très bien compte de son existence à l'œil nu et mieux à la loupe par la fine trainée de liquide troublé qui s'en échappe."

We have previously explained that we have never, in numerous series of sections, been able to satisfy ourselves that such openings definitely exist; ruptures, quite possibly artificial, may occur in the epithelial lining of the œsophagus, and in this way the tunnels may be in communication with the œsophageal lumen. For example, a crack in the lining epithelium of the œsophageal lumen, in fig. 13, would place one of the tunnels in communication with the lumen. Such ruptures may possibly occur at times when the tunnels are full of secretion during life, and would be not unlikely to occur when the œsophagus was opened and its interior displayed, owing to the transverse stretching to which the epithelium would be subjected. It is in this way that we think the appearances of the escape of milky fluid from the hinder end of the glands, as seen by both HARRINGTON and COMBAULT, are to be explained. In any case there is no question of the whole, or the majority, of the sixty or so tunnels being in communication with the œsophageal lumen at their hinder ends—but merely of an occasional one here and there which bursts, so to speak; and COMBAULT's description of the glands as "un organ unique, cavité periœsophagienne ouverte aux deux bouts" is altogether inadmissible.

An appearance which we met with only in *Lumbricus* in our own preparations, and which is described and explained by CLAPARÈDE and COMBAULT, is the presence of a double circle of tunnels in some sections, one within the other. This led RIBAUCOURT to the mistaken idea of a continuous internally-placed series of tunnels and, superposed on this, a separate series in each of the segments occupied by the glands. The condition may be illustrated by text-fig. 1; it is a simple consequence of the bulging of the glandular mass between the septa, and its restriction at the sites of the implantation of the septa; a section taken along the line *a b* will evidently cut a double or even treble series of tunnels, which will appear as concentric circles. This external lobulation of the glands is very variable, even in the same species, as COMBAULT remarks: and he is quite right in maintaining that there is one single organ extending from end to end. Differences in the degree of lobulation had previously been shown for a considerable number of species by Ribaucourt.

Combault's main thesis is that the glands are respiratory organs; and though the present communication does not deal with the physiology of the glands, a few remarks seem called for on this subject. A primary contention is that the earthworms are really aquatic; "les lombrics sont en fait des animaux aquatiques au même titre que tous les animaux qui respirent dans la vase"; "les 'vers de terre,' ne pouvant vivre que dans la terre humide, s'accommodent très bien du régime purement aquatique, et, périssant à la moindre sécheresse, doivent être considerés, au point de vue respiratoire, comme des animaux aquatiques." The epithelium of earthworms is compared with that of the frog as a respiratory organ, to the disadvantage of the former; "l'épiderme est recouvert (in the earthworm) d'une cuticule très épaisse . . . l'épaisseur de la cuticule vient encore s'opposer aux échanges gazeux." Or again, "il suffit d'ailleurs, à notre avis, d'étudier la structure des téguments d'un Lombric, pour être persuadé de l'impossibilité d'une respiration uniquement cutanée."

Respiration takes place, according to Combault, by the aspiration of water into the œsophagus: "Des mouvements musculaires continuels aspirent et chassent l'eau dans une chambre œsophagienne, située en avant de l'organe de Morren." The presence of the glandular tissue in the substance of the œsophageal wall causes a narrowing of the œsophageal lumen, so that the water is forced to traverse the gland (*i.e.* the tunnels of the gland): "Les organes autrefois décrits sous le nom de glandes digestives de Morren constituent en réalité une chambre branchiale periœsophagienne; il s'agit d'un veritable manchon œsophagien communiquant avec l'œsophage à ses deux extremités par deux paires d'orifices. Ce manchon creusé dans le tissu conjonctif qui sépare l'épithelium œsophagien de la couche musculaire produit un rétrécissement de l'œsophage qui force l'eau à les traverser."

The glands are therefore gills—internal branchiæ; and "leur aspect est tel qu'ayant montré ces coupes à des histologistes sans leur donner aucun renseignement sur la provenance, ils prononcèrent tous le nom de 'branchies.'" This comparison leads the author to certain revolutionary morphological ideas; the insertion of the septa into the glands represents a first hint of the branchial arches of Vertebrates: "L'insertion des dissepiments semble chez les types évolués pénétrer l'organ de Morren et les lamelles branchiales sont en quelque sorte soutenues par un arc de tissu conjonctif, véritable ébauche d'arc branchial." Or again: "Nous tenons dès maintenant à rapprocher l'organe respiratoire des Lombrics, des glandes en T des Scyllidiens, et surtout de la corbeille branchiale de l'Amphioxus . . . la corbeille branchiale de l'Amphioxus peut être rapprochée de l'organe branchiale de Morren: par sa forme, par sa situation, par sa fonction et enfin par son aspect histologique. Un coup d'œil jeté sur une coupe passant par la corbeille branchiale de l'Amphioxus évoque aussitot le souvenir des coupes passant par l'organe de Morren."

These latter expressions of the author's views scarcely require criticism. With regard to the former—earthworms as aquatic animals—while some certainly can and do live in water or mud, and others in damp earth, a number even among the Lumbricidæ can endure a considerable degree of dryness. According to SZÜTS (29), though *Allobophora* lives mostly in damp soil, it may be found under very various conditions; *Eiseniella* is found in damp or swampy meadows; *Eisenia rosea* may be found in luxuriant garden earth, and also in less nutritive loamy soil, or even between the stones of pavements in towns; *Lumbricus* and *Octolasium* can live on high mountains, and in stony, sandy, siliceous or loamy earth. The idea of a current of water passing through the glands (even were there a definite opening at the hinder end) may be dismissed as fanciful.

SUMMARY AND CONCLUSIONS.

(1) The calciferous glands of earthworms were rightly interpreted by the older authors as foldings of the œsophageal epithelium. The simplest condition is that where there occur slight segmental bulgings of the canal, within which are a number of transverse folds of the epithelium.

(2) In many forms the bulgings become diverticula, with wide or narrow mouth. The extreme form under this head may be seen in, for example, *Octochætus barkudensis*, where the glands are large lobed sacs, in the interior of which are numerous thin lamellæ extending nearly across the lumen; the sacs communicate with the œsophageal canal only by a narrow neck or "duct."

(3) The condition in *Eutyphœus* may be considered to have arisen from the fusion, along their edges, of a series of parallel epithelial lamellæ, transverse in direction, on each side of the œsophagus. The interlamellar spaces are here open above near the dorsal wall of the œsophagus, but are closed below by the ventral œsophageal wall. The glands here cause but little external swelling, being as it were withdrawn within the œsophageal wall. This is the end term of a type of evolution which starts with simple transverse lamellæ.

(4) The condition in the Lumbricidæ originated in a series of longitudinal lamellæ. The mode of evolution has been comparable to what has happened in *Eutyphœus*—the inner edges of the lamellæ have fused. In this way a series of longitudinal tunnels has been formed, in and part of the epithelial coat of the œsophagus, and entirely within the muscular coat. These tunnels open in front, where the longitudinal folds begin, into the œsophageal pouches in segment x; they become progressively smaller, and cease in xiv without posterior openings.

(5) The epithelium of the glands is in all cases continuous with that of the œsophagus, and comparative anatomy shows that the various forms of glands are essentially due to various forms and degrees of complexity of the epithelial folds. The glands are therefore not mesodermal in origin, and are not merely the walls of blood-vessels, as has recently been contended.

REFERENCES TO LITERATURE.

(1) Beddard, F. E., *A Monograph of the Order of Oligochæta*, Oxford, 1895.

(2) Beddard, F. E., "On the Anatomy of *Ocnerodrilus* Eisen," *Trans. Roy. Soc. Edin.*, vol. xxxvi, 1892.

(3) Benham, W. B., "Notes on two Acanthodriloid Earthworms from New Zealand," *Quart. Journ. Micr. Sci.*, vol. xxxiii, 1892.

(4) Bourne, A. G., "On *Megascolex cœruleus* Templeton from Ceylon, together with a Theory of the Course of the Blood in Earthworms," *Quart. Journ. Micr. Sci.*, vol. xxxii, 1891.

(5) Claparède, E., "Histologische Untersuchungen über den Regenwurm," *Zeit. für wiss. Zool.*, vol. xix, 1869.

(6) Combault, A., "Sur l'histologie des glandes calcifères des Lombrics," *C. R. Soc. Biol.*, vol. lxii, 1907.

(7) Combault, A., "Quelques expériences pour déterminer le rôle des glandes calcifères des Lombrics," *ib.*, *id.*

(8) Combault, A., "Contribution à l'étude de la respiration et de la circulation des Lombriciens," *Journ. de l'anat. et de la physiol.*, vol. xlv, 1909.

(9) Eisen, G., "Anatomical Studies on New Species of *Ocnerodrilus*," *Proc. Calif. Acad. Sci.*, ser. ii, vol. iii, 1893.

(10) Freudweiler, H., "Studien über das Gefässsystem niederer Oligochäten," *Jena. Zeit. f. Naturw.*, vol. xl, 1905.

(11) Gurwitsch, A., *Vorlesungen über allgemeine Histologie*, Jena, 1913.

(12) Harrington, N. R., "The Calciferous Glands of the Earthworm, with Appendix on the Circulation," *Journ. Morphol.*, vol. xv, Suppl., 1899.

(13) Heidenhain, M., *Plasma und Zelle*, vol. i, pt. 2, Jena, 1911.

(14) Lang, A., "Beiträge zu einer Trophocöltheorie," *Jena. Zeit. f. Naturw.*, vol. xxxviii, 1903.

(15) Lankester, E. R., "The Anatomy of the Earthworm," *Quart. Journ. Micr. Sci.*, n.s., vol. iv, 1864.

(16) Michaelsen, W., "Beiträge zur Kenntnis der Oligochæten," *Zool. Jahrb.: Abth. f. Syst.*, vol. xii, 1899.

(17) Michaelsen, W., "The Oligochæta of Natal and Zululand," *Ann. Natal Mus.*, vol. ii, 1913.

(18) Michaelsen, W., "Oligochæta," in *Beiträge zur Kenntnis der Land- und Süsswasserfauna Deutsch-Sudwestafrikas*, Hamburg, 1914.

(19) Perrier, E., "Études sur l'organisation des Lombriciens terrestres," *Arch. Zool. exp. et gen.*, vol. iii, 1874.

(20) Raff, Janet W., "Contributions to our Knowledge of Victorian Earthworms: the Alimentary Canal," pt. 1, *Proc. Roy. Soc. Vict.*, vol. xxii, 1910.

(21) Ribaucourt, E. de, "Étude sur l'anatomie comparée des Lombricides," *Bull. Scientifique France et Belgique*, vol. xxxv, 1901.

(22) Rohde, E., "Untersuchungen über den Bau der Zelle: IV. Zum histologischen Wert der Zelle," *Zeit. f. wiss. Zool.*, vol. lxxviii, 1904.

(23) Schafer, E. A., *The Essentials of Histology*, London, 1910 ed.

(24) Schiller, I., "Über den feineren Bau der Blutgefässe bei den Arenicoliden," *Jena. Zeit. f. Naturw.*, vol. xliii, 1907.

(25) Schneider, K. C., *Lehrbuch der vergleichenden Histologie der Tiere*, Jena, 1902.

(26) Stephenson, J., "On Intestinal Respiration in Annelids; with considerations on the Origin and Evolution of the Vascular System in that Group," *Trans. Roy. Soc. Edin.*, vol. xlix, 1913.

(27) Stephenson, J., "On a Collection of Oligochæta belonging to the Indian Museum," *Records Ind. Mus.*, vol. xii, 1916.

(28) Sterling, S., "Das Blutgefässsystem der Oligochäten," *Jena. Zeit. f. Naturw.*, vol. xliv, 1909.

(29) Szüts, A., "Die Archæo- und Neolumbricinen," *Zool. Anz.*, vol. xlii, 1913.

(30) Vejdovsky, F., "Zur Hämocöltheorie," *Zeit. f. wiss. Zool.*, vol. lxxxii, 1905.

(31) Vejdovsky, F., "Zweiter Beitrag zur Hämocöltheorie," *ib.*, vol. lxxxv, 1906.

EXPLANATION OF FIGURES.

a., axis of lamella; *b.m.*, basement membrane; *cil.*, cilia; *crys.*, crystals, probably of calcium carbonate, within the gland; *d.v.*, dorsal vessel; *epi. œs.*, epithelium of œsophagus; *h.*, heart; ***int.***, dilated internal end of lamellar sinus; *l.*, lamellæ of gland; *lam. sin.*, lamellar sinus; *l.p.*, lamellæ of œsophageal pouch, here not united to form tunnels; *lum.*, central lumen of œsophagus; *m.*, muscular coat; ***n.***, nucleus in lamellar sinus; *œs.*, œsophagus; *œs. p.*, œsophageal pouch; *part.*, vertical partition (in ***Eutyphœus***); *perit.*, peritoneum; *per. sin.*, peripheral sinus; *r.*, rodlets; *ret.*, reticular tissue and loose spaces beneath œsophageal epithelium; *sem. ves.*, seminal vesicle; *sept.*, septum; *s.i.v.*, supraintestinal vessel; *t.*, tunnel; *v.*, vessel in dorsal edge of vertical partition; *vent. v.*, ventral vessel; *x*, incomplete roof of tunnel; *y*, flat cell roofing tunnel; *z*, dilated end of lamellar sinus closed in by basement membrane and a thin protoplasmic layer.

Fig. 1. *Pheretima hawayana*; horizontal longitudinal section through the œsophagus in segment xii. × 50.

Fig. 2. The same; cells of a fold of the œsophageal epithelium; formalin, Delafield's hæmatoxylin and eosin. × 570.

Fig. 3. *Ocnerodrilus occidentalis*; transverse section through a calciferous gland, in front of its junction with the œsophagus. × 160.

Fig. 4. The same; epithelium of œsophagus in segment x, behind the entry of the calciferous glands; rodlets well marked; Zenker, Delafield's hæmatoxylin and eosin. × 290. No muscular coat is visible.

Fig. 5. *Octochætus barkudensis*; transverse section of œsophagus with calciferous gland of one side; rodlets on œsophageal epithelium not visible at this magnification. × 130.

Fig. 6. The same; part of calciferous gland, outer wall with lamellæ arising from it. Fixative not known; Delafield's hæmatoxylin and eosin. × 300.

Fig. 7. *Eutyphœus gigas*; dissection of œsophagus in segment xii, which is opened to show the calciferous glands within.

Fig. 8. *Eutyphœus waltoni*; calciferous gland of one side in horizontal longitudinal section. × 40.

Fig. 9. The same; lamellæ of calciferous gland in vertical longitudinal section; formalin, Delafield's hæmatoxylin and eosin. × 145.

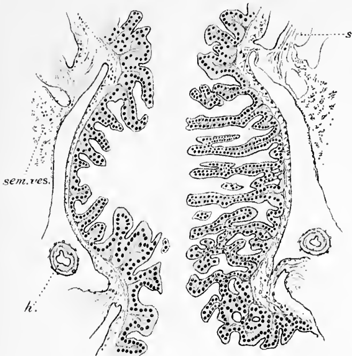
Fig. 10. The same; transverse section of part of calciferous gland, the vertical partition being cut transversely; one or two of the lamellæ are also cut, perhaps owing to the section being slightly oblique; formalin, Delafield and eosin. × 160.

Fig. 11. *Helodrilus parvus*; transverse section through alimentary tube in segment x of a young sexual specimen. The section is slightly oblique, and therefore shows a slightly different level on the two sides; on the right the section passes through the œsophageal pouch anterior to the appearance of prominent lamellæ; on the left lamellæ are present, which below are fusing together to form tunnels. Fixative not known; van Gieson's stain. × 180.

Fig. 12. *Helodrilus caliginosus*; transverse section through œsophagus of a young specimen in segment xi; tunnels established, rodlets as a fine border. Formalin, Delafield and eosin. × 125.

Fig. 13. The same; a portion of the œsophageal wall more highly magnified. Same preparation. × 550.

J. STEPHENSON AND BAINI PRASHAD: CALCIFEROUS GLANDS OF EARTHWORMS.



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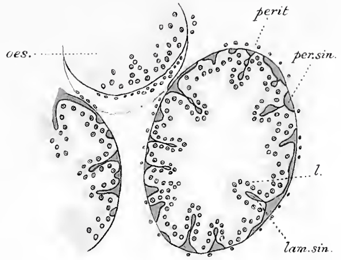

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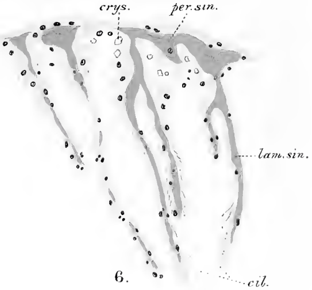

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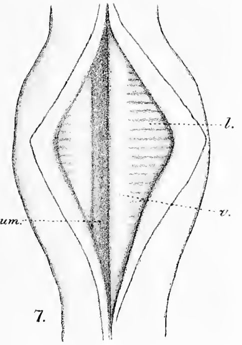

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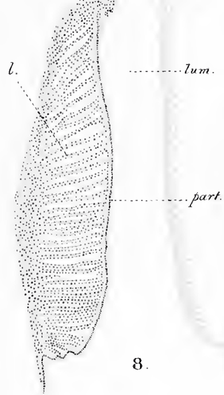

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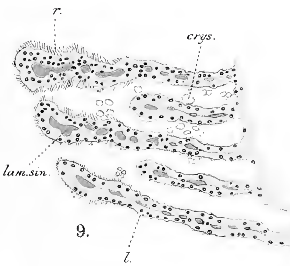

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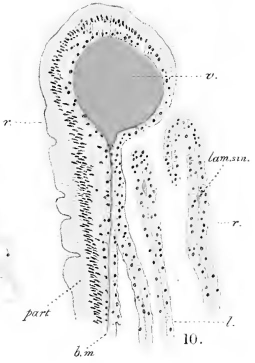

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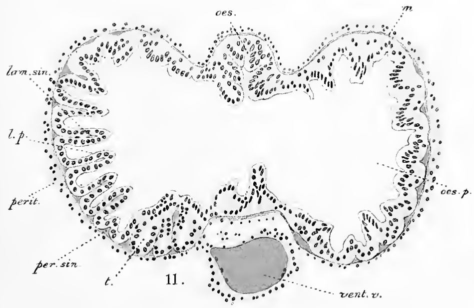

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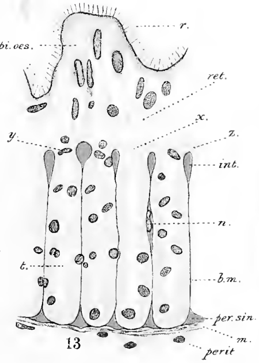

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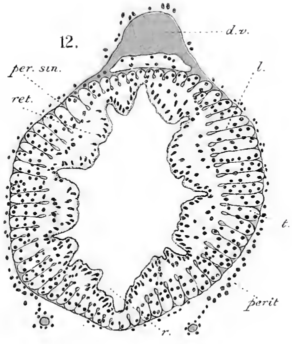

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McFarlane & Erskine Lith. Edin.

XVIII.—The Morphology of the Prosencephalon of Spinax as a type of Elasmobranch Fore-brain.

By **J. Stuart Thomson**, M.Sc., Ph.D., Lecturer and Senior Demonstrator in Zoology in the Victoria University of Manchester.

(With Two Plates and Three Text-figures.)

(MS. received January 26, 1918. Read February 4, 1918. Issued separately April 25, 1919.)

CONTENTS.

Part I.—Gray Masses.

Part II.—Fibre Tracts.

Introduction and Gross Morphology.

This investigation on the morphology of the Fore-brain or Prosencephalon of Elasmobranchii was suggested to me by Professor G. Elliot Smith, F.R.S., and I am indebted to him for introducing me to an interesting if somewhat difficult and perplexing subject. A glance at the literature on the morphology of the prosencephalon will readily convince one of two things—firstly, of the endless field for work in endeavouring to ascertain the true homologies of the neurone areas and fibre tracts in the brain throughout the Phylum Vertebrata; and secondly, of the somewhat unnecessary obstacles which have been introduced into the problem by the more recent additions to a terminology, already overburdened and encumbered, of new terms for equivalent parts. It would appear to be very advantageous if mutual agreement could be arrived at among workers on this subject regarding the use of descriptive terms, and, if such is at present impracticable, that each new worker should refrain as far as possible from applying a new term to a structure already previously described. In one case, namely, that of the tuberculum olfactorium, five different terms have apparently been applied to the same area. I obtained a large amount of material for my study of the brain of Elasmobranchs during periods of work at the marine biological stations of Naples, Plymouth, and Cullercoats, and to the authorities at these institutions I have pleasure in acknowledging my cordial indebtedness.* Some of my sections were cut in paraffin, others in celloidin, and were variously stained, but chiefly by Mayer's hæmalum and eosin and by the Wiegert-Pal method. The earlier drawings for this paper were drawn with the aid of the Edinger Projection Apparatus, for the use of which I have to thank Professor G. Elliot Smith; the later drawings were made with the Zeiss Projection Apparatus, which has been more recently introduced into the Zoological Department at Manchester University by Professor S. J. Hickson. The external characters of the brain of Spinax as seen from the dorsal surface are shown in fig. 1, the usual parts of the Elasmobranch brain being observed. The brain is of the more slender type, and the more massive part of the prosencephalon or fore-brain is connected with the olfactory bulbs by slender stalks, the olfactory peduncles. The prosencephalon has a fairly deep median groove on the rostral wall and extending over one-half to two-thirds of the medio-dorsal and medio-ventral walls. On the dorsal surface of the prosencephalon, towards the posterior end, two not very prominent rounded swellings or elevations are situated lateral to the part in which there is no median groove; these are parts of the primordium hippocampi (fig. 1*d*). Anterior to these swellings of the primordium hippocampi, a more flattened part of the roof with very faint transverse lines is situated; this area suggests the anterior pallial commissure as depicted on the dorsal surface of some Elasmobranch brains, but in the case of Spinax this is evidently slightly developed. On the ventral surface of the prosencephalon, towards the posterior end, a narrow cleft occurs, which is the point through which blood-vessels and the nervus terminalis of Locy enter the brain and penetrate to the internal tissues. The other points relating to the morphology of the prosencephalon or fore-brain will be dealt with in Parts I and II of this paper, in which the gray masses and the fibre tracts are considered.

Part I.—THE GRAY MASSES.

A transverse section through the most anterior part of the free lateral lobe of the prosencephalon, and passing through the base of the olfactory peduncle, shows a comparatively simple arrangement of the nerve cells or neurones (fig. 2). In the lateral lobe of the prosencephalon itself the neurones are distributed in rather an irregular manner, without aggregation at any special part. In the peduncular part the neurones are aggregated around the immediate margin of the cavity of the peduncle, and further at two places of the wall, namely, firstly, near the lateral wall opposed to the main mass of the prosencephalon, and secondly, near the dorsal wall. These two aggregations of neurones become linked up slightly posteriorly with areas of neurones which appear in the prosencephalon lobe proper. These areas in the

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* I have also to express my indebtedness to the Royal Society of London for a grant of £10 in aid of the printing of this paper.

prosencephalon are at first only slightly defined, but they gradually become more and more definite as one examines sections in a posterior direction. Fig. 3, which illustrates the condition in which the hemispheres are completely fused ventrally in the median line over an extent of about half their height, shows the various areas of neurones. The roof of the prosencephalon is occupied by a mass of neurones, which has been regarded as the forerunner of the hippocampus, and has therefore been termed the Primordium hippocampi (*d*). The Corpus paraterminale (*e*) is commencing to appear as a ventral extension in the medial direction of the Primordium hippocampi. The somewhat saucer- or cap-shaped area which runs latero-ventrally parallel with the margin of the section is the Tuberculum olfactorium (*b*). The mass of neurones which the latter partly encloses is the Corpus striatum (*a*). The area lateral to the dorsal half of the ventricle is the Formatio pallialis (*c*).

If fig. 3 is compared with ELLIOT SMITH'S[*] fig. 1, representing a coronal section through the left cerebral hemisphere of an adult Lepidosiren, the corresponding areas are readily recognised. In both the formatio pallialis is readily seen, and its medial continuation the hippocampus; the tuberculum olfactorium running round the latero-ventral edges of the hemispheres is evident. The tuberculum olfactorium is, as described by ELLIOT SMITH, a "peculiar cortical formation covering, like a closely fitting cap, the corpus striatum." The paraterminal body is commencing to become defined as an extension in the ventral direction of the primordium hippocampi.

These five main areas, as recognised in the Dipnoan cerebral hemispheres, may be followed in sections of the fore-brain of Spinax from the point depicted in fig. 3 in an anterior and posterior direction. Fig. 3 also shows two grooves in the wall of each lateral ventricle (pr', pr''), opposite to which lie two more or less cell-free zones (x', x''). The groove has been termed the sulcus limitans, and the zone the zona limitans, and these may be further distinguished, according to their position, as lateral and medial. I have used the terms adopted by ELLIOT SMITH in his description of the Dipnoan cerebral hemisphere throughout this paper. They imply a certain view regarding the structure of the fore-brain which I have not space to enter into here; but this is on the whole unnecessary, as this conception has been repeatedly emphasised by ELLIOT SMITH.[†] I would therefore reiterate that the main area of neurones which I recognise in the Elasmobranch fore-brain, as exemplified by that of Spinax, and as seen in my figures, are the following: the formatio pallialis, the primordium hippocampi, the corpus paraterminale, the tuberculum olfactorium, and the corpus striatum.

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[*] GRAFTON ELLIOT SMITH, "The Cerebral Cortex of Lepidosiren," etc., *Anatomischer Anzeiger*, Bd. xxxiii, Nos. 20 and 21, Jena, 1908.

[†] GRAFTON ELLIOT SMITH, "On the Morphology of the Cerebral Commissures in the Vertebrata," etc., *Trans. Linn. Soc. London*, Ser. 2, Zoology, vol. viii, 1902, pt. xii.

An attempt may, however, be briefly made to compare the areas of neurones in the fore-brain, as described above, with the descriptions of other workers, but this can only be done and should only be accepted with caution owing to the extreme difficulty in some cases of arriving at any degree of certainty regarding the homologies of the parts described by different authors. The well-marked saucer- or cap-shaped area running latero-ventrally parallel with the margin of the hemisphere, the tuberculum olfactorium, is apparently identical with the cortex olfactoria of EDINGER, the nucleus tæniæ of KAPPERS, the nucleus post-olfactorius of HOUSER, the hypostriatum of CATOIS, and the area superficialis basalis of JOHNSTON.* In the dorsal part of the hemisphere (pars pallialis of GAUPP) above the zona limitans, in which I distinguish the formatio pallialis (lateral), the primordium hippocampi (dorsal), and the commencing corpus paraterminale (medial), GAUPP † describes and figures in the fore-brain of the frog the formatio pallialis lateralis, the formatio pallialis dorsalis, and the formatio pallialis medialis in corresponding order. In the same region JOHNSTON distinguishes the primordium pallii somatici and the primordium hippocampi in various Selachian fore-brains. Further posteriorly and ventrally in the pars subpallialis of GAUPP he distinguishes the precommissural (paraterminal) body, but regards the latter as part of an area of central gray, which he terms the area olfactoria medialis. This last area, according to JOHNSTON, lies below the zona limitans medialis, filling the "septum." The medial olfactory area I do not recognise as independent, regarding it as chiefly composed of the paraterminal body, which appears as a ventral extension of the primordium hippocampi, and partly of a more lateral part, a portion of the corpus striatum. This view I have not arrived at without very careful study of my sections. I have already indicated the position of the corpus striatum, situated in the ventral half of the hemisphere (pars subpallialis of GAUPP) dorsal to the tuberculum olfactorium. JOHNSTON has described another area in this region, "the area olfactoria lateralis." He writes, "this occupies a part of the lateral wall of the olfactory lobe, meeting the medial area at the olfactory peduncle and at the ventral angle of the ventricle." In this paper I do not describe this area as distinct from the others which I have noted, as it appears to me (as no doubt JOHNSTON will admit) that it has no sharp boundaries. It merges to a large extent dorsally into the formatio pallialis and ventrally into the corpus striatum. The "area olfactoria lateralis" apparently corresponds with the "epistriatum" of KAPPERS.

From the condition described as occurring in the section figured in fig. 3 one gradually passes to the arrangement in which the two lateral hemispheres form one united mass with the velum transversum on the dorsal surface and a groove on the ventral surface. The arrangement of the areas of neurones at this stage is shown in

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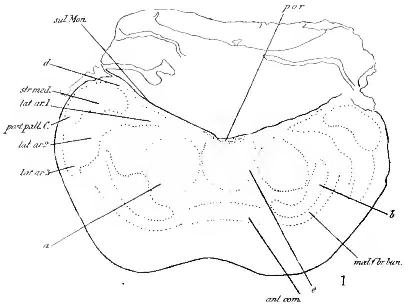
* J. B. JOHNSTON, "The Telencephalon of Selachians," *Journal of Neurology and Psychology*, vol. xxi, No. 1, February 1911.

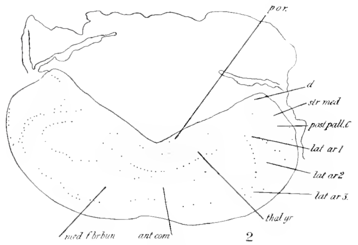
† GAUPP, ECKER'S and WIEDERSHEIM'S *Anatomie des Frosches*, Braunschweig.

fig. 4, in which one observes an aggregated central mass (*e*), namely, the paraterminal body (infra-foraminal precommissural body of JOHNSTON), a lateral mass on each side of this adjacent to the medial wall of the ventricle (*a*), part of the corpus striatum. In fig. 56 of JOHNSTON'S paper a transverse section of the brain of Acanthias is given, which represents practically the same condition as in my figure, but I draw different conclusions. The tuberculum olfactorium (*b*) (area superficialis basalis of JOHNSTON) is clear in both. The paraterminal body (*e*) is also evident, and there projects towards the lateral ventricle a zone of cells (*a*), which JOHNSTON terms the nucleus medialis septi. GAUPP'S description of this subpallial part may be summarised as follows. The subpallial part of the hemisphere can be distinguished into three regions—lateral, medial, and angular. The lateral part is the area of the basal ganglion of higher Vertebrata from which the basal fore-brain bundle takes its origin. The medial part of the hemisphere wall ("the septum," *s. str.*) can be differentiated into two areas of gray matter, namely, the central gray of the septum (Epistriatum P. R. y Cajal) (*e* of my figure), and the area lying more in the concavity of the ventricular wall (*a* of my figure), which he terms the Ganglion mediale Septi (Ganglion primordial, Ganglion basal P. R. y Cajal). The pars angulare is situated round the ventral angle of the ventricle (fig. 4), and is to be regarded as a continuation of the gray masses which lie on the floor of the recessus superior of the thalamencephalon. The pars angulare of GAUPP is clear in my sections at the region previous to the occurrence of the foramen interventriculare. It is, as GAUPP states, only obvious for a short distance. I regard it as part of the corpus striatum. The tuberculum olfactorium in the Amphibian brain does not appear to have the same definiteness as in that of the Selachian, but the facts seem to point to the probability that the pars lateralis of GAUPP corresponds to part of the tuberculum olfactorium, likewise, however, to part of the corpus striatum. The central gray of the "septum" of GAUPP appears to correspond with the paraterminal body (*e* of my fig. 4). A comparison of these areas of neurones with those given by GAUPP in the pars subpallialis is, however, a matter of some difficulty.

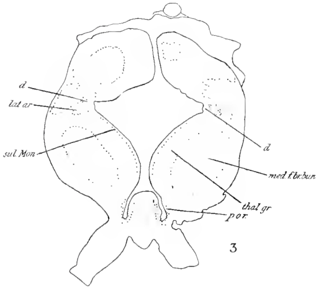
The areas of neurones already noticed in the prosencephalon pass in the præthalamus and thalamencephalon into the arrangement shown in the text-figs. 1–3. Text-fig. 1 represents a diagram through the thalamencephalon. The tuberculum olfactorium, corpus striatum, corpus paraterminale, primordium hippocampi, and formatio pallialis are present in a modified condition. The formatio pallialis lies dorsal to the upper extremity of the tuberculum olfactorium. It is a zone of cells which are grouped into three sets, namely, first a more medial area of scattered cells; secondly, an intermediate lying nearer the circumference of the section; and third, an external area of large cells (*lat. ar.* 1, 2, 3). This zone, which I have carefully traced in an anterior and posterior direction, is clearly a continuation of the formatio pallialis. The term given to this area by JOHNSTON, namely, the somatic area, does not, however, appear suitable. The stria medullaris (see p. 498) and the primordium



TEXT-FIG. 1.



TEXT-FIG. 2.



TEXT-FIG. 3.

hippocampi are situated dorsal to the formatio pallialis. Ventrally, the tuberculum olfactorium forms the bed in which the medial fore-brain bundle is later situated, as seen in text-fig. 2, which illustrates the arrangement slightly posterior to the last. The tuberculum olfactorium is no longer so obvious, and the position formerly occupied by the corpus paraterminale and the corpus striatum is now represented by a transverse area which has been termed the thalamic gray. Text-fig. 3 illustrates the arrangement of the parts further posteriorly in the thalamencephalon at the region from which the optic nerves originate. The areas have naturally undergone further re-arrangement, and the medial fore-brain bundle is much more pronounced.

PART II.—THE FIBRE TRACTS.

The following account is mainly concerned with the course of the medullated fibres in the prosencephalon, dealing more especially with those which apparently vary from the results attained by other authors.

Tractus olfactorius.—The course of this tract in Spinax mainly agrees with that described by JOHNSTON in Scyllium and Acanthias, after allowing for the divergence in the method of viewing the neurone areas of the fore-brain.

The following four tracts appear to be confined to the prosencephalon proper:—

Tractus olfacto-corticalis lateralis.—A few medullated fibres are seen on the lateral side of the dorsal end of the lateral ventricles (fig. 5). These fibres have an oblique course, and apparently run from the formatio pallialis to the primordium hippocampi. JOHNSTON has described a similar set of fibres as the tractus olfacto-corticalis lateralis rectus and the tractus olfacto-corticalis cruciatus in Scyllium and Acanthias. He states that some of these fibres enter the large roof commissure and pass to the opposite half of the primordium hippocampi; but in the fore-brain of Spinax I have been unable to detect such fibres crossing over to the opposite side. The fibres of the tractus olfacto-corticalis lateralis are firstly seen far anteriorly, when the peduncular part of the fore-brain is still evident, and when the small anterior part of the lateral ventricle is seen for the first time. These fibres are situated lateral and dorsal to the apex of the ventricle, and are sometimes not clearly separated from the fibres of the tractus olfactorius.

Tractus olfacto-corticalis medio-dorsalis (*fasciculus marginalis* of ELLIOT SMITH in Ornithorhynchus).—Fig. 6 shows part of the distribution of the fibres of this tract. The fibres are seen in the anterior part of the prosencephalon, when the lateral lobes are fused in the median line for a considerable extent. They run dorsally and medially from the zona limitans medialis, and then parallel with the dorsal margin of the prosencephalon until they meet the fibres of the tractus olfactorius lateralis, hence the term fasciculus marginalis appears appropriate.

The tractus olfacto-corticalis medio-dorsalis has been described by JOHNSTON in Acanthias as continuing in a caudal direction until it meets the pallial tract as the latter proceeds anteriorly over the tractus olfactorius lateralis. He states that when the pallial tract and the olfacto-corticalis medio-dorsal tract meet and intermingle the number of fibres in each has diminished very much, and that both enter the lateral border of the primordial hippocampus. The distribution of this tract appears to vary in Elasmobranchs. It has been found to be large and prominent in Acanthias, but has not been recognised in Scyllium. In Spinax its distribution appears to differ from that in Acanthias, as apparently it does not extend in a caudal direction to meet the pallial tract. It appears that this tract runs from the paraterminal body to the primordial hippocampus, and then passes on to the formatio pallialis.

Tractus cortico-medialis, BOTAZZI, GAUPP, and KAPPERS; *tractus olfacto-corticalis septi*, JOHNSTON, etc.; *fasciculus medianus*, CATOIS.—Some ventral fibres of this tract are seen in fig. 7. They pass dorsally on either side from the ental surface and medial end of the tuberculum olfactorium. Though not shown in my figure, I have traced long continuous fibres passing far dorsally (internal to the medial walls of the lateral ventricles) and external to another set of fibres (see figure) lying nearer the medial line, which will be described under the title tractus medianus in a later paragraph.* With the exception of one difference, this tract apparently agrees with the course described by JOHNSTON. The main facts are that in the so-called "septum" the fibres form a very diffuse bundle dorso-ventral in direction, that the bundle collects from the ental surface of the medial part of the tuberculum olfactorium and passes up into the primordium hippocampi. In fig. 34, p. 82 of his paper on the "Telencephalon of Selachians," JOHNSTON gives a drawing combined from several transverse sections to show the relations of the so-called "fornix" and the tractus olfacto-corticalis septi in *Scyllium caniculi*. In his drawing the tractus olfacto-corticalis septi is represented as extending dorsally as far as the upper extremity of the lateral ventricles. This is at least not true for Spinax, in which the fibres of this tract only extend into the paraterminal body or the ventral part of the primordium hippocampi. My other drawings of the distribution of this tract agree with those of JOHNSTON which are not combined, and I am therefore inclined to suspect that an error may possibly be present in his combined drawing. JOHNSTON terms this tract the tractus olfacto-corticalis septi, but I retain the older name, the tractus cortico-medialis of BOTAZZI and KAPPERS, etc.

Tractus olfacto-corticalis medialis cruciatus.—Regarding this tract JOHNSTON writes (p. 16): "In the area of secondary fusion of the medial olfactory nuclei in Acanthias appear a few medullated fibres (figs. 58, 59, 69), which arise in the

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* Fig. 8 shows the fibres of the tractus cortico-medialis situated lateral to the fibres of the more medial tractus medianus.

medial olfactory nucleus, cross to the opposite side and enter the primordium hippocampi. A similar decussation is seen in my preparations of the frog brain, and has been described by Snessarew." In his figures this tract forms a well-defined cross, but in Spinax there exists only the slightest indication of these fibres, and one is not certain that they are the same (fig. 8).

The following two tracts lead to the thalamencephalon :—

The *tractus olfacto-hypothalamicus.*—Figs. 7 and 8 show part of the distribution of the lateral portion of this tract. Its course corresponds, allowing for the difference regarding the homologies of the neurone areas of the brain, with that described by Johnston. There is a lateral and a medial portion, which form a diffuse bundle lying in front of and terminating posteriorly in the anterior commissure and medial fore-brain bundles (figs. 9, 11). The anterior commissure is apparently largely composed of decussating fibres from the medial fore-brain bundles.

Tractus tæniæ of Edinger, Kappers ; *tractus olfacto-habenularis* of Johnston.—Part of this tract is seen in fig. 11, and its course apparently agrees with that described by Johnston. It consists of a number of fibres, among those of the lateral olfactory tract, which gradually come into view as one follows a series of sections posteriorly, becoming more and more definite.

The following five tracts are connected either with the primordium hippocampi or with the formatio pallialis :—

Tractus pallii (fig. 10) represents part of this tract. It was firstly described by Edinger, and has also been noted by later writers on the Selachian fore-brain. It does not require further description, but I may note that it appears to be less developed in Spinax than is the case in some related forms.

Tractus cortico-habenularis (Johnston) ; *tractus olfacto-habenularis* (Kappers).—This tract is very small, but I have observed a few fibres dorsally behind the interventricular foramen, which are apparently joined by several fibres proceeding from the primordial hippocampus. They are not very clear, but the probability is that these constitute the above tract, which is apparently more developed in Scyllium than in Spinax and Acanthias.

Commissura hippocampi (fig. 10).—This commissure, situated in the roof of the fore-brain, has been described by various authors. It has been termed the upper part of the anterior commissure, the pallial commissure, and the psalterium. This tract is not so well developed in Spinax as in Acanthias. Johnston writes (p. 19): "It is certain, however, that there are fibres which arise in the primordium hippocampi itself and cross to the opposite side. In Scyllium and Raja these fibres are diffusely scattered among the olfactory decussations, but in Acanthias part of them at least form a distinct bundle whose course is worth describing." In Spinax I have not been able indubitably to detect fibres crossing to the opposite side, but as apparently only some of these fibres are medullated, it is possible they may have escaped my observation. The condition in Spinax thus appears to resemble that of Scyllium and Raja more than that of Acanthias in this respect.

Commissura pallii posterior.—This is a large bundle of non-medullated nerve fibres, the position of which is indicated in fig. 12. Many authors have held that a part of the tractus tæniæ (see p. 495) forms a true commissure in various fishes. It is apparently a commissure of the pallial area, and is probably homologous with the posterior pallial commissure in amphibians and reptiles.

Tractus medianus (Kappers and Theunissen); *median-bundle* (Edinger); *fasciculus cortico-medialis* and *median bundle* (Botazzi).—This tract has been the subject of much difference of opinion, and I still have some doubts, despite the certainty entertained by Johnston, as to this tract really being the homologue of the "fornix" of Reptilia and Mammalia, but it is possible that Spinax does not form such a good subject as Scyllium for tracing the course of this tract. Kappers and Theunissen have apparently been led into an error regarding the course of the tractus medianus by a wrong identification of certain fibres, which I have not space enough to enter into in this paper. Johnston writes (p. 23): "The tractus medianus undoubtedly arises in the roof, descends through the septum and runs to the hypothalamus. This is the description of the fornix in reptiles and mammals, and I think there can be no doubt of the homology." I am certain that I am dealing in Spinax with the same tract as that described and figured by Johnston in Scyllium and Acanthias under the term "fornix," for I largely agree with his description of the ventral part of its course and its relations to the so-called tractus cortico-medialis septi (fig. 8). The part with which my investigations on Spinax does not correspond is in regard to the more dorsal part of its course. He writes of fibres which collect from the dorsal part of the primordium hippocampi, pass meso-ventrally, and form two dense bundles medial to the inner walls of the lateral ventricles and dorsal to the zona limitans medialis. They cross the zona limitans, pass caudally over the anterior commissure, and enter the medial fore-brain bundle. The part of the bundle which they enter runs to the hypothalamus. I have, however, been unable to detect in the fore-brain of Spinax fibres of this tract so far dorsal as he has described and figured in other types. The tractus medianus and the tractus cortico-medialis are for part of their courses situated so close together in the "septum" that it is almost impossible to say that they are separate tracts. When, however, one examines sections further posteriorly, it is clear that these two tracts are distinct, and arise ventrally from different parts. The tractus medianus lies nearer the median line than the tractus cortico-medialis, and I have definitely traced fibres of the former tract running to the medial fore-brain bundle; further, when traced posteriorly after the fibres of the tractus cortico-medialis have disappeared, those of the tractus medianus may still be seen. The ventral ends of the fibres of the tractus cortico-medialis pass to the ental medial end of the tuberculum olfactorium. The fibres of the tractus medianus, as seen in transverse section, run in a different direction from those of the tractus cortico-medialis, namely, more longitudinally or obliquely. The course of the tractus medianus, as I have found it in the prosencephalon of Spinax, is that of fibres rising in the ventral part of the primordium hippocampi just on the dorsal side of the zona limitans medialis, which run ventrally on either side lateral to the median line and medial to the fibres of the tractus cortico-medialis, and finally proceed to the medial fore-brain bundle. The following additional points have, however, to be noticed. I have definitely traced a few fibres from the formatio pallialis lying external and fairly far lateral to the saucer-shaped tuberculum olfactorium, which pass to the more medially situated tractus medianus. I hold that the tractus cortico-medialis is also connected by fibres with the more external, lateral olfactory tracts. At this region of the brain (that in which the posterior ends of the tractus medianus and tractus cortico-medialis are situated) one has a great convergence of different tracts which pass directly or indirectly into the medial fore-brain bundle or the anterior commissure; such tracts are the tractus cortico-medialis, tractus olfacto-hypothalamicus lateralis and medialis, and the tractus medianus. These tracts are in connection by fibres passing here and there from one to the other. I have noted these connections in detail during my examination of the sections, but for the sake of brevity must here omit them.

Basal Fore-brain Bundle (fig. 11).—From the work of authorities on the structure of the brain of Teleostean and Ganoid fishes, it has been recognised that the basal fore-brain bundle consists of (*a*) a median portion, the tractus strio-thalamicus, EDINGER, etc. (anterior commissure, medial fore-brain bundle, and tractus olfacto-hypothalamicus medialis of JOHNSTON), and (*b*) of a lateral portion, the tractus olfacto-hypothalamicus lateralis. JOHNSTON has noted the presence of "a third portion of the basal fore-brain bundle which has hitherto been overlooked." He terms this part the lateral fore-brain bundle, but admits that at the region of the optic chiasma there is no clear distinction between lateral and medial fore-brain bundles. The lateral fore-brain bundle is, according to JOHNSTON'S views, similar to the basal fore-brain bundle described by GAUPP in Amphibia. The tractus thalamo-corticalis, which is said to make up the greater part of the lateral fore-brain bundle in Selachians, is partly seen in figs. 11 and 12, but owing to the limits of space I must here omit its discussion.

Corpus callosum.—JOHNSTON has described and figured on the lateral and dorsal surface of the prosencephalon medium of *Scyllium canicula* a set of fine fibres, of which he writes, "the commissure of the somatic areas in the lamina supra-neuroporica resembles in every way the corpus callosum, with which the writer believes it to be homologous." In fig. 9 one sees dorsally to the ventricle several fibres running more or less vertically to the margin, and ventrally to these other fibres passing parallel with the circumference. The more dorsal of these fibres may perhaps correspond to part of the corpus callosum, and the more ventral to part of the pallial tract as described by Johnston, but the former constitute the only trace of a similar condition so far as I have found it in Spinax. The small dorsal fibres, which one observes in my fig. 9, may only be branches of the olfactory or pallial tracts, for I have been unable to find in Spinax such a comparatively, well-defined tract and commissure as figured by Johnston in *Scyllium canicula* (fig. 20, p. 76, Johnston).

Tractus tæniæ (of Johnston).—To the tractus tæniæ of Edinger, Kappers, and others, Johnston has given the name tractus olfacto-habenularis, and has then described and figured "fibres . . . probably not noticed before" under the term tractus tæniæ. In the case of Spinax, I have not been able to arrive at any clear distinction between these two tracts, which it is allowed are closely associated together, and in the explanatory lettering of my figures I have therefore used the term tractus tæniæ in a comprehensive manner.

Summary of Fibre Complexes.

I may here briefly notice the summary of certain fibre complexes as given by Johnston.

Commissura pallii anterior.—This term is used to include in Selachians all the fibre decussations in the roof of the telencephalon. This position distinguishes it from the anterior commissure on the ventral surface. It consists of the following: (*a*) the hippocampal commissure, (*b*) the corpus callosum, (*c*) decussating fibres from the "area olfactoria lateralis" and from the "area olfactoria medialis." The anterior pallial commissure as regards the sub-commissures (*a*) and (*b*) is apparently, to say the least, not developed to the same extent in Spinax as in the types investigated by Johnston.

The Basal Fore-brain Bundle, consisting of the medial and lateral fore-brain tracts, the former including the tractus olfacto-hypothalamicus medialis, the "fornix" and somatic projection tract (part of the tractus strio-thalamicus of authors); the lateral chiefly composed of the thalamo-corticalis tract.

The Stria medullaris (corresponding in part to the tractus tæniæ of Edinger and other authors), in which he recognises seven separate bundles, including the tractus tæniæ *s. str.*, the tractus olfacto-habenularis lateralis, and the commissura pallii posterior. An adequate discussion of these bundles is beyond the scope of the present paper.

The Commissura anterior.—The Selachian fore-brain is not favourable for the study of the anterior commissure.

SUMMARY OF FIBRE TRACTS.

I have located the following nerve fibre tracts in the prosencephalon of Spinax:—

1. The tractus olfactorius, the course of which in the fore-brain of Spinax agrees with that described by JOHNSTON in other Selachian types.
2. The tractus olfacto-corticalis lateralis (fig. 5), which is not developed to the same extent in Spinax as in other types.
3. The tractus olfacto-corticalis medio-dorsalis (fasciculus marginalis) (fig. 6), the distribution of which apparently slightly differs from that in Acanthias.
4. The tractus cortico-medialis (BOTAZZI, KAPPERS, GAUPP); tractus olfacto-corticalis septi (JOHNSTON), which does not extend so far dorsally in Spinax as in Scyllium (fig. 7).
5. The tractus olfacto-corticalis medialis cruciatus (fig. 8), of which there is only the slightest indication in Spinax.
6. The tractus olfacto-hypothalamicus (fig. 9), the course of which mainly corresponds with that described by JOHNSTON in other types.
7. The tractus tæniæ (EDINGER, KAPPERS); tractus olfacto-habenularis (JOHNSTON) (fig. 11).
8. The tractus pallii (fig. 10) has been frequently noticed by other authors.
9. The tractus cortico-habenularis (JOHNSTON); tractus olfacto-habenularis (KAPPERS). This tract is not well defined; it is apparently more developed in Scyllium than in Spinax and Acanthias.
10. Commissura hippocampi (fig. 10). Fibres crossing over to the opposite side have not been definitely observed in the brain of Spinax.
11. The tractus medianus (KAPPERS and THEUNISSEN) (fig. 8), which is held by JOHNSTON to be the homologue of the "fornix" of Reptilia and Mammalia, is not developed dorsally in Spinax as described for Scyllium and Acanthias.
12. The commissura pallii posterior (figs. 11 and 12). A large bundle of non-medullated nerve fibres.
13. The basal fore-brain bundle, consisting of a median portion (tractus strio-thalamicus, EDINGER) and a lateral portion, the tractus hypothalamicus lateralis (fig. 11).
14. The corpus callosum. The fore-brain of Spinax does not show a tract and commissure such as has been described and figured for Scyllium.

With the object of curtailing the letterpress of this paper a list of the literature on the Elasmobranch brain is not given, but reference may be made to the bibliography at the end of JOHNSTON'S Memoir on the "Telencephalon of Selachians," already cited. Finally, the author would express his regret that, for the same reason, many points worthy of discussion and elaboration have had to be omitted.

EXPLANATION OF PLATES.

Fig. 1. The brain of Spinax from the dorsal surface.

Fig. 2. Transverse section of the left side of the anterior end of the prosencephalon, passing through the peduncle and its canal.

Figs. 3 and 4. Transverse sections of the prosencephalon further posteriorly showing the areas of neurones.

Figs. 5–12. Transverse sections showing parts of most of the fibre tracts described in the text.

REFERENCE LETTERS.

a	corpus striatum
ant. com.	anterior commissure.
ant. pall. c.	anterior pallial commissure.
b	tuberculum olfactorium.
c	formatio pallialis.
d	primordium hippocampi.
dec. tr. olf. lat.	decussation of lateral olfactory tract.
dor.	dorsal side.
e	paraterminal body.
int. for.	interventricular foramen.
lat. ar. 1, 2, 3	lateral area with three sub-areas.
lat. ven.	lateral ventricle.
med. f. br. bun.	medial fore-brain bundle.
nuc. hab.	nucleus habenulæ.
olf. ped.	olfactory peduncle.
o. n.	optic nerve.
p. o. r.	pre-optic recess.
post. pall. c.	posterior pallial commissure.
pr′, *pr″*	sulcus limitans lateralis, sulcus limitans medialis.
r.	recess.
str. med.	stria medullaris.
sul. Mon.	sulcus Monroi.
thal. gr.	thalamic gray.
tr. cort.-med.	tractus cortico-medialis.
tr. hipp.	tractus (commissura) hippocampi.
tr. med.	tractus medianus.
tr. olf.-cort. lat.	tractus olfacto-corticalis lateralis.
tr. olf.-cort. m.-c.	tractus olfacto-corticalis medio-cruciatus.
tr. olf.-cort. m.-d.	tractus olfacto-corticalis medio-dorsalis.
tr. olf.-hyp. lat.	tractus olfacto-hypothalamicus lateralis.
tr. olf.-hyp. med.	tractus olfacto-hypothalamicus medialis.
tr. olf. lat.	tractus olfactorius lateralis.
tr. pall.	tractus pallii.
tr. tæn.	tractus tæniæ.
tr. thal.-cort.	tractus thalamo-corticalis.
v. tr.	velum transversum.
x′, *x″*	zona limitans lateralis, zona limitans medialis.

Dr J. Stuart Thomson: "The Morphology of the Prosencephalon of Spinax as a type of Elasmobranch Fore-brain."—Plate I.

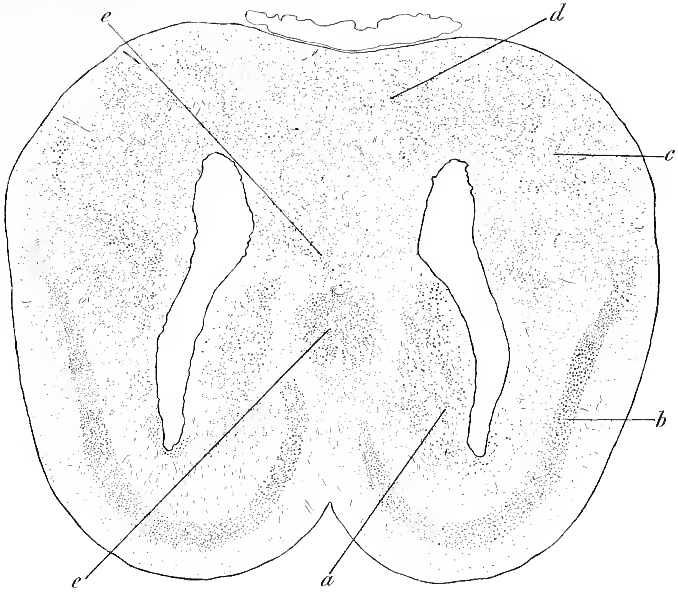

Fig. 4.

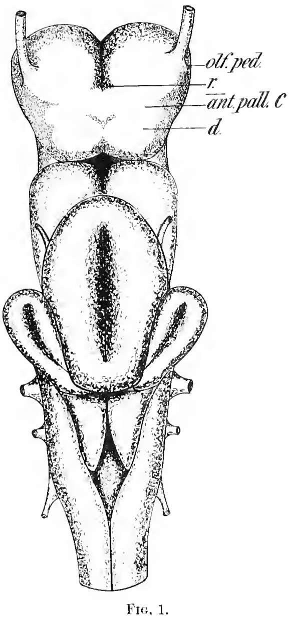

Fig. 1.

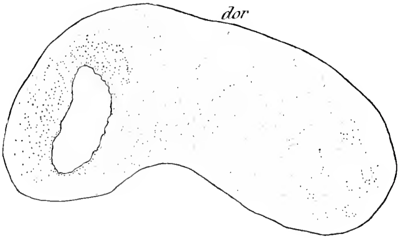

Fig. 2.

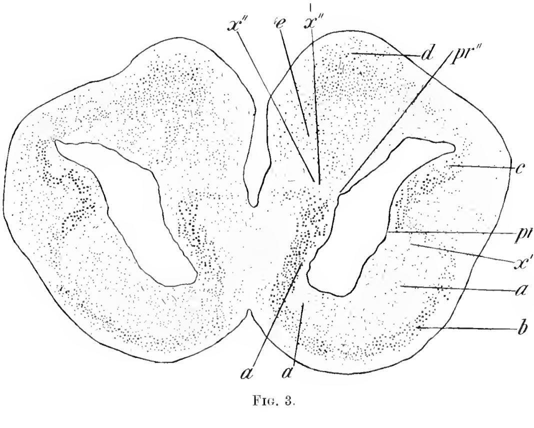

Fig. 3.

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Dr J. STUART THOMSON : "The Morphology of the Prosencephalon of Spinax as a type of Elasmobranch Fore-brain."—PLATE II.

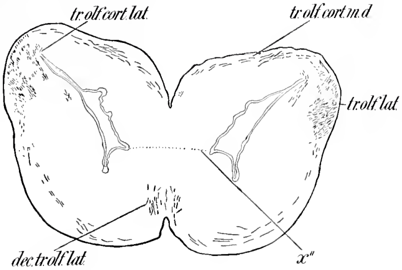


FIG. 5.

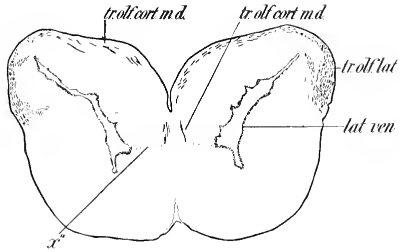
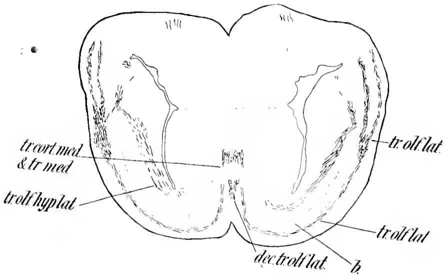


FIG. 6.



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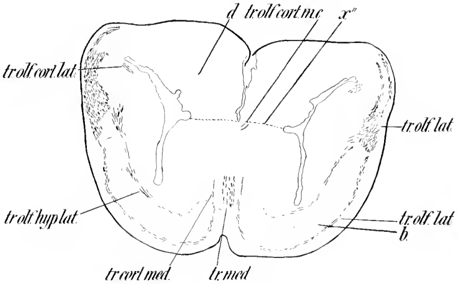

FIG. 8.

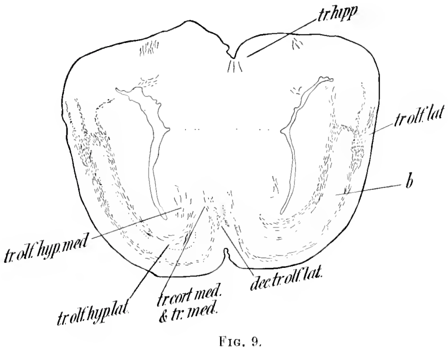

FIG. 9.

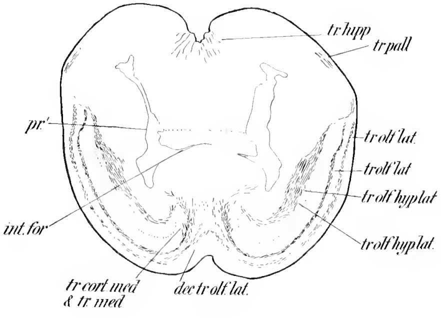

FIG. 10.

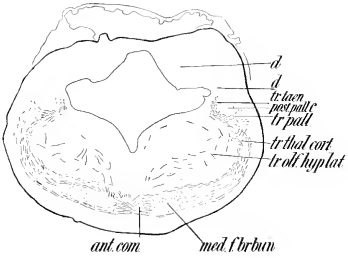

FIG. 11.

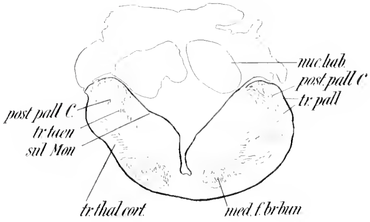

FIG. 12.

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