XV. On some recent Contributions to our Knowledge of the Morphology and Physiology of the Cell. By PATRICK GEDDES, F.R.S.E., Lecturer on Zoology in the School of Medicine, and Demonstrator of Botany in the University of Edinburgh. [Plate III.]

(Read 1st March 1881, with additions 15th March 1882.)

After the establishment of the cell theory, and more especially after Max Schultze had shown that the cell was not of necessity definitely walled, but was essentially a naked lump of protoplasm with an embedded nucleus, the attention of histologists was for some years almost withdrawn from the scrutiny of the minute structure of this unit-mass, to be concentrated upon the study of the modes of arrangement and differentiation of these unit-masses into the systems of tissues into which the genius of Bichât had analysed the organism. With the discovery of the remarkable changes which are to be observed in dividing cells, however, a return from the study of the cell-aggregate to that of the cell itself commenced, and this newer movement has been so fruitful and so suggestive that the question of cell structure is again paramount in histology. It is the object of the present paper briefly to summarise and discuss some of the later contributions-excepting, however, those relating to the changes which go on during cell-division—partly because the enormous and rapidly increasing literature on this subject is already admirably treated in the well-known works of Flemming, Strasburger, and others, which excellent summaries have been from time to time published in English,* but also because the rapid increase of our knowledge of the wonderful phenomena exhibited by the dividing nucleus has naturally tended to throw into the shade numerous other scarcely less important lines of research which may profitably be considered.

Assuming, then, a knowledge of at least the ultimate result of these researches—the fundamental similarity of the process of cell-division in animal and vegetable cells alike,—

^{*} Quart. Journ. Miero. Sci., xvi., xviii., xx., etc.; and Journ. Roy. Micro. Soc. Lond., passim.

let us consider what steps have been taken towards the solution of the numerous cognate inquiries.

1. Is a nucleus universally present? The group Monera was erected by Hæckel* in 1868 for the reception of the numerous very simple protoplasmic organisms in which no nucleus had been detected, and in which he assumed none to exist. The discovery of a distinct nucleus in Foraminifera by F. E. Schultze+ and Richard Hertwig # cast serious doubts upon the distinctness of the group, so that Claus § and others have proposed its entire abandonment. Among plants, too, a vast number of the lower algae and fungi, formerly considered destitute of nuclei, have been shown always to possess one or even many, so that Schmitz holds that Thallophytes destitute of a nucleus are altogether unknown. || The Bacteria, however, still remain, and although a re-examination of such forms as *Protomyza* is very desirable, it seems more probable that there really exist certain low forms in which the protoplasm may be non-nucleated.

2. Passing over the numerous investigations as to the internal structure of the nucleus, it may be noted that Macfarlane \P has recently drawn attention to a minute spheroidal body commonly present within the nucleolus, which, though occasionally figured, has never been thought of any importance. He terms this the endo-nucleolus; and in later papers he points out the great constancy of its occurrence in both animal and vegetable cells, and asserts that the division of the cell starts from this innermost body, which divides before the nucleolus and this before the nucleus.

3. Great attention has recently been paid to multinucleate cells. Schmitz** found numerous nuclei in Siphonocladaceæ, etc. Maupas ++ counts as many as from 150 to

+ Rhizopoden Studien. Archiv. f. Mikrosk. Anat., i.

^{*} Monographie Moneren. Jena Zeitschr., iv., 1868.

[‡] Bemerk. z. Organ. u. systemat. Stellung d. Foram. Jena Zeitschr., x., 1876.

[§] Lehrbuch d. Zoologie. 4te Auflage, Wien, 1880.

^{||} Journ. Roy. Micro. Sci., 1880, p. 482.

[¶] Trans. Bot. Soc. Edin., 1880.

^{**} Op. cit.

⁺⁺ Journ. Roy. Micro. Sci., 1880, p. 106.

200 nuclei in tubes of Cladophora, many also in Vaucheria, Empusa, and Infusorians. Hegelmaier* finds multinucleate cells in the suspensor of Dicotyledons; and Treub,+ whose researches are earliest and most elaborate of all, has proved the plurality of nuclei of constant occurrence in the vegetative cells of phanerogams, especially in the laticiferous cells and bast fibres of Euphorbia, Vinca, etc. All the nuclei in one cell sometimes divide simultaneously, division just stopping short of the formation of septa. Considerable light has also been thrown on the multinucleate condition by the recent observations of Macfarlane on the development of Chara.[±] He finds that the internodal cells partially keep pace with the division of the nodal cells, their nucleolus first dividing repeatedly, and the multinucleolate nucleus then breaking up into many portions. In the nodal cells the nucleolus also proliferates when division ceases, and the nucleus may break up.

The multinucleate condition thus loses much of its apparently anomalous character, and seems to be readily assumed by large cells, such as giant cells, in which abundant nutrition continues after maturity. A special term—such as *syncytium*, proposed by Gegenbaur—seems unnecessary.

4. The generalisation Omnis cellula e cellula being accepted, are we also to admit the similar maxim, Omnis nucleus e nucleo? In the majority of cases this is, of course, true; but do no exceptions occur—is free nucleus formation in protoplasm impossible? In this relation, while by no means intending to commit myself unreservedly to the maintenance of that (on the whole less probable) view, I am desirous of calling the attention of other investigators to two cases already described and figured by myself, which appear decidedly to support it. The first case was observed in a species of Enteromorpha § (see fig. 2), in which the new cells

‡ Trans. Roy. Soc. Edin., 1882

§ On the Phenomena of Variegation and Cell Multiplication in a species of *Enteromorpha* (Trans. Roy. Soc. Edin., 1879-80).

^{*} Journ. Roy, Micro. Sci., 1880, p. 979.

⁺ Niederland Archiv., 1879.

arising by the process which I have termed interlaminar gemmation appeared at first perfectly homogeneous, never exhibiting a nucleus, even on treatment with reagents, while the older and larger ones possessed a distinct nucleus and nucleolus. Secondly, in the even more remarkable case of endogenous cell formation presented by the brown corpuscles of *Echinus* * (fig. 1), no nucleus is distinguishable until the adult corpuscle has reached its full development. Such cases as these demand careful reinvestigation, before the invariable origin of nuclei from pre-existing nuclei can be safely maintained.

5. Passing now from the morphological aspects of the nucleus to the physiological, the older view—of the nucleus as a mere inert dense lump—need not detain us. Not only do the wide chemical differences between the nucleus and the surrounding protoplasm oppose this view, while the phenomena of all multiplication tend to show that it is, on the contrary, the seat of the activities of the cell, but it is sometimes possible even to observe its movements. The nucleus of many ova is capable of amœboid movement; + Unger \ddagger has observed similar movements both in normal and in inflamed tissues. Schleicher § describes an easy method of watching the movements of the nucleus in the living cartilage cells of the frog's omosternum, and I || have described a regular oscillation of the nucleus from side to side within the body of an infusorian.

6. Thanks to the investigations of Flemming, Strasburger, Klein, and others, we now know that the so-called granules of the protoplasm of cells belonging to all kinds of animal tissues are really the optical expressions of the thickened intersections of a delicate network of denser filaments—the *stroma*, between the meshes of which lies the more fluid

- + Balfour, "Comp. Embryology," i., 1880.
- ‡ Ueb. amœboid. Kernbewegung, etc., Med. Jahrb. Wien, 1878, p. 393.
- § Journ. Roy. Micro. Sci., 1880, p. 407.

 \parallel (a) Observations on the Histol. and Physiol. of Convoluta (Proc. Roy. Soc., Lond., 1879); (b) Sur une nouvelle sous-classe d'Infusoires (Comptes Rendus, 19th Dec. 1881).

^{*} Sur le Fluide Périvisceral des Oursins. Arch. d. Zool., Exp. VIII.

protoplasm. There is little doubt that a similar structure exists in the vegetable cell, although there the frequently enormous development of sap vacuoles presses the protoplasm into threads, as in Spirogyra, which cannot be fairly compared to a stroma. There is considerable evidence for believing that in muscle the fibrils represent the stroma; and Professor Haycraft * suggests that the pseudopodia amœboid cells are mere outflows of semi-fluid protoplasm, squeezed from between the meshes of the stroma by its contraction, the subsequent retraction of the pseudopodia being accounted for by the relaxation of the stroma, the viscosity of the interstromal matter, and surface tension. While no one who has observed the wonderful activity and the varied forms of pseudopodia emitted by many Protozoan forms (some amœbæ having two distinct forms of pseudopodium,+ and some protruding cup-shaped processes ‡), or by the corpuscles of many invertebrates, particularly when uniting into a common ameeboid mass, § will accept the above as a satisfactory explanation; it is, of course, by no means impossible that we have here one of the factors of the process : nor indeed does Dr Haycraft demand much more.

7. The transformation of ciliated or flagellate cells into the amœboid state has been long known among such organisms as *Protomyxa*, Monads, etc.; and Huxley || has insisted on the importance of the alternation between these forms, which he terms mastigopod and myxopod, in the morphology of the Protozoa.

(May not the *Mastigamæba* of Schultze and the similar organisms figured by Butschli and Savile Kent \P — which are possessed of both pseudopodia and flagella—be simply forms of mastigopod, sketched during their assumption of the myxopod state ?)

* Proc. Roy. Soc. Edin., 20th Dec. 1880.

+ Korotneff, Arch. d. Zool., Exp., 1878.

‡ (Plakopus).

§ Geddes, "Sur le Fluide Périvisceral des Oursins" (Arch. d. Zool., Exp. VIII.); and "On the so-called Coagulation of Invertebrate Corpusculate Fluids" (Proc. Roy. Soc. Lond., 1880).

|| Huxley, "Anatomy of Invertebrated Animals," 1877.

¶ Manual of the Infusoria, London, 1881.

I am very strongly of the opinion that the same metamorphosis or degeneration from the ciliated to the amœboid state is of great importance in the histology of invertebrates. Not only does it frequently take place among ciliated embryos, but the amœboid corpuscles of many invertebrates (e.g. Echinus) develop in the same way from the ciliated epithelium of the perivisceral cavity.* So, too, I have elsewhere + described the remarkable transformation which occasionally takes place (doubtless as a pathological change) in the ciliated ectoderm of a planarian; and it is here possible to watch the actual transformation of cilia into pseudopodia, and even to see the two slowly contracting together. May not the assumption of this change with diminishing vitality throw light upon diseases of the ciliated epithelium of the trachea?

Chun has recently shown that, as had often been surmised, the vibratile bands of Ctenophores are simply united cilia, for when macerated they separate.

8. While the principal forms of contractile tissue are, of course, the muscular, the ciliated, and the amceboid, it is by no means correct to suppose that no other forms are known. The remarkable contractile collar of Torquatella, + the heart of Appendicularia, § the extraordinary infusorian Pulsatella, which moves by the rapid rhythmical contraction of internal fibrillæ around the large vacuole, are instances of new and strange modes of contractility; while the spermatozoa of Urodeles, which are provided with an undulating membrane along one side, or those of certain planarians, where a regular series of waves runs continuously from one end of the spermatozoon to the other, increasing in velocity, though not in amplitude, towards the end which bears the flagellum, are, if possible, even more valuable as illustrations

* Op. cit., Arch. d. Zool., Exp., 1880.

+ Op. cit., Proc. Roy. Soc. Lond., 1879.

‡ Lankester, Torquatella typica (Quart. Jour. Micro. Sci., vol. xiv., 1874).

§ Lankester, On the Heart of Appendicularia (Quart. Jour. Micro. Sci., vol. xiv., 1874).

|| Sur une nouvelle sous-classe d'Infusoires (Comptes Rendus, 19th Dec. 1881).

¶ Geddes, On the Histology of Convoluta (Proc. Roy. Soc. Lond., 1879). VOL. VII. 0

of the great variety of ways in which contraction may take place.

9. The circulation of protoplasm, which has so long been known and studied in such plants as Chara, Nitella, Vallisneria, etc., and which is believed to be of very wide distribution in vegetable cells, though little searched for in the animal kingdom, has been observed * in the cartilage cells of Geryonia. Unfortunately, no observations have been made upon the still more remarkable phenomenon of "aggregation of the protoplasm," discovered by Darwin+ in the cells of the glands of Drosera, and observed by him also in the sensitive hairs of Dioncea and in the roots of various plants, save a single confirmatory paper by Francis Darwin; ± and it still remains to be investigated whether this remarkable process takes place in animal cells, whether it is related to circulation, and whether both are modifications of that irregular streaming which may be observed within the body of an amœba. Perhaps these phenomena may have something in common with those movements of the nucleus in animal cells above referred to; in any case a thorough comparative study of all these modes of protoplasmic motion is highly desirable.

10. In this relation, too, the contractile vacuoles of many zoospores, infusorians, etc., are worthy of attention. It has long ago been pointed out how the irregular disposed and non-contractile vacuoles of the lowest amœboid organisms become differentiated on one side into the large sap cavities of vegetable cells, and on the other into the regularly contractile vacuoles of many Protozoa. The most remarkable specialisation, however, is certainly that which I have recently described in *Pulsatella* § (see section 8, *supra*).

11. The coalescence of many ameeboid cells into a continuous mass or *plasmodium* was discovered by De Bary to be a regular stage in the life-history of the Myxomycete fungi.

* Gegenbaur, Comparative Anatomy, p. 26.

+ Insectivorous Plants, London, 1877.

[‡] Aggregation in the Tentacles of Drosera (Quart. Jour. Micro. Sci., xvi., 1876).

§ Op. cit.

Hæckel has figured one of the Monera-his Protomyza aurantiaca, which forms similar cell fusions. One or two similar Rhizopods have also been observed, and my own observations have shown that this tendency to union, apparently unimportant and rare, is really one of the best marked tendencies of the amoeboid cell. For the corpuscles of invertebrates taken from various groups-urchins, starfishes, bivalves, gasteropods, worms, or crustaceans, all form plasmodia. The phenomenon can be best observed in the sea urchin, by suspending a drop of the perivisceral fluid from the under surface of a cover-glass placed upon a glass ring, of which the under side should be oiled to prevent evaporation. A little carmine or ultramarine may with advantage be added. Union takes place only between the finely granular corpuscles, which soon form an immense amœboid mass, which differentiates into granular endosarc and hyaline ectosarc, the latter of which sends out pseudopodia of extraordinary length and activity, which readily absorb any free corpuscles of the finely granular sort,-the coarsely granular corpuscles, like the foreign pigment granules, being simply taken into the interior of the mass.*

12. In my former papers on this subject I have compared these plasmodia to such Rhizopods as *Microgromia* socialis (Hertw.),† *Raphidiophrys*, etc., in which several constituent units are united by bridges of protoplasm. The well-known structure of Volvox, the beautiful *Moneron*, *Monobia confluens*, recently figured by Schneider,‡ and the remarkable recent announcement of Frommann § that the meristem cells of *Dracana*, *Rhododendron*, etc., are in direct protoplasmic continuity by means of delicate filaments passing through foramina in the cellulose wall, however, when viewed together with the case of such Rhizopods, fur-

^{*} Obs. s. l. Fluide Périviscéral des Oursins, Arch. d. Zool., Exp. VIII.; On the Coalescence of Amæboid Cells, etc. (Proc. Roy. Soc. Lond., No. 202, 1880).

⁺ R. Hertwig, Ueb. Microgromia socialis, etc., Arch. f. Mikr. Anat. Bd. and Taf. 1, 1874.

[‡] Arch. d. Zool., Exp., 1880.

[§] Beobacht. üb. Structur, etc. d. Pflanzenzelle. Jena, 1880.

nish us with a type of the morphological arrangement and the physiological relations of vegetable cells alike distinct from this and from the ordinary one. The very deep pits in such thickened cell walls have often led vegetable histologists erroneously to imagine their protoplasm continuous; but the cases above mentioned, however, appear to me to furnish a considerable amount of new evidence in favour of that view; which, however, while very attractive, especially as serving plausibly to explain many remarkable physiological phenomena—such, for instance, as the propagation of an impulse through the leaf of Drosera—will require much farther research for its verification.

13. The question so long debated during the early days of the cell theory as to the nature and respective homologies of such structures as the cellulose wall and primordial utricle of the vegetable cell, the cysts of Amœbæ or Gregarines, the skeletons of Diatoms and Thalamophora, etc., the gelatinous investment of many Radiolarians, the matrix of cartilage, sarcolemma, neurilemma, intercellular substance, etc., still affords room for many detailed inquiries. We remain as yet completely ignorant of the laws of formation of such "organic crystallisations" as the skeletons of Radiolarians and Diatoms, though such siliceous deposits may yet furnish a transition from the chemistry of the carbon compounds to that of the analogous silicon compounds; or, still better, a glimpse into the play of forces within the protoplasm which produces them.

Nageli's theory of the growth of starch grains and cell walls by intussusception has recently been vigorously attacked by Schimper,* and I have pointed out that the cell wall in *Chlamydomyxa labyrinthuloides* is "distinctly formed by the deposition of successive laminæ, not by intussusception and subsequent differentiation, an important fact in view of the wide prevalence of the latter and somewhat overstrained theory "+ (see fig. 4). The laminated structure of the cel-

^{*} Bot. Zeit. 1880-81.

⁺ Observ. on the Resting-Stage of Chlamydomyxa (Quart, Jour. Micro. Sci., Jan. 1882). See Strasburger's recently published work, "Ueb. d. Ban u. Wachsthum d. Zellhäute," Jena, 1882, in which a vast mass of similar evidence is adduced.

lulose coat in many algae, e.g., Enteromorpha (fig. 2), is also very evident.

14. Passing to the consideration of the modes of cell division, I shall not at present venture upon any bibliographical account, but content myself for the present by briefly referring to such contributions as I have already published.* The first relates to the process of cell multiplication by means of interlaminar gemmation (fig. 2). The second describes the origin of the brown corpuscles of *Echinus* by a process (highly suggestive of comparative researches) which appears to be a variety of that of free cell formation, from certain of the pigment granules which occur in masses in certain portions of the blood vessels and water-vascular system (fig. 1). Finally, I have figured specimens of Chlamydomyxa, which at least closely simulate, if they do not, as is much more probable, absolutely represent all the main modes of cell multiplication -transverse division, gemmation, free cell formation, and rejuvenescence-with which we are acquainted, and which at any rate assist us in imagining how these processes have arisen (see fig. 3).

EXPLANATION OF PLATE.

Fig. 1. Endogenous (?) development of brown amœboid corpuscles of sea urchin : \dagger a, three of the yellow granule-masses from the ambulacral pouch, with one free brown corpuscle (at left hand upper corner); b, c, d, similar granule-masses from intestinal blood vessel, the two latter showing one or two of their constituent spherical bodies enlarged and darkened in colour; e, a granule-mass with dark coloured body, now of irregular form; f, the same under pressure; at g, completely expressed (born, in fact) as a brown amœboid corpuscle; h, another brown corpuscle, more highly magnified, and showing dark coloured granules in colourless protoplasm; i, the same corpuscle killed and decolorised; j, a corpuscle crushed; k, proliferation and escape of small spherical yellow bodies (nucleoli?) from nuclei of epithelial cells of ambulacral pouches, by union or division of which the yellow granule-masses seen in figs. a, b, appear to originate.

Fig. 2. Cell-multiplication by *interlaminar gemmation* in *Enteromorpha*: ‡ a, a filament with laminated structure of cellulose brought out by weak

* Op. cit.

+ S. l. fluide Périviscéral d. Oursins, Arch. d. Zool., Exp., vol. viii., pl. 38.

‡ On the Phenomena of Variegation, etc., in Enteromorpha (Trans. Roy. Soc. Edin., vol. xxix., pl. 12).

214 Proceedings of the Royal Physical Society.

potash; b, c, d, e, f, filaments showing small new cells destitute of chlorophyll, single, or forming colourless shoots; g, h, filaments more highly magnified, showing origin of the colourless cells by gemmation of the protoplasm (from below the chlorophyllaceous layer) of the green cells, into the lenticular or angular spaces between the laminæ of cellulose. The same is seen two-thirds down b.

Fig. 3. Union of amœboid cells into a plasmodium :* a, amœboid cells of perivisceral fluid of a star-fish, freshly drawn; b, the corpuscles sticking together in a group; c, the same completely fused into a plasmodium; d, a corner of the large and active plasmodium formed by finely granular amœboid corpuscles of the sea urchin. With the most trifling modifications, the same figures, more especially a, b, c, would serve to represent the formation of plasmodia; (1) in the so-called coagulation of any invertebrate corpusculate fluid; (2) in Hackel's *Protomyxa aurantiaca*, and other forms of Protozoa; (3) in Myxomycete fungi.

Fig. 4. Diverse modes of multiplication in *Chlamydomyxa labyrinthuloides* (Archer): + a, a spherical specimen; b, c, mass divided two and four respectively, recalling the transverse division of *Protococcus*; d, a specimen recalling the transverse division of an amœba; c, a flat amœboid mass just beginning to throw out a cellulose coat, apparently after rejuvenescence; f, a specimen in process of gemmation, recalling the process of cell-multiplication in *Torula*; g, a specimen containing several smaller encysted masses—endogenous division. The formation of the cell-wall from successively deposited laminæ is particularly well marked in e, g.

XVI. Notes of an Entomological Excursion to the New Forest, Hampshire, in July 1880. By WILLIAM EVANS, Esq.

(Read 21st December 1881.)

ABSTRACT.

In this paper the author gave an account of a three weeks' excursion to the New Forest undertaken by him in July 1880. A small hamlet called Bank was chosen for headquarters, and in its immediate neighbourhood, as well as in those parts of the forest stretching out to Lyndhurst on the one hand and Brockenhurst on the other, the bulk of the collecting was done.

Having indicated the position of the forest, and referred to its antiquity and historical associations, the author proceeded

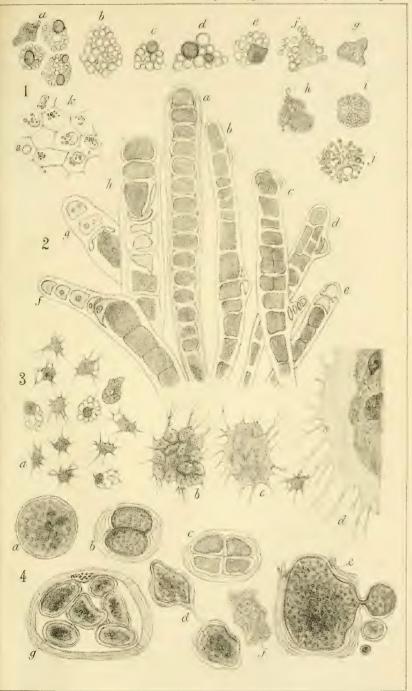
^{*} On the Coalescence of Amœboid Cells, etc. (Proc. Roy. Soc. Lond., vol. xxx., pl. 5).

⁺ Observ. on the Resting Stage of Chlamydomyxa, etc. (Quart. Journ. Micro. Sci., vol. xxix., pl. 5).

Vol. VII.

PLATE III.

Royal Physical Society, Edinburgh.



MSFarlane & Erskine, Lith!" Edm!