larger ungulates, including giraffe, rhinoceros and elephant, are doomed to disappear from the French colonies unless special measures are taken for their protection. Even the hippopotamus has been seriously reduced in numbers, and more in the French areas than elsewhere.

Complementary to Rode's volume is that of Dr. Gromier¹⁶ on African big game. Dr. Gromier is an excellent representative of the sportsman-naturalist type, who studies and photographs as well as shooting his quarry. After a general introduction which includes various valuable practical suggestions, he treats at some length of the African elephant (which, he considers, has the right to the title of 'King of Beasts'), with shorter sections on rhino, hippo, lion, buffalo, eland, giraffe, and both sub-species of gorilla. The book is illustrated with numerous photographs by the author, some of considerable interest, and by plates of footprints of the animals described in the text and of some others.

The African elephant is a species of extremely wide ecological tolerance, combined with an interesting plasticity of behaviour. Thus Dr. Gromier says it uses its tusks for digging only in dry areas. The eland, giraffe and lion have a lesser but still very considerable range of ecological tolerance.

The individual variability of elephants is very unusual among animals (in this respect the species bears a resemblance to our own). Among the many variants Dr. Gromier notes is one remarkable individual, the tusks of which were crossed in front of the trunk after the fashion of some of the mammoths. He unfortunately refrains from giving the measurements of the largest specimen he shot, "for fear that he might have been mistaken"! He notes, however, that they exceeded those of the animal recorded by Foa, which was 3.69 m. (just over 12 ft.) at the withers.

Though both the lion and the giraffe are often to be found in thorn-bush, the latter takes little account of thorns (on account of its thick hide), whereas to the lion they are formidable obstacles. Dr. Gromier mentions the prevalence of mutual licking in giraffes—an interesting social habit, reminiscent of the trophallactic mutual licking of termites. He considers that this has arisen through the inability of the giraffe, owing to the length of its neck, to lick its own body clean—a fact which he thinks is also the cause of their pronounced smell.

The alimentary demands of the gorilla may be appreciated by the fact that, in two specimens, Dr. Gromier found in the stomach the remains of a single meal of about forty bananas, together with other materials. Gorillas also show more marked individual variation than do most wild species (for example, in colour); as do lions. The two subspecies of gorilla differ interestingly in social habits; the forest race lives in small family bands, usually with only one (or two) adult females, while the mountain race forms extended family groups of twenty to thirty individuals, including several females and young males.

He gives some interesting examples of variations in rhinoceros horns, including some which are quite straight and others which are curved forwards, indicating a reversal of the normal growth-gradient in this region.

For those who like a macabre flavour to their ecology, I recommend Dr. Gromier's account of the "orchestre scabreux et scatologique" resulting from the pressure of gas inside a decomposing rhinoceros carcass. "Les moindres fissures ou érosions de la

peau jouaient leur petit air de flûte, les cuivres étaient tenus bruyamment par les anses intestinales qui s'échappaient des voies naturelles, et un morceau du colon énorme, qui avait réussi à passer par le sphincter, tonitruait un air de trombone triomphant". The observations of the field naturalist can add both realism and surrealism to those of the systematist and the anatomist!

- ¹ Les anguilles : variation, croissance, euryhalinité, toxicité, hermaphroditisme juvénile et sexualité, migrations, métamorphoses. Par Léon Bertin. (Bibliothèque scientifique.) Pp. 218+8 plates. (Paris : Libr. Payot, 1942.) 50 francs.
- ² Les coléoptères : formes, mœurs, rôle. Par Dr. Renaud Paulian. (Bibliothèque scientifique.) Pp. 396 (14 plates). (Paris : Libr. Payot, 1943.) 125 francs.
- ³ La vie des scarabées. Par Dr. Renaud Paulian. (Histoires naturelles, 5.) Quatrième édition. Pp. 234. (Paris : Libr. Gallimard, 1944.) 95 francs.
- ⁴ Les colibris. Par J. Berlioz. Pp. 198. (Paris : Libr. Gallimard, 1944.) n.p.
- ⁵ (Paris : Boubée et Cie., 1942 and later.) n.p.
- ⁶ L'Homme et les plantes cultivées. Par André G. Haudricourt et Louis Hédin. (Géographie humaine, 19.) Huitième édition. Pp. 234+16 plates. (Paris : Libr. Gallimard, 1943.) 110 francs.
- ⁷ Les fondements biologiques de la géographie humaine : essai d'une écologie de l'homme. Par Prof. Max Sorre. Pp. 440. (Paris : Armand Collin, 1943.) n.p.
- ⁸ Oiseaux de mon pays. Par H. Noll. Pp. 182. (Neuchâtel et Paris : Delachaux et Niestlé S.-A., 1939.) n.p.
- ⁹ La formation du système nerveux. Par Raoul-Michel May. (L'Avenir de la science, 20.) Pp. 302+45 plates. (Paris : Libr. Gallimard, 1945.) 330 francs.
- ¹⁰ L'Origine des cellules reproductrices et le problème de la lignée germinale. Par Prof. L. Bounoure. (Collection des Actualités biologiques.) Pp. xii+272. (Paris : Libr. Gauthier-Villars, 1939.) 120 francs.
- ¹¹ Continuité germinale et reproduction agame. Par Prof. L. Bounoure. (Collection des Actualités biologiques.) Pp. iv+84. (Paris : Libr. Gauthier-Villars, 1940.) 56 francs.
- ¹² L'Hérédité. Par Prof. Émile Guyénot. (Encyclopédie scientifique : Bibliothèque de biologie générale.) Troisième édition. Pp. 717. (Paris : G. Doin et Cie., 1942.) n.p.
- ¹³ Organisme et sexualité. Par Prof. Maurice Caullery. (Encyclopédie scientifique : Bibliothèque de biologie générale.) Pp. 342. (Paris : G. Doin et Cie., 1942.) n.p.
- ¹⁴ Faune de l'Empire français. 1 : Orthoptéroïdes de l'Afrique du nord. Par Lucien Chopard. Pp. 450. (Paris : Libr. Larose, 1943.) 300 francs.
- ¹⁵ Faune de l'Empire français. 2 : Mammifères ongulés de l'Afrique noire. Par Paul Rode. Première partie : Famille des bovidés (buffles, antilopes, gazelles). Pp. 124. n.p. Deuxième partie : Tragulidés, girafidés, suidés (phacochère, potamochoère, hylochère), hippopotamidés (hippopotame), périssodactyles (rhinocéros), proboscidiens (éléphant), hyraciens (damans). Pp. 125-212. n.p. (Paris : Libr. Larose, 1943-1944.)
- ¹⁶ La vie des animaux sauvages de l'Afrique. Par Dr. Émile Gromier. (Bibliothèque géographique.) Pp. 344+36 plates. (Paris : Libr. Payot, 1938.) 100 francs.

GENETICS OF THE MICROFUNGI

By PROF. C. T. INGOLD

AT its morning meeting in London on December 19, 1945, the Society for General Microbiology, with Sir Alexander Fleming in the chair, discussed the question of "Variation of Cells having Bi-parental Inheritance", and the papers and discussion dealt largely with the genetics of the microfungi. After a brief survey of reproduction in the microfungi by the present writer, Prof. Ö. Winge, of the Carlsberg Laboratory, Copenhagen, dealt with his genetical work on yeasts, which has revolutionized our ideas of these organisms. He was followed by Dr. D. G. Catcheside, who discussed the importance of the heterothallic Ascomycetes as tools for the geneticist.

Apart from the first discovery of conjugation in a fungus by Ehrenberg in 1818, perhaps the greatest advance in the study of sexuality in these organisms was due to Blakeslee, who in 1904 described the phenomenon of heterothallism in the Mucorales. This opened the way for experimental breeding, and in 1925 Burgeff¹ succeeded in mating *Phycomyces Blakesleeanus* with *P. nitens* and obtaining zygospores which germinated to give a hybrid—the first true

interspecific hybrid to be produced experimentally in fungi. However, members of the Mucorales are unlikely to become popular with the geneticist, since germination of the zygospores is usually difficult, the nuclei are so small that the fundamental cytological facts of the life-cycle are still in doubt and the multinucleate condition of the sporangiospores introduces possible complications.

In 1914 Egerton², working with *Glomerella*, reported heterothallism in Ascomycetes, and since that time many more examples of this phenomenon have come to light in that group. However, it soon became apparent that the nature of heterothallism in Ascomycetes was not quite analogous to that in Mucorales. In Mucorales, although there is usually no consistent difference in size between the two cells which fuse to form the zygospore, it is a reasonable theory that the difference between + and - strains is essentially one of sex. This explanation does not hold for the Ascomycetes. In *Ascobolus magnificus*, for example, apothecia are produced only where + and - mycelia meet, but each is hermaphrodite, producing well-defined male and female organs. Thus the difference between + and - is not a sexual one. Each strain is bisexual, but self-incompatible.

In Ascomycetes the asci are borne on ascogenous hyphae which usually arise from the female organ. In the ascogenous hyphae the nuclei occur in pairs and, in heterothallic species, it seems likely that each pair consists of a + and a - nucleus. The bi-nucleate ascus-initial cell likewise has a + and a - nucleus.

The cytology of ascus development has given rise to considerable controversy. Most mycologists and cytologists would probably now agree that the two nuclei of the ascus-initial are haploid, that these fuse to form a diploid nucleus, that the two nuclear divisions which then occur constitute meiosis, and that the four haploid nuclei then undergo a final mitosis giving eight haploid nuclei, around each of which a spore is organised. This is the only picture of ascus development which is supported by genetical evidence.

Because we know where meiosis occurs and because of the orderly arrangement of the eight spores in the ascus, the heterothallic species of Ascomycetes are valuable tools in the hands of the geneticist, especially because the products of a single meiosis, being conveniently wrapped up in an ascus, can readily be isolated and studied.

Starting with the pioneer work of B. O. Dodge on *Neurospora*, much attention has been given to the genetics of this genus in recent years, and it bids fair to become as notable a genus in the history of genetics as *Pisum*, *Drosophila*, *Zea* and *Datura*. In heterothallic species of *Neurospora*, Lindegren³ has made important studies on the segregation of the gene pair, + and -, in the ascus. There are always four + and four - spores. If segregation occurs at the first division of meiosis, the four upper spores are + and the four lower -, or vice versa, but if segregation occurs, following a cross-over, at the second division of meiosis, then four other arrangements are possible. Lindegren found that all these are realized. Other allelomorph pairs, besides + and -, have been studied in *Neurospora* and these have been found to segregate in the same manner, half the spores of the ascus carrying one gene and the other half its allelomorph. A specially beautiful example was described by Zichler⁴ in *Bombardia lunata*. In a cross between a dark-spored and a light-spored variety the asci in the resulting perithecia had each four dark and four pale ascospores. All six

possible arrangements of these spores in the ascus were encountered, and Zichler gave extensive data of the number of asci exhibiting each pattern of spore-distribution. His data have recently been carefully analysed by Catcheside⁵, who finds that the gene for dark spores, whether segregation occurs at the first or second division of meiosis, tends to pass more often to the apical than to the basal end of the spindle. The solution of the cause of this curious 'polarized segregation' may throw additional light on chromosome and cell dynamics.

A great landmark in the genetical study of the microfungi was Prof. Ö. Winge's discovery that species of *Saccharomyces*, far from being apogamous, exhibit a definite diplophase and haplophase. The beautiful papers on the genetics of yeast which have been issued from the Carlsberg Laboratory during the past ten years have already become classics of mycological literature*. Winge⁶ found that when an ascospore of *Saccharomyces cerevisiae* germinates, it buds to produce small round haplophase cells. Sooner or later these may fuse in pairs, and from each fusion cell a large oval diplophase cell buds out which can originate a giant colony of diploid cells. He further found that most naturally occurring yeasts are highly heterozygous, with the result that the four colonies arising from the four isolated spores of an ascus are quite unlike and all different from the parent colony. The giant colonies formed by yeasts of different genotype are often strikingly different and the great beauty of some of them is illustrated in the fine plates of the Carlsberg papers. In the strains of yeast investigated by Winge, homothallism appears to have been the rule and the haplophase was short-lived. However, in recent years another school of yeast genetics has developed in America under Lindegren⁷, who reports heterothallism—though not very strict heterothallism—in the strains of yeast with which he worked. He found that more or less stable colonies of small-celled haplophase yeast could be produced from single ascospores which showed little tendency to give rise to the diplophase.

A big step forward in the study of yeast genetics was made by Winge⁸ when he succeeded in producing a hybrid between *Saccharomyces ellipsoideus* and *S. validus* by placing an ascospore of each species side by side. The two spores fused and from the fusion cell a hybrid bud grew out from which a hybrid colony originated. The hybridization of yeasts offers great possibilities in the industrial field.

Winge⁹ also studied mutations in yeast. A colony arising from a uninucleate haploid ascospore might be expected to remain true to type. However, even in such a colony sectors of a new type may occur, presumably as a result of gene mutation.

The Ascomycetes with their illegitimate cousins in the Fungi Imperfecti make up the vast majority of the microfungi. On the other hand, the Basidiomycetes are mainly large forms with the very important exceptions of the rusts and smuts. It is interesting to note that most rusts and smuts appear to be heterothallic. In recent years much attention has been paid to the genetics of smuts, and interspecific hybrids have been produced. In rusts, different physiological races have been crossed and as a result new races have arisen. In the life-cycle of the black stem rust of wheat due to *Puccinia graminis*, the barberry has developed a new significance. It is no longer to be regarded merely as

* E. R. Sansome has given a recent review of yeast genetics in *Nature*, 157, 52 (1946).

OBITUARIES

Prof. J. Stanley Gardiner, F.R.S.

an alternate host on which the rust gathers its strength for its attack on the wheat; it is also a common ground on which the various physiological races of the rust can meet and hybridize with the production of new races.

In 1938 Hansen¹⁰ described the 'dual phenomenon' in Fungi Imperfecti and explained this by the hypothesis of heterokaryosis. In *Botrytis cinerea*, for example, the conidium has several nuclei and it is suggested that they are not necessarily genetically alike. When such a spore gives rise to a colony a sector may develop differing from the rest. This sector may have arisen from a branch which, instead of having a mixture of nuclei of two or more different genotypes, has received nuclei of only one. It is well known that, in Nature, such a fungus as *Botrytis* occurs as a number of strains. When two strains meet, anastomoses (vegetative fusions) occur freely, and through these the nuclei can pass from one strain into the other, thus producing the heterokaryotic condition. The freedom with which nuclei can move through a mycelium of septate cells has been emphasized by Buller¹¹, who directed attention to the fact that the central pore existing in the cross-wall of higher fungi allows free streaming of protoplasm and transport of nuclei from cell to cell.

This peculiar heterokaryotic condition which may arise in the higher fungi offers interesting possibilities to the geneticist, in spite of the fact that no karyogamy is involved. The question has been discussed by Pontecorvo and Gemmel^{12,13} in recent contributions to *Nature*.

Recent work by Beadle and Conrardt¹⁴ on heterokaryosis in physiological mutants of *Neurospora* is especially interesting and suggestive. For the growth of fungi certain vitamins are necessary. Some fungi are capable of synthesizing some or all of these, others can grow only if the necessary ones are provided. Both vitamin B₁ (thiamin) and B₆ (pyridoxin) are necessary for the vegetative growth of *Neurospora*. Beadle and Conrardt obtained a strain which could synthesize B₁ but not B₆ and another which could make B₆ but not B₁. Neither would grow by itself on a standard basal medium. When, however, macroconidia belonging to the two strains were sown together, vegetative fusions occurred and the heterokaryotic mycelium, capable of synthesizing both B₁ and B₆, grew freely.

Something is now known of the genetical causes of the instability of pure cultures originating from single cells or single spores. In yeasts genetical segregation may occur, in cultures started from a single cell, at ascus formation. In conidial fungi with multinucleate spores heterokaryosis may be the cause of variation. Finally, in any cell and at any time gene-mutation may occur.

The genetics of fungi is an exciting and rapidly expanding subject, but one must bear in mind the warning words of Albrecht von Haller more than two hundred years ago when he described fungi as "a mutable and treacherous tribe".

¹ Burgeff, B., *Flora N.F.*, 18-19, 40 (1925).

² Egerton, C. W., *Amer. J. Bot.*, 1, 244 (1914).

³ Lindgren, C. C., *Bull. Torr. Bot. Club.*, 59, 119 (1932).

⁴ Zichler, H., *Planta (Arch.wiss. Bot.)*, 22, 573 (1934).

⁵ Catcheside, D. G., *Ann. Bot. N.S.*, 8, 119 (1944).

⁶ Winge, O., *C.R. Lab. Carlsberg s. Physiol.*, 21, 77 (1935).

⁷ Lindgren, C. C., *Ann. Miss. Bot. Gar.*, 32, 107 (1945).

⁸ Winge, O., *C.R. Lab. Carlsberg s. Physiol.*, 22, 235 (1939).

⁹ Winge, O., *C.R. Lab. Carlsberg s. Physiol.*, 24, 79 (1944).

¹⁰ Hansen, H. N., *Mycologia*, 30, 442 (1938).

¹¹ Buller, A. H. R., "Researches on Fungi", 5 (1933).

¹² Pontecorvo, G., and Gemmell, A. R., *Nature*, 154, 514 (1944).

¹³ Pontecorvo, G., and Gemmell, A. R., *Nature*, 154, 532 (1944).

¹⁴ Beadle, G. W., and Conrardt, V., *Genetics*, 29, 291 (1944).

JOHN STANLEY GARDINER, emeritus professor of zoology in the University of Cambridge and one of the outstanding figures in British zoology, died suddenly on February 28 at the age of seventy-four. His research career began in 1896 when he took part in the Royal Society's well-known expedition of Funafuti; from then onwards he was recognized as an authority on the distribution of marine animals in general and on the madreporarian corals in particular. Between 1897 and 1909 he organised and led three major expeditions to the Indian and Pacific Oceans, each of which threw considerable light on the broad relationships between the physical and biological aspects of oceanography. Perhaps the most interesting of these expeditions was that to the Maldivic Archipelago, for it led to the theory that a large land mass could be eroded to a depth of about 150 fathoms, thus giving rise to a submerged plateau which would later provide a foundation for coral reefs. From 1909 onwards, university duties prohibited further expeditions, but at least three other major projects owe much to Gardiner's inspiration and active support: the Suez Canal expedition under Munro Fox (1924), the Indian Ocean expedition (1933) under Seymour Sewell and the Lake Titicaca expedition under H. C. Gilson (1937). Gardiner's work was recognized by his election to the Royal Society at the relatively early age of thirty-six, and in later years he received the Agassiz Medal of the U.S. National Academy of Science, the Gold Medal of the Linnean Society, and the Darwin Medal of the Royal Society. He delivered the Lowell Lectures at Harvard in 1930.

After each of his expeditions, Gardiner returned to Cambridge to play an active part in college and university life. He became a fellow of Caius in 1898, dean in 1903 and senior proctor in 1907. In 1909 he succeeded Adam Sedgwick as professor of zoology and for the next twenty-eight years remained in residence in the University. He was, above all else, a man of wide scientific vision, and his influence was felt far beyond the limits of his own research interests. He was in no sense a physiologist, but he saw clearly that the study of animal form could acquire new significance when considered in relation to function. As head of his Department at Cambridge, he did all in his power to weld morphology and physiology into one indivisible science. Between 1909 and 1914 his own lectures on "The Principles of Zoology" gave to students this new point of view, but perhaps of even greater significance was Gardiner's ability to gather round him men of inspiring personality. In 1910 Leonard Doncaster and Cresswell Shearer joined his staff, and these with Gardiner formed a nucleus around which advanced students rapidly gathered.

On the outbreak of war in 1914, Gardiner shouldered an extremely heavy burden of teaching, but nevertheless devoted a great deal of energy to the organisation of fishery research, of which he acted in the official capacity of director of scientific investigations until 1920. At the end of the War of 1914-18, Gardiner, with characteristic foresight and generosity, gave to each returning member of his staff a full year's freedom from teaching, and he encouraged them by every means in his power to develop their research interests. During the next fifteen years he continued to foster the functional outlook, but, at the same time, developed other aspects of zoology, notably ento-