Ann. Soc. belge Méd. trop.
1964, **44**, 2, 267-272.

Travail dédié au Professeur A. Dubois à l'occasion de son 75e anniversaire.

The Subgenera of *Plasmodium* in Mammals

BY

P. C. C. GARNHAM,
Department of Parasitology,
School of Hygiene and Tropical Medicine,
London.

Summary. — A third subgenus — *Vinckeia* — is added to *Plasmodium* and *Laverania* in the genus *Plasmodium*, with type species *Plasmodium (Vinckeia) bubalis* Sheater, 1919. The subgenus *Plasmodium* is slightly redefined, in consequence of this change. A list of species belonging to the subgenus is given and the main differentiating characters are discussed.

The genus *Plasmodium* was created by Marchiafava and Celli in 1885 to accommodate parasites, living within human erythrocytes, unpigmented and with lively amoeboid movements; they named the organism *Plasmodium malariae*. Malaria parasites were found in birds shortly after their discovery in man, and these received a variety of generic names which sufficed to confuse the taxonomic relationships for some years. But early in the present century, the « Oscillarias », « Polymitus », « Proteosoma », etc., were discarded, and all species of malaria parasites were lumped into the single genus *Plasmodium*. At least, this was the treatment accorded to them by most workers, though some zoologists still retained the names of *Laverania* (for the « malignant tertian » parasite of man) and of *Proteosoma* (for the avian parasites).

The discovery of the tissue cycle of malaria parasites revealed that profound differences existed amongst the various species, and it was generally recognised that a new classification was desirable; Lily Mudrow (1950) foresaw what loomed ahead, but recommended patience until the entire cycles had been studied and their details clarified. The entire cycles will perhaps never be discovered, and the writer feels that the view of the German worker, although shared by other prominent malariologists (e.g. Huff, 1963), is a counsel of perfection and at the 5th and 6th Congresses of Malaria, held respectively in Istanbul (1953) and Lisbon (1958), suggested that the malaria parasites should be placed in several genera. The names *Laverania* and *Haemamoeba* were revived and

applied by the writer and others to *P. falciparum* and the species found in birds and lizards, respectively. Many workers, however, found this change distasteful and continued to use the old names, even for parasites so patently distinct as *Hepatocystis* (= *Plasmodium*) *kochi*.

Another solution to the nomenclature of the avian parasites was proposed by Corradetti, Garnham and Laird (1963), in which a single genus *(Plasmodium)* was preserved, but the species were regrouped into four subgenera. Thus the name *Plasmodium* is retained for use in a general context, while the subgeneric names are available for zoological or taxonomic purposes. At a later date these subgenera may well be raised to generic rank. Bray (1963) followed this course in regard to *Laverania,* and reduced this name (as approved by Hemming, 1954) to a subgenus with *Plasmodium (Laverania) falciparum* as the type species, while at the same time placing the remaining malaria parasites of mammals in the subgenus *Plasmodium,* with *Plasmodium (Plasmodium) malariae* as the type. Bray's definition of the subgenus *Plasmodium* (1955) is thus « parasites which reproduce sexually and by sporogony in an anopheline mosquito and asexually by schizogony in two cycles, one producing pigment in non-nucleated red blood cells and the other in parenchymal cells of the liver producing considerably more than 1,000 merozoites and in successive generations of exoerythrocytic schizogony ». Bray (see 1958) defined the subgenus *Laverania* as « parasites which reproduce sexually and by sporogony in an insect host and asexually by schizogony in two phases in a vertebrate host, one in red blood cells producing pigment and the other for one generation only in liver cells ».

The characters of the two subgenera, *Plasmodium* and *Laverania,* are shown in the table, and the essential difference between them is seen to lie firstly in the shape of the gametocytes, spherical in the former and crescentic in the latter, and in the persistence of exoerythrocytic schizogony, secondary forms being present in the former and absent in the latter.

Such a classification of the mammalian malaria parasite proves quite adequate for the species found in primates, but is less applicable to species in other mammals. For instance, no persisting exoerythrocytic stages (with a single possible exception) have been discovered in any of the latter; yet all possess spherical gametocytes. The following is a list of the non-primate mammalian malaria parasites :

P. anomaluri	from	*Anomalurus*
P. atheruri		*Atherurus*
P. berghei		Sylvatic rodents
P. bubalis		Water buffalo
P. cephalophi		Antelope

P. girardi	from	Lemurs
P. roussetti		Fruit bats
P. sandoshami		Colugo
P. traguli		Chevrotain
P. vinckei		Sylvatic rodents

A perusal of this list reveals two striking points — firstly the exotic nature of the host and, secondly, the fact that four of the species, including *P. berghei,* were discovered by members of the Antwerp School of Tropical Medicine, of which Professor A. Dubois is the late Director. A study of the parasites themselves will quickly show how greatly they differ from the primate species, and for this reason a third subgenus in the genus *Plasmodium* is created, namely, *Vinckeia,* in honour of Dr Ignace Vincke (of the same School) who has done so much to elucidate the mystery of some of these rare parasites, and who discovered, first as sporozoites and later in the blood form, *P. berghei,* a parasite of supreme importance in malaria research.

The subgenus *Vinckeia* is defined as follows :

Vinckeia, subgen. n., includes species of malaria parasite found in various mammals below the simian level. The erythrocytic schizont does not fill the corpuscule and gives rise to eight or fewer merozoites. True stippling of the erythrocyte is absent. Gametocytes are spherical and sporogony proceeds in anopheline mosquitoes. Exoerythrocytic schizogony is rapid, taking three days or less, and secondary tissue stages are rare or missing. The type species is *Plasmodium (Vinckeia) bubalis* Sheather, 1919. *P. (Vinckeia) bubalis* has been selected as the type species, instead of the earlier described *P. (V) cephalophi,* Bruce *et al.,* 1913, because the latter parasite has never been seen since its original discovery, and its description is not very acceptable. The creation of a third subgenus renders the previous definition of *Plasmodium (Plasmodium)* rather less broad, as the subprimate species of parasites are now removed from it, and *Plasmodium (Plasmodium)* is restricted to parasites of supralemuroid primates, with the characters as enumerated by Bray.

The definition of *Vinckeia* is subject to various exceptions, but is very largely applicable to the species named in the above list. The asexual blood stages are essentially small, though in certain species, e.g. *P. berghei,* the number of merozoites may exceed eight, at least in some strains of laboratory hosts.

With the exception of a single instance of exoerythrocytic schizogony of the falciparum type in *P. (V.) traguli* found in the liver of a chevrotain, no tissue stages have been seen in any species of

TABLE.

Differential characters of the Subgenera of Mammalian Species of *Plasmodium*.

Subgenus	Blood schizont and merozoites	Stippling of Erythrocyte	Shape of gametocytes	Pre-patent period	EE stages	Site of EE	Vertebrate Host
Plasmodium	Large; 8 or more merozoites	Present	Spherical	Five days or more	Primary and Secondary	Liver Parenchyma	Primates
Laverania	Large; 8 or more merozoites	Present	Crescentic	Five days or more	Primary	Liver Parenchyma	Primates
Vinckeia	Small; 8 of fewer merozoites (*)	Absent	Spherical	Three days or less	Primary	? Mesoderm	Lemurs and lower mammals

(*) Occasional exception is *P. (V.) berghei*.

the subgenus, in spite of, for instance, prolonged searches in experimental infections of *P. berghei*. It would be premature to conclude that the liver parenchyma is *not* the site of exoerythrocytic schizogony, but it seems more likely that the primary stages occur in more generalised mesodermal cells, in which they might well remain undetectable without the application of optimum techniques. There is another reason also for thinking that this tissue may be the developmental site : the duration of the pre-patent period was shown by the Belgian workers to be three days or less — such a period corresponds better to the length of the cryptozoic stages of avian parasites in macrophages than to the minimal five days required by primate species in the hepatic cells. Moreover, Wolcott (1957) considered *P. berghei* to be closer to the avian and saurian species of malaria parasites, because of the presence of two dot-like chromosomes of equal size in the nucleus of the schizont, in contrast to the unequal chromosomes of human species of parasites.

The malaria parasites of the three classes of vertebrates — mammals, birds and reptiles — exhibit some similarity in grouping, and we might expect to find certain types of subgenera reflected in each; certainly, this is true of the parasites of the birds and lizards. This new subgenus — *Vinckeia* — of mammals resembles the small avian parasites now classified under the subgeneric name of *Novyella,* although the shape of the gametocytes is different; possibly the course of evolution has taken the track from *Novyella* to *Vinckeia,* while *Haemamoeba* has led to *Plasmodium (Plasmodium)*.

BIBLIOGRAPHY.

Bray, R. S., Studies on the exo-erythrocytes cycle in the genus *Plasmodium,* Lewis, London, 1957.

Bray, R. S., Amer. J. Trop. Med. Hyg., 1958, **7**, 20.

Bray, R. S., Trans. Roy. Soc. Trop. Med. Hyg., 1963.

Bruce, D., Harvey, D., Hamerton, A. E. and Lady Bruce, Proc. Roy. Soc., B., 1913, **87**, 45.

Corradetti, A., Garnham, P. C. C. and Laird, M., Parasit., 1963, **5**, 1.

Garnham, P. C. C., Proc. 5th Internat. Congr. Trop. Med. & Malaria, Istanbul, 1953, **2**, 228.

Garnham, P. C. C., Proc. 6th Internat. Congr. Trop. Med. & Malaria, Lisbon, 1958, **6**.

Hemming, F., Opinions of Internat. Comm. Zool. Nomenclature, 1954, **7**, 226.

Huff, C. G., In « Advances in Parasitology ». Acad. Press, London, 1963.

Mudrow-Reichenow, L., Ärtzliche Forschung, 1950, **4**, 457.

Marchiafava, E. and Celli, A., Fortschr. Med., 1895, **11**, 24.

Sheater, A., J. Confr. Path. Therap., 1919, **32**, 223.

Wolcott, G., J. Protozool., 1957, **4**, 48.