

The Terminology of Parthenogenesis.

By

Sir Ray Lankester, K.C.B., F.R.S.

THE word "parthenogenesis" has become established in biological science to signify the production of offspring by a virgin mother. The term does not embrace reproduction by buds or by fission, but refers to parentage by a mother who produces egg-cells identical in character with those which, in the vast majority of instances, fuse with male sperm-cells before proceeding to develop. In those instances which are distinguished as instances of "parthenogenesis," the egg-cells proceed to develop *without* fusion with the male reproductive element or sperm-cell.

Parthenogenesis may accordingly be defined as an exceptional and historically super-induced modification of the normal process of sexual reproduction or gamogenesis in which the female gamete or egg-cell does not unite with a male gamete or sperm-cell to form a "zygote," but proceeds to develop independently.

The term should not be applied to reproduction by unfertilised unicellular "spores" common in the lower plants and Protozoa, nor to any cases except those in which the "parthenogenetic" reproductive cell is either (1) a normal egg-cell capable of sexual zygosis, or (2) demonstrably a comparatively recent modification of such an egg-cell. The latter is an important special group, and at one time these modified egg-cells—incapable of fertilisation—were incorrectly described as "pseud-ova" (Huxley). The egg-cell

thus independently developing may be described as "autoblastic" and the process as "autoblastesis." And again the autoblastic egg-cell may be described as "lipospermic" and the embryonic history as one characterised by "lipospermy" or "lipospermia."

A difficulty of nomenclature has lately arisen in describing and discussing the offspring so produced—for instance, when the eggs of the frog have been experimentally induced by the mechanical method of Bataillon (scratching with a needle) to develop so as to give rise to tadpoles, and even adult frogs, without fertilisation by sperm-cells. By oversight the tadpoles so produced have been referred to as "parthenogenetic," and by a similar error the broods of green-fly produced without the intervention of a male parent have been called "parthenogenetic young." Clearly the word "parthenogenetic" has been, and must be, used to describe the virgin mother, and therefore cannot at the same time be applied to her offspring without causing confusion. It seems to me that the word "impaternate," or "fatherless," should be used for the offspring. I have failed to excogitate any other term which will so well meet the case.

If we call individuals so produced "autoblastic"—a term applicable to the egg-cells which give rise to them—we leave it doubtful as to whether we may not be referring to their future reproductive capacity rather than to their origin; and if we call them "lipospermic" we may possibly intend by this word to indicate that they are devoid of male reproductive gonads, and not merely that no sperm-cells were concerned in their genesis. The term "impaternate" is readily intelligible and admits of no such ambiguity.

A further difficulty in regard to the nomenclature of virgin reproduction or parthenogenesis is that the word "virgin" and its Greek equivalent refer to the condition of the mother, and not to the history of the egg-cells which she produces and passes from her body. The "virgo intacta" is an adult female who has not been "covered" or "impregnated" by a male, or, to use another term, has not been

"mated." In most species of frogs and fishes, and in many other aquatic animals, the female parent is always a "virgo intacta." Such females are always "parthenogenetic" in the strict sense of the word. The fact that the eggs are not "autoblastic," but are fertilised after they leave the mother's body, does not alter her physiological condition or "status" in any way as compared with that of a mother whose eggs on being deposited by her are capable of "lipospermic" embryogenesis. She is never "mated" or "impregnated." The difference between her and the more familiar impregnated or fecundated mother arises from the persistence in the one case of the original and primitive method of free discharge of both the female and the male reproductive cells into the water in which the parents live, and, by contrast, the secondary development in the other case (comprising a vast variety and number) of arrangements for the fertilisation of the egg-cells while still actually within the protective body of the mother or in close contact with it. These secondary developments are determined by the fact (1) that they favour both economy and certainty in the operation of the male gametes or spermatozoa, and (2) by their provision of advantageous maternal protection to the minute egg-cells and the early stages of their growth when fertilised. It is obvious that in non-aquatic animals intra-maternal fertilisation of the egg-cells is obligatory.

The egg-cells which are freely discharged and fertilised by free-swimming sperm-cells "in the open" may be called "planktogamic" (plankton = freely swimming), whilst egg-cells which are subjected to the secondary protective arrangements may be called either "hysterogamic" (hysteron = uterus), if fertilised within the oviductal chamber of the mother, or "propylogamic" (propylon = a gateway), if fertilised on the surface of the mother's body or in immediate relation thereto (as in the case of many Crustacea and of some Amphibia).

There is no word in use to indicate the physiological status of an adult female which is no longer a "virgin," but has been

"mated" or "covered," and has received into her oviduct sperm-cells from a male. We might designate such a female as a "mate" in contrast to a "virgin," but "mate" is in ordinary use for any kind of comrade. Though the words "wife" and "spouse" have too definite a reference to human legal and social status, yet the Latin word "conjux," implying as it does a "conjugium" (the significance of which is given in Virgil's account of wind-fertilised mares, "sine ullis conjugii vento gravidæ"), may well be used as the antithesis of "virgo." Any female bearing hystero-gamic egg-cells is accordingly a "conjux," whilst one discharging "plankto-gamic," or it may be "propylogamic," egg-cells is a "virgin."

The existence of "hystero-gamesis" leads on to that phenomenon which was by Aristotle regarded as a highly important "differentia" in the classification of animals, and is loosely described as "viviparity." Animals which pass a large part of their embryonic growth within the mother's body and are born naked and with much of the shape and locomotive capacity of the adult are called "viviparous." But really all animals are viviparous, for the birth product is a living thing whether it is a naked egg-cell or more or less advanced in development. The enclosure of the birth-product in a shell or case, which has given rise to the term "oviparous," is not of any value as indicating the real degree of development of the young at birth, for in some cases unfertilised egg-cells, in others mere discs of developing embryonic cells (as in birds, etc.), and in yet other cases well-shaped young ranging from the early larva up to the completely formed miniature of the adult, as in some of the shell-bearing snails, may be enclosed within an egg-shell when "laid" by the mother. There is accordingly no great general importance to be attached to the distinction between "viviparous" and "oviparous" animals. The egg-shell has, of course, its protective value, but the exact phase and nature of the living thing within it must be considered in any comparison of the reproductive processes of different animals.

I may now show how far the considerations and the des-

criptive terms here suggested apply to certain typical cases of what is usually called parthenogenesis, but is better designated "autoblastesis" or "lipospermia."

(1) The greenflies, or Aphides, are, as are all insects, characteristically hystero-gamic. They are propagated by males and mating females (conjuges) in autumn. But the spring and summer broods are females only. They are virgins, and produce true egg-cells which are autoblastic and develop into impaternate females (lipospermia or parthenogenesis). These impaternate females in their turn produce impaternate females, and this process may continue for several generations. The egg-cells of these virgin mothers are modified and enclosed so as to be incapable¹ of zygosis, whilst the maternal structures connected with hystero-gamesis (intra-maternal fecundation) are aborted, although the intra-uterine gestation is retained and the young are born naked in a fully formed condition, and are accordingly said to be "viviparous."

(2) The phyllopod Crustacean *Apus* normally gives birth to egg-cells encased each in a delicate egg-shell. These are autoblastic, and produce with very rare exceptions only impaternate females. At rare intervals, owing to conditions not ascertained, a few impaternate males are hatched from some of the eggs, and "propylogamic" fertilisation of the eggs of some of the virgin mothers of the same generation then takes place.

(3) The breeding queen bee (*Apis*) and the breeding queens of some other hymenopterous insects are at the same time both parthenogenetic and gamogenetic! They are definitely "conjuges," or mated females, but some of their eggs are hystero-gamic and give rise to females only, whilst others are agamic (lipospermic) and give rise by autoblastesis to impaternate males (drones) only. This remarkable double character of the "queen" is due to the fact that the sperm-cells of the drone received and stored by her in her spermatheca can be withheld from contact with the egg-cells about to be laid or

¹ Possibly a skilful experimentalist might succeed in artificially fertilising these eggs with the appropriate spermatozoa.

admitted to them according to circumstances. Fertilisation of the egg-cell is (to use a French term) "facultative."

(4) Silkworm moths and some other female Lepidoptera sometimes lay eggs without having mated or come into contact with a male. Not infrequently these eggs, which in normal conditions should be hysterogamic, proceed to develop by autoblastesis, and produce impaternal males and females. This lipospermic reproduction is stated to have been experimentally carried out through three successive generations. The autoblastesis can be favoured, if not determined, by brushing the shell of the egg with a camel's-hair pencil.

(5) The female of the common frog is in all circumstances a "virgin." Her eggs are planktogamic. The eggs of some other Amphibia may be propylogamic or even hysterogamic. When received into carefully purified water, the unfertilised eggs of the common frog, which are naturally enveloped, each in a jelly-like coat, can be caused to enter upon the curriculum of cell-division and embryonic growth by scratching the surface of the dark-brown egg-cell with a needle. The impaternal offspring thus produced have been reared to late stages of the tadpole phase, and more rarely to the adult form. The impaternal or fatherless young thus reared have, so far as present records stand, always proved on examination to be males.

(6) Female bony fishes with a few exceptions, such as the viviparous blenny, are, like the female frog, virgins. Their eggs are planktogamic—that is to say, are fertilised when floating in the water.

Other cases of lipospermia or autoblastesis, such as those revealed by the experiments of Loeb, Deslages, and others, could, I think, be with advantage summarised by the use of some such nomenclature as that here suggested. Autoblastesis is contrasted with gamoblastesis, but its occurrence is not "spontaneous." It depends upon either mechanical or chemical conditions which could be enumerated and classified.

[The present article is a revision of one which was printed in 'Nature,' August, 1917.—E.R.L.]