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Parthenogenesis

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'Behold, a virgin shall conceive, and bear a son, and shall call his name Immanuel.' The most famous reference to virgin birth is actually based on a mistranslation, for the Hebrew word *almah*, in Isaiah 7, 14, means a young woman, and not necessarily a virgin. In the New English Bible the quotation begins: 'A young woman is with child.'

In non-human mammals also claims of virgin births have not so far withstood the rigours of scientific examination. Nevertheless, parthenogenesis is a phenomenon of undoubted biological interest which leads to the production of living young in many types of animals, as well as in plants. White (1977) has estimated that the proportion of animal 'species' which reproduce exclusively by parthenogenesis, and are therefore all female, is of the order of one in a thousand. Parthenogenesis may initiate early embryonic development in mammals, and its lack of success in this class poses some fundamental and as yet unresolved problems regarding the significance of fertilisation in the physiology of reproduction and embryonic development. This is one of the reasons why parthenogenesis is once again an area of active research.

An individual resulting from the development of an unfertilised egg is variously referred to as 'parthenogenone', 'parthenogen', or 'parthenote'. The last term is American, while 'parthenogenone' is preferred in the British literature (Graham, 1974).

Definitions of parthenogenesis

The fact that in certain animals, females may produce eggs capable of development without previous copulation has been known for a long time and was called *'lucina sine concubitu'*. The term 'parthenogenesis' is due to Richard Owen (1849) who defined it as 'procreation without the immediate influence of a male'; this includes various processes such as fission and budding in addition to the development of unimpregnated ova. Several authors have since attempted to redefine the term.

According to Suomalainen (1950) parthenogenesis means 'the development of the egg cell into a new individual without fertilization', and this simple definition is adequate for many lower animals. In other animals, however, embryos produced without fertilisation suffer a high mortality, a fact that is reflected in the definition of parthenogenesis by Beatty (1957) as 'the production of an embryo from a female gamete without the concurrence of a male gamete, and with or without eventual development into an adult'. Beatty (1967) subsequently modified this definition by substituting 'without any genetic contribution from a male gamete' for 'concurrence of a male gamete'. The purpose of thus extending the definition was to include the special case of gynogenesis, in which a spermatozoon enters an egg and activates it to complete the second meiotic division and to develop into an embryo, but does not contribute any chromosomal material (see below). Whether or not this process should be included within the province of parthenogenesis is clearly a matter of choice.

It will be clear, however, that parthenogenesis does not necessarily imply that the mother has had no access to a male. In different groups of animals both fertilised and unfertilised eggs of the same female may proceed to form embryos. For instance, in aphids parthenogenetic generations alternate with others in which fertilisation takes place. This is known as 'cyclical parthenogenesis'. In bees an egg may be either fertilised or develop parthenogenetically. This process is known as 'facultative parthenogenesis'. Indeed, the possibilities for parthenogenesis in the life cycle of different types of animals are many and varied. This subject has been reviewed by Suomalainen (1950), by Narbel-Hofstetter (1964), and by White (1973, 1978). Parthenogenesis in plants has been discussed by Stebbins (1950) and by Nygren (1954).

On any definition, however, parthenogenesis is distinct from asexual reproduction since it involves the production of egg cells, whereas in asexual reproduction new individuals are formed from somatic cells of the parent. As will be shown below, parthenogenesis can occur in the absence of meiosis, so that the

egg will have the same chromosome constitution as the mother. For this reason, the processes are sometimes equated, particularly in the literature of theoretical genetics (Maynard Smith, 1971; Williams, 1975). From a physiological point of view, however, the processes are different since an egg is a specialised reproductive cell which exerts an undoubted influence on the development of the embryo. Parthenogenesis is, therefore, better regarded as an incomplete form of sexual reproduction.

Lastly, parthenogenesis must be distinguished from hermaphroditism, that is the production of male and female gametes by the same organism. Some hermaphrodites are capable of self-fertilisation, but this process, involving as it does the union of male and female gametes, is clearly distinct from parthenogenesis.

Nuclear fusion is not a bar to parthenogenesis, provided both nuclei are of the same gametic sex, that is female, as exemplified by the fusion of the egg nucleus and a polar body. This process is known as 'automixis', whereas the term 'amphimixis' relates to the fusion of male and female gametes. Development of a new individual in the absence of amphimixis is known as 'apomixis'. This term, however, has been defined in different ways by different authors. According to Beatty (1957), apomixis in animals is synonymous with parthenogenesis, whereas White (1977) restricts the term to parthenogenesis in the complete absence of meiosis. The term 'apomixis' is commonly used with reference to plants and here modes of reproduction other than parthenogenesis may be included (Suomalainen, 1950). The process of sexual reproduction in plants differs from that in animals, since in plants a diploid sprophyte generation alternates with a haploid gametophyte generation, and so the breakdown of fertilisation may have different consequences. In the present review the term 'apomixis' will henceforth be avoided.

Haploid, diploid, and polyploid parthenogenesis

Parthenogenetic development may proceed by various routes depending on whether meiosis of the egg cell is completed normally or, failing this, which of the stages has been omitted. Alternatively, meiosis may be completely suppressed and the egg develop as a result of mitotic divisions only. The number of chromosome sets in the embryo can further be varied by failure of cell division as a result of DNA synthesis, either before meiosis or afterwards, in what would otherwise have been a cleavage division. This process is known as endoreduplication. Different routes of parthenogenetic development are illustrated in Fig. 1. Their genetic implications have been discussed by Beatty (1957) and by Uzzell (1970).

If a diploid oogonium completes the two meiotic divisions and continues development in the absence of nuclear fusion, the resultant embryo will be haploid, at least initially. As will be shown below, the somatic cells of such embryos may subsequently become diploid or polyploid.

Haploid parthenogenesis has been achieved experimentally, particularly in amphibia. In this class also, artificial fertilisation with sperm which had been previously inactivated with *x*-rays has led to the production of gynogenetic embryos. Such embryos resemble those produced by parthenogenesis in not possessing any paternal chromosomes, but they differ in the mode of origin and possibly also in the possession of non-nuclear material derived from the sperm.

Haploid parthenogenesis forms part of the sex determining mechanism in certain insects, spiders, and rotifers in which males are formed from haploid, unfertilised eggs, whereas diploid, fertilised eggs give rise to females.

Diploid or polyploid parthenogenesis can proceed via a number of routes, some of which are illustrated in Fig. 1. Diploid eggs may be formed by the suppression of either the first or second polar bodies. Alternatively, polar bodies may be extruded and subsequently fuse with the egg cell. The second meiotic division may be completed without extrusion of the second polar body and the resultant diploid egg cell then undergoes cleavage. It is also possible, however, that the two products of the second meiotic division are separated by immediate cleavage, thus initiating haploid parthenogenesis (Witkowska, 1973a). If neither polar body is extruded, the resulting egg would be tetraploid, since the primary oocyte contains the duplicated number of chromatids in preparation to undergoing two meiotic divisions.

Since homologous chromosomes normally segregate during the first meiotic division, suppression of the second polar body will result in the egg receiving either two paternal or two maternal partners of any pair of chromosomes, though some recombination will have occurred as a result of crossing-over. This process can be achieved in mammals experimentally (see below). Since crossing-over occurs during prophase in the primary oocyte, recombination is likely to have occurred even in cases where the first polar body has been suppressed. However, if diploid parthenogenesis occurs via the route of premeiotic chromosome doubling, the first meiotic division occurs with the diploid number of bivalents. In some species it is known that pairing is restricted to sister chromosomes. Therefore, in spite of the fact that meiosis is completed, no effective crossing-over takes place.

Diploid parthenogenesis can also arise from a normally reduced haploid egg which develops in the

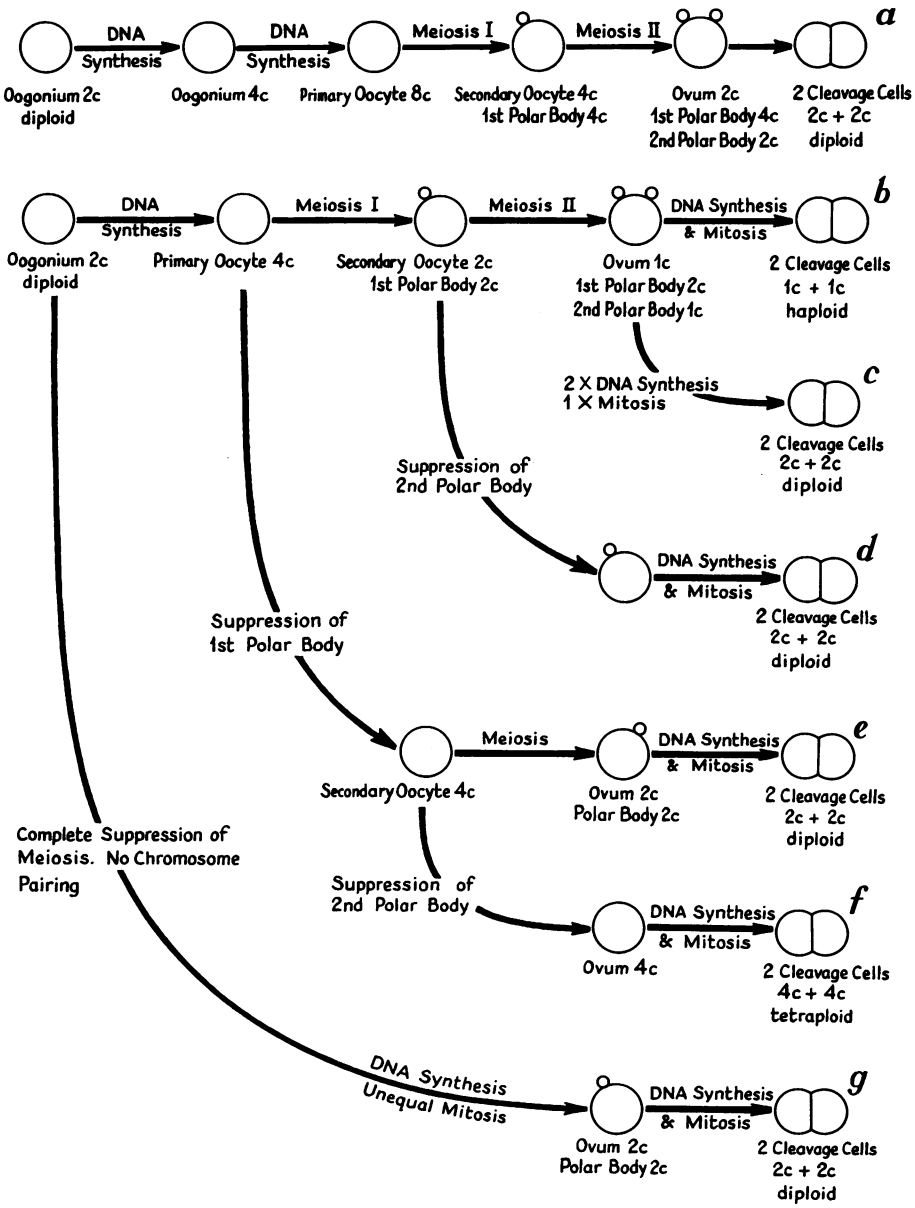

Fig. 1 *Different routes of parthenogenesis in diploid females. (a) Premeiotic endoreduplication; (b) development of normally reduced egg; (c) postmeiotic endoreduplication; (d) suppression of 2nd polar body; (e) suppression of 1st polar body; (f) suppression of 1st and 2nd polar bodies; (g) ameiotic parthenogenesis. Additional routes are described in the text. The symbol* c *refers to the amount of DNA present in the chromosomes of a haploid cell before DNA synthesis. If parthenogenesis were to occur in a polyploid female, routes (a) and (g) would result in similarly polyploid daughters.*

absence of fertilisation and in which the first cleavage division is suppressed. The same process occurring in a diploid egg would result in tetraploid parthenogenesis. A diploid egg which is fertilised in the normal way would give rise to a triploid embryo.

Diploid egg cells can be formed in which meiosis has been completely suppressed. In this system the homologous chromosomes of the oocyte fail to pair and no crossing-over takes place. One mitotic division gives rise to a diploid egg and a single polar body

(Darlington, 1958). The chromosome constitution of the egg will, therefore, be exactly the same as that of the mother, apart from the rare occurrences of mutations and chromosomal changes.

As was pointed out by White (1978), ameiotic parthenogenesis removes all those restraints that meiosis normally imposes. As a result successful reproduction can be achieved by triploid and aneuploid forms, as well as by heterozygotes for chromosomal rearrangements, provided they are capable of undergoing mitosis. This mechanism can also serve as a stable reproductive process in species hybrids. The same considerations apply to the process of meiosis following premeiotic chromosome doubling, if pairing is restricted to sister chromosomes so that no effective recombination takes place. Parthenogenesis in the absence of recombination resembles asexual reproduction in that the chromosomes of the offspring are faithful replicas of the maternal ones. Nevertheless, the lack of meiosis or recombination is clearly a secondary effect which is superimposed on the sexually differentiated oocyte in the absence of fertilisation. Thus, even ameiotic parthenogenesis is not synonymous with asexual reproduction. Though both fertilisation and recombination have been abandoned, the production of specialised egg cells has been maintained. In as much as the new organism originates in an egg, its early development resembles that of a zygote.

Parthenogenesis and sex determination

Whenever sex is determined by the chromosome constitution, offspring produced by parthenogenesis in the absence of effective meiosis will all be female (if we exclude the possibility of non-disjunction giving rise to XO males). Any system of parthenogenesis in which females give rise exclusively to females is known as 'thelytoky' (from the Greek meaning 'giving birth to a female child').

The opposite situation in which parthenogenesis leads to the production of exclusively male offspring is called 'arrhenotoky' ('giving birth to a male child'). This term is generally applied to the haploidiploid system of sex determination, particularly well known in bees, in which males originate by haploid parthenogenesis while diploid females are produced by fertilisation in the normal way. The production of diploid males by parthenogenesis has been reported in birds (see below). In this class the female is the heterogametic sex.

Lastly, parthenogenesis may give rise to both males and females. This condition is known as either 'deuterotoky' or 'amphitoky' (see Suomalainen, 1950). All four terms date from the late nineteenth century.

Some examples of parthenogenesis in invertebrates

THELYTOKY IN INSECTS

The formation of female parthenogenetic offspring is widespread among many order of insects. Thelytoky may be obligatory, being apparently the sole mode of reproduction, as in some stick insects belonging to the order Phasmida and in certain Diptera and Psychids (Lepidoptera—see below); it may be an occasional occurrence in species in which fertilisation occurs normally; or there may be a regular alternation of generations when individuals produced by thelytokous parthenogenesis finally give rise to sexually produced ones. The last process is known as 'cyclical parthenogenesis' and is best known in aphids (greenfly). The subject has been reviewed by White (1973).

Thelytoky in Diptera is of interest because the presence of polytene chromosomes in the salivary glands gives information on the cytological state of parthenogenetic species. White (1973) lists a total of 17 species which appear to reproduce solely by parthenogenesis. All 12 species in which data on polytene chromosomes were available were found to be heterozygous for at least one chromosomal inversion. Moreover, 7 of the 12 species were triploid. In some of the species there was no evidence of meiosis, in others meiosis took place and was followed by automixis. The latter group includes a member of the Drosophilidae, *Drosophila mangabeirai*. Structural heterozygosity is maintained by the fusion of non-sister nuclei resulting from the second meiotic division.

It should be added that in populations with obligatory parthenogenesis the term 'species' is not entirely appropriate, since males are absent and breeding does not take place. It seems that thelytokous parthenogenesis may be a means of perpetuating certain chromosomal arrangements, such as structural heterozygosity or triploidy, in groups of organisms in which this mode of reproduction leads to the formation of viable offspring. The findings of Basrur and Rothfels (1959) on the blackfly, *Cnephia mutata*, support this view. Diploid individuals consisted of males and females in approximately equal numbers, whereas triploid invididuals were all female and were thought to reproduce parthenogenetically. Investigations of salivary gland chromosomes showed that triploid larvae were highly heterozygous for chromosome inversions and that such inversions were absent from the diploid individuals. Thus, though the two types occurred side by side, it appeared that no breeding occurred between them.

Parthenogenesis is known to occur in many species of *Drosophila*, though this process usually results in embryonic death. In *D. parthenogenetica* a small proportion of eggs laid by virgin females completes their development to produce adult offspring. The large

majority of these flies are females, which may be diploid or triploid (Stalker, 1954). A few contain both diploid and triploid cells. The production of triploid daughters from unfertilised mothers is evidence that meiosis leading to the formation of haploid nuclei had taken place. In addition, a small number of sterile diploid males were produced, which proved to have XO sex chromosomes.

The proportion of viable offspring from diploid virgin females could be much increased by selection. In Stalker's original strain 0·9% of unfertilised eggs started development and of these 9% formed viable larvae. After 17 generations of selection these proportions had risen to 8% and 19%, respectively. The fertility of triploid virgins was lower. After 6 to 8 generations only 0·9% of eggs began development and 19% of these survived. Keeping the flies at a higher temperature also resulted in an increased proportion of offspring by parthenogenesis, though the effect was less pronounced. In another species, *D. mercatorum*, Carson (1967) obtained a sixtyfold increase in the rate of diploid parthenogenesis leading to viable female offspring following hybridisation between strains and selection. The resulting stocks could be maintained in the absence of males.

Thelytoky occurs sporadically in many groups of insects belonging to the Orthoptera. A particularly instructive example is the parthenogenetic grasshopper *Warramaba* (formerly *Moraba*) *virgo* whose cytogenetics have recently been worked out by White *et al.* (1977). The species consists of females only. The diploid chromosome number is 15 and various chromosome arms are heterozygous for fixed structural rearrangements. This heterozygosity is transmitted from mother to daughter by a mechanism of meiotic thelytoky: the chromosome number doubles before meiosis and pairing takes place between sister chromosomes.

Although it was originally thought that the structural heterozygosity had gradually built up since the adoption of the parthenogenetic mode of reproduction, Hewitt (1975) suggested that *W. virgo* had arisen by hybridisation between two as yet undescribed species, provisionally designated as 'P169' and 'P196', respectively, and evidence presented by White *et al.* (1977) supports this hypothesis. Crosses between P169 females and P196 males resulted in some viable female hybrids with a diploid number of 15 chromosomes (8 derived from P169 and 7 from P196) which were essentially similar to the standard karyotype of *W. virgo*. Moreover, when *W. virgo* females were crossed with males of P169 or P196, triploid hybrids of both sexes were obtained. The males were sterile, but the females produced a further generation of female progeny by parthenogenesis by the route of premeiotic chromosome doubling. The parthenogenetic mode of reproduction in *W. virgo* can thus be explained as a necessary adaptation by a structurally heterozygous hybrid for the production of viable offspring, even though the cellular events leading to premeiotic doubling are not yet understood.

Thelytoky is also known in Hymenoptera, in Coleoptera, and in Lepidoptera (White, 1973). The beetle, *Adoxus obscurus* (order Coleoptera) consists of diploid males and females in North America and of triploid parthenogenetic females in Europe. Lokki *et al.* (1976a) studied the genetic variability at 16 enzyme loci in 52 Scandinavian triploid populations and found that 80% of all beetles had the same genotype, while the remainder consisted of 6 different genotypes. This low level of variability contrasts with the situation found in a weevil, *Polydrosus mollis*, examined by Lokki *et al.* (1976b). Of 52 parthenogenetic populations, 2 were found to be diploid and the rest triploid. Enzyme studies carried out among 69 triploid individuals from Finland and Sweden revealed the existence of 21 different genotypes.

Among Lepidoptera, thelytokous parthenogenesis has been described in the Psychidae, or bagworms, moths in which the females are wingless, though the males are swift fliers. The occurrence of parthenogenesis in this family was described by von Siebold in 1856, at a time when the role of the spermatozoon in fertilisation was still entirely unknown. One of the species mentioned by von Siebold, *Solenobia triquetrella*, has been investigated by Seiler (1963). Three main forms may be distinquished: (1) diploid fertilising; (2) diploid thelytokous; (3) tetraploid thelytokous. The diploid chromosome number is about 60.

Experimentally induced parthenogenesis has been described in the silkworm *Bombyx mori* (reviewed by Tazima, 1964; Strunnikov, 1975). However, the offspring thus produced will not necessarily be all female, since in the Lepidoptera, to which the silkworm belongs, the female is heterogametic, so that some parthenogenetic routes will result in males. When silkworm eggs were treated with hydrochloric acid, meiosis was thought to proceed normally but diploid males as well as females resulted. The males, which were mostly homozygous, were thought to arise by fusion of two cleavage nuclei, while the most likely origin of females is by the fusion of an egg with a polar body. By contrast, heat treatment of eggs resulted in all female offspring, either by suppression of the first polar body, if the eggs had been laid, or by ameiotic parthenogenesis in eggs which had been dissected out.

Earlier reports of parthenogenesis in different species of Lepidoptera have been reviewed by Cockayne (1938).

THELYTOKY IN OTHER INVERTEBRATES

The brine shrimp, *Artemia salina*, which belongs to

the order Crustaceae, is one of the best known invertebrates reproducing by thelytokous parthenogenesis. The 'species' (also referred to as 'superspecies' or 'biotype'), which occurs only in waters of high salinity, has been investigated by many cytologists with somewhat varying results. The topic has been reviewed by White (1973).

In some strains fertilisation is obligatory, while in others females reproduce by parthenogenesis. It appears that in both cases the diploid chromosome number is 42 and that 21 bivalents are formed also in parthenogenetic females. The exact route by which diploid eggs are produced in these females is uncertain. Polyploid forms have also been described, but these appear to be mostly ameiotic.

Polyploidy also occurs in earthworms (Muldal, 1952; Omodeo, 1955). The order of Oligochaetes to which earthworms belong is basically hermaphrodite; the usual mode of reproduction is cross-fertilisation between two hermaphroditic individuals. The thelytokous condition seems to have been secondarily derived by suppression of testicular development. In some parthenogenetic forms, however, sperm is still formed and may be necessary to activate the egg into normal development, though nuclear fusion does not take place (Christensen, 1961). Though parthenogenesis is widespread among polyploid earthworms it is not obligatory in this group, since cross-breeding takes place in many polyploid species. In the family Lumbricidae, which has been the most widely investigated, four different genetic systems have been described (Omodeo, 1955; White, 1973): (1) diploid fertilising; (2) polyploid fertilising; (3) polyploid without nuclear fusion; and (4) polyploid automictic. In the last group, meiosis is thought to be preceded by a doubling of the chromosome number, a route allowing regular segregation of chromosomes even in triploid or pentaploid karyotypes.

The flatworms also are normally cross-fertilising hermaphrodites and parthenogenetic forms are common in this class. By contrast, parthenogenesis seems not to occur in the hermaphroditic order of Pulmonata which includes the majority of snails (White, 1973).

Parthenogenesis occurs in some nematodes. *Aphelenchus avenae* is normally a parthenogenetic species consisting of females only. However, Hansen *et al.* (1972) found that eggs kept at high temperatures (30°C to 32°C) would develop into males. Male development could be prevented by the action of mitomycin C which resulted in the production of adult females at 30°C (Buecher *et al.* 1974). Since mitomycin C is an inhibitor of DNA synthesis, these findings support the hypothesis that in *Aphelenchus avenae* male development requires a burst of mitoses at a critical time of development (Mittwoch, 1969).

CYCLICAL PARTHENOGENESIS IN APHIDS

The parthenogenetic modes of reproduction which have been described so far occur either sporadically in species which normally reproduce sexually, or parthenogenesis may have become the accepted mode of reproduction often in species which are hermaphroditic, or where the existence of polyploidy would lead to difficulties in meiosis. In cyclical parthenogenesis, generations consisting of females only are succeeded by one in which both males and females are present and fertilisation takes place; this usually coincides with the onset of winter. The situation is best known in aphids (greenfly—order Hemiptera) and in gallwasps (order Hymenoptera), most of which are parasites on oak trees.

The life cycle of the aphid *Tetraneura ulmi*, a member of the aphids, has been described by Schwartz (1932) (see Fig. 2). During May in Europe, small wingless olive-green females make a gall each on the leaves of elm trees. The female known as 'fundatrix' remains in the gall all her life and produces up to 40 winged young. All are female and viviparous; indeed, they are pregnant before birth. Known as 'emigrantes', they fly to the roots of grasses where they give birth to a generation of 'exules', wingless females, which for a while may give rise to similar individuals to themselves. Eventually, however, during late summer, a winged generation is born which again fly to elm trees. The 'sexuparae' are all females, but each one is capable of giving rise to both male and female offspring, the 'sexuales'. The females are yellowish brown and the males which are smaller are green. They hatch in the bark of the trees and eventually copulate. A fertilised female lays a single egg which is two-thirds her body size. After laying the egg the female dies and the egg winters in the bark. The fundatrix emerges in the spring, makes her way to the leaves of the elm, and starts the cycle once more.

The diploid chromosome number of females is 14 and that of males 13. Females have XX sex chromosomes, while males are XO. The chromosomes are distinguishable by size.

During the development of parthenogenetic eggs, only a single polar body is formed; the division of the chromosomes appears to be lengthwise, as in an ordinary mitosis. Eggs destined to develop into males also undergo a single division, in which the autosomes are thought to divide lengthwise, while one of the X chromosomes passes undivided into the polar body.

During spermatogenesis two meiotic divisions occur. The first is unequal, giving rise to a secondary spermatocyte and a small cell which degenerates. The single X chromosome passes into the secondary spermatocyte, which on completion of the second meiotic division gives rise to two female-determining

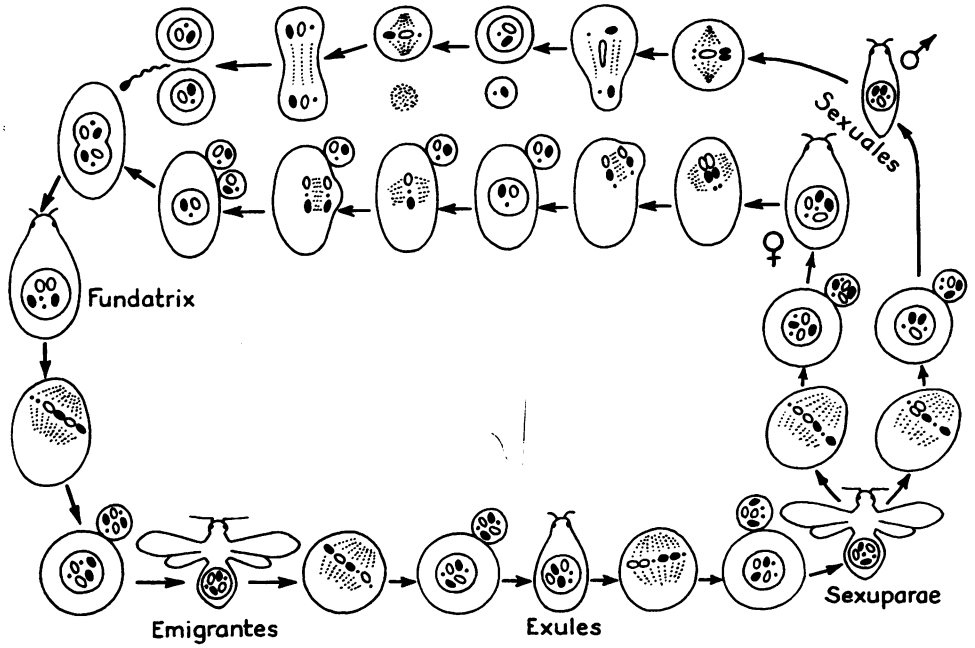

Fig. 2 *Life cycle in the aphid,* Tetraneura ulmi. *Three pairs of chromosomes have been drawn, of which one is monosomic in the male. From Schwartz (1932).*

spermatozoa. The oocytes of the female sexuales also undergo two meiotic divisions, giving rise to eggs containing the haploid chromosome number including an X chromosome.

Tetraneura ulmi is an outstanding example of a species in which individuals can vary in such fundamental characteristics as presence or absence of wings (Fig. 3), type of foodplant, size and colour, as well as the presence or absence of fertilisation, all within the framework of the same chromosome constitution. The only chromosomal difference is that between the two sexes. The phenotypic differences shown by the various female generations suggest that cytoplasmic and environmental differences may account for a large amount of such variation. That various environmental agents may affect wing production in aphids has been claimed (see Morgan, 1919).

The life histories of other species of aphids are essentially similar to that found in *Tetraneura ulmi*, though differences in detail may occur. In some the sexual stage has been lost altogether so that parthenogenesis has become obligate rather than cyclical, while in certain species of *Phylloxera* studied by Morgan (1912) there are two kinds of sexuparae which give

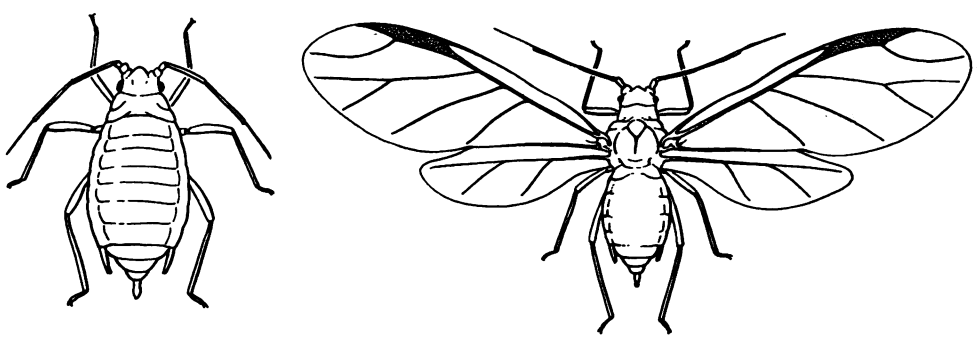

Fig. 3 *Winged and wingless forms in the reproductive cycle of an aphid. From Morgan (1919).*

rise to males and females, respectively. The eggs differ in size as well as in chromosome number, the male-producing eggs being smaller than those which develop into females, but the cytogenetical phenomena which precede the formation of these eggs have still not been elucidated (White, 1973).

HAPLOID PARTHENOGENESIS (ARRHENOTOKY) IN HYMENOPTERA

Parthenogenesis is more widespread among Hymenoptera than any other order of animals. It is best known in the honey bee, *Apis mellifera*.

Aristotle knew not only that bees could procreate without copulation, but also that the offspring so produced were different from their mothers (see White, 1973). That unfertilised eggs give rise to males and fertilised eggs to females was discovered more than a hundred years ago by Johann Dzierzon, who was pastor in Carlsmarkt, Silesia. Dzierzon described his findings in a book on the theory and practice of bee breeding, published in 1848.

When a queen bee is mature she undertakes one or several nuptial flights and mates with a drone high up in the air. Henceforth, the queen is able to lay two types of eggs, fertilised and unfertilised, apparently at will. However, as noted by Dzierzon, the unfertilised eggs are laid into special drone cells which are wider and deeper than the cells in which worker bees develop.

The sperm is stored in the queen's spermathecae and lasts throughout her reproductive life. If an unfertilised egg is to be laid it must pass down the oviduct either without meeting any sperm or, if sperm should be present, fertilisation must somehow be prevented (Butler, 1962).

An egg which has been fertilised may develop either into a worker or queen bee. Queens are reared in special, large cells called 'queen cups' and the larvae are liberally fed with special food known as 'royal jelly'. It seems, however, that even ample supplies of royal jelly do not necessarily lead to the production of queens in the laboratory (Butler, 1962), and unequivocal evidence on the nutritional requirements leading to the development of queens rather than workers is still lacking (Weaver, 1974). It has been established, however, that for the first three days a female larva can be made to develop into a queen or worker by transferring her into an appropriate cell in the hive.

As pointed out by White (1973), a male bee has only one parent, while a female has two; but females have only three grandparents, five greatgrandparents, etc. Since a drone receives all his chromosomes from his mother, all his genes should show the sex-linked mode of inheritance, and in general this condition is fulfilled (Rothenbuhler, 1958). Nevertheless, in spite of their origin from a haploid egg, the majority of a drone's body cells are not haploid. In the growth of insects mitotic divisions play only a partial role. A large part of the often very rapid increase in size can be accounted for by the process of endoreduplication which results in the formation of large polyploid cells in many tissues (White, 1973). Mittwoch *et al.* (1966) found that the interphase cells of worker larvae aged between 10 and 20 hours ranged between diploid and 16-ploid, while corresponding drone cells varied between haploid and 32-ploid. However, most of the mitoses were diploid in the female larvae and haploid in the males. Very similar results have recently been reported by Rasch *et al.* (1977) in two other species of Hymenoptera. Dividing cells of male and female embryos of *Habrobracon juglandis* and of *Mormoniella vitripennis* were haploid and diploid, respectively. However, in adults both sexes had equivalent ploidy levels. Haemocyte and brain cells were either diploid or tetraploid, while Malpighian tubule cells ranged between octoploid and 32-ploid in both males and females. Mello and Takashashi (1971) reported higher levels of polyploidy in the nuclei of queen larvae compared with those of workers.

The way in which haploid and diploid cells give rise to male and female development, respectively, provides a challenge to our understanding of chromosomal mechanisms of sex determination. Heterozygosity versus hemizygosity at certain chromosomal regions might be one of the factors involved, since diploid drones have been produced by artificial inbreeding (Woyke, 1963). In addition, we may be dealing with general effects of the chromosome constitution on mitotic rates and growth (Mittwoch, 1973); diploid drones have much smaller testes than haploid ones (Woyke, 1974) and they apparently produce diploid spermatozoa (Woyke, 1975).

Parthenogenesis in vertebrates

Present-day interest in experimentally induced parthenogenesis is centred mainly on work in mammals, though many of the available techniques were first used on frogs as well as sea urchins.

The classical technique for obtaining embryos without a paternal set of chromosomes used inactivated spermatozoa. This process which is known as 'gynogenesis' or 'pseudogamy' will be described first.

GYNOGENESIS IN FISH AND AMPHIBIA

Oscar Hertwig (1911) discovered the apparently paradoxical effect when frog eggs were fertilised with irradiated sperm. Sperm treated with low doses of radium gave rise to normal offspring, while higher doses of radium resulted in abnormal embryos. However, when the dose of irradiation was further

increased the eggs once again gave rise to near normal embryos. Hertwig interpreted these results by assuming that the high doses of radium destroyed the chromosomes of the sperm and that the development of the eggs was a type of parthenogenesis. Essentially similar results were obtained by Gunther Hertwig (1924) as a result of 'fertilising' amphibian eggs with irradiated sperm from a different species. True hybrids between the toad *Bufo vulgaris* and the frog *Rana fusca* died before the gastrula stage, but if the frog sperm had been irradiated, the embryos developed more or less normally into haploid larvae. Gunther Hertwig (1924) showed subsequently that haploid larvae could be obtained also by treating sperm with trypaflavin (3,6 diaminoacridinium chloride). Briggs *et al.* (1951) obtained typical haploid larvae by the action of sperm from the bullfrog, *Rana catesbeiana*, treated with toluidine blue, with eggs from the leopard frog, *R. pipiens*. Similar results were obtained by irradiating the *Catesbeiana* sperm with *x*-ray doses of at least 65 000 R, while untreated sperm gave rise to invariable hybrids. The ploidy of the embryos was determined from ectoderm cell size.

Recently Jones *et al.* (1975) reported that in *Xenopus laevis* treatment of spermatozoa with ethyleneurea induced abnormalities in the resulting embryos, but that the frequency of abnormalities decreased with increasing doses of the chemical. With high doses haploid embryos resulted. Gynogenesis has been described in several species of fish. In populations of the 'silver fish', *Carassius auratus giblio*, which is native in Eastern Asia and is thought to be the ancestral form of the goldfish (*C. auratus auratus*), Lieder (1955) found males to be rare or absent. When eggs were artificially 'fertilised' with sperm from the related species *C. carassius*, young fish developed which had all the characteristics of *C. auratus giblio* and none of the paternal species.

An essentially similar situation has been described in the Amazon molly, *Poecilia formosa*, an all-female species native in Texas and Mexico (Schultz and Kallman, 1968). In the northern part of their range, fertilisation is achieved by males of *P. latipinna* and in the southern part by a species of the *P. sphenops* complex. *Poecilia formosa* has been maintained in laboratories for many generations, where it could be confirmed that reproduction is almost invariably by gynogenesis. Since the males do not contribute any chromosomes to the offspring, all the offspring of a given female behave as if they were a clone, and several such clones which differ in histo-incompatibility characteristics are in existence. However, in the Genetics Laboratory of the New York Aquarium a total of 18 hybrids was obtained, representing about 1% of the offspring, by using either *P. sphenops* or *P. vittato* as the paternal species. The hybrids proved to be triploid which strongly suggests that they originated from diploid eggs.

Triploidy has also been observed in field populations associated with *P. formosa* and here it is assumed that *P. mexicana* provided the third set of chromosomes (Prehn and Rasch, 1969). Balsano *et al.* (1972) found that *P. mexicana, P. formosa*, and the triploids could all be distinguished on the basis of electrophoretic variants of plasma proteins. Their data suggested that triploid individuals comprised a significant, though variable, proportion of at least five natural populations of *P. formosa*.

OTHER TYPES OF PARTHENOGENESIS IN FISH AND AMPHIBIA

In the guppy, *Poecillia reticulata* (formerly *Lebistes reticulatus*), Spurway (1953) reported the birth of fish thought to be the result of parthenogenesis. Histological investigation revealed, however, that the fish which had given birth to young in the absence of a male contained testicular as well as ovarian tissue (Spurway, 1957). Hermaphroditism is a rare abnormality in this species. Subsequently, Stolk (1958) described parthenogenesis in the same species, as well as in the swordtail, *Xiphophorus helleri*, in the absence of spermatozoa in fish which had been infected by the phycomycete *Ichthyonophonus hoferi*. It was suggested that the toxin produced by the parasite acted as the stimulus for the development of unfertilised oocytes.

Experimentally induced parthenogenesis leading to the development of viable adults has been described in several species of amphibia including *Rana japonica, R. nigromaculata*, and *R. pipiens* (see Beatty, 1967, for review).

PARTHENOGENESIS IN REPTILES

Most of our knowledge about the reproductive behaviour of reptiles refers to lizards and snakes belonging to the order *Squamata*; and it is a remarkable fact that there are about 27 species known to belong to this order (26 lizards and 1 snake) which consist entirely, or almost entirely, of females whose natural mode of reproduction is by parthenogenesis (reviewed by Cole, 1975). In 10 species there is evidence that they originated through hybridisation. In 3 species no evidence of hybridisation has been forthcoming; 2 of these exist as bisexual[1], fertilising populations in some localities and as unisexual[1], parthenogenetic populations in others. In 17 species, additional evidence regarding their origin is required,

[1]When applied to species, as in the context of this article, 'unisexual' means consisting of members of one sex only, that is females, while 'bisexual' means consisting of males and females. (Unfortunately the terms have different meanings when applied to individuals: 'unisexual'—either male or female, not hermaphrodite; 'bisexual'—hermaphrodite.)

though evolution through hybridisation has been suggested for several of them.

In the whiptail lizard belonging to the genus *Cnemidophorus*, which is widespread in the western hemisphere, 13 out of approximately 40 species reproduce by parthenogenesis. At least 600 specimens of *C. neomexicanus* have been examined, all of which were female. The reproductive cycle of these females is similar to that of related bisexual species, except that during the mating season, when the oviducts of bisexual species contain sperm, no sperm are found in the oviducts of *neomexicanus*.

C. neomexicanus is a diploid species with 46 chromosomes (Pennock, 1965). One of its haploid complements, including the X chromosome, appears indistinguishable from that of *C. tigris*, while the other resembles that of *C. inornatus* (Fig. 5). These two species which are bisexual differ in appearance, *C.*

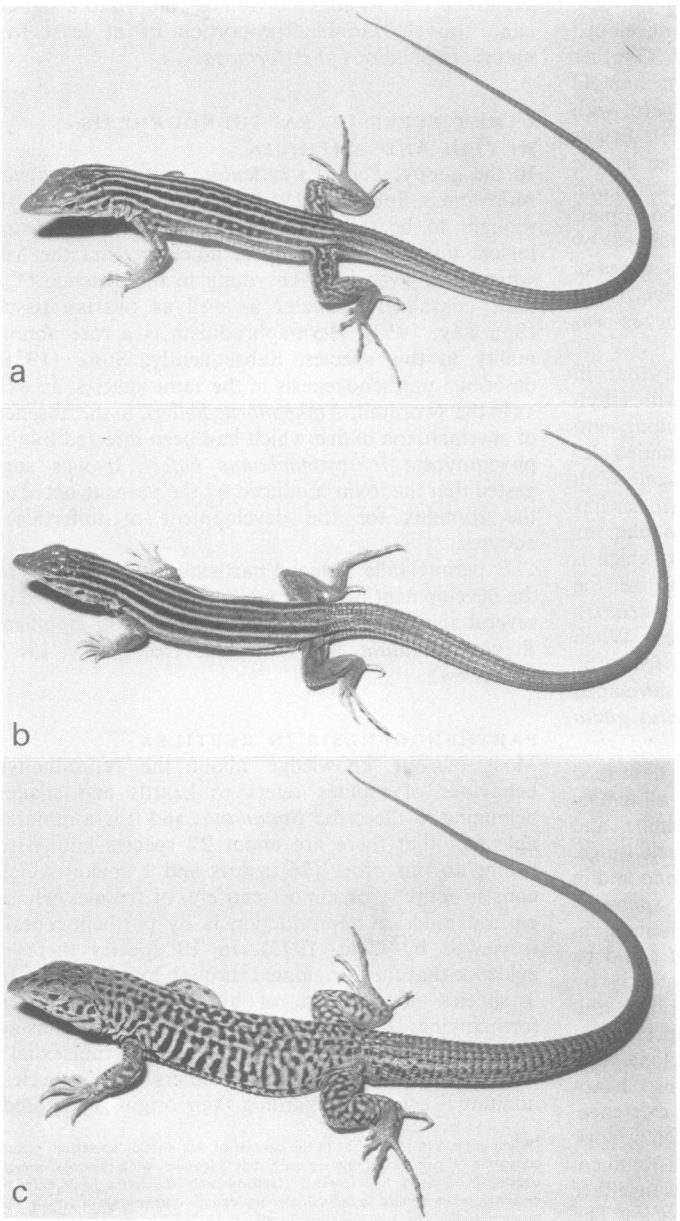

Fig. 4 Cnemidophorus neomexicanus, *an all-female species and its two bisexual parent species.* (*a*) C. neomexicanus ♀, *parthenogenetic, diploid;* (*b*) C. incornatur ♀, *bisexual, diploid;* (*c*) C. tigris ♂, *bisexual, diploid. Photographs contributed by Dr C. J. Cole.*

tigris being spotted and *C. inornatus* being striped; *C. neomexicanus* is intermediate (Fig. 4). Further evidence in favour of a hybrid origin of *C. neomexicanus* comes from electrophoretic studies and from the fact that *C. neomexicanus* and *C. inornatus* produce viable hybrids with a 1:1 sex ratio.

Another species in which parthenogenetic reproduction was observed in the laboratory is *C. uniparens*. This species is triploid, and Cuellar (1971) studied the maturation of the oocytes from sectioned material of germinal discs, the eggs being large-yolked. He observed two meiotic divisions, each giving rise to a polar body. Since as many as 69 bivalents were seen during the first meiotic division, it was concluded that the somatic chromosome number was doubled early in oogenesis, presumably by a premeiotic endoreduplication.

Triploidy arises from occasional matings between parthenogenetic diploid females with diploid males of one of the parent species, or another related species (Cuellar, 1974; Cole, 1975). With male heterogamety, the triploid offspring would be expected to consist of both sexes. The males would almost certainly be sterile, but the females have the chance to evolve into a new parthenogenetic species.

The parthenogenetic species *C. tesselatus* consists of both diploid and triploid populations. The former arose as hybrids between *C. tigris* and *C. septemvittatus*, while the triploid populations contain an additional chromosome set of *C. sexlineatus*. Parker and Selander (1976) examined isozyme variants at 21 loci and found a greatly increased level of heterozygosity in the parthenogenetic compared with the parent species (0·560 and 0·714 in diploid and triploid *C. tesselatus*, respectively, compared with a mean of 0·059 for the two parental species). On the basis of isozyme variants, the authors conclude that all triploid individuals represent a single clone, whereas 12 different diploid clones can be distinguished.

In recent years, Cole and Townsend (1977) have succeeded in raising parthenogenetic lizards of the genus *Cnemidophorus* in the laboratory. Three generations of the Chihuahua whiptail lizard, *C. exsanguis*—a triploid species—were obtained in the complete absence of males. The authors suggest that raising parthenogenetic lizards is an efficient way of obtaining reptiles for research purposes.

PARTHENOGENESIS IN BIRDS

As we reach the warm-blooded vertebrates, parthenogenetically produced offspring become increasingly less viable, and there is no known instance of parthenogenesis as a normal mode of reproduction. Nevertheless, parthenogenetic development may be initiated, and in both turkeys and chickens there are well-authenticated cases of birds having reached adult life in spite of their parthenogenetic origin.

The question whether an abortive parthenogenesis may occur in infertile chicken eggs has been debated for over a century. Oellacher (1872) described the occurrence of cleavage processes in unfertilised eggs which, however, differed from those in fertilised eggs.

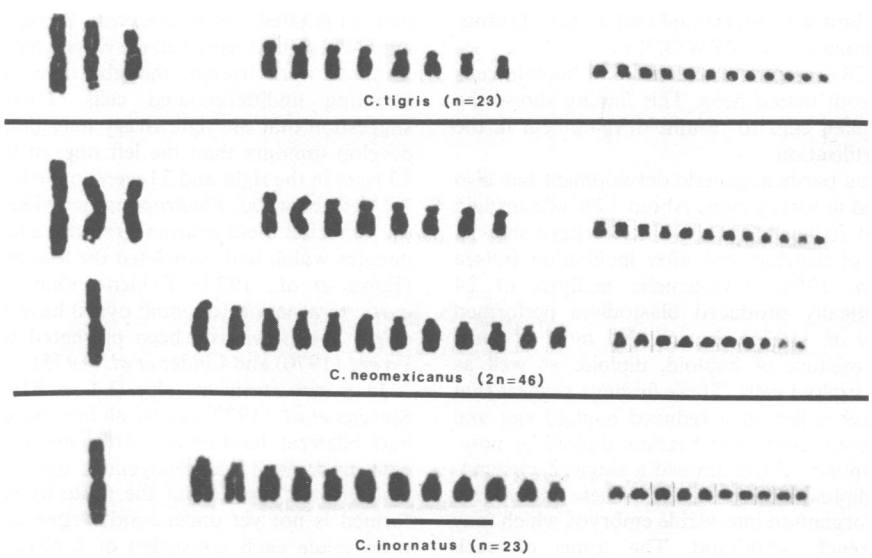

Fig. 5 *Karyotypes of* C. tigris (½ *karyotype*), C. neomexicanus, *and* C. inornatus (½ *karyotype*). C. neomexicanus *contains an X chromosome from* C. tigris *shown in third position in the top two rows. The other X chromosome is not known. Bar = 10 μm. (From Lowe and Wright, 1966).*

Some investigators confirmed this finding while others denied it. Kosin (1945) used Feulgen staining and found evidence of mitosis in about 15% of unfertilised blastodiscs in eggs of unmated Barred Rock and White Leghorn hens. Such mitoses were infrequent, however, suggesting that the developmental potential of such blastodiscs was low.

Subsequently, Olsen (1966) investigated different breeds of chickens and found wide variations in the ability of eggs to initiate parthenogenetic development. In some breeds none of the eggs showed any parthenogenetic development, while others, including White Leghorn and Barred Plymouth Rocks, had a low incidence. The highest incidence was found to be in Dark Cornish of the Beltsville strain in which 6·38% of eggs showed parthenogenetic development.

In some eggs parthenogenetic development was resumed on incubation, and in a few cases this has led to the production of adult chickens. Sarvella (1973) described 4 Dark-Cornish-type chickens which resulted from a total of 8532 eggs laid by virgin mothers. Three other chicks were hatched, but died during the first week. The mothers had been sexed at 6 weeks of age and were then separated from males. When the hens approached reproductive age, they were placed in separate cages. The chicks required special care during and after hatching. All 4 which survived to adulthood were males, of which 1 proved to be fertile. This male as well as 2 others was diploid. The sex chromosomes were thought to be ZZ(XX). One other parthenogenetically produced adult chicken which had been described previously (Sarvella, 1970) proved to be triploid. This bird was intersexual and its sex chromosomes were thought to be ZZW(XXY).

Bloom (1970) showed the existence of haploid cells in embryos from mated hens. This finding shows the ability of chicken eggs to resume development in the absence of fertilisation.

Spontaneous parthenogenetic development has also been described in turkey eggs. About 17% of eggs laid by non-mated Beltsville Small White turkeys showed some degree of development after incubation (Olsen and Marsden, 1954). Cytogenetic analysis of 24 parthenogenetically produced blastodiscs performed by Darcey *et al.* (1971) showed that most of them contained a mixture of haploid, diploid, as well as aneuploid or triploid cells. These findings suggest that parthenogenesis arises in a reduced haploid egg and that subsequently cells may become diploid or polyploid. The haploid cells contained a single Z chromosome while diploid cells were ZZ. These latter cells may become organised into viable embryos which may hatch and reach adulthood. The testes of such parthenogenetically produced turkeys are small and their fertility is reduced (Sarvella, 1974).

Although it had earlier been assumed that parthenogenesis in birds arises by the suppression of the second polar body (see Beatty, 1957), recent findings point either to an origin from a normally reduced egg or, alternatively, to a process of spontaneous cleavage in lieu of polar body extrusion (see below). Since it is likely that cells lacking a Z chromosome are inviable in birds, either route may be expected to give rise to all male offspring.

PARTHENOGENESIS IN MAMMALS

Spontaneous parthenogenesis

Spontaneously occurring cleavage divisions in ovarian or tubal eggs have been described in mice and in guinea pigs (Pincus, 1936) as well as in the human ovary, particularly in atretic follicles (Krafka, 1939). In hamster eggs, almost 80% were found to show spontaneous activation, extruding the second polar body within 24 hours of fertilisation (Austin, 1956). Some of these eggs underwent a haploid cleavage division.

More recently Stevens and Varnum (1974) described an inbred strain of mice (LT) in which parthenogenesis occurred regularly in a small percentage of virgin females. Most of these parthenogenones resembled embryos aged 5 or 6 days. After superovulation, most females contained eggs which had undergone cleavage and some contained blastocysts. Chromosome preparations made from some of the blastocysts revealed cells with haploid, diploid, or polyploid numbers. The same mouse strains also showed a high incidence of ovarian teratomata, which had originated from oocytes. About half of the animals aged 90 days had developed teratomata. Most of these were benign, though some contained proliferating undifferentiated cells. There was some suggestion that the right ovary may be more likely to develop tumours than the left one: of 97 teratomata, 53 were in the right and 31 were in the left ovary, while 13 were bilateral. Electrophoretic evidence supported the view that these ovarian teratomata had arisen from oocytes which had completed the first meiotic division (Eppig *et al.*, 1977). Evidence that human benign cystic teratomata (dermoid cysts) have a post-meiotic origin had previously been presented by Linder and Power (1970) and Linder *et al.* (1975).

In a new strain of mice (LT × BJ) developed by Stevens *et al.* (1977) nearly all females aged 3 months had bilateral teratomata, while about 30% of their eggs underwent parthenogenetic development. These embryos are diploid but the route by which they are formed is not yet understood. Triple chimaeras have been made each consisting of 2 eight-cell parthenogenetically produced embryos fused to an eight-cell normally produced embryo belonging to an albino strain. A total of 55 triple embryos were introduced

into the uteri of pseudo-pregnant females and resulted in 2 young, 1 male and 1 female, containing parthenogenetical cell lines. The male was smaller than his 3 litter mates and had pigmented hair on the back of his head and irisis containing pigmented as well as non-pigmented areas. There was also evidence that some of the blood cells were of parthenogenetic origin, but this was not apparent in the testes. The male sired 27 offspring all of which were albino and showed no evidence of a parthenogenetic component. These results indicate that cells derived by parthenogenesis in mice can take part in organ formation provided the embryo also contains cells derived by fertilisation. There is as yet no explanation for the lack of viability of embryos derived wholly by parthenogenesis.

Even if we accept that the chance of a mammalian parthenogenone developing to term is minimal, there is the corollary that if one did survive, its parthenogenetic origin might be difficult to detect (Beatty, 1957). Since such parthenogenones would be female, Whitten (1971) examined genetic markers of female mice from crosses which resulted in an excess of females. All the females investigated proved to be hybrids between the two parental strains.

The subject of human parthenogenesis appears to be of perennial interest and in 1955 a Sunday newspaper carried an article asking mothers who thought they had a parthenogenetic child to come forward; the article added that such children should be girls. As a result 19 pairs of mothers and daughters were examined by Balfour-Lynn (1956). Eleven of the pairs could be immediately eliminated and 8 were blood grouped. Six of the pairs showed blood group incompatibility and a seventh differed in eye colour. On the remaining pair skin grafting was carried out and a graft from daughter to mother was shed within 4 weeks.

Induced parthenogenesis

The experimental induction of parthenogenesis in mammals began with the pioneering studies of Pincus and his collaborators in the rabbit. In 1936 Pincus and Enzman showed that the extrusion of polar bodies could be induced *in vitro* not only by contact with sperm suspension, but also by heat treatment or exposure to butyric acid and hypertonic solutions. Subsequently Pincus and Shapiro (1940) described the effect of cold treatment on unfertilised tubal eggs *in vitro* and claimed not only an increased incidence of cleavage but also the production of a living young. There has since been abundant confirmation of the possibility of inducing parthenogenetic development in mammals by experimental procedures but none of the embryos so formed has survived the embryonic period.

Graham (1974) has reviewed the various agents used to induce parthenogenesis in mammals and the results achieved. Most of the techniques rely on exposing ovulated eggs to conditions which are as extreme as they can withstand without actually killing them. It is thought that the activating stimuli act directly on the cell membrane which induces subsequent changes in the cytoplasm of the egg.

Hot shocks were found to activate up to one-half of treated mouse eggs and to induce a smaller proportion of diploid morulae and blastocysts. The same treatment was ineffective in rats. By contrast, cold shocks were ineffective in the mouse, but induced up to 100% activation in rat eggs. Cleavage was rare in this species and development was haploid. Osmotic shock caused activation in a proportion of eggs in the rat and the rabbit, and ether anaesthesia had a similar effect in the mouse and the rat. The two most effective techniques for producing parthenogenetic mouse embryos are electrical activation and treatment with hyaluronidase.

The electrical technique, which had originally been designed to activate amphibian eggs, was developed by Tarkowski *et al.* (1970) for use in mice. A female mouse containing newly ovulated eggs is anaesthetised and a brief electric shock (20 to 50 volts from a 8 μF capacitor) is passed between electrodes placed on either side of the part of the oviduct containing the eggs. The electric shock is thought to cause abrupt and local heating of the eggs and may directly depolarise the egg membrane. As a result up to three-quarters of the eggs are activated and 9 out of 10 of these may develop into morulae and blastocysts. This is the most successful technique available, its only disadvantage being that the eggs cannot be directly observed as they cleave. The method developed by Graham (1970) overcomes this disadvantage. Eggs removed from virgin females after injection of human chorionic gonadotrophin are placed into culture medium containing hyaluronidase which causes the cells of the cumulus oophorus to fall away from the zona pellucida. Up to three-quarters of the cells may be activated, but in culture less than 10% develop into blastocysts. However, if the activated eggs are transferred into foster mothers, about two-thirds develop into morulae and blastocysts.

Parthenogenetic embryos produced by either electricity or hyaluronidase treatment may be either haploid, diploid, aneuploid, or polyploid. Witkowska (1973a) succeeded in carrying out chromosome analysis in 60 morulae and blastocysts obtained by electricity treatment and found that 36 were haploid, 10 were diploid, 1 was tetraploid, and 13 were haplodiploid mosaics, derived from haploid eggs. Freshly ovulated mammalian eggs are usually in metaphase of the second meiotic division. Haploid parthenogenesis will result either if meiosis is completed normally or if the egg cleaves in half, so that one cell contains the egg

nucleus and the other cell the nucleus of what should have been the polar body (immediate cleavage). If the nucleus of the polar body is retained in the egg, diploid parthenogenesis will result (Witkowska, 1973a; Graham, 1974). The mechanisms involved in the production of aneuploid, haplodiploid, and polyploid embryos have not yet been explained.

The pattern of death has been studied in parthenogenones induced by both electricity (Witkowska, 1973b) and hyaluronidase treatment (Kaufman and Gardner, 1974). Witkowska (1973b) found that the number of living embryos decreased every day, so that on the 9th and 10th days only 2 out of 86 embryos were alive. Almost all embryos appeared to be retarded. The cause of death, particularly of the diploid embryos, remains unexplained (Tarkowski, 1975). Since the majority are formed from two products of the second meiotic division they would not be expected to be fully homozygous. Moreover, since inbred strains of mice are involved, death caused by homozygosity of lethal genes is not a convincing explanation.

Mintz and Gearhart (1973) found that the zona pellucida of parthenogenetic mouse embryos produced by electrical stimulation was more sensitive to proteolytic enzymes than that of normal embryos. At the level of ultrastructure, Solter *et al.* (1974) reported numerous differences between parthenogenones and embryos derived by fertilisation, whereas Van Blerkom and Runner (1976) detected only one difference in the number of crystalloid bodies. While the methods used in the experimental induction of parthenogenesis might add to the abnormalities of the embryos, it is clear that the cause of death in mammalian parthenogenones is at present unknown.

Significance of fertilisation

Austin (1974) distinguishes two phases of fertilisation: plasmogamy and karyogamy. The latter is of genetic importance whereas plasmogamy is of reproductive importance. It involves the close attachment of the cell membrane of egg and sperm followed by fusion. At this point the gamete membranes form a single continuum, so that spermatozoon and egg form a single cell. Egg cytoplasm flows around the sperm nucleus and gradually engulfs its tail. It is still an open question whether the sperm contributes any extranuclear material to the zygote. The mid-piece of the spermatozoon which is characterised by the mitochondrial layer has been seen to penetrate the egg of the rabbit (Hadek, 1969), though it is thought that the mitochondria of the penetrating sperm degenerate and dissolve. However, Beatty (1972) found a positive correlation between mean body weight and mean mid-piece length in strains of mice which had been selected for different body weights; and he suggested the possibility that the mitochondrial content of the spermatozoon may have been the prime target of selection. Fawcett (1972) has discussed the possible role of centrioles in spermatogenesis and fertilisation and in addition has described a special cytoplasmic body present in germ cells. The multitude of spermatozoa which remain trapped in the uterine cavity also undergo regressive changes as a prelude to their total degeneration. Subsequently the uterus becomes the site of a massive leucocytic invasion (Zamboni, 1972). There appears to be a number of unknown factors regarding the role of spermatozoa in reproduction other than their function in karyogamy.

This circumstance casts serious doubts on the claims of theoretical geneticists that sexual reproduction needs to be explained in evolutionary terms. According to Maynard Smith (1971) parthenogenetic females producing only progeny like themselves have twice the fitness of sexual females producing equal numbers of male and female offspring. He admits, however, that if both parents care for their offspring males are not entirely wasted. Apart from the fact mentioned earlier that parthenogenesis is an incompletely sexual, rather than an asexual form of reproduction, these considerations seem to be totally irrelevant to mammals, in which no parthenogenone has yet been known to survive to birth.

Furthermore, even in animals in which parthenogenesis can be an effective means of reproduction, the facts do not support the view that the process is more efficient than reproduction by fertilisation. Williams (1975) writes that 'it would appear that as soon as parthenogenesis is possible in any vertebrate population, sexual reproduction is 'immediately' lost. There are no heterogonic vertebrates, with periodic or facultative sexuality'. As we have seen, however, cytogenetic studies of parthenogenetic lizards have confirmed that many species are of hybrid origin; in addition, there is a high incidence of triploidy. In such species, the usual process of reproduction by fertilisation is impossible and their only hope of survival lies in the adoption of parthenogenesis, if it is physiologically feasible. It may be significant that structural heterozygosity and triploidy seem to be frequent also in thelytokous insects. All in all, the estimated incidence of one in a thousand animal species reproducing solely by parthenogenesis suggests that the disadvantages of the process tend to outweigh its obvious advantages.

It should be noted that in contrast to the situation in reptiles, neither parthenogenesis nor triploidy seems to be compatible with viability in mammals. The reasons for these differences cannot as yet be explained by any known genetic mechanism. It is of interest, however, that chimaeras of parthenogenones and products of

fertilisation can be viable in mammals and the same applies to triploid/diploid chimaeras.

At present it has to be stated categorically that an origin in sexual reproduction including fertilisation appears to be necessary for viability in mammals. It is to be hoped that current research on parthenogenesis will shed light on the reproductive significance of fertilisation.

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Note added in proof

A recent article by Cuellar (1977) deals with ecological and evolutionary factors assumed to be of importance in the establishment of parthenogenesis in animals. Some of the assumptions made have been questioned by Cole (1978).

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