

Viewpoints in Biology

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VIEWPOINTS IN BIOLOGY

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Edited by

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INTRODUCTION

Viewpoints in Biology publishes broadly based reviews of biological subjects which may be extensively illustrated. These reviews are not only summaries of the state of the subject but also indicate the direction in which progress may be expected, and stress unsolved problems. While putting a cogent, well-argued point of view the authors are, however, not necessarily asked to give exhaustive documentations of all the work in the subject. Considerations of the theoretical aspects of biology, criticisms of well-established methods and discussions of material from an evolutionary point of view are all welcome. Descriptions of the practical details of methods are not accepted unless they are involved in the consideration of a subject of general biological interest.

As far as possible the reviews are readily understandable to other scientists as well as biologists. With increasing specialization within biology as well as the sundering of science into departments, it is more and more necessary that the problems facing one sort of scientist should be presented in a way which is understandable to others, so that if their interests are aroused they can bring to bear their own specializations on to the problems of another department of science.

The editors wish to thank all authors, societies and publishers for permission to reproduce diagrams and tables which have appeared in previous publications.

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MARSUPIALS AND THE EVOLUTION OF VIVIPARITY

G. B. SHARMAN

The great strength of this marsupial work, which I regard as functional morphology, lies in the fact that it has always been considered in the light of the possible course of evolution, and, without this reference, I think that morphology is likely to be barren and to fall into errors of homology. Nevertheless one must caution our Australian friends that it would be prudent to get more of the facts and to explore them more fully before embarking into speculations that may lead us into difficulties. *E. C. Amoroso*¹.

INTRODUCTION

THERE are many resemblances between the egg-laying mammals (monotremes) and the marsupials but evidence indicates that an ancestral stock, from which both metatherian (marsupial) and eutherian mammals evolved, existed after the monotremes had begun their separate evolution. Primitive eutherians and metatherians are known from the late Cretaceous and all the more complete specimens fall unequivocally into either Eutheria or Metatheria². If the apparent similarity between the ear regions of primitive insectivores and marsupials are due to convergence then the eutherians and marsupials may be more widely separated than is at present suspected³. Whatever the case the marsupials and eutherians, once separated, followed their separate evolutionary lines culminating in the forms existing today which nowhere differ so much as in their methods of reproduction.

The marsupial young is born while of small size and in a generally embryonic condition after a shorter gestation period than usually occurs in eutherian mammals of comparable size. The gestation period (here regarded as the interval between fertile copulation and birth during which continuous embryonic development occurs) varies between 13 days in *Didelphis virginiana* (the American opossum)⁴ and about 38 days in the rat-kangaroo, *Potorous tridactylus*⁵. Some marsupials such as *Dasyurus viverrinus* (the Australian native cat) and *Didelphis* produce 30, 40 or more eggs at a single ovulation^{6,7}. Apparently not all of these are fertilized and intra-uterine death may further reduce the number of young produced but *Dasyurus* may give birth to as many as 18 living young⁸. Many phalangers and macropodid marsupials (Phalangerioidea) produce a single egg at each ovulation and only one red kangaroo (*Megaleia rufa*) of each thousand carrying young in the pouch had twins⁹.

In marsupials as in eutherian mammals the secretions of the corpus luteum—the endocrine organ formed following shedding of the eggs from the ovary—induce changes resulting in the onset of a luteal phase in the reproductive organs. These changes, of a secretory nature, apparently serve to nourish the embryo during its intra-uterine development. They are developed alike in pregnant and non-pregnant marsupials carrying a functional corpus luteum and, so far as is known, always last the same length of time in the non-pregnant female as they do in its pregnant counterpart. Hill and O'Donoghue, pioneers in the study of marsupial reproduction, used the term 'pseudopregnancy' to designate the period which, in the non-pregnant animal, follows ovulation,

and in which the changes in the ovary, mammary glands and uteri are essentially similar to those in the pregnant female¹⁰. This early, if not the first, use of what is now a familiar term in reproductive physiology serves as a reminder that in the early part of this century as much was known about reproduction in marsupials as about reproduction in eutherian mammals. The early interest in marsupial reproduction was not, however, maintained and extensive study of Australian marsupials has only been renewed comparatively recently. Although the uterine luteal phase lasts the same length of time in pregnant and non-pregnant marsupials of the same species the phase varies in length from species to species. In *Didelphis* the luteal phase lasts until about the thirteenth day after oestrus at which time the pregnant female gives birth¹¹. In *Trichosurus vulpecula* (the Australian brush possum) the luteal phase is extended to the sixteenth or seventeenth day after oestrus¹² and in *Setonix brachyurus* (the quokka) it lasts until about the twentieth day and the young is retained in the uterus for a further 7 days. In animals, such as *Setonix*, in which the embryo is retained in the uterus beyond the limits of the luteal phase the gestation period is extended to nearly the length of one oestrous cycle but pregnancy does not prevent the recurrence of oestrus at the expected time. At the oestrus subsequent to birth (post-partum oestrus) copulation, ovulation and fertilization may occur and marsupials having post-partum oestrus exhibit delayed implantation—the prolonged storage in the uterus of a dormant embryo while a young is suckled in the pouch¹³.

The embryonic membranes which are concerned with nourishment of, and excretion by, the embryo in the uterus vary from the exceedingly simple type found in *Trichosurus*¹⁴ to the exceedingly complex type, in which the allantois or embryonic bladder forms an intimate connection with the uterine wall in *Perameles* (bandicoots)¹⁵.

After birth marsupial young attach more or less firmly to the teats and are reared in very close association with their mothers, generally being protected from the external environment by the pouch¹⁶. The number of teats in the pouch limit the number of young that may be reared and those which cannot find an unoccupied teat when they reach the pouch must die¹⁷. The development of the pouch shows all variations from the condition in *Myrmecobius fasciatus* (the numbat) which has no pouch at all¹⁷ through the condition in *Antechinus flavipes* (the yellow-footed marsupial mouse), in which the young are protected in their early stages by a mere shallow depression¹⁸, to the condition in the Phalangeroidea in which the young are usually nourished for long periods in a deep bag-like pouch. The time the young spend in the pouch before becoming semi-independent varies from 8 weeks in *Isodon macrourus* (the short-nosed bandicoot)¹⁹ to nearly a year in *Macropus kanguru* (the great grey kangaroo)²⁰.

J. P. Hill, who did outstanding early work on marsupial embryology and reproduction, maintained that the stock which gave rise to marsupial and eutherian mammals had a placenta, simple in structure, composed of vascularized yolk-sac and vascularized allanto-chorion²¹. In *The Mammals of South Australia*, which contains the best general account of marsupial natural history yet written, Wood Jones wrote that the marsupials had 'developed along a line expressed by, among other things, the degeneration of the allantoic placenta, the curtailment of intra-uterine life, the begetting of immature offspring and

the development of a marsupium or pouch in which to shelter them'²². It is proposed, in this review, to examine these and other theories about marsupial reproduction in the light of recent advances in knowledge.

This review does not claim to be comprehensive; the reader is referred to an earlier work, which reviews progress in the field of marsupial reproduction up to 1959 for an account of processes not dealt with here¹⁶.

EGGS, EMBRYOS AND TEATS

It has long been recognized that evolution in marsupials was accompanied by reduction in the number of eggs produced at each ovulation with consequent reduction in the number of young born and suckled and that there has been an associated reduction in the number of teats and mammary glands⁶.

Didelphis virginiana may produce as many as 44 eggs at a single ovulation but 'about 10 per cent of the eggs found in the first half of gestation are defective, the majority of which are actually unfertilized'⁷. In *D. aurita* about 25 per cent of 69 early embryos from 3 females were reported to be abnormal or of small size²³. Similarly *Dasyurus viverrinus* produces a large number of eggs and in one case 12 of a total of 35 blastocysts were abnormal⁶. *Pseudocheirus* normally raises 2 or, occasionally, 3 pouch young but up to 6 developing embryos have been found in the uteri²⁴. In the family Macropodidae, and in *Trichosurus vulpecula*, double ovulations are very rare and multiple ovulations have never been recorded^{9,25}.

In *Didelphis* between 11 and 17 (usually 13) teats are found in the pouch but 'in spite of the progressive mortality of eggs and embryos *in utero* it happens that very often more young are born than can be accommodated by the teats'⁷. Litters of 18, 21 and 25 newborn young have been recorded^{4,7}. *Dasyurus* with 6 (sometimes 8) teats may produce as many as 18 living young⁸. *Pseudocheirus* has 4 teats 2 of which were regarded as non-functional²⁴ but a female rearing 3 pouch young has been recorded. Marsupial young in excess of the number of teats are doomed to death by starvation since only those that win the race to occupy the teats can be reared (Table 1.1).

Table 1.1. Numbers of eggs shed, young born and teats present in various marsupials

Family	Species	No. of eggs shed		No. of young born	No. of teats
		Usual	Maximum		
Didelphidae	<i>Didelphis virginiana</i>	22	44	up to 25	11-17
	<i>Didelphis aurita</i>	25	35		
Dasyuridae	<i>Phascogale penicillata</i>	20	35	≥ 8 up to 18	10
	<i>Antechinus flavipes</i> <i>Dasyurus viverrinus</i>				8 6-8
Peramelidae	<i>Perameles nasuta</i>	3	5	up to 5	6
Phalangeridae	<i>Dromicia concinna</i>	1	2	ca. 6	6
	<i>Trichosurus vulpecula</i>	2-3	6	1	2
	<i>Pseudocheirus</i> spp.	1		2-3	4
	<i>Phascolarctos cinereus</i>	1		1	2
Macropodidae	Numerous species	1	2	1	4

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Intra-uterine mortality undoubtedly occurs also in those marsupials which bear a single young but its incidence may not be as high as in monovular eutherian mammals⁹.

The incidence of births in female macropodid marsupials exposed to males for one day or less at the time of oestrus indicate a high percentage of successful fertilizations, low intra-uterine mortality and great efficiency by the neonatal young in reaching the pouch and teat. In *Megaleia rufa* 102 of 124 copulations (82 per cent) were followed by the appearance of young in the pouch. Comparable figures for monovular eutherian mammals are hard to obtain but the percentage of mares which become pregnant varies from 53 to 95 per cent depending on the amount of time they have access to the stallion over the long (1-37 day) heat period. Apparently only about 65 per cent of dairy cows conceive at first service and an average of 1.8 heat periods elapse before pregnancy occurs. Up to 82 per cent conceive as the result of a single artificial insemination²⁶. It would appear that, even by eutherian standards, reduction in the number of eggs shed has been accompanied by the development of efficient methods of caring for the single egg and the derived embryo in monovular marsupials.

Pouch mortality occurs and it is likely that this is heavy in polytocous species, although Reynolds stated that in *Didelphis* 'no disadvantages have been demonstrated for the conditions that exist during the two-month period that the young spend in the marsupium before they attain a stage of development that is approximately comparable to that of placental mammals at the time of birth'. He thought, however, that the vulnerability of the family to predators during later stages of pouch development may have been a disadvantage⁴. Mortality of pouch young during late stages of pouch development in *Megaleia* was exceedingly heavy under drought conditions although it was not demonstrated that this was heavier than mortality of newborn young of eutherian mammals under similar conditions. Indeed, during the drought in which the heavy mortality of *Megaleia* young was demonstrated the management of the pastoral property where the study was made did not allow the sheep to mate⁹.

In general, reduction in the number of teats in the marsupial pouch is correlated with reduction in the number of young born, greater size of the newborn young and greater development of the birth canal to allow the passage of larger young (see later). However, in the macropodid marsupials which bear but a single offspring 4 functional teats are retained. This is apparently of selective advantage since overlapping periods of suckling in and out of the pouch normally occur and there is evidence that only two of the four teats are readily available to a young born during the period in which an earlier young is suckled^{5,27}.

If only one of the many young born reaches the pouch of *Didelphis* lactation is initiated, continues for a short time, and then ceases. The young starves and is lost from the pouch and the mother returns to oestrus since the suckling stimulus exerted by a single young is not sufficient to maintain lactation⁴. This finding was overlooked by Talice and Lagomarsino who could not explain why single young were lost from the pouches of two females of *Didelphis azarae*²⁸.

OESTROUS CYCLE AND PREGNANCY

In general, proliferative luteal and post-luteal phases may be distinguished in

the uteri of marsupials during the oestrous cycle and during pregnancy. The pro-oestrous proliferative phase is characterized by cell multiplication in the uterine epithelia and growth of one or more Graafian follicles in the ovaries. Cell multiplication in the uterine epithelia continues during oestrus, the follicle or follicles become mature and the stratified epithelia in the posterior vaginal region become more or less cornified resulting in characteristic composition of the oestrous or post-oestrous vaginal smear. Copulation usually occurs at oestrus if the female is placed with a male. The sexually receptive phase usually lasts less than one day in *Didelphis virginiana*¹¹, *Trichosurus vulpecula*¹², *Setonix brachyurus*¹³ and *Megaleia rufa*²⁷ but much longer in *Potorous tridactylus*⁵ and *Antechinus flavipes*¹⁸. In *Trichosurus*, *Setonix* and *Megaleia*, ovulation and corpus luteum formation occur one or two days after oestrus irrespective of the occurrence or non-occurrence of copulation^{12,13,27}. Definite instances of copulation-induced ovulation are unknown in marsupials¹⁶. Uterine epithelial cell multiplication and some cornification of the lateral vaginal epithelia continue after oestrus but the post-oestrous proliferative phase is soon replaced by the luteal phase induced by progesterone secreted by the corpus luteum in both pregnant and non-mated females. During the luteal phase the uterine gland epithelia, especially those of the peripheral glands, are of increased height with basally situated nuclei. Mitoses no longer occur. The post-luteal phase is a regressive phase in corpus luteum and uterus. In *Dasyurus*, *Didelphis* and *Trichosurus* the young are born at the end of the luteal phase (Table 1.2) and the ensuing post-luteal phase is followed by the quiescent phase of lactation while the young are suckled in the pouch. In non-pregnant females of *Didelphis* and *Trichosurus* the post-luteal phase is followed by pro-oestrus and another oestrus. If the young of these marsupials are removed at birth there is a recurrence of oestrus at the time it would have occurred had the females not been pregnant^{11,12}

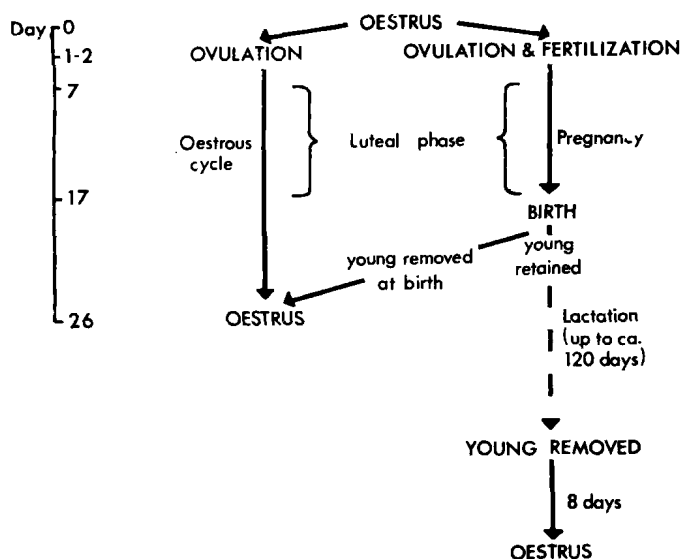


Figure 1.1. Diagrammatic representation of possible events after oestrus in *Trichosurus vulpecula*¹². Alternative paths indicated by arrows

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(Figure 1.1). *Dasyurus* is stated to be monoestrous so the post-luteal phase is followed by anoestrus in the event of non-occurrence of pregnancy¹⁰.

The embryo is retained in the uterus during and after the post-luteal phase in *Setonix* and in *Megaleia* and is born at the end of the pro-oestrous proliferative phase^{13,27}. The next oestrus after fertilization in those marsupials in which the gestation period is extended into the pro-oestrous phase thus becomes a post-partum oestrus. Post-partum oestrus may fail to occur in wild females of *Megaleia* under extreme environmental stress²⁹. As happens when the neonatal *Didelphis* or *Trichosurus* is removed from the pouch just after birth, pregnancy in *Setonix* and *Megaleia* does not delay the onset of the ensuing oestrus but oestrus occurs post-partum whether the young are removed at birth or not (Figure 1.2). This is presumably because pro-oestrous changes are already well advanced at parturition whereas in those marsupials in which the young is born during the post-luteal phase the suckling stimulus prevents the recurrence

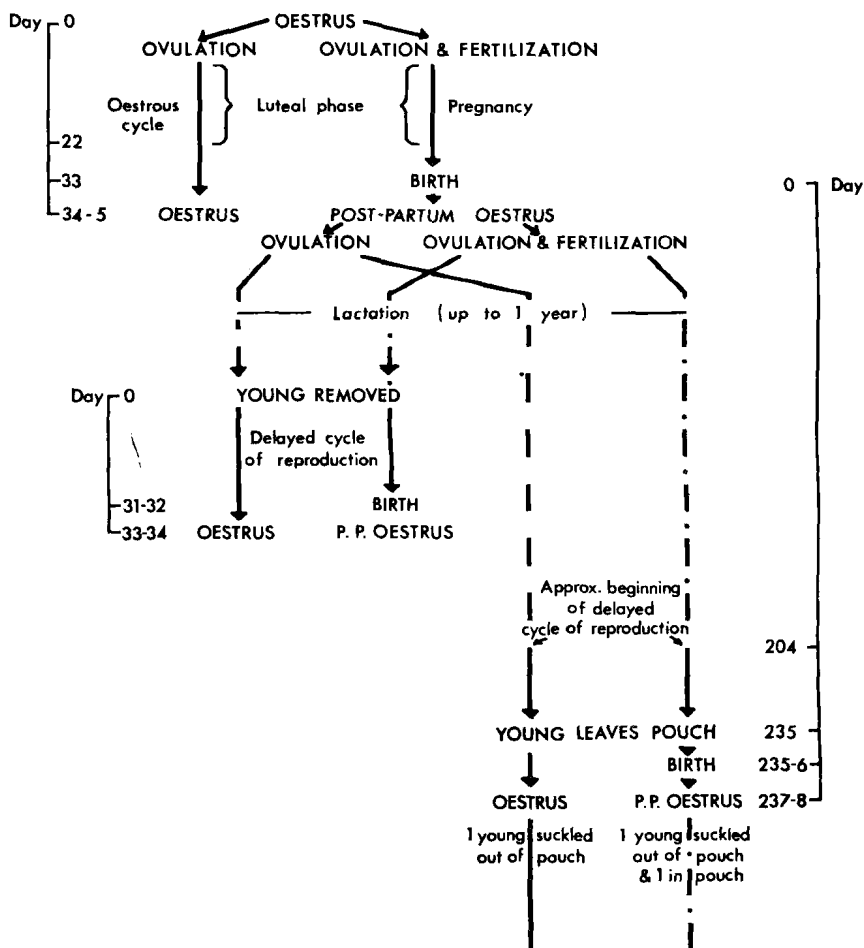


Figure 1.2. Diagrammatic representation of possible events after oestrus in *Megaleia rufa*²⁷. Alternative paths indicated by arrows, quiescent phase of lactation (lactation anoestrus) indicated by a broken line, dots indicate time when quiescent blastocyst present

of oestrus since it is exerted before the pro-oestrous phase is initiated. In *Setonix* and *Megaleia* changes, like those following normal oestrus, occur after post-partum oestrus but as the suckling stimulus becomes effective the quiescent phase of lactation is initiated. A similar sequence of events presumably occurs in other marsupials exhibiting post-partum oestrus. The embryos of marsupials which have a post-partum oestrus may be retained in the uterus as dormant, but viable, blastocyst stages for long periods while young are suckled in the pouch. This is equivalent to the phenomenon of delayed implantation in some eutherian mammals³⁰.

In all marsupials so far studied, with a single possible exception^{20,31}, the gestation periods are shorter than the length of one oestrous cycle (*Table 1.2*). In a variety of these an identical, or near identical, sequence of events to those occurring after oestrus in the non-mated female have been demonstrated in the pregnant female¹⁰⁻¹³. That the anatomical and histological similarities indicate a physiological equivalence of the pregnant and non-pregnant states has been demonstrated by a variety of experiments. In *Potorous*, *Trichosurus*, *Setonix*, and *Megaleia* no constant differences could be detected between the post-oestrous vaginal smears of pregnant and non-mated females^{5,12,13,27}. Non-pregnant females of *Trichosurus* excreted similar amounts of pregnanediol to those excreted by pregnant females at the same number of days after oestrus¹². The normal development of early embryos, transferred to the uteri of non-pregnant females, demonstrated the physiological equivalence of pregnant and non-pregnant states in *Setonix*. Development continued in embryos, derived from dormant blastocysts, which were transferred 6 days after resumption of growth was initiated, following removal of the pouch young. The maximum discrepancy between donor and recipient, allowing continued development, was much greater than that in any eutherian mammal so far examined³².

Table 1.2. Intervals from oestrus to end of uterine luteal phase, from oestrus to birth (gestation period) and from oestrus to next oestrus (oestrous cycle length) in various marsupials

Family	Species	Days after oestrus		
		End of luteal phase	Birth	Next oestrus in absence of pouch feeding
Didelphidae	<i>Didelphis virginiana</i>	13	13	29
Dasyuridae	<i>Antechinus flavipes</i>	at parturition	32	365
	<i>Dasyurus viverrinus</i>		8-20	365
Peramelidae	<i>Isodon macrourus</i>		ca. 13	26
	<i>Perameles nasuta</i>		ca. 12	
Phalangeridae	<i>Trichosurus vulpecula</i>	17	17.5	26
Macropodidae	<i>Setonix brachyurus</i> *	20	27	28
	<i>Protemnodon eugenii</i> *		29	30
	<i>Protemnodon rufogrisea</i> *		30	30-31
	<i>Megaleia rufa</i> *	≥ 22	33	35
	<i>Macropus kanguru</i>		29-38	32-55
	<i>Potorous tridactylus</i> *		38	42

*Post-partum oestrus and delayed implantation occur.

MARSUPIALS AND THE EVOLUTION OF VIVIPARITY

It has long been known that the post-ovulatory changes in the mammary glands of non-mated female marsupials are like those occurring in pregnant females³³. The ability of the mammary glands of non-mated or parous virgin females of *Megaleia* and *Trichosurus* to produce milk and maintain living young was tested by transferring newborn young to their pouches or teats^{27,34}. Transfers to foster-mothers which were at that stage after oestrus at which they would have given birth had they been mated were successful and it was conclusively demonstrated that, in the absence of copulation or pregnancy, the glands were capable of producing milk and nourishing newborn young weighing less than one gram without a prior period of stimulation. The growth rates of the foster-young, many of which were reared until the completion of lactation, were not different from those of control young reared by their own mothers. It thus appears that all the hormones necessary for mammary gland differentiation are present in the non-mated female marsupial.

The above experiments while not proving that there is no enhanced hormone secretion during gestation in marsupials suggest that this is the case. The placenta of most marsupials, and of all marsupials for which anatomical or experimental evidence of equivalence of pregnant and non-pregnant states exists, is simple in structure. In eutherian mammals the placenta is an important, secondary source of hormones during pregnancy and it is probable that secretion of a placental hormone, which increased the period of functional activity of the corpus luteum, was the initial adaptation which enabled the gestation period of eutherians to be extended beyond the limits of the oestrous cycle³⁵. Pregnancy does not extend the interval between successive oestrous periods in marsupials: neither does it result in extension of the uterine luteal phase which is known to be induced and maintained by the secretion of progesterone from the corpus luteum³⁶. In many eutherian mammals ablation of the corpora lutea or complete removal of the ovaries has no effect on the maintenance of pregnancy and it is likely that the loss of these endocrine organs is compensated for by placental hormone production³⁵. In *Didelphis* complete ovariectomy is followed by the collapse of the uteri and death of the intra-uterine embryos³⁷. In *Trichosurus* and *Setonix* the embryos may develop to term following ablation of the corpora lutea and in *Setonix*, at least, the same may occur after complete removal of the ovaries but these results do not suggest compensation for loss of ovarian structures by placental secretion. Ablation of the single corpus luteum, removal of the entire ovary containing the corpus luteum, or even removal of both ovaries does not, if performed after certain stages, result in abbreviation of the uterine luteal phase irrespective of the presence of an intra-uterine embryo and its placenta. The results suggest that the luteal phase, induced in the uterus by secreted or injected progesterone, usually persists in the absence of corpora lutea once it is initiated^{36,38}. Presumably the progesterone is less rapidly metabolized than in some other mammals.

Viviparity may be viewed as a process by which the uterus was enabled to tolerate and nourish the developing embryo for extended periods. It is suggested that an early step in the evolution of viviparity in marsupials was the retention of the egg, with its developing embryo, in the uterus until the cessation of the uterine luteal phase. The living marsupials *Dasyurus*, *Didelphis*, and *Trichosurus* appear to have progressed very little beyond this stage other than in reduction of yolk with associated reduction of shell to allow a better exchange between

uterine wall and placenta. In all three a well-developed shell membrane persists for much of the gestation period^{6,7,14}. The duration of the luteal phase, and hence the gestation periods, differ in these marsupials so that an early adaptation allowing longer pregnancy may have been an extension of the period of secretory activity of the corpus luteum resulting in a longer luteal phase. In other marsupials the embryo is retained in the uterus beyond the limits of the luteal phase and is born just before the next expected oestrus. Since it is probable that the secretions of the corpus luteum are not supplemented by hormones secreted by the placenta any further extension of the period of secretory activity of the corpus luteum must also occur in the non-pregnant animal and thus increase the length of the oestrous cycle. This theory supposes that marsupials, such as *Potorous tridactylus*, which have a long (38 days) gestation period have only evolved this after extension of the period of active secretion by the corpus luteum.

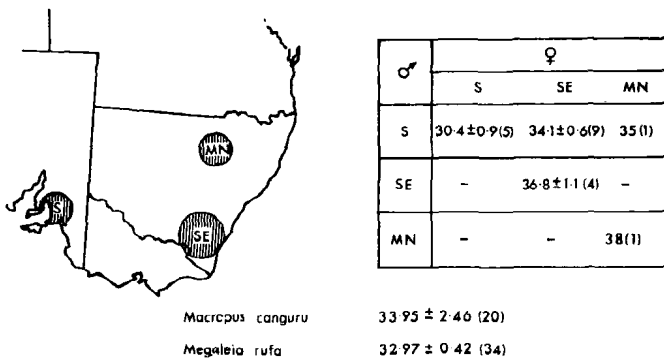


Figure 1.3. Variation in the gestation period of grey kangaroos (*Macropus kanguru*) from different regions and variation in females when crossed with males of different geographical origin²⁰. Mean length of gestation periods in days ± standard deviation and number of observations in brackets. S—Adelaide area South Australia; S.E.—south-east New South Wales; MN—mid-north New South Wales, Australia. The mean and standard deviation of the gestation period in red kangaroos (*Megaleia rufa*) from several widely separated areas should be compared with that in the combined samples of grey kangaroos from the three areas

Post-partum ovulation did not occur in *Macropus kanguru* and if copulation took place at about the time of parturition it was not accompanied by fertilization. It is suggested elsewhere that delayed implantation may have been abandoned during evolution of *Macropus*. Poole and Pilton found that the gestation period in this species was not as regular as in *Megaleia* and other marsupials and that it varied according to the geographical origin of the individuals and was apparently determined by the genetic constitution of the intra-uterine embryo²⁰. In the colony the gestation periods ranged from 29 to 38 days and females had different gestation periods when fertilized on successive occasions by males from different localities (Figure 1.3). The 25 per cent extension of the gestation period in some females and the possible inhibition of ovulation during late pregnancy and post partum suggest special hormone mechanisms of pregnancy in *Macropus* not so far detected in other marsupials.