fluted points, crescents, Borax Lake points (with one possible exception), or "long stem points." On the other hand, the Mendocino complex shares 8 of its 12 point types with Borax Lake, although the Mendocino specimens are smaller, on the average, than Borax Lake points of the same type. The Mendocino complex shares six point types with the Middle Central California complex; all but one of these is also shared with the Borax Lake site. Finally, while the Mendocino complex has metates as grinding stones, it has a much more prominent assemblage of mortars than Borax Lake has. When the Borax Lake age estimates are used as a guide, it appears that the Mendocino complex would have to be more recent than the wide-stem Borax Lake points—that is, less than 7000 years. The smaller point size and the use of mortars in the Mendocino complex suggest a Middle Central California affinity, although not a strong one. If a rough age of 1000 B.C. is accepted for Middle Central California, this places the Mendocino complex between 1000 and about 5000 B.C., there being some feeling that the true age is likely to be closer to the more recent end of that time span. This is not very precise dating, but it is a substantial revision toward greater age than the "guess" date of A.D. 500 to 1000 previously published.

25. C. W. Meighan, in *The Quaternary of the United States*, H. E. Wright, Jr., and D. G. Frey, Eds. (Princeton Univ. Press, Princeton, N.J., 1965).

26. This work is in part supported by National Science Foundation grants GP-5548 to P. E. Damon and GA-1288 to C. V. Haynes. The cooperation and assistance in the field of Charles Rozaire, Freddie Curtis, Robert and Melva Orlins, Richard Muers, and George and Mary McLeod are gratefully acknowledged. A special word of gratitude is due Willard Hodges of the Lake County Realty Company for permission to excavate trenches in the company's walnut orchard and to Edward Fitts for a masterful job of backhoe excavation. Microscope slides and illustrations were prepared at the University of California, Los Angeles, by Leonard Foote and Paul Aiello. The costs of laboratory work were paid by a Faculty Research Grant from UCLA to C. W. Meighan. The Southwest Museum, through Director Carl Dentzel and Curator Bruce Bryan, permitted access to the original Borax Lake collection and generously allowed us to cut small pieces from many important specimens for purposes of obsidian dating. This cooperation made possible the first objective sequencing of Borax Lake artifact types.

Reproductive Physiology of Marsupials

Unique features of marsupial reproduction suggest two evolutions of viviparity in therian mammals.

G. B. Sharman

The marsupial mother bears her young after a shorter gestation period than that usually occurring in other mammals of comparable size, and the young are born in a generally embryonic condition. Although the pouch, or marsupium, from which the marsupial order takes its name, is not a universal feature of the group, the young are always firmly attached to the teats for a period after birth which roughly corresponds to the latter part of intrauterine gestation in eutherian or true mammals. It was once believed that the eutherian mammals were descended from marsupials, but this view is no longer held. However, it has more recently been suggested that marsupials are descended from ancestors with a true allantoic placenta, such as that occurring in all eutherians and few marsupials, or that the marsupial type of reproduction is derived from the fully viviparous reproduction of eutherians (*1*). It is at least equally probable that marsupials and eutherians are derived from common oviparous ancestors and that viviparity evolved independently in each group. Accordingly, I examined the physiology of marsupial reproduction and compared analogous processes in marsupials and eutherians.

Chromosomal Sex Determination

Diploid chromosome numbers of marsupials vary from 10 in the female and 11 in the male to about 32. Chromosome numbers are known for about 60 species, or about 26 percent of extant marsupials, and in all but four of these sex is determined by XX female chromosomes and XY male chromosomes. In the American superfamily Didelphoidea (opossums), two species, *Caluromys derbianus* and *Marmosa mexicana* have 14 chromosomes. The two X chromosomes are less than half the size of the smallest autosomes, and the Y chromosome is minute, much smaller than the X, and less than 1 micrometer in length (*2*). All of the Australian superfamily Dasyuroidea (marsupial "mice" and "cats," for example) thus far studied also have 12 autosomes, a small X chromosome and a minute Y chromosome (*3*). *Burramys parvus* (superfamily Phalangeroidea), an Australian marsupial known until 1966 only as a Pleistocene fossil, and related animals grouped by Kirsch as Burramyidae have similar karyotypes to the dasyuroids and are always distinguishable on sex chromosome morphology from the remaining phalangeroids (*4*). The occurrence of similar karyotypes in *Caluromys*, which Reig (*5*) regarded as being one of three surviving genera of the otherwise extinct subfamily Microbiotheriinae, in the dasyuroids, and in the most generalized of the phalangeroids suggests that the small X and minute Y chromosome of these animals may represent the ancestral marsupial condition.

Sixteen species of marsupials have 22 chromosomes, and in most of these, and in those with various other chromosome numbers, the sex chromosomes are larger than those of the 14 chromosome didelphoids, the dasyuroids and the burramyids. The X chromosome is about the same size as the smallest autosome, and the Y is the smallest chromosome of the set. The X and Y chromosomes are thought to associate by chiasmata at meiosis. In both mitosis and meiosis they show a cycle of condensation different from that of the autosomes, and, although they separate first at the anaphase of meiosis, they lag on the spindle and reach the poles after the other chromosomes. Failure of prophase pairing during meiosis and loss during mitosis occur, and it is suggested that the sex chromosomes are at some disadvantage during division as compared to the autosomes (*6*).

Intersexual marsupials with sex chromosome aberrations are apparently produced from union of gametes with unbalanced sex chromosome complements. The incidence of intersexuality

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in marsupials is not, however, higher than in eutherian mammals. We found a tammar wallaby (*Macropus eugenii*) of female phenotype (weight basis) with pouch, teats, mammary glands, and penis, but no scrotum; the sex chromosomes of this animal were XXY. Unlike eutherian mammals, XY male marsupials lack rudimentary teats and mammary glands. The internal reproductive organs of the XXY intersex are essentially male, and the testes are aberrant, undescended, and nonfunctional. Another phenotypic female with an essentially female reproductive system, pouch, teats, and mammary glands has but one X and no Y sex chromosomes. The gonads of the XO intersex are of ovarian size but nonfunctional and contain both testicular and ovarian elements. A small empty scrotum is present in addition to the pouch (*7*). Men with XXY chromosomes are sterile, of male phenotype with descended testes, and they frequently exhibit breast enlargement in later life (*8*). The XXY mouse of male phenotype has libido but is apparently sterile (*9*). In man, XO individuals are phenotypically female and agonadal or with rudimentary gonads in which germ cells do not occur (*10*), but XO mice are of female phenotype and fertile (*9*). Notwithstanding the differences of the marsupial chromosomal intersexes from their eutherian counterparts, these cases demonstrate that the marsupial Y chromosome, like that of eutherian mammals, is strongly male determining. Sex determination does not depend, as in *Drosophila*, on the ratio of the X chromosomes to the autosomes.

In four species of marsupials, extra sex chromosomes occur normally without accompanying sex modifications. These animals have multiple sex chromosome systems derived by incorporation of autosomal material into the sex-determining system (*3, 11, 12*). In the XX female and XY_1Y_2 male chromosome systems of *Macrotis* (= *Thylacomys*) *lagotis, Wallabia bicolor* (= *Protemnodon bicolor*), and *Potorous tridactylus*, the ancestral X chromosomes are fused to autosomes whereas in *Lagorchestes conspicillatus* both X and Y chromosomes are fused to autosomes (Fig. 1). *Wallabia bicolor, P. tridactylus,* and *L. conspicillatus* have fewer chromosomes than related species, and the first two species have the lowest chromosome numbers known in mammals. The incorporation of autosomal material into the sex chromosomes apparently reduces the possibility of their loss because of nondisjunction during cell division (*11*). The short arm of only one of the two compound X chromosomes exhibits asynchronous synthesis of DNA in *W. bicolor* and *P. tridactylus*. One of the X chromosomes of *P. tridactylus* frequently has its achromatic region reduced, and this is believed to be the "inactive" chromosome (*13*). The results are interpreted in terms of the Lyon hypothesis which postulates functional inactivation of one of the two X chromosomes in the normal female mammal (*14*).

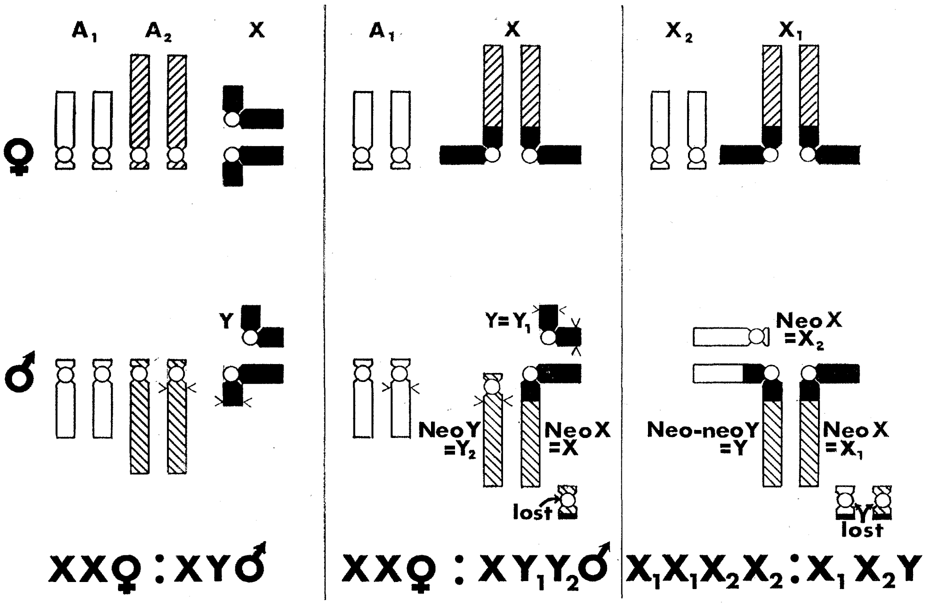

Fig. 1. (Left) The chromosomes of a marsupial with an XX ♀ —XY ♂ sex-determining mechanism and two pairs of autosomes (A_1, A_2). Further autosomal pairs not shown. (Center) A reciprocal translocation between one autosome and the X chromosome converts the system to an XX ♀ —XY_1Y_2 ♂ sex-determining mechanism and reduces the number of pairs of autosomes by one. (Right) Further reciprocal translocations between Y_1 and Y_2 chromosomes of the XY_1Y_2 system and between Y_1 and another autosome convert the system to an $X_1X_1X_2X_2$ ♀–X_1X_2Y ♂ system reducing the number of autosomes by a further pair. > <, Points of chromosome breakage and reunion; open circles, centromere regions of chromosomes.

At least three species of the Australian superfamily Perameloidea have sex chromosome mosaicism. In *Isoodon obesulus, I. macrourus,* and *Perameles nasuta* the chromosome number in the male germ line is 12 autosomes plus X and Y sex chromosomes, and in the ovarian tissue there are 12 autosomes plus two X chromosomes. The chromosome number in liver and spleen cells and in leukocytes of both males and females is $2n = 13$. One X chromosome is eliminated from somatic tissues of females, and the Y chromosome is eliminated from male somatic tissues. Hayman and Martin (*15*) suggest that the difference in X chromosome constitution between female germ and soma lines can be explained in terms of a mechanism for dosage compensation and that a parallel exists between somatic elimination of X and Y chromosomes and delayed duplication of DNA during mitosis. The delay in DNA synthesis of one X chromosome in somatic cells of female mammals can be explained in terms of the "inactive X hypothesis" (*14*), but there is considerable evidence that the Y chromosome is also late replicating in many eutherian mammals and in some marsupials. Somatic elimination or deletion of one X chromosome in eutherian mammals has been attributed to an inactive X chromosome (*16*). Analyses of the chromosome constitutions of various tissues in the pouch young of *P. nasuta* and *I. macrourus* showed that X chromosome elimination from somatic tissues occurred over a long period during morphogenesis. Gut and skin cells of newborn animals retain both sex chromosomes, and elimination is not complete in the spleen of 10-day-old *P. nasuta* or the liver of 24-day-old *I. macrourus*. All cells in the cornea of the 55-day-old female *I. macrourus* retain both X chromosomes. In the early embryo of eutherian mammals, no sex chromatin bodies are found and presumably both female X chromosomes are active. The sex chromatin body appears at the late blastula or early primitive streak stage, and X inactivation is presumed to occur at, or near, this stage (*14*). Sex chromatin bodies, which differ between sexes, have not thus far been demonstrated in bandicoots, and thus there is no criterion by which to detect inactivation before a sex chromosome disappears from the relevant cell or tissue. However, even if inactivation occurs some time before sex chromosome elimination it might be assumed that it occurs at different stages of morphogenesis in the various tissues in view of the fact that elimination itself occurs over a long period.

Reproductive System and Birth

All mammals pass through an embryonic "sexually indifferent" stage when, regardless of sex chromosome constitution, the undifferentiated ducts of the reproductive systems of both sexes are present. These are the Wolffian and Müllerian ducts, and it is the relation of these to the developing kidney ducts (ureters) that at once distinguishes marsupials from true mammals. In both groups the ureters arise as budlike outgrowths on the dorsomedial side of the Wolffian ducts, but, as development proceeds in the marsupial, their point of origin is shifted to a medial position. In eutherians the point of origin is shifted to the lateral aspect of the Wolffian ducts. The end result is that in adult marsupials the ureters pass to the base of the bladder between the Wolffian ducts while in eutherians they pass to the outside of the Wolffian ducts (*17*). The Müllerian ducts appear after the Wolffian ducts but grow along the same course so that the ureters of marsupials lie also between the Müllerian ducts. In summary, the differences between marsupial and eutherian reproductive systems, amounting only to a variation in point of origin of ureters in the embryo, are slight early in development and profound in the adult (Fig. 2). In descent of the marsupial testis the Wolffian duct derivative, the vas deferens, is outside the ureter, whereas the descending eutherian vas deferens must loop over the ureter. The Müllerian duct derivatives —uterus and vagina—are free to undergo fusion in the eutherian for they are outside the ureters. If similar fusion occurred in marsupials it would impede the ureters. Marsupials thus have two lateral vaginas (Fig. 2), and these are the canals up which the sperms travel at insemination. Many male marsupials have a bifid penis, the right and left prongs apparently being placed in the corresponding lateral vaginal canals during copulation (*18*).

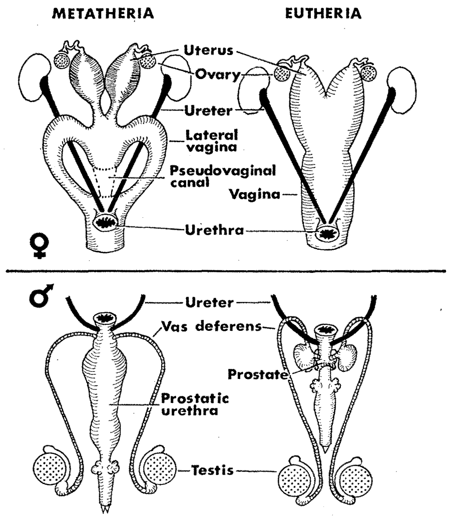

Fig. 2. A comparison of the reproductive systems of female and male metatherian (marsupial) mammals with those of eutherian mammals.

In ancestral marsupials birth presumably occurred through the lateral vaginal canals, the homolog of the eutherian mid-line vagina, but in most if not all recent marsupials birth occurs through a mid-line passage (*19*). This is the pseudovaginal canal—a shortcut to the urogenital sinus from the cul-de-sac formed where each lateral canal loops around a ureter (Fig. 2). In didelphoid, dasyuroid, and perameloid marsupials, and in most of the phalangeroids except kangaroos, the pseudovaginal canal is transitory, being formed anew at each parturition. Its formation, in the Australian brush possum, appears to be dependent on secretions of progesterone from the corpus luteum, although mechanical rupture may be responsible for the final stages of canal formation (*20*). Relaxin, a nonsteroid substance secreted by the ovarian corpus luteum, is known to relax the pelvic girdle of the guinea pig before parturition and to affect the reproductive tract of other eutherian mammals. A corresponding secretion from the corpus luteum of the brush possum has relaxin activity but no apparent effect on the vaginal canal of this animal.

In the Macropodidae (kangaroos and wallabies) and in the unique Australian marsupial *Tarsipes*, whose relation to other marsupials is uncertain, the epithelium of vaginal culs-de-sac and urogenital sinus become contiguous at the time of the first parturition and, thereafter, form a permanent mid-line birth canal (*19*). Removal of both ovaries, or of the ovary bearing the single functional corpus luteum, in the wallaby *Setonix* usually prevents parturition, but Tyndale-Biscoe found that administration of relaxin to ovariectomized animals allowed better intrauterine survival and a higher percentage of births (*20*). The relaxin appears to be produced in the ovary rather than in the corpus luteum.

Notwithstanding the makeshift nature of the marsupial birth canal, a very high percentage of pregnancies result in live young, and those marsupials which almost invariably give birth to a single young (monotocous species) are reproductively very efficient. I found that 102 of 124 (82 percent) red kangaroo (*Megaleia rufa*) females which had access to a male for 1 day or less at the time of estrus gave birth to a young which reached the pouch. This compares more than favorably with the reproductive efficiency of monotocous eutherian mammals in which between 53 and 95 percent become pregnant after a single insemination (*19*).

The female red kangaroo about to give birth first cleans the inside of her pouch by licking. Just before parturition occurs the female assumes the "birth position"—a sitting posture in which the tail is passed forward between the hind legs, the weight largely being taken on the dorsal surface of the butt of the tail (*21*). Birth is preceded by the appearance of a few milliliters of viscous fluid from the ruptured yolk sac and of the unruptured embryonic allantoic sac. The young appears at the urogenital opening enclosed in the fluid-filled amnion and, after breaking free, crawls unaided to the pouch. During the first part of its climb up the mother's ventral surface, the young is connected by the umbilical cord to the yolk-sac placenta which is still within the birth canal. The journey to the pouch is accomplished in a few minutes, and the young crawls into the pouch where it attaches to one of the four teats. After the umbilical cord is severed the placenta is expelled from the urogenital opening. No recent observers have been able to confirm the observations of earlier authors that the mother licks a track in the fur for the young to follow. Fur licking is, however, continuous throughout the climb to the pouch but it is confined to the region behind the young—all traces of blood, birth fluids, and embryonic membranes being eaten, except the allantoic sac.

We have evidence that an essentially similar process of parturition to that in the red kangaroo occurs in many other macropodid marsupials (*22*). The gray kangaroo appears to be an exception—it gives birth in a standing position with the tail behind, instead of between, the hind limbs. All kangaroos give birth to a single young; the birth position and process of parturition in the polytocous American opossum (*23*) essentially resemble similar phenomena in the red kangaroo.

Lactation

The marsupial young is born in a less-developed condition after a generally much shorter fetal life than that of eutherian mammals of comparable size. The discrepancy between weights of newborns of marsupial and eutherian mammals disappears if marsupials are regarded as being "born again" when they leave the mother's pouch, at which time they weigh about as much as the newborn young of eutherians of comparable size (*24*). A further period of suckling, roughly corresponding to the postnatal suckling period of eutherians, occurs after marsupial young leave the pouch.

The composition of marsupial milk, like that of eutherian mammals, changes continuously through the period of suckling. A clear fluid is secreted from the teats at the time of parturition (*25*), and the early milk appears to contain little, if any, fat although sufficient quantities for chemical analysis are difficult to obtain. Milk produced in later stages of lactation has a higher fat content, and the milk on which advanced young are suckled may contain up to 20 percent fat. The total solid content is variable and shows no definite increase as lactation proceeds, but fat increase is accomplished by a decrease in the percentage of solids that are not fats. There is a tendency for increased protein content and reduced reducing sugar content as lactation proceeds (*26*). Some marsupials, notably kangaroos, have overlapping periods of lactation—a young on foot being suckled on one of the four teats while another, much smaller, young is suckled in the pouch on another teat. The two milks, secreted concurrently by separate mammary glands of the same female, appear very different, and because the young on foot is over 200 days older than the pouch young (*21*) the two milks apparently differ in composition. Analyses that have been done during the period of double suckling do indicate differences; the advanced gland produces milk with three times as much fat as the second gland (*27*).

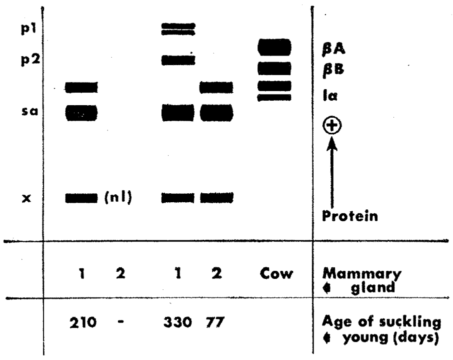

Fig. 3. Starch-gel electrophoresis of whey proteins from the milk of a red kangaroo and a cow. (Left) Electropherogram of the milk from the single lactating mammary gland of a red kangaroo suckling a pouch young 210 days old. (Center) Two electropherograms from the same red kangaroo 120 days later; the young suckling on gland 1 has left the pouch and another young, 77 days old, is suckling from gland 2. (Right) Cow's milk. Abbreviations: βA, β-lactoglobulin A; βB, β-lactoglobulin B; *la*, bovine α-lactalbumin; *nl*, gland not lactating; *p1* and *p2*, whey proteins specific to the kangaroo which appear at late stages of suckling; *sa*, serum albumin; and *x*, undefined protein with same mobility as haptoglobin. [Results from Lemon and Bailey (*28*)]

Using electrophoretic methods, Bailey and Lemon (*28*) clearly demonstrated a specific protein difference between the milks secreted by two different mammary glands in the same red kangaroo (Fig. 3). They considered that specific whey proteins appeared in the milk of the first gland suckled while intrauterine development of the second young was proceeding but were absent from the milk secreted by the second gland after the new young began suckling. Lemon and Poole (*29*) have subsequently shown that the association postulated between appearance of the whey proteins and intrauterine development is fortuitous. The new protein bands appear in the electropherogram after a more or less constant period of suckling apparently independent of changed pituitary or ovarian hormone secretion. It is, however, clear that kangaroos commonly produce, at the same time from separate mammary glands, two milks which differ vastly in chemical composition and that these are produced under the same endocrine environment.

Reproductive Cycles

The changes which occur between successive periods of estrus in the nonfertilized female constitute the estrous cycle. In marsupials the hormone-induced changes which occur in the reproductive organs after ovulation (which is closely associated with estrus) are identical in pregnant and nonmated females. For these similarities of the estrous cycle to pregnancy Hill and O'Donoghue in 1913 proposed the term "pseudopregnancy" (*30*). This early usage of the term and its subsequent loose adaptation to a number of different phenomena in various eutherian mammals illustrates (i) the early attention which was paid to some aspects of marsupial reproductive processes and (ii) the long hiatus between early and recent studies on marsupial reproduction. Recent workers (*31*) have avoided usage of the term pseudopregnancy for any phase of the marsupial reproductive cycle largely because pseudopregnancy arrests the reproductive cycle of rodents which are foremost in mind as laboratory animals. In marsupials neither pseudopregnancy, in the sense of Hill and O'Donoghue (*30*) and Hartman (*32*), nor true pregnancy interrupts the estrous cycle.

The proestrous phase of the marsupial estrous cycle is characterized by enlargement of one or more of the graafian follicles, by mitotic proliferation of the uterine lumen and gland epithelia, and by increase in the size of the elements of the vaginal complex (*30–32*). These changes may be induced in the spayed or intact female by the injection of estrogens (*20, 33*). In the intact female changes induced by estrogen reach their peak at about the time of estrus when copulation occurs. Ovulation occurs one to several days after estrus (*31, 32*), and uterine epithelial proliferation continues at and after this time and is accompanied by desquamation of the vaginal epithelia and by decrease in size of the vaginal complex. Corpora lutea are formed at the site of ruptured ovarian follicles. All marsupials thus far investigated ovulate spontaneously, there being no evidence that copulation or other stimuli are necessary to induce shedding of the ovarian eggs.

The postestrous proliferative phase is eventually replaced by the luteal phase which is characterized by one or more functional corpora lutea in the ovaries and the onset of a secretory phase in the uteri (*30–32*). Just as the proliferative phase is induced in the castrate female by the injection of estrogen so the luteal phase is induced by the injection of progesterone (*34*). The uterine luteal phase, which varies in length in different marsupials, is followed by anestrus in monestrous marsupials and by the postluteal phase, which grades into the next proestrus, in polyestrous marsupials. The relations of size of the uteri to the accompanying ovarian events during the estrous cycle of marsupials are shown in the top line of Fig. 4.

If insemination occurs at estrus, the resulting pregnancy does not interrupt the estrous cycle of any marsupial. Provided that the newborn young are prevented from reaching the teat or removed soon after birth, the next estrus recurs when expected. In species that exhibit postpartum estrus, the relation between parturition and estrus is fortuitous—estrus and mating occur at the same time as they would have occurred had the animal not been pregnant. There is considerable interspecies variation in the time after insemination at which the marsupial young is born. Those born at the end of the luteal phase arrest the cyclic reproductive activity of their female parent before the recurrence of estrus, whereas those which are carried through the postluteal and proestrous phases arrest postestrous cyclic reproductive activity (Fig. 4). In the swamp wallaby (*Wallabia bicolor*), alone among marsupials thus far studied, the young is carried in the uterus during estrus and is born in the ensuing postestrous phase. The average length of the estrous cycle is 32 days, and the gestation period is 35 days. Pregnancy does not inhibit the cyclic recurrence of estrus, but suckling-induced ovarian inactivity occurs postpartum (Fig. 4). Ovulation strictly alternates between left and right ovaries so that the closing stages of gestation in one uterus may be accompanied by the segmentation of a newly fertilized egg in the alternate uterus (*22*).

The close anatomical and histological similarities between postestrous phases of pregnant and nonpregnant marsupials and the failure of pregnancy (but not of lactation) to inhibit the cyclic recurrence of estrus and ovulation suggest an endocrine equivalence of the pregnant and nonpregnant states. Other results confirm that this is so. Equivalent postovulatory mammary gland development occurs both in pregnant and nonmated marsupials (*18, 25, 32*). Mammary glands of virgin, or nonmated, marsupials become functional at an equivalent postestrous stage to that at which parturition occurs in gravid females. Newborn foster young attached to the teats of virgin or nonlactating females at this stage are suckled, show normal growth rates, and are raised to maturity (*21, 25, 35*). The endocrine equivalence of postovulatory pregnant and nonpregnant states in the quokka (*Setonix*) was demonstrated by the development of early embryos transferred to the uteri of nonpregnant recipients. Embryos that had completed up to 6 of the total of 25 days after the blastocyst stage, the normal period for development in the uterus, continued normal growth in a recipient uterus (*36*). Compared to their pregnant counterparts (*31*), nonmated female marsupials have equivalent concentrations of pregnanediol in the urine and Lemon has shown that progesterone concentrations are equivalent at similar postovulatory stages in bloods of pregnant and nonpregnant animals (*37*). These various results strongly indicate that there is no extraovarian hormone secretion during pregnancy; the placenta is not an endocrine organ in marsupials, as it is in eutherian mammals (*38*).

Embryonic Diapause

Embryonic diapause is apparently confined to macropodid marsupials where it is known to occur in at least 14 species (*39*). It may not, however, be universal in the macropodids, for no unequivocal instance has yet been found in the western gray kangaroo *Macropus fuliginosus* (*40*). The term "embryonic diapause" is used in preference to "delayed implantation," an analogous phenomenon in various eutherian mammals (*41*). During diapause a viable but totally quiescent embryo (blastocyst) consisting of 70 to 100 cells and about 0.25 millimeter in diameter is carried in one uterus. The blastocyst differs from the equivalent stage in eutherian mammals by being surrounded by a shell membrane and albumin layer. These membranes have the remarkable property of perfectly preserving for many months the numerous accessory spermatozoa which become entrapped within the membranes at fertilization (*42*). The blastocyst proper is composed of a single spherical layer of cells, all of the same type, called protoderm which is not divisible into embryonic and extraembryonic regions. By contrast the eutherian mammal blastocyst has an inner cell mass, certain formative cells of which form the embryo proper, while

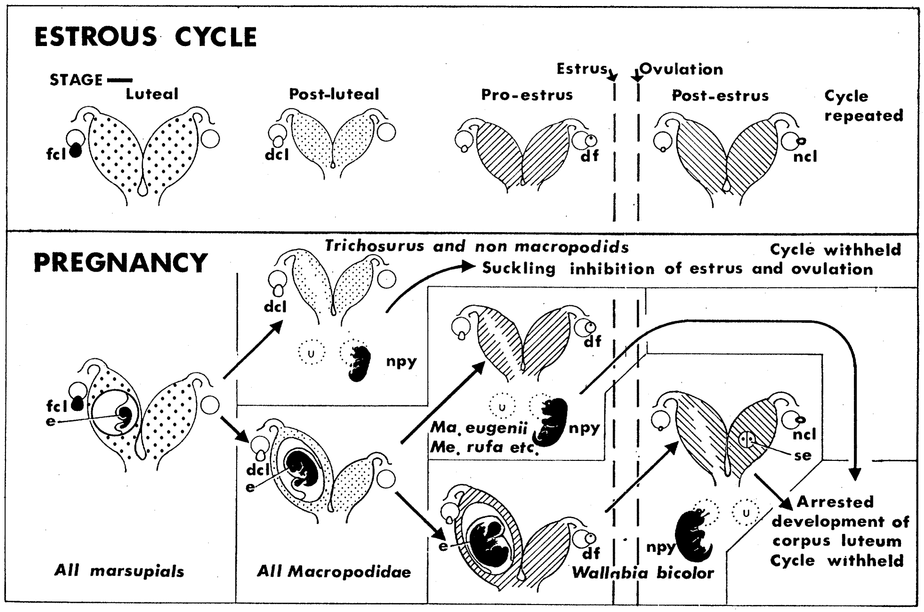

Fig. 4. (Top, left to right) The size and functional relations of ovary and uterus during succeeding phases in the estrous cycle of marsupials. Abbreviations: *dcl*, degenerating corpus luteum; *df*, developing graafian follicle; *fcl*, functional corpus luteum; and *ncl*, new corpus luteum. (Bottom) Size and functional relations during pregnancy and lactation. Abbreviations: *e*, intrauterine embryo; *npy*, newborn pouch young attached to teat; and *se*, segmenting egg.

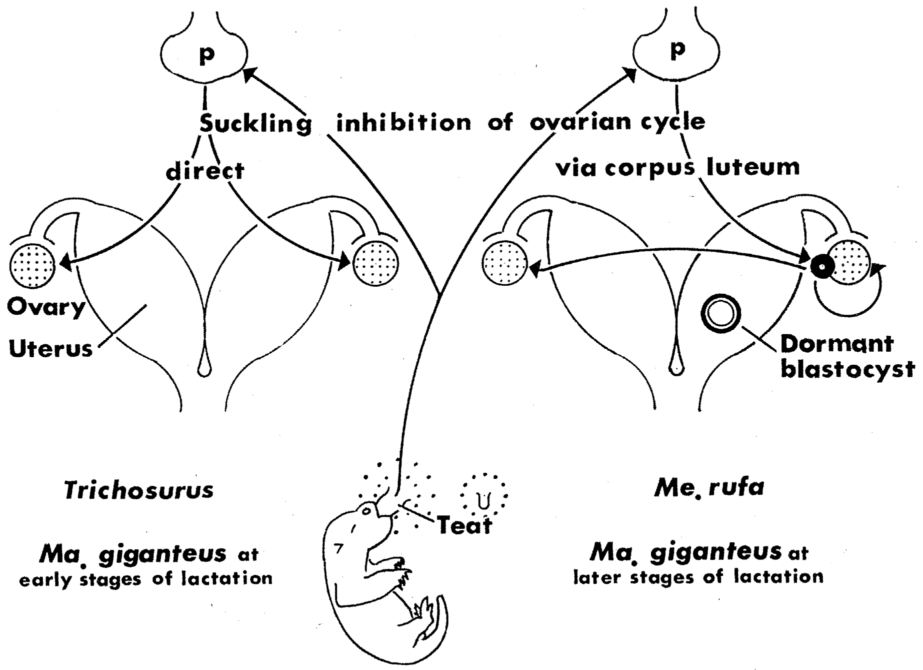

Fig. 5. Diagrammatic representation of the two methods of suckling inhibition of the ovarian cycle in marsupials. *Trichosurus vulpecula* and *Macropus giganteus* at early stages of lactation (left) return to estrus soon after the young is removed from the pouch. *Megaleia rufa* and *Macropus giganteus* at later stages of lactation (right) do not return to estrus for about a month after the young are removed from the pouch. *Megaleia rufa* returns to estrus soon after the corpus luteum is removed surgically and while pouch suckling continues. Abbreviation: *p*, pituitary gland.

the remaining cells give rise to extraembryonic membranes.

In the eastern gray kangaroo (*Macropus giganteus*) the gestation period, unlike that of most other macropodids, is rather shorter than the length of one estrous cycle. In this respect the gray kangaroo resembles nonmacropodid marsupials which do not exhibit embryonic diapause (Fig. 4). Suckling by the early pouch young inhibits ovarian function because the estrous cycle is withheld during the early part of lactation. If the pouch young is removed during this period, estrus and ovulation occur about 9 days later (*22*). During later stages of lactation, up to 75 percent of wild animals ovulate and may become fertilized some 120 or more days before the young leaves the pouch. Development of the corpus luteum which forms at the site of the ruptured follicle is arrested before its development is complete, and the embryo resulting from fertilization during pouch suckling becomes dormant. Development of the arrested corpus luteum and of the dormant blastocyst is resumed if the young is lost or removed from the pouch or after the completion of pouch suckling (*43, 44*). An essentially similar situation is found in other macropodid marsupials that exhibit embryonic diapause except that fertilization of the egg which becomes the dormant blastocyst occurs earlier in the life of the pouch young than it does in the case of the gray kangaroo. In a number of species in which the length of the gestation period approximates that of one estrous cycle, fertilization occurs postpartum. In the swamp wallaby preparturition fertilization occurs (Fig. 4). Suckling induces a resting phase in the post- or prepartum corpus luteum (the corpus luteum of lactation), and a dormant blastocyst is present during pouch suckling (*22*).

On analogy with nonmacropodid marsupials and with the gray kangaroo during the early part of pouch suckling, it might be expected that pouch suckling would inhibit ovulation in those marsupials in which the gestation period is just shorter than the length of one estrous cycle. This is not so; postpartum ovulation is delayed in red kangaroos that give birth during periods of severe drought, but it may occur after rainfall while a large young is suckled in the pouch (*45, 46*). Red kangaroos suckling a young in the pouch return to estrus and ovulate 14 to 21 days after surgical removal of the corpus luteum of lactation (*46*). The stimulus of suckling is sufficient to prevent return to estrus, in the absence of a corpus luteum of lactation, during about the first 160 days of lactation in the gray kangaroo. However, once ovulation does occur and the corpus luteum of lactation is formed, further ovulation is prevented (*44*). There are thus two mechanisms of lactational inhibition of ovulation in marsupials. In nonmacropodids and in the gray kangaroo during the early part of lactation, the suckling stimulus prevents ovulation by a direct effect on the ovaries. In macropodids, such as the red kangaroo, the inhibiting effect is mediated via the corpus luteum of lactation (Fig. 5). Evolution of ovulation inhibition via the corpus luteum presumably evolved within the Australian macropodid marsupials, and it is assumed to be mediated via the pituitary gland. The pituitary is however implicated only on analogy with related phenomena in eutherians because the pituitary-ovarian axis has not been investigated experimentally in marsupials.

The pituitary is also directly implicated, but again by inference only, in the embryonic diapause of the tammar wallaby. In this species, diapause is usually initially controlled by lactation and postdiapause development of the dormant blastocyst occurs if the young is removed from the pouch during the breeding season (January to July). When the young leaves the pouch in spring each year, the breeding season is over and the corpus luteum of lactation does not resume development until the following summer at the beginning of the new breeding season. The dormant blastocyst, carried throughout pouch life, is also carried during the nonbreeding period and begins growth after onset of renewed corpus luteum activity (*47*). Ovulations at the close of the breeding season may be immediately followed by corpus luteum arrest, in which case embryonic diapause occurs in the nonlactating animal during the nonbreeding season (*48*). Presumably the factor stimulating development of the corpus luteum of lactation at the start of the breeding season and the missing factor at the close of the breeding season are one and the same, and this is assumed to be a luteotropic hormone of pituitary origin. Neither of the pituitary hormones, luteinizing hormone or prolactin, which have luteotropic activity in various eutherian mammals, cause renewed development of the marsupial corpus luteum of lactation. An extract of horse anterior pituitary, having both follicle stimulating hormone and luteinizing hormone activity, caused corpus luteum hypertrophy in two of five quokkas which were suckling pouch young, but the dormant blastocyst, carried by but one of the animals, did not resume development (*49*).

Interest in embryonic diapause centers on the mechanisms by which the host animal is able to maintain a totally quiescent, but viable, embryo for very long periods. The importance of the suckling stimulus was demonstrated in experiments in which an extra young on foot was fostered onto red kangaroos already suckling one young on foot. Two young, suckling from outside the pouch, both induce and maintain diapause as does the single young suckled inside the pouch (*50*). Oxytocin, the hormone which stimulates milk flow, may play a key role in preventing development of the corpus luteum of lactation because injected oxytocin both prevents corpus luteum hypertrophy and maintains embryonic diapause in red kangaroos experimentally deprived of their pouch young (*51*). Since renewed development of the dormant blastocyst normally occurs in red kangaroos at the end of the pouch suckling period but before the cessation of lactation, it is possible that the corpus luteum responds to reduced concentrations of circulating oxytocin consequent on the less-frequent suckling of the young at the close of its pouch life.

Fertilized eggs develop to the blastocyst stage and enter diapause if the ovaries are removed 2 days after mating. Ovariectomy during diapause is without effect on the dormant blastocyst (*42*). Diapause thus appears to be initiated and maintained in the absence of ovarian hormone secretion rather than because of a specific hormone-induced environment. The resting corpus luteum of lactation does not induce a luteal (secretory) phase, such as that induced in the uterus by the cyclic corpus luteum or by the injection of progesterone. Progesterone injected during diapause, to both intact and ovariectomized animals, both induces a luteal phase and starts blastocyst development. Injected estrogen also starts blastocyst development, but with less overall success than with progesterone (*52*). Both hormones may act by increasing the metabolic activity of the uterus and thus overcome a restraint, exerted by the uterus, on development. Fertilized eggs restrained in the fallopian tube apparently fail to develop to blastocysts, because none are found 10 days after ligation of the posterior end of the tube. Blastocysts transferred to the anterior chamber of the eye fail to develop and undergo degenerative changes. Those sealed in diffusion chambers in the peritoneal cavity sometimes undergo limited cell division alongside degenerative changes in other cells, while blastocysts in the uteri of equivalent females remain dormant (*53*). By contrast, mouse blastocysts, transferred to the kidney during delayed implantation, develop normally and "implant," while similar blastocysts in the uterus remain in delay (*54*).

Evolution of Marsupial Reproduction

Clemens (*55*) suggested that *Pappotherium* and other mammals of early Cretaceous (Albian) age had the dental characters of the most recent common ancestors of marsupials and eutherians. Slaughter (*56*) has described a new genus, which he regards as a didelphid marsupial, from Albian deposits of Texas, which also contain material referable to the Eutheria. On the basis of these finds he regards the marsupial-eutherian dichotomy from a common ancestor to have been pre-Albian, a concept earlier proposed on other grounds (*57*). Although separate evolutions of marsupials and eutherians from reptilian ancestors have been proposed, it is generally agreed that both groups are descended from the pantotheres—a group of middle and upper Jurassic mammals. It is unknown whether the pantotheres were oviparous or viviparous, and paleontological findings are unlikely to provide the answer. It is therefore relevant to compare the marsupial and eutherian methods of reproduction, because they may represent separate evolutions of viviparity. Regardless of their long evolutionary history, marsupials are expected to have retained some features of reproduction inherited from ancestors common also to the eutherian mammals. Purely marsupial innovations have presumably evolved within the group while some features of reproduction, common to both marsupials and eutherians, have undoubtedly had parallel evolutions within each group.

Sex determination involving the XX female and XY male chromosomes is common to both marsupials and eutherians and probably evolved before their separate existences. The Y sex chromosome is male determining in marsupials (*7*), as it is in eutherians (*58*). Multiple sex chromosome systems have their parallel in similar systems in eutherians (*59*), and since they occur in two marsupial families and among distantly related members of the same family, they have presumably originated a number of times in both marsupials and eutherians. Somatic elimination of the Y chromosome is, on present evidence, a typically marsupial innovation confined to one group of bandicoots.

The marsupial reproductive system is superficially specialized; yet it retains, in common with reptiles and monotremes, a medial position of the ureters in relation to the paired Wolffian and Müllerian ducts of the embryo (*17*). In the eutherian reproductive system, migration of the point of origin of ureters to the lateral aspect of the developing Wolffian ducts allows complete fusion, in the adult, of the vaginal portion of the reproductive tract. This modification may have allowed the birth of young which could only achieve extended uterine growth after the adoption of placental secretion—another purely eutherian innovation. The failure of marsupials to evolve placental secretion, which in eutherians both extends the secretory phase and inhibits ovulation, sets limits to the period of intrauterine development.

A secretory, or luteal, phase of the estrous cycle is found in all mammals (*60*). If, as suggested (*61*), the monotreme and marsupial-eutherian lines are separate derivations from mammal-like reptiles then the luteal phase may be a premammalian evolution. It is not necessarily associated with viviparity, because, in the monotremes, the uterine fluid is absorbed by the fertilized egg that undergoes a limited amount of embryonic development during its passage through the oviduct (*62*). Estrogen and progesterone are apparently responsible for cyclic changes in the reproductive organs of both marsupials and eutherians. These hormones have a long history in vertebrate, and perhaps prevertebrate, evolution, although progesterone may function as a hormone only in mammals (*63*).

The simultaneous production of two milks, differing greatly in composition, in the same animal and the occurrence of a unique type of embryonic diapause are, apparently, purely macropodid marsupial innovations. The first is an adaptation allowing two generations of young to be fed simultaneously (*21*), while the second is an adaptation preventing concurrent occupation of the pouch by two young of different ages (*19*). However, even though diapause is confined to the macropodids, and may have evolved in the group, a blastocyst similar to that which becomes dormant is a universal feature of the marsupials.

All major groups of vertebrate animals more advanced than the jawless fish have at least some viviparous members, excepting only the birds. There have thus been many evolutions of viviparity so a separate evolution in marsupials is not unlikely on general grounds. The many unique features of marsupial reproductive physiology suggest that viviparity evolved separately in eutherian and marsupial stocks after their derivation from a common oviparous ancestor.

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NEWS AND COMMENT

Psychology: Apprehension over a New Communications System

Dissension has arisen in the American Psychological Association (APA) over a multimillion dollar plan to establish a "national information system for psychology." The plan would supplement the existing psychology journals with a computerized system for distributing unedited manuscripts on a rapid-fire basis. Proponents of the new system see it as an imaginative effort to cope with problems arising from the rapid growth of the scientific literature. But critics charge that a "cabal" at APA headquarters, operating in relative secrecy, is rushing pell-mell into a radical change without taking adequate care to ensure that the quality of scientific communication remains high.

The internal squabbles of an organization are generally of interest only to its members, but the fracas at APA seems worth examining on two counts. For one thing, the problems besetting the psychology literature are similar to the problems faced in virtually all scientific disciplines, so the APA's experience may have widespread relevance. For another thing, the dispute at APA stems partly from a deep feeling of distrust between some psychologists in the field and the central office staff. This is a malady that strikes many organizations that become large enough to establish bureaucracies with an inertia and mind of their own. "The engineers and technicians have moved in and are pushing aside the psychologists," complains Jane Loevinger, a gadfly who is a research associate at Washington University and a member of the APA's policy and planning board. "They want to do their thing rather than our thing. It's upside down."

The proposed information system has been designed under a $960,000 "program definition" grant from the National Science Foundation (NSF). The system would be comprehensive and would seek to improve the entire range of scientific communications. It would include, among other things, a system for computerized bibliographic control and information retrieval; a system for exchanging informal communications, such as memos, letters and research