SEX CHROMOSOMES AND REPRODUCTIVE ANATOMY OF SOME INTERSEXUAL MARSUPIALS

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Summary. Two intersexual tammar wallabies (*Macropus eugenii*), one intersexual euro (*Macropus robustus*) and one intersexual brush possum (*Trichosurus vulpecula*) were studied.

One tammar had 17 chromosomes instead of the 16 characteristic of the species. There were 14 autosomes and two X and one Y sex chromosomes (XXY intersex). The animal was of female body phenotype (weight basis) and had a pouch containing four everted and well-developed teats with underlying mammary tissue. Undescended non-functional testes were present, one of which was distinctly abnormal. The accessory reproductive structures (apart from the pouch and mammary glands) were of the male type and the penis was well developed.

In the second tammar, dividing cells resembling spermatogonia in one gonad had 14 autosomes and one X chromosome (XO intersex). This animal was of female body phenotype and had a pouch containing two very small teats on one side, with underlying rudimentary mammary tissue. A small scrotum was present. The gonads were nonfunctional, undescended ovo-testes. Both gonads had tissue resembling the interstitial tissue of the normal ovary, and structures containing cells resembling undifferentiated spermatogonia. The accessory reproductive structures were essentially of the female type.

The intersexual euro and the intersexual brush possum (XY intersexes) had well developed pouches containing rudimentary mammae but on dissection were found to have normal male reproductive systems, the testes being within the body cavity. These had small testicular tubules and a greater than normal quantity of interstitial tissue. There were no meiotic stages of spermatogenesis.

It is concluded that the Y chromosome is strongly male-determining and that there is no obvious correlation between karyotype and occurrence of pouch and mammary tissue in marsupials.

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INTRODUCTION

In recent years a great deal of information has accumulated on the chromosomal basis of various intersexual conditions in man, and, to a lesser extent, similar evidence is available for some other eutherians. Jacobs (1966), Mittwoch (1967) and many others have discussed this subject in considerable detail. Up till now, however, there appear to be no reports concerning sex chromosome abnormalities associated with intersexuality in marsupials. Biggers & McFeely (1966) defined an intersex as "an animal with congenital anatomical variations that confuse the diagnosis of sex" and the term is used in the same sense here.

Intersexual marsupials are known to occur, but few cases have been recorded. Hartman & League (1925) described an intersexual American opossum (*Didelphis*) and Gilmore (1965) an intersexual Australian brush possum (*Trichosurus*) but in neither case was the chromosome constitution studied. Marsupials have larger and fewer chromosomes than eutherian mammals (Sharman, 1961) and are thus ideal for a study of the chromosomal basis of intersexuality.

This paper is a description of the chromosomes and reproductive systems of two intersexual tammar wallabies (*Macropus eugenii*), one intersexual euro (*Macropus robustus*) and one intersexual brush possum (*Trichosurus vulpecula*). The chromosomes of the tammar were described by Sharman (1954), those of the euro by Sharman (1961) and those of the brush possum by Altmann & Ellery (1925) and Koller (1936). Sharman (1954) described the vaginal complex of the tammar and brush possum and a description of the female reproductive system of the brush possum may be found in Pilton & Sharman (1962). A general description of the male marsupial reproductive system is given by Eckstein & Zuckerman (1956).

MATERIALS AND METHODS

Animals

All the intersexual animals came from wild populations; the two tammars (*Macropus eugenii* Desm.) from Kangaroo Island, South Australia, the euro (*Macropus robustus* Gould) from near Broken Hill, western New South Wales, and the brush possum (*Trichosurus vulpecula* Kerr) from Canberra, Australian Capital Territory. The intersexual forms were compared with mature males and females of the same species.

Chromosome cytology

Blood was obtained from a normal male (SP54), a normal female (SP52) and one intersexual tammar (SP67/85) from a lateral vein on the tail of the living animals and the leucocytes were cultured using a modification of the technique of Moorhead, Nowell, Mellman, Battip & Hungerford (1960). Later the same tammars were injected intraperitoneally with colchicine (5 ml of 0.1% solution), 2 to 3 hr before being killed with veterinary Nembutal (Abbott) injected into the heart. Spleen and bone marrow tissues were removed and treated as cell suspensions according to Ford & Hamerton (1956).

One intersexual tammar (TK507) was shot in the field and preparations for

the study of chromosomes were obtained from its gonads (fixed in alcohol-formalin-acetic acid). These were compared with chromosome preparations obtained from the testis of a normal male, fixed and stained according to the method of Sharman (1961). The intersexual euro (E68/45) was also shot in the field and preparations for the study of chromosomes were obtained from its gonads fixed in 3:1 absolute alcohol-acetic acid. These were compared with chromosome preparations obtained from the spleen and bone marrow of normal animals. The chromosome complement of the intersexual brush possum (86339) was studied from Feulgen squashes of testis, bone marrow and spleen after injection of the living animal with colchicine.

Anatomy and histology

Reproductive systems and mammary glands (if present) were fixed in alcohol-formalin-acetic acid and transferred to 80% alcohol after 1 to 2 days. Organs for histological study were embedded in paraffin wax and cut at 6 to 20 μ thickness. Sections were stained in Ehrlich's haematoxylin and eosin or in iron alum haematoxylin.

RESULTS

Body phenotype and sex chromosomes

Tammar SP67/85 was classified, on being brought to the laboratory from the wild population, as a female and was discovered to be intersexual when attempts

TEXT-FIG. 1. Regression of body weights on molar eruption stages of male, female and intersexual *Macropus eugenii*. $\circ$ = male; $\bullet$ = female; points for SP67/85 (XXY intersex) and TK507 (XO intersex) are indicated. Both animals fall within the female range of body phenotypes on a weight basis.

were made to perform ovariectomy for an experiment not connected with this investigation.

Unless the penis is extruded, and apart from the presence or absence of scrotum and pouch, the only obvious sexual dimorphism in the tammar is in body weight, both sexes being the same colour. Males are, on the average,

TABLE 1
DISTRIBUTION OF CHROMOSOME COUNTS IN NORMAL AND INTERSEXUAL
Macropus eugenii

Sex and no. of animal	Cell types	No. of counts of:			Total no. of counts	Karyotypes
		15	16	17		
Male (SP54)	Leucocytes	1	25	0	26	16/XY
	Bone marrow	1	24	4	29	
	Spleen	0	16	0	16	
	Totals	2	65	4	71	
Female (SP52)	Leucocytes	0	3	0	3	16/XX
	Bone marrow	0	73	0	73	
	Spleen	0	26	0	26	
	Totals	0	102	0	102	
Intersex (SP67/85)	Leucocytes	0	4	28	32	17/XXY
	Bone marrow	0	0	21	21	
	Spleen	0	5	24	29	
	Totals	0	9	73	82	
Intersex (TK507)	Gonad	10	0	0	10	15/XO

slightly larger and heavier than females. The molar eruption stage of macropodid marsupials gives an approximate indication of age (Sharman, Frith & Calaby, 1964) so a comparison was made of weights and molar eruption stages of male, female and intersexual tammars (Text-fig. 1). SP67/85 was lighter than all males at the same molar eruption stage (MIII. 4), weighed about the same as females of comparable age and on close inspection did not appear to have the more heavily built forebody characteristic of mature males. The body phenotype was thus female.

About 1 week after the intersexual condition was diagnosed, blood was

EXPLANATION OF PLATE 1

Figs. 1 to 3 from leucocyte cultures, Fig. 4 from bone marrow of animal pretreated with colchicine and Fig. 5 from testis tubule of animal not treated before fixation.

FIG. 1. The 14 autosomes and X and Y chromosomes of a normal male *Macropus eugenii*. $\times 1520$.

FIG. 2. The 14 autosomes and two X chromosomes of a normal female *Macropus eugenii*. $\times 1680$.

FIG. 3. The 14 autosomes, two X and one Y chromosomes of the XXY *Macropus eugenii*. $\times 1280$.

FIG. 4. The 14 autosomes and X and Y chromosomes of a normal male *Macropus robustus*. $\times 1520$.

FIG. 5. The 14 autosomes and X and Y chromosomes of the XY intersex *Macropus robustus*. The chromosomes are much smaller than those of the normal male (Fig. 4) because there was no colchicine treatment before fixation. $\times 1520$.

PLATE 1

(Facing p. 60)

PLATE 2

(Facing p. 61)

drawn and leucocyte cultures prepared. SP67/85 was found to have 17 chromosomes (see Table 1) instead of the 16 reported as normal by Sharman (1954). Comparison of the chromosomes with those of male and female tammar (Pl. 1, Figs. 1 and 2) showed that the complement consisted of a normal diploid set of 14 autosomes with two X and one Y sex chromosomes (Pl. 1, Fig. 3). This was confirmed from chromosome counts of dividing bone marrow and spleen cells after the animal was killed.

Tammar TK507, of female body phenotype (Text-fig. 1), was shot during a field survey. A study of the abundant mitotic figures which occurred in the gonads failed to reveal any cell containing more than 15 chromosomes and in ten cells which were completely analysed, no chromosome resembling the small Y chromosome was found (see Table 1). The X chromosome is the second smallest of the set and has a characteristic constriction near the centromere. The gonadal tissue of TK507 was thus XO in sex chromosome constitution although the possibility cannot be excluded that the animal may have been a tissue mosaic with both X and Y chromosomes, or two X chromosomes, present in other cells.

The normal diploid complement of male euros is $2n = 14 + XY$ (Pl. 1, Fig. 4). The chromosomes were studied in thirty-three dividing cells from the undescended testis of the intersexual euro, E68/45. All had 14 autosomes and an X and a Y chromosome (Pl. 1, Fig. 5) except two, one of which contained no Y chromosome. Presumably the Y chromosome was lost from this cell during preparation of the squash. The other aberrant cell doubtfully contained 17 chromosomes. The intersex weighed 39.0 kg compared with a mean weight of 39.7 kg for males and 20.1 kg for females at the same molar eruption stage. It was also dark in colour like the normal males of the collecting area and was thus of male phenotype.

Intersexual brush possum 86339 was, like tammar SP67/85, mistaken for a female until the penis was everted during attempts to take a vaginal smear.

EXPLANATION OF PLATE 2

Haematoxylin and eosin stained sections of gonads of normal male, intersexual and normal female *Macropus eugenii*. All photos $\times 320$, except Fig. 5, $\times 400$.

FIG. 1. Portions of testicular tubules from normal, sexually mature male. Note sparse interstitial tissue (IT) and well developed tubules with active spermatogenesis.

FIG. 2. Tunica albuginea (at top) and one of the three types of testicular tubule surrounded by plentiful interstitial tissue from the left gonad of XXY intersex SP67/85.

FIG. 3. Junctional area between large and small tubules in the left gonad of XXY intersex SP67/85. Large tubule at top, small tubules (ST) surrounded by plentiful interstitial tissue at bottom.

FIG. 4. Left gonad of XO intersex TK507. Note tunica albuginea (top right), interstitial tissue (IT) and portion of large tubule at bottom. Compare with right gonad of same animal (Fig. 6).

FIG. 5. Cluster of cells from possible abnormal ovarian follicle in right gonad of XO intersex TK507. The cell cluster surrounds a central space containing a larger cell.

FIG. 6. Right gonad of XO intersex TK507. Note germinal epithelium (at top), probable abnormal ovarian follicles embedded in tissue resembling ovarian stroma (cf. Fig. 7) and interstitial tissue (lower left).

FIG. 7. Portion of ovary of normal mature female SP52 showing germinal epithelium (top left), primordial follicles (at left) and interstitial tissue (IT).

The chromosomes of fifty dividing cells from testis, bone marrow and spleen were studied. Forty-nine of these had 20 chromosomes and one had, doubtfully, 21 chromosomes. The small and readily recognisable Y chromosome was present in every cell. Each cell had a chromosome of similar size and shape to the X chromosome although this could not always be distinguished with certainty from the smallest pair of autosomes. There was thus no evidence of a chromosomal basis for the intersexual condition, the animal having the chromosome number and sex chromosome constitution typical of the male.

The reproductive systems

The reproductive system of tammar SP67/85 (XXY intersex) consisted of two gonads within the body cavity, a well-developed Wolffian duct derivative, consisting of epididymis and vas deferens and the prostatic urethra typical of

TEXT-FIG. 2. Comparison of reproductive systems of normal XY male *Macropus eugenii* (left), XY intersex *Macropus robustus* (centre) and XXY intersex *Macropus eugenii* (right). Cross hatching indicates structures derived from the Wolffian ducts, bladder and ureters indicated by dotted lines in normal male. B = bulbo-urethral glands; C = cauda epididymidis; H = caput epididymidis; M = mammary gland; P = pouch; PE = penis; PU = prostatic urethra; S = scrotum; T = teat; TA = tunica albuginea; TE = testis; V = vas deferens. The distribution of interstitial tissue is indicated by crosses and the relative sizes of testicular tubules by dots.

male marsupials (Text-fig. 2). The penis was larger than that of the mature male dissected for comparison. No Müllerian elements were recognizable in the reproductive system and none was found in histological sections prepared from the various regions. The vas and epididymis were normal histologically except

that the tubules when seen in section were smaller than in the mature male used for comparison, and were nowhere distended with seminal elements. Typical male bulbo-urethral glands were present at the base of the penis.

The gonads were kidney-shaped rather than of the roughly spherical shape characteristic of the descended testes of mature male tammar and, in the unfixed condition, were flaccid rather than firm to the touch. In this respect, they differed from the undescended testes of brush possum 86339 and euro E68/45 (see later). Both gonads were invested by a well developed fibrous tunica albuginea (Pl. 2, Fig. 2) such as was present on the testis of the normal male. The right gonad was homogeneous throughout and consisted of testicular tubules, without lumina, embedded in abundant interstitial tissue. The left gonad was not homogeneous in structure and two types of tissue were recognizable macroscopically when it was sliced with the scalpel prior to histological preparation. Three sorts of tubule were found on microscopic examination. The smaller of the two macroscopically distinguishable regions situated near the cauda epididymidis consisted of large testicular tubules separated by abundant connective tissue in which few interstitial cells occurred. This region was separated by a thin layer of connective tissue from the remainder of the gonad (second region) which consisted of very much smaller, ill-defined, testicular tubules separated by abundant interstitial cells and very little connective tissue (Pl. 2, Fig. 3). This second region was composed of elements resembling those which made up the entire right gonad but it also contained a small area of tubules of a third type. These were intermediate in size between the small and large tubules occurring elsewhere in the left gonad and more nearly normal. Some had an ill-defined lumen (Pl. 2, Fig. 2). All three types of tubule were composed of cells which resembled spermatogonia and occasional mitoses were observed. No meiotic stages of spermatogenesis, such as are found in the normal male with descended testes (Pl. 2, Fig. 1), were seen.

The well-developed pouch contained everted teats and the underlying tissue was sectioned revealing the presence of mammary tissue consisting of scattered ducts and poorly developed alveoli.

Tammar TK507 (XO intersex) was of female body phenotype (Text-fig. 1). The pouch was well developed but a small empty scrotum was also present. The reproductive system was essentially of the female type. Paired gonads, occupying the same position as the ovaries in females, and essentially normal Fallopian tubes were present. The uteri were well developed and glandular, the glands being as well developed as those of lactating female tammars. The vaginal complex was normal (Text-fig. 3) and essentially as described for the female tammar by Sharman (1954) who found that, contrary to the condition in many other marsupials, no vestigial Wolffian element was present. Wolffian elements were nowhere found in the reproductive system of TK507. The urogenital sinus was exactly like that of the normal female but the clitoris could not be examined since it was removed during dissection in the field.

The gonads were about the size of ovaries but contained both testicular and ovarian elements. The right gonad was surrounded by a complete germinal epithelium (Pl. 2, Fig. 6) but this was present only as a remnant near the hilus in the left gonad. Apart from the remnant near the hilus the tissue surrounding

the left gonad (Pl. 2, Fig. 4) greatly resembled the tunica albuginea of the testis. The hilar end of each gonad contained a mass of interstitial tissue resembling that of the normal ovary (Pl. 2, Figs. 4 and 6) there being more in the left gonad than in the right. Structures in the non-hilar end of the left gonad, when seen in section, resembled testicular tubules and contained cells resembling spermatogonia (Pl. 2, Fig. 4). They were, however, irregular instead of circular when seen in cross-section, contained no lumen and were of greater diameter than mature

TEXT-FIG. 3. Comparison of reproductive systems of normal XX female (left) and XO intersex (right) *Macropus eugenii* reproductive systems. Vertical hatching indicates structures derived from the Müllerian ducts, bladder and ureters indicated by dotted lines in the normal female. C = clitoris; F = Fallopian tube; G = germinal epithelium; GF = Graafian follicle; I = interstitial tissue; L = lateral vagina; M = mammary gland; MV = median vagina; P = pouch; S = scrotum; T = teat; TA = tunica albuginea; U = uterus; US = urogenital sinus.

testicular tubules of normal male animals. Numerous mitoses were seen but there were no normal meiotic stages. The right gonad showed more resemblance to an ovary than did the left. The tissue beneath the germinal epithelium resembled the stroma of the normal ovary (cf. Pl. 2, Figs. 6 and 7) and contained structures surrounded by a stratified epithelium reminiscent of the undifferentiated theca of normal primary and secondary ovarian follicles. These structures, which were perhaps abnormal ovarian follicles, were seen in serial section to contain irregular spaces, presumably filled with fluid in the living animal. On the periphery of the spaces, some of the cells were grouped in clusters enclosing a hollow central cavity sometimes containing a larger cell which appeared to be in the prophase stage of meiosis (Pl. 2, Fig. 5).

The pouch was well developed but teats were absent on the left side and present only as minute projections on the right side. Serial section of the tissue below the teats on the right side revealed the presence of a few poorly developed mammary gland ducts but no alveolar tissue was found.

A small empty scrotum was present caudad to the pouch in the position it normally occupies in the male. On the left side, that is on the side where teats were absent and the gonad had the least development of germinal epithelium, a solid cord of tissue descended from the anterior end of the uterus to the neck of the scrotum. This consisted of bundles of striated muscle surrounded by a connective tissue sheath. In spite of the presence of striated muscle, this was at first considered to be a persisting gubernaculum, so the left half of the scrotum was compared, in serial section, with the left half of the scrotum of a 76-day-old tammar in which the gubernaculum was seen to connect the cauda epididymidis to the scrotal sac. It was composed of mesenchyme-like connective tissue and contained no striated muscle. No such structure occurred in the scrotum of the intersex.

Euro E68/45 and brush possum 86339 (XY intersexes) both had typically male reproductive systems except that the testes were undescended (Text-fig. 2). Each testis was spherical, firm to the touch in the unfixed condition, and surrounded by a typical tunica albuginea. They were homogeneous in structure and made up of testicular tubules without developed lumina, separated by plentiful interstitial cells. Numerous mitoses were seen in the spermatogonia of the seminiferous tubules but there were no later stages of spermatogenesis. No Müllerian elements were found in either reproductive system and each had a well developed penis and bulbo-urethral glands.

Neither XY intersex had a scrotum and in each case a pouch was present in the position normal for females. Brush possum 86339 was a young animal. There were two small depressions in places occupied in the mature female by the two teats. Similar depressions occurred in normal immature females prior to eversion of the teats. Sections of the tissue below the teat pits revealed a few rudimentary structures resembling mammary gland ducts. The pouch of euro E68/45 was large and contained four everted teats, as in the normal female, arising from mammary glands consisting of scattered ducts and poorly developed alveoli.

DISCUSSION

In man, the Y chromosome is strongly male determining and it appears that the female determinants are predominantly located on the autosomes (Lewis & John, 1968). A similar situation is found in the mouse and the domestic cat and may be general for eutherians. These conclusions are drawn from the results of detailed studies on individuals with abnormal sex chromosome constitutions.

The discovery of a tammar, with an XXY sex chromosome constitution and a basically male reproductive system suggests that in marsupials also the Y chromosome is strongly male determining. In man, mouse, cat and tammar, while the sex phenotype of XXY individuals is basically male, the expression or modification of male-ness varies considerably. XXY men are sterile and of

male phenotype with descended testes which, at least in later life, show atrophy of the seminiferous tubules. Gynaecomastia is a typical, but not obligatory, feature of the XXY condition in man (Overzier, 1963). XXY mice are of normal size and of male phenotype. They exhibit male mating behaviour but are sterile (Russell, 1961). Sterile tortoiseshell male domestic cats with XXY sex chromosomes have been described but the situation in cats remains puzzling in view of reports of occasional fertile tortoiseshell males. For brief backgrounds to this problem see Biggers & McFeely (1966) and Mittwoch (1967). The XXY tammar (SP67/85) had a male phallus and a completely male reproductive system and was, in these respects, like XXY individuals of eutherian species. It differed from XXY eutherians in having undescended testes and in being of female body weight.

In man, individuals with one X chromosome and no Y chromosome are phenotypically female and agonadal, or with rudimentary gonads in which germ cells do not occur. Fallopian tubes, uterus and vagina are present (Hauser, 1963). On the other hand, XO mice are of female phenotype and fertile (Russell, 1961). The XO tammar (TK507) was phenotypically female and the accessory reproductive structures, like those of XO mouse and man, were typically female, indicating that in the absence of the Y chromosome, female characteristics appeared. In the tammar, however, a certain amount of masculinization had occurred as evidenced by a rudimentary scrotum and by the presence of gonads with a tunica covering and internal tubules reminiscent of testicular structures.

The question of whether or not the presence of a Y chromosome is necessary for the development of testicular tissue has been raised several times. Ferguson-Smith (1966) and McFeely, Hare & Biggers (1967) have discussed mechanisms which might account for the development of testes in eutherians of female genotype. In TK 507, the cytological evidence is slight, since the chromosomes were studied in only one of the body tissues—the gonads—and masculinization was not marked. The possibility cannot be excluded that TK507 was a sex chromosome mosaic with an undetected XY cell line of low frequency.

Intersexuality in marsupials apparently does not always have an obvious chromosomal basis since euro E68/45 and brush possum 86339 had apparently normal male sex chromosomes. Thus, as in eutherians (McFeely *et al.*, 1967) marsupials may exhibit intersexuality in the absence of an obvious sex chromosome aberration.

Hartman & League (1925) studied a 'sex intergrade' American opossum (*Didelphis marsupialis*) which had a male habitus but also had a small misshapen pouch and a normal but empty scrotum. The reproductive system was essentially female but included structures, called Gärtner's ducts by the authors, which were apparently persisting Wolffian elements. The uterine glands were simple and not so well developed as in the XO tammar described above. The gonads were the size of ovaries and appear to have been very like the right gonad of the XO tammar. They were considered to contain anovular Graafian follicles.

Gilmore (1965) described 'gynandromorphism' in the brush possum, the specimen apparently having similar reproductive morphology to the XY brush

possum intersex. Two small teats were present but the presence of mammary gland tissue was not specified.

We have been unable to find teats or mammary glands on the pouch young, juvenile or adult of any male of a variety of Australian species of marsupials examined although Hartman (1952) stated that "in the infant pouch young (of *Didelphis*) the males do possess the rudiments of mammary glands, variable in number". Sharman (1962) stated that mammary glands did not occur in male marsupials but were well developed in male monotremes. The XXY, XO and XY intersexes reported on above had pouches containing at least rudimentary teats and mammary tissue. Several intersexual marsupials of other species, mainly red kangaroo (*Megaleia rufa*), have been studied (G. B. Sharman, unpublished) and most had pouches and mammary tissue including those which were otherwise essentially cryptorchid males. However, one 'intersexual' red kangaroo had a normal female reproductive system and a pair of persisting Wolffian ducts each of which ended in a small, otherwise empty, scrotum. There was no pouch or mammary tissue but the essential female nature of the animal was confirmed by it being at the immediate post-oestrous stage when shot and having recently copulated and ovulated.

McCraday (1938) considered, on embryological grounds, that the pouch and scrotum of the marsupial *Didelphis* were homologous structures and Bolliger (1946) reached the same conclusion about the pouch and scrotum of the brush possum. However, these two structures existed together in an intersexual *Didelphis* (Hartman & League, 1925) and in the XO tammar (TK507). Pocock (1926) also recorded the simultaneous occurrence of pouch and scrotum in *Didelphis*. In the marsupials *Notoryctes* (Stirling, 1891), *Thylacinus* (Pocock, 1926) and *Chironectes panamensis* (Enders, 1937), the pouch is a normal development in the male. Bolliger (1946) based his conclusion of homology on what he considered to be transformations of scrotum to pouch by ovarian hormone administration but his findings were questioned by Sharman (1959) who could not obtain the same results with *Setonix*. Burns (1956) failed to modify either pouch or scrotum of *Didelphis* with hormone treatments which profoundly modified the reproductive organs. No author has recorded the presence of mammary tissue in hormone-treated male marsupials. The occurrence of pouch and mammary tissue thus has no obvious chromosomal basis since it occurs in XXY, XO and XY intersexes and in XX females, but not in XY males.

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