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# The significance of striated muscle in the mammary glands of marsupials

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## INTRODUCTION

The nonapeptide oxytocin has been used in various laboratories to facilitate removal of milk from the mammary glands of marsupials (Gross & Bolliger, 1959; Bergman & Housley, 1968; Griffiths, McIntosh & Leckie, 1972; Messer & Green, 1979; Green & Renfree, 1982). The target tissue for oxytocin is myoepithelium, the contraction of which is responsible for milk ejection or 'let-down' (Linzell, 1955). Myoepithelium has been demonstrated in the mammary glands of the red kangaroo *Macropus rufus* (Griffiths, Elliott, Leckie & Schoefl, 1973; see also CSIRO film 'Comparative Biology of Lactation', 1974) and an oxytocin-like nonapeptide, mesotocin, has been identified in the partes nervosae of macropodid marsupials (Chauvet, Hurpet, Chauvet & Acher, 1983). Recently Lincoln & Renfree (1981) carried out some elegant experiments demonstrating that electrical stimulation of 'presumptive oxytocinergic neurones' in the basal region of the hypothalamus raised intra-galactophore pressure in the mammary glands of lactating *Macropus agilis*. Intravenous injection of oxytocin also resulted in increased pressure in galactophores.

All this evidence indicates that milk let-down mechanisms in marsupials are similar to those in eutherians. However, Bolliger & Gross (1960) and Barbour (1963) found that extensions of striated or voluntary muscle from the ilio-marsupialis muscle penetrate deeply into the parenchyma of the mammary glands of the possum *Trichosurus vulpecula*. Griffiths *et al.* (1972) found similar swathes of striated muscle in the mammary glands of the red kangaroo *Macropus rufus*. This muscle tissue, as will be described below, also occurs in the mammary glands of *Macropus eugenii*, the tammar wallaby. Bolliger & Gross (1960) and Barbour (1963) thought it possible that contraction of the internal striated musculature could expel milk from the *Trichosurus* mammary gland. Recently, without reference to the above, Barnes (1977) came to a similar conclusion concerning slips of striated muscle in the mammary glands of the pouchless marsupial *Marmosa robinsoni*, that run from the deep fascia "perpendicular to the skin surface or at shallow angles like the poles in a tepee converging upon the dermis around each nipple".

The notion that contraction of voluntary muscle is involved in expulsion of milk into pouch young of marsupials was propounded early in the nineteenth century (Seiler, 1828; Morgan, 1829), but the mechanism envisaged was different from that discussed by Bolliger & Gross, by Barbour and by Barnes. Both Seiler and Morgan thought the mammary glands could be compressed, at their periphery, by the contraction of the ilio-marsupialis or 'compressor mammae' muscles, and that this would force the milk through the teat into the young. These authors were convinced that compression of the mammary gland "exerted at the will of the mother for the purpose of ejecting its secretion" was a necessity since the "imperfect state of organization" of the marsupial neonate would preclude ability to suck (Morgan, 1829). However, marsupial neonates can suck (see Enders, 1966 for review of the evidence) and can even suck up fluid from a non-distortable plastic tube inserted into the mouth aperture alongside the teat (Jurgelski, 1971). Enders (1966) also tested the notion of voluntary ejection of milk by stimulating electrically the motor nerves of various ventral muscles, in particular that of the illio (*sic*)-marsupialis muscle in lactating *Didelphis* and *Marmosa* carrying young 20–50 days old. Marked contraction of the muscle was observed, so presumably the internal strands of striated muscle, whose existence was apparently unknown to Enders, also contracted but milk was not ejected at the teats. Some years later Renfree (1979) observed that five out of nine lactating tammar wallabies whose mammary glands had been denervated by an operation involving complete severance of the ilio-marsupialis muscle continued to suckle successfully their 35–60 days old pouch young for a further 22 days until they were killed for histological examination.

It would appear from the above that contraction of striated muscle within the mammary gland is not involved in milk let-down in the tammar or other marsupials. It may, however, have other functions; in order to gain some insight into what they may be, the occurrence and distribution of striated muscle within the mammary glands of pouched and pouchless marsupials of Australia and South America have been studied and are described, along with the effects of anaesthesia on the ability of pouchless marsupials to support young attached to the teats. Observations on the milking, with and without the aid of oxytocin, of marsupial mammary glands sustaining very small pouch young, and on the imbibition of fluid by marsupial neonates from rigid, non-distortable tubes are also described.

## MATERIALS AND METHODS

### *Animals and histological procedures*

The histology of mammary glands, both lactating and non-lactating, including teats, was studied in the following pouched marsupials (numbers in parentheses): *Macropus rufus* (15), *Macropus eugenii* (6), *Petrogale xanthopus* (1), *Trichosurus vulpecula* (1), *Pseudocheirus peregrinus* (1), *Vombatus ursinus* (1), *Tarsipes rostratus* (3), and in the following pouchless or pseudo-pouched marsupials: *Antechinus swainsonii* (1), *Antechinus stuartii* (2), *Dasyuroides byrnei* (2), *Dasyurus viverrinus* (2), *Caenolestes obscurus* (1), *Dromiciops australis* (1), *Rhyncholestes raphanurus* (1) and *Monodelphis brevicaudata* (1). The last four specimens are South American marsupials.

The animals were killed by exsanguination following anaesthesia induced by ether or by intraperitoneal injection of Nembutal or of Brietal (Eli Lilly) and blocks of tissue, some with teats attached, were cut from mammary glands for fixation; in the instance of very small species whole glands and teats were cut into halves longitudinally and fixed. Three fixatives were used: Bouin's fluid, formalin and acetic acid–formol. After embedding in paraffin all specimens were serially sectioned. Some sections were left unstained, others were stained with Heidenhain's iron haematoxylin without counterstain or with haematoxylin and eosin. The unstained sections were viewed with polarised light using a quarter wave plate and crossed polarisers. With this, striated muscle could be detected by its birefringence.

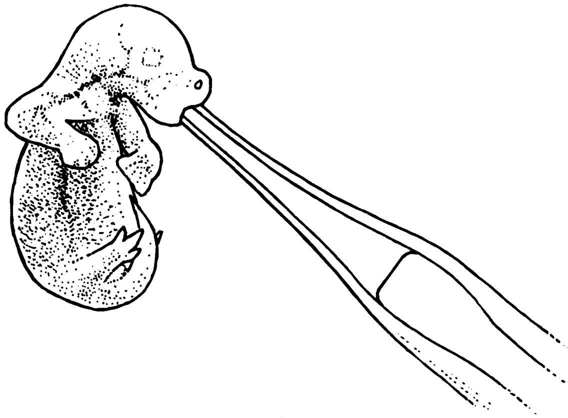

Fig. 1. *Macropus rufus*; 3 days old young sucking up cow's milk from an Ostwald pipette.

*Anaesthesia procedures*

Ether anaesthesia was induced in two lactating specimens of *Antechinus stuartii* each bearing eight young attached to her teats. When the animal was quiet it was held by scruff and tail, photographed from side and ventral aspects, allowed to recover consciousness, and photographed again; this experiment was carried out twice for one animal, and four times for the other. Two lactating specimens of *Dasyuroides byrnei* and two of *Dasyurus viverrinus* were anaesthetised by intravenous injection of 2·5% Brietal (Eli Lilly), via a tail vein, at the rate of 0·5 ml/kg body weight. Two of the young, weighing 5–6 g, were removed from the teats of each of these females, which were carrying 4–5 young, so that observations could be made on the teats as well as on the attached young.

*Demonstration of uptake of fluids from non-distortable tubes by marsupial neonates*

For observation of imbibition of fluid by very young marsupials, seven pouch young of *Macropus eugenii* aged 6–14 days were offered warm water from glass opsonic pipettes of sizes that allowed of insertion into the anterior end of the buccal cavity. A newborn *Petrogale xanthopus* was offered water from a capillary tube, since its mouth was too small to allow of insertion of a pipette. (The newborn of *M. eugenii* weigh *ca.* 400 mg, of *P. xanthopus* 460 mg and of the red kangaroo 800 mg). A 3 day pouch young of *Macropus rufus* was offered warm cow's milk from an Ostwald pipette as shown in Figure 1; the opsonic pipettes and the capillary tube were also held at the angle shown. The water imbibed by the *M. eugenii* pouch young was measured by weighing them before and after offering.

*Milking procedures*

The milking of seven specimens of *Macropus rufus*, lightly anaesthetised with ether and suckling young 1–7 days old, was carried out before and after intramuscular injection of oxytocin (Syntocinon, Sandoz) at the rate of 0·4 i.u./kg B.W.. The single pouch young of each mother was removed from the teat 17–20 hours before milking, which was carried out by gently squeezing the gland. The milk was taken up from the teat in capillary tubes, the amount being measured by the difference in weight.

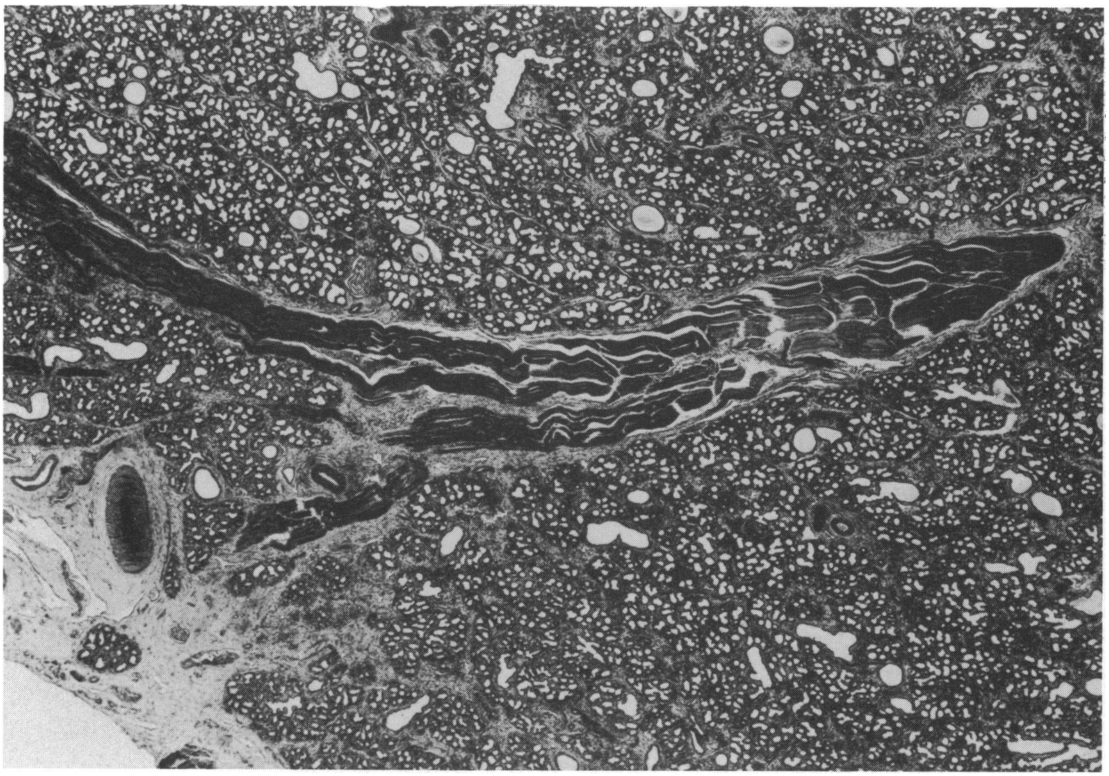

Fig. 2. *Macropus rufus*; section at periphery of mammary gland at oestrus showing invasion of the secretory parenchyma by a striated muscle swathe. Heidenhain's iron haematoxylin. ×23·8

## RESULTS

### *Striated muscle in the mammary glands of pouched marsupials*

The mammary glands of marsupials, like those of the monotremes, consist of a collection of lobules separated by connective tissue sheaths (Eggeling, 1905; Griffiths, 1978). In the mammary glands of *Macropus rufus* sustaining newborn, 6, 19, 26 and 55 days old pouch young and at oestrus, the alveoli are small, lined by a cuboidal epithelium, and exhibit a very thick stroma of connective tissue (Griffiths *et al.* 1972). In these glands it can be seen that swathes or ribbons of striated muscle pass in diffuse array from the ilio-marsupialis muscle into the interior of the gland. The muscle swathes are located between the connective tissue sheaths separating contiguous lobules (Figs. 2, 3), but not all connective tissue sheaths are invaded. A few of the bands of muscle penetrate almost to the junction of the mammary parenchyma with the base of the teat where they are inserted on to connective tissue raphes; the musculature within the teat proper is smooth muscle. In mammary glands of *M. rufus* sustaining larger pouch young (85, 100, 128 and 190 days old) the alveoli are large, thin-walled, and the connective tissue sheaths are reduced to thin laminae between the greatly enlarged lobules. In these glands striated muscle can be detected but it is not as noticeable as in the glands sustaining small young. In quiescent non-lactating glands* taken from does supporting 6, 16, 52, 84, 96, 100 and 190 days old young the

* Macropodid marsupials have four mammary glands and four teats but only one pouch young, which is firmly attached to a teat. The doe may also be suckling a large young at heel; in this case she makes two kinds of milk, one for the pouch young and one for the heeler. The two unsuckled glands remain in a quiescent state; if she has no young at heel there are three quiescent glands.

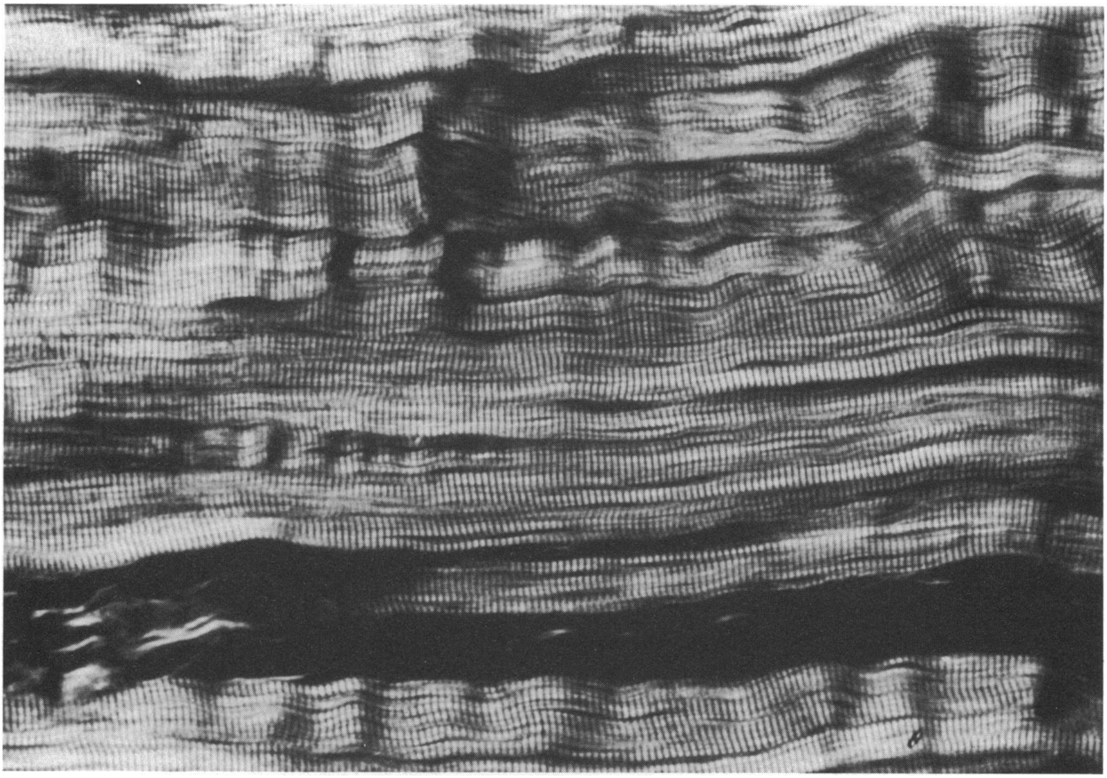

Fig. 3. *Macropus rufus*; section at periphery of mammary gland at oestrus showing invasion of the secretory parenchyma by a striated muscle swathe. Heidenhain's iron haematoxylin. ×418.

striated muscle appears as a prominent element since the parenchyma is reduced to a system of ducts of narrow bore embedded in a stroma of connective tissue, smooth muscle and blood vessels (Griffiths *et al.* 1972).

The distribution and extent of striated muscle, and the structure of the parenchyma in the mammary glands of two other species of macropodid marsupial, *Macropus eugenii* and *Petrogale xanthopus* suckling neonates, were found to be similar to those observed in the glands of *M. rufus* suckling small young. The *Vombatus ursinus*, *Trichosurus vulpecula* and *Pseudocheirus peregrinus* specimens were fully lactating, their mammary glands exhibiting thin-walled large alveoli and relatively little striated muscle.

The mammary glands of the honey possum, *Tarsipes rostratus*, were of particular interest since they exhibited, between the lobules, swathes of striated muscle which were prominent even in the fully lactating gland. The distribution of this musculature also was different from that in the other pouched marsupials examined in that 4 or 5 well developed strands of muscle from the ilio-marsupialis enter the gland from the periphery and fan out towards the teat (4 teats present) and actually penetrate to its base, inserting there on to connective tissue raphes (Fig. 4). Some of the strands, however, terminate in the dermis of the skin of the pouch.

### *Striated muscle in the mammary glands of pouchless marsupials*

*Antechinus swainsonii* and *A. stuartii* have Type 1 mammary areas (Woolley, 1974), i.e. they are pouchless and the naked young attached to the teats looks like a tight bunch of grapes closely applied to the mammary area of the mother (Fig. 10). The three

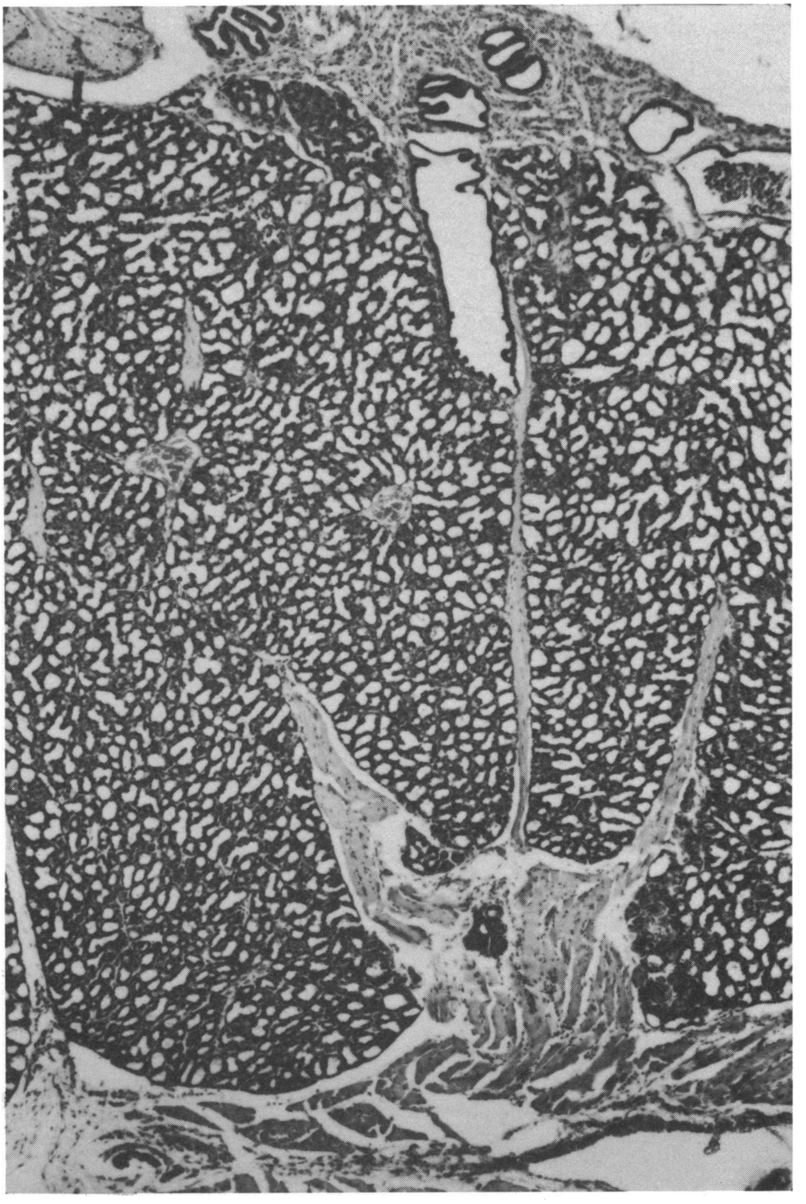

Fig. 4. *Tarsipes rostratus*; longitudinal section through mammary gland and teat showing insertion of a strand of striated muscle from m. ilio-marsupialis on to base of teat (upper portion of photo). Haematoxylin and eosin. ×4·25.

specimens examined each had eight teats, four on each side arranged in a semicircle, and each teat had a young one attached. The ilio-marsupialis muscle on each side is robust and strap-like, extending from the pelvis round the abdominal musculature to the dorsal surface of the mammary glands. Here, on each side it divides into four discrete well defined muscles which penetrate into the mammary glands (Fig. 5), and each is inserted on to connective tissue raphes at the base of a teat (Fig. 6). These internal muscles run to the teats only (Fig. 7); there is no diffuse distribution of strands of voluntary muscle as seen in the glands of the pouched marsupials.

Fig. 5. *Antechinus swainsonii*; dissection of left side mammary glands and m. ilio-marsupialis showing entrance of four branches into the gland each passing to one of four teats. Top of photo rostral.

*Dasyuroides byrnei* also has a Type 1 mammary area exhibiting six teats; the mammary glands exhibited robust, discrete muscles identical to those in *Antechinus*. *Dasyurus viverrinus* has a Type III pouch (Woolley, 1974). This may be termed a pseudo-pouch, since the mammary area is surrounded by a circular flap of skin but the centre is not closed, and the young are visible, unlike those in the pouched marsupials. There are usually six teats but some specimens may have seven or eight. Discrete robust muscles arising in the ilio-marsupialis muscle penetrate the secretory parenchyma and run to the bases of the teats as in the marsupials with Type 1 mammary areas.

The *Caenolestes obscurus* specimen examined was non-lactating but in oestrus (Tyndale-Biscoe, personal communication). The mammary area exhibited four teats (Kirsch & Waller, 1979; Tyndale-Biscoe, 1980) to each of which prominent discrete striated muscles ran from the ilio-marsupialis muscle to be inserted right into the teat. The parenchyma consisted of convoluted ducts, the lumina of which were lined by a cuboidal epithelium; the ducts converged towards the teat. The other caenolestid mammary gland examined was that of *Rhyncholestes raphanurus*. This was in full lactation or perhaps at the stage of weaning of the young. The alveoli of the parenchyma were large, thin-walled and distended, with a coagulum that appeared to be milk. However, *postmortem* changes were apparent. The gland was markedly lobulate, and in between the lobules were long swathes of degenerate tissue which in parts exhibited the characteristics of muscle tissue and which were inserted into the

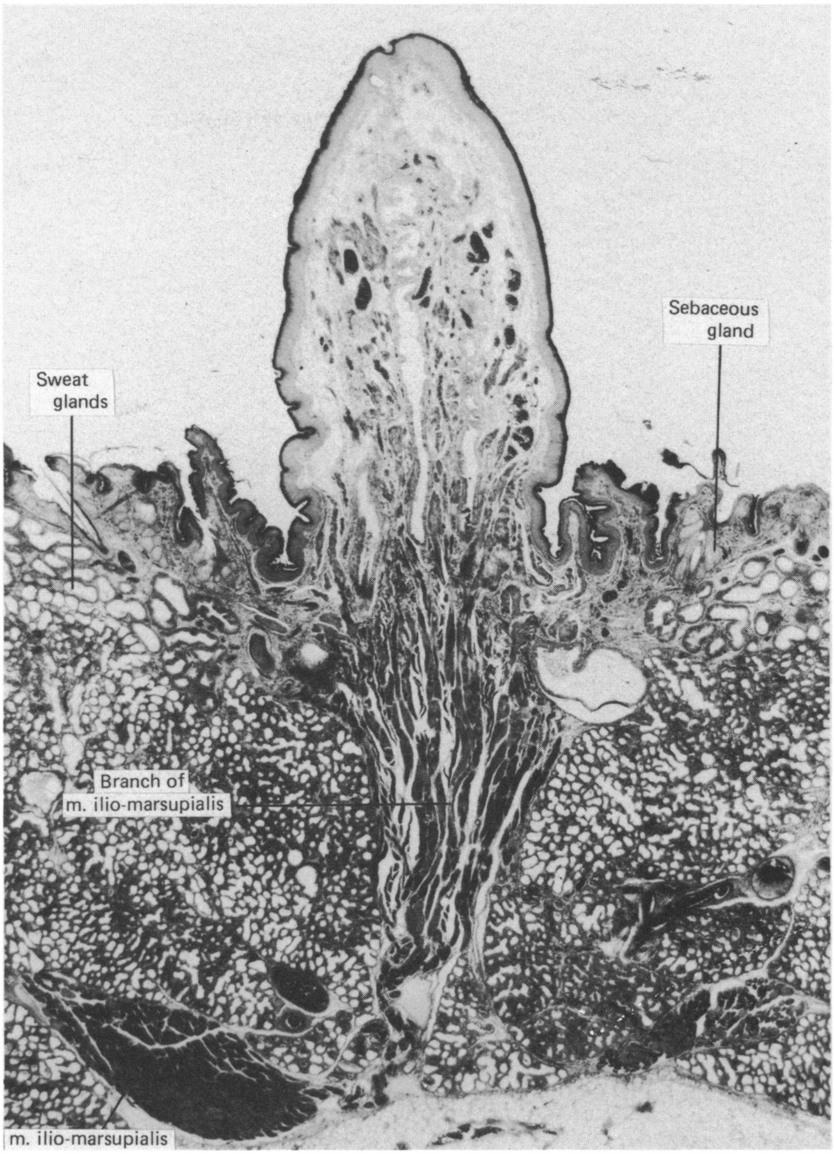


Fig. 6. *Antechinus swainsonii*; sagittal section of teat and a branch of m. ilio-marsupialis inserted on to base of the teat. Heidenhain's iron haematoxylin. ×28.

bases of the teats. This presumptive muscle exhibited no striations but invasions of lymphocytes were apparent. This specimen had six teats, three on each side of the pouch area; the only other specimen of a female *Rhyncholestes* ever taken had five teats (Osgood, 1924).

The mammary glands of the *Dromiciops* specimen were at an early stage of lactation, exhibiting thick-walled tubules some of which were sprouting alveoli; in fact the parenchyma was very like that illustrated in Figure 2. The mammary area exhibited four teats, to each of which a very small young was attached. The parenchyma was invaded by massive swathes of striated muscles running from the ilio-marsupialis muscle, parallel to one another, to the teats and to the overlying dermis.

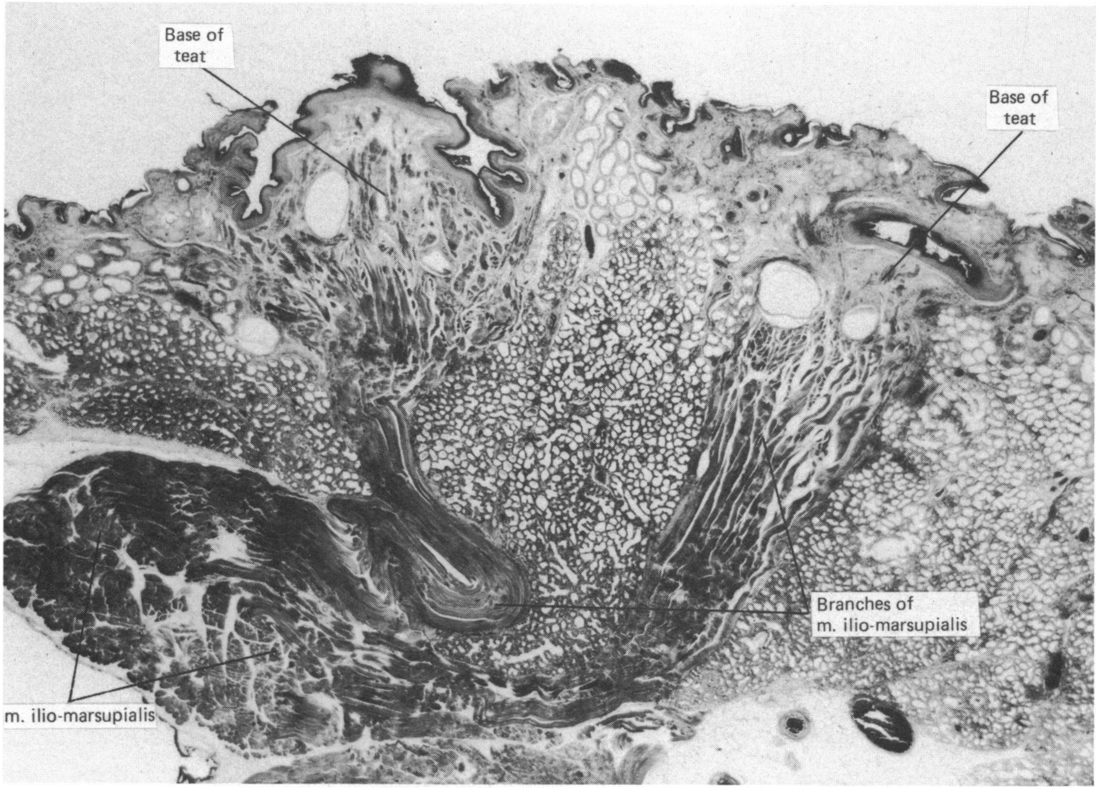


Fig. 7. *Antechinus swainsonii*; parasagittal section of two contiguous teats showing discrete branches of muscle running to bases of teats from their parent m. ilio-marsupialis (lower left). Heidenhain's iron haematoxylin. × 20·9.

The mammary area of *Monodelphis brevicaudata* exhibits at least nine teats (Tyndale-Biscoe, 1980); in the mammary gland of the specimen available a deep penetration of the parenchyma (non-lactating) by strands of striated muscle was observed. These strands run more or less parallel to one another from the ilio-marsupialis muscle to the dermis near the teats and to the bases of the teats.

*Effect of anaesthesia on the ability of pouchless marsupials to retain their young in the mammary area*

*Antechinus swainsonii* and *A. stuartii* are very active mouse-like mammals whose food consists of, *inter alia*, moths and other insects found under and on top of forest litter (Wood, 1970); it is known that *A. stuartii* climbs trees as high as 25 m. This activity, along with the presence of a robust discrete musculature to the teats, suggests that the function of the muscles is to ensure, by their tonic contraction, that the heavy load of naked young attached to the teats does not scrape along the substratum when the mother is hunting for prey. (One of the specimens of *A. stuartii* weighed only 25 g, yet her load of 8 young weighed 11·76 g, individual weights ranging from 1·35 to 1·53 g.) This notion was tested by the following experiments: two recently trapped lactating *A. stuartii* carrying 8 young each were anaesthetised as described in Materials and Methods. In this condition when they were held up by the scruff of the neck and the tail the young hung down well below the general level of the ventral surface (Fig. 8). When the effect of the anaesthetic wore off and the mother became conscious, as

Fig. 8. *Antechinus stuartii*; lateral view of female anaesthetised with ether showing young hanging down below ventral surface. Scale indicated in Fig. 10.

judged by opening of the eyes and struggling, the young were hauled up and held tightly to the mammary area (Figs. 9, 10). Six experiments were carried out on these two animals with the same result each time. In two of those trials the anaesthetised female was held in the hand lying on her back and her young were pulled out of the mammary area, still attached to the teats,* four to one side and four to the other. As the females became conscious the young were all drawn back into the mammary area by a concerted convulsive movement, resulting in the tight packing of the young in the mammary area shown in Figure 10.

Events identical to the above were observed in the *Dasyuroides* and *Dasyurus* specimens; in the latter when the female was anaesthetised the young hung down out of the pseudo-pouch and were drawn back up into it upon recovery. The observations on the teats from which the young had been removed were particularly interesting; when fully anaesthetised the teats of these animals projected out well above the general level of the mammary area, but as the effects of the anaesthetic wore off the teats were slowly drawn back into the skin of the mammary area, which was deformed into saucer-shaped depressions around each teat. In the final stage of retraction the teats were scarcely discernible. When this happened with the young still attached the anterior portions of their heads were drawn into the depressions.

* Attachment to the teat at this stage of development appears to be a matter of voluntary effort on the part of the young, since they have a gape and the mandibles are capable of opening and shutting the mouth. Furthermore, it was observed some hours after one of the young had been accidentally removed that it had reattached to its teat and remained there for the duration of the experiments.

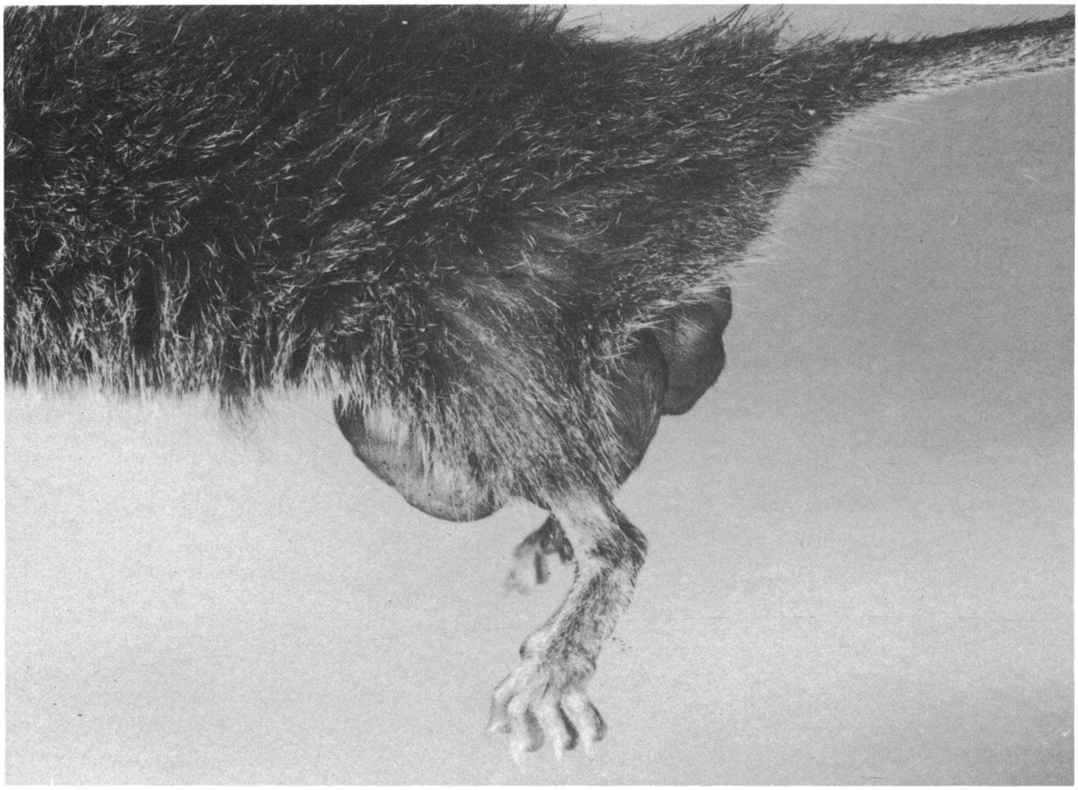

Fig. 9. Same after recovery from anaesthesia.

*Removal of milk from mammary glands of red kangaroos suckling very small pouch young*

For the first few days of lactation milk supplied to the pouch young of the marsupials so far examined is a transparent or pellucid fluid (Barton, 1806; O'Donoghue, 1911; Griffiths & Barton, 1966) containing very little lipid (Griffiths *et al.* 1972). In anaesthetised red kangaroos this can be obtained at the teat, from which the pouch young had been removed 17–20 hours before, without the aid of oxytocin by gently squeezing the gland. In one instance milk appeared at the teat, without squeezing, at the touch of a finger. The amounts obtained by squeezing are shown in Table 1. However, if the gland is stripped in this way intramuscular injection of oxytocin immediately after stripping brings about 'let-down', and more milk can be obtained following squeezing of the gland (Table 1).

*Ingestion of fluid from glass tubes by very young macropodids*

A neonatus of *Petrogale xanthopus* sucked up water from a capillary tube inserted into its mouth, the removal being accompanied by a jerky, reciprocating motion of the meniscus of the fluid in the tube. Similarly a 3 day pouch young of *Macropus rufus* sucked up cow's milk from an Ostwald pipette held at the angle shown in Figure 1; a reciprocating movement of the meniscus was apparent. It was also found that *Macropus eugenii* pouch young aged 6–14 days could remove water from opsonic pipettes held as in Figure 1; the jerky reciprocating motion of the meniscus was again observed. The amounts of water sucked in and the times taken are shown in Table 2.

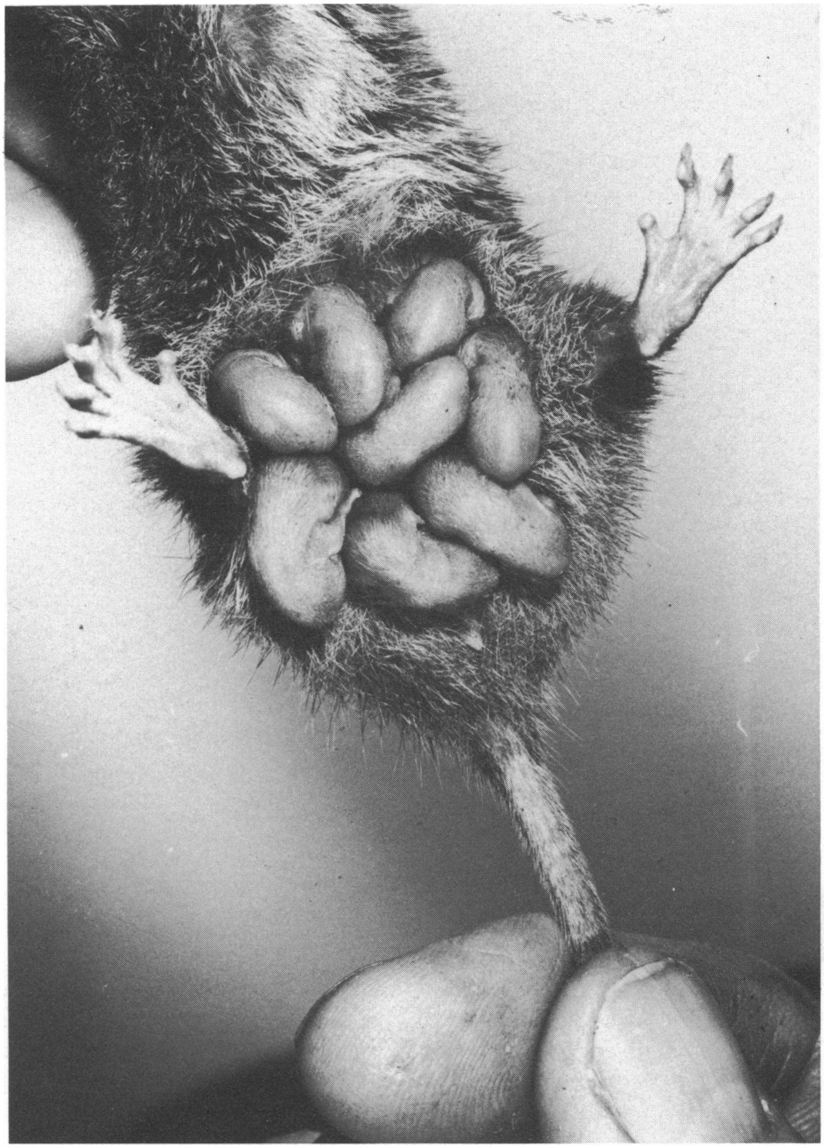

Fig. 10. Same, ventral view after recovery from anaesthesia.

DISCUSSION

It would appear from the experiments on the pouchless marsupials that contraction of the discrete muscles inserted on to the teats enables the mother to carry her heavy load of young high above the substratum, so protecting the young from injury or removal. The name retractor mammae is proposed for these muscles.

In the pouched honey possum *Tarsipes rostratus* this musculature is much reduced, but strands still run to the teats. In the other pouched marsupials examined the musculature is reduced still further and only occasionally does a strand of muscle reach a teat. This suggests that in these it has become vestigial, since it is no longer called upon to support the young. The reduction in the musculature in *Tarsipes* may represent the process of becoming vestigial.

Table 1. *Effect of intramuscular injection of oxytocin on milk flow of the mammary glands of red kangaroos sustaining small pouch young*

| Age of pouch young (days) | Weight of milk obtained before injection (mg) | Substance injected | Weight of milk obtained after injection (mg) |
|---|---|---|---|
| 1 | 26·9 | Oxytocin | 50·9 |
| 2 | 230·1 | Oxytocin | 111·5 |
| 2 | 7·5 | Oxytocin | 83·8 |
| 3 | 20·8 | Water followed | 24·4 |
| | | by oxytocin | 113·2 |
| 5 | 18·1 | Water | 3·3 |
| 7 | 159·9 | Oxytocin | 305·7 |
| 7 | 348·4 | Oxytocin | 344·1 |

Table 2. *Imbibition of water from an opsonic pipette by small pouch young of Macropus eugenii*

| Age of pouch young (days) | Body weight (g) | Weight of water sucked up (mg) | Time taken (minutes) | Remarks |
|---|---|---|---|---|
| 6 | 1·01 | 22·8 | 2·5 | Sucking commenced soon after insertion of pipette. Meniscus in pipette exhibited pumping reciprocal motions during removal of water |
| 7 | 1·18 | 22·4 | 3·5 | As above |
| 7 | 1·30 | 17·4 | 1·9 | As above |
| 8 | 1·28 | 23·5 | 2·0 | As above |
| 9 | 1·32 | 24·0 | 2·5 | As above |
| 13 | 2·10 | 37·1 | 0·75 | As above |
| 14 | 2·23 | 10·0 | 5·0 | As above |
| | | 28·5 | 2·6 | Left in incubator in saturated air at 35 °C for 2 hours and re-offered pipette |

It would not be profitable to speculate about the function of the muscle in the mammary glands of the pouchless South American marsupials, until it has been studied in lactating specimens in conjunction with experiments on the effect of anaesthesia on the ability of the mothers to retain their young in the mammary area. This would be easy to carry out with *Marmosa* since it is amenable to laboratory life. Indeed, Hunsaker & Shupe (1977) have observed that *Marmosa* adopts a different walking posture immediately after attachment of the neonates to the teats: the female raises the lumbar section of her back which "kyphotic posture protects the embryons from contact with the substrate and from mechanical abrasion"; doubtless the musculature observed by Barnes (1977) assists this function. In the case of caenolestids this would not be so easy. Caenolestids (*Caenolestes*, *Lestoros* and *Rhyncholestes*) carrying young have never been trapped. Kirsch & Waller (1979) took four lactating *Caenolestes obscurus* in the Páramos de Puracé, Colombia, but none was accompanied by young; possibly *C. obscurus* leaves its young in a nest when they get too big to carry around, just as *Antechinus stuartii* does with its young (Wood, 1970).

The putative vestigial nature of the striated musculature in the mammary glands of the pouched marsupials, and the fact that complete resection of the m. ilio-marsupialis does not prevent successful suckling of relatively large pouch young in the tammar (35–60 days old), does not exclude the possibility that it has a function. The observation that milk can be obtained from the mammary glands of red kangaroos suckling very small pouch young 1–14 days old without the aid of oxytocin could be interpreted as the result of a 'tap' response, i.e. myoepithelium is contracting in response to mechanical stretching. This has been shown to occur in the mammary glands of rabbits (Cross, 1954) and of rats (Grosvenor, 1965), probably in response to pummelling of the gland by the relatively robust young. It is inconceivable that the minuscule neonate of a marsupial (that of *Tarsipes* weighs < 5 mg) could exert a pummelling action, but it is conceivable that contraction of striated muscle within the gland could stretch myoepithelial fibres and thus elicit a tap response. This notion is supported by the observations that striated muscle is concentrated relative to parenchyma in the earliest stages of lactation, and that apparently the gland suckling a neonate is more sensitive to the action of oxytocin than the gland supporting a large young at heel (Lincoln & Renfree, 1981). It will be recalled that it is difficult to detect striated muscle in such glands. It may well be that striated muscle and oxytocin act synergistically in promoting contraction of myoepithelium at birth, thus pumping milk to the neonate which is capable of vigorous sucking.

The observations that marsupial neonates can imbibe fluid from rigid non-distortable tubes (Jurgelski, 1971 and the present work) show that the process of imbibition of milk by marsupials is different from that of Eutheria. Cowie (1972) found, by cineradiography, that the main method of imbibition of milk by eutherian young is not by sucking but by expressing it from nipple or teat. He found that the base of the teat is compressed between the tongue and the palate, and that the milk is then stripped out of the teat by the tongue compressing the teat from its base towards its tip against the palate. The pressure on the base of the teat is then released to allow it to fill up with milk. This happens rapidly, since the milk is under pressure brought about by contraction of the myoepithelium. The process in marsupials is different: the dorsal surface of the deep narrow tongue is grooved for reception of the teat and the base throughout its length is anchored to the floor of the buccal cavity. Vertically arranged striated muscle fibres extend from the base to the dorsal surface of the tongue, thus contraction of these lowers the dorsal surface leading to decreased pressure in the buccal cavity. This draws in the milk from teat or from glass tubes inserted into the mouth.

The mechanism of imbibition of milk by the young of tachyglossid monotremes is different again, but the agent is suction. In fact there must be two different mechanisms depending on the stage of differentiation of the young: the structure of the tongue at hatching is quite different from that in the adult, which condition is achieved, at the most, by 100 days of life when the animal is still suckling (Griffiths, McIntosh & Coles, 1969; Griffiths, 1978; Griffiths, 1988).

## SUMMARY

The distribution and amounts of striated muscle within the mammary glands of pouched and pouchless marsupials from Australia and South America are described. Invasions into the mammary secretory parenchyma in pouchless marsupials by swathes of striated muscle from the ilio-marsupialis muscle are massive, in some instances concentrated into discrete muscles, which are inserted on to the bases of the teats; the name retractor mammae is proposed for these muscles. In pouched marsupials striated muscle penetrates the parenchyma, but the distribution is diffuse and the muscle strands are not inserted on to teats except in the instance of the glands of the honey possum *Tarsipes rostratus*.

The young of anaesthetised pouchless marsupials hang down from the teats; as

anaesthesia wears off they are hauled up tightly into the mammary area. It is concluded that this is a result of contraction of the retractor mammae muscles and that it is a means of protecting the naked young from injury by rough terrain. The mammary gland musculature in pouched marsupials is considered to be vestigial, but its contraction may have the function of initiating a 'tap-response' contraction of myoepithelium acting synergistically with the 'let-down' hormone mesotocin.

Mechanisms of imbibition of milk by marsupial neonates, based on observations that they can suck fluid from non-distortable tubes, are discussed.

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