



FAUNA *of* AUSTRALIA

33. TARSIPEDIDAE

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DEFINITION AND GENERAL DESCRIPTION

The single species of the Family Tarsipedidae, the Honey Possum, *Tarsipes rostratus*, is differentiated from all other small marsupials on the combined basis of its long pointed snout, three longitudinal dorsal stripes and its teeth which, other than the procumbent lower incisors, are reduced to tiny pegs.

HISTORY OF DISCOVERY

Paris Museum specimens, as *Tarsipes rostratus*, were described by M. Paul Gervais who, in his own name and that of M. Jules Verreaux, read a lengthy description and presented illustrations at the Scientific Meeting of the Zoological Society of London on January 11, 1842 (Gervais & Verreaux 1842). Specimens sent to the British Museum by Capt. George Grey, later Governor of South Australia, were described as *T. spenserae* by J.E. Gray, also in 1842 (Gray 1842). Mahoney (1981) showed that the senior synonym is *rostratus* as the description given by Gervais & Verreaux to the Zoological Society of London appeared in the account of the 19th February meeting of the Société Philomatique de Paris published in *L'Institut, Paris* on March 3, 1842, (Anon 1842), thus preceding Gray's published description by a mere 5 days.

Gould (1845a) illustrated the Honey Possum in his work on Australian mammals, having directed his collector Gilbert to obtain several specimens from Swan River and King George Sound. Gilbert apparently had difficulty obtaining specimens.

‘The Tarsipes is generally found in all situations suited to its existence from Swan River to King George's Sound, but from its rarity and the difficulty with which it is procured, notwithstanding the high rewards I offered, the natives only brought me four specimens; one of these, a female, I kept alive for several months, and it soon became so tame as to allow itself to be caressed in the hand without evincing any fear or making any attempt to escape. It is strictly nocturnal, sleeping during the greater part of the day and becoming exceedingly active at night: when intent upon catching flies it would sit quietly in one corner of its cage, eagerly watching their movements, as, attracted by the sugar, they flew around; and when a fly was fairly within its reach it bounded as quick as lightning and seized it with unerring aim, then would eat it at leisure, sitting tolerably erect and holding the fly between its fore-paws, and always rejecting the head, wings and legs. The artificial food given it was sopped bread made very sweet with sugar, into which it inserted its long tongue precisely in the way in which the Honey-eaters among birds do theirs into the flower-cups for honey; every morning the sop was completely honey-combed, as it were, from the moisture having been drained from it by the repeated insertion of the tongue; a little moistened sugar on the end of the finger would attract it from one part of the cage to the other; and by this means an opportunity may be readily obtained for observing the beautiful prehensile structure of the tongue, which I have frequently seen protruded for nearly an inch beyond the nose; the edges of the tongue near the tip are slightly serrated. The tail is prehensile, and is used when the animal is climbing precisely like that of the Hepoona. The eyes, although small, are extremely prominent and are placed very near each other; the ears are generally carried quite erect. When sleeping the animal rests upon the lower part of the back, with its long nose bent down between its fore-feet and its tail brought over all and turned down the back. Mr. Johnson Drummond shot a pair in the act of sucking the honey from the

blossoms of the *Melaleuca*; he watched them closely, and distinctly saw them insert their long tongues into the flower precisely after the manner of the birds above-mentioned' (Gilbert, quoted in Gould 1845a).

Gould's description remained the best and most detailed for over 100 years. In our experience, however, we have never seen captive Honey Possums eating insects and examination of gut contents of wild caught animals showed no insect remains (see below). Several common names for *Tarsipes rostratus* have been recorded: honey possum, honey mouse and the Aboriginal term noolbenger (Ngool-boon-gor) (Gould 1845a).

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

The general colour of the coarse fur is a grizzled greyish brown above and cream below. The transition between the grey and cream areas has a marked reddish tinge. The dorsal markings consist of a distinct, dark brown central stripe from the back of the head to the base of the tail flanked by less distinct, lighter brown stripes.

The Honey Possum is a small mouse-sized mammal in which the females are larger. Head and body length for adult females ranges 70–90 mm, tail 75–105 mm and weight 8–16 grams. For adult males, head and body length are 65–85 mm, tail 70–100 mm and weight 7–11 grams.

The head has a long, slender, sharply pointed snout. The tongue is elongate and protrusible, with an obvious tuft of long papillae at the tip. The vibrissae are long. The eyes are close together, chiefly looking upwards and forwards. The ears are rounded and of medium size.

The tail is about 1.2 times longer than the head and body, thinly haired, tapering and prehensile. The forefoot has five more or less equal digits. The hind foot also has five digits: the second and third are syndactylous, the first opposable to the others and the fourth considerably elongated (Fig. 33.1). The digits have large rough apical pads. The claws resemble nails and do not project beyond the toe pads.

The pouch of females is deep and completely encloses the mammary area. There are two teats anterior and two posterior to the opening. The male has a very large, pendulous, furry scrotum.

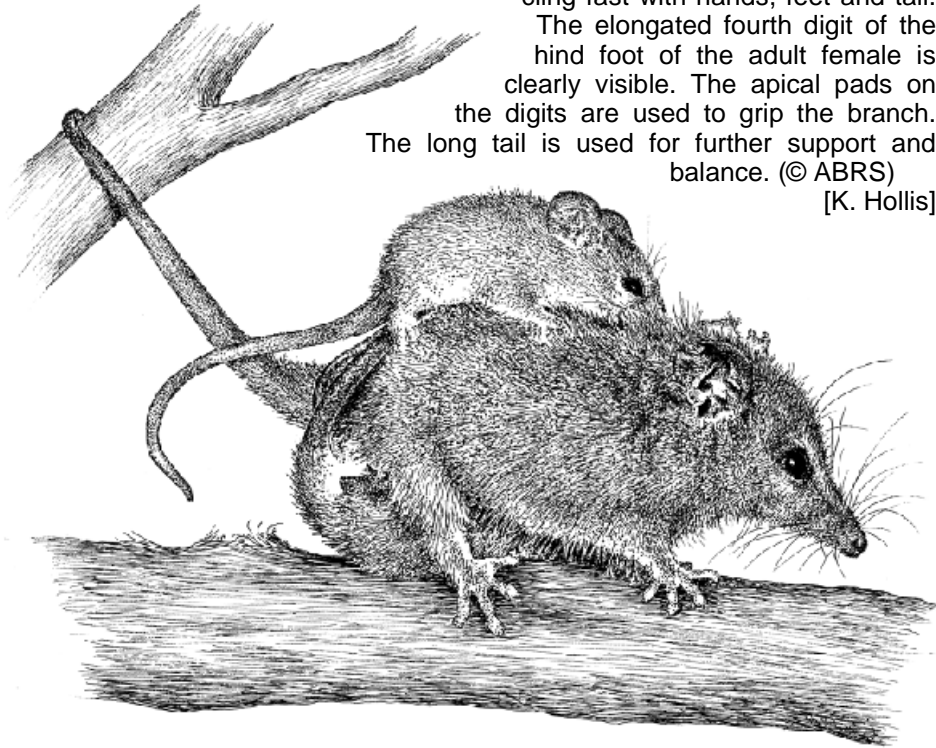
Skeletal System

The skull of the Honey Possum (Fig. 33.2) exhibits certain distinctive features which reflect its extreme dietary specialisation, as discussed by Archer (1984b). The teeth are vestigial and food collection is performed by means of the tongue (see below). The parts of the skull which carry teeth or the muscles involved in chewing also are reduced. The skull is more elongated than in any other small diprotodont. The snout, with elongate nasals, maxillae and premaxillae, tapers to a narrow point. The frontals are small and the area of contact between the nasals and lacrymals is broad. The zygomatic arch is slender and the posterior margin of the palate is incomplete. The dentary is a splint-like bone with a much reduced coronoid process and no inturned angular process. Teeth are minute and few, with 22 at most. The dental formula is I (1-2)/1 C 1/0 PM-M (1-4)/(1-3), the premolars and molars undifferentiated. All these features reflect the absence of chewing in food collection.

There is no published information on the postcranial skeleton.

Figure 33.1 Female *Tarsipes rostratus* with two young, about 10 days after the young left the pouch for the first time. At this age, young can ride on their mother's back, but also may be carried on her belly. They cling fast with hands, feet and tail.

The elongated fourth digit of the hind foot of the adult female is clearly visible. The apical pads on the digits are used to grip the branch. The long tail is used for further support and balance. (© ABRS)
[K. Hollis]



Locomotion

The two main forms of locomotion in the Honey Possum are running and climbing. On the ground and on thick branches which do not slope too steeply (45°), the animal moves at a fast run with the heel raised from the ground and the tail held out behind. In climbing on steep slopes, thin branches or leaves, the tail is used much more (Fig. 33.1). Often, it is curled round a branch as the possum moves slowly up or down or is held straight and pressed hard against a surface, acting as a brake when the animal pauses in ascending vertical surfaces. It is rarely seen suspended only by the tail; more often it holds on with the tail and one pair of limbs while the other pair is moved. Use of the tail and hind limbs frees the forelimbs to manipulate blossoms, if necessary. The arrangement of apical pads on the digits described above further improves their adhesion to a surface. As in other phalangeroids, the first digit of the hindfoot or pes is opposable to the other four. The fourth digit is much longer than either the fifth or the syndactylous second and third digits and the span which can be gripped by the first and fourth digit is large for such a small animal (Fig. 33.1).

Its small size, general agility, prehensile tail and grasping digits allows the Honey Possum to move along the underside of a small branch or to the terminal flowers of slender branches.

Feeding and Digestive System

The Honey Possum feeds almost exclusively on nectar and pollen. For the collection and processing of this diet, there are considerable morphological specialisations of the oral cavity, tongue and alimentary tract.

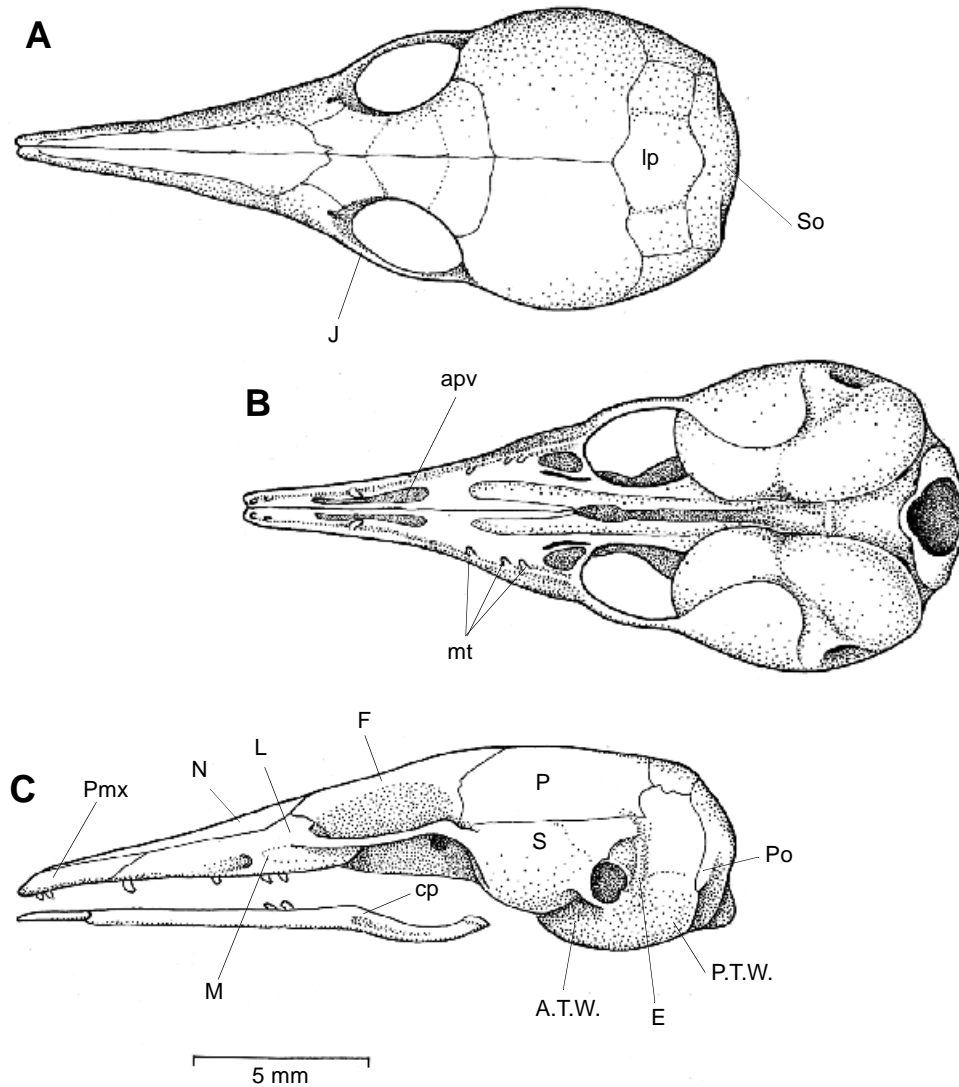


Figure 33.2 The skull and left dentary of a young individual of *Tarsipes rostratus*. The whole skull is 21.5 mm long: **A**, dorsal view; **B**, ventral view; **C**, lateral view. Distinctive features include the vestigial dentition, the virtual lack of a coronoid process on the dentary, the elongate snout, nasal-lachrymal contact, relatively small frontal, palatine and vomer bones, very large interparietal and squamosal bones, large ventral flange of the squamosal, splint-like jugal (and zygomatic arch) and incomplete posterior margin of the palate. Abbreviations: Pmx = premaxilla; N = nasal; M = maxilla; L = lacrimal; F = frontal; J = jugal; P = parietal; Ip = interparietal; So = supraoccipital; S = squamosal; Po = paroccipital; E = ectotympanic; P.T.W. = tympanic wing of the periotic (mastoid portion?); A.T.W. = tympanic wing of the alisphenoid; D = dentary; (c.p.) = position where coronoid process develops in other mammals; a.p.v. = anterior palatal vacuity; m.t. = posterior maxillary teeth (not clearly differentiated into premolars and molars). (After Archer 1984b; © ABRS) [S. Weidland]

The main instrument of food collection is the tongue, which is long (about 18 mm) and extensible to about 10 mm beyond the tip of the snout. Studies of the morphology of the feeding apparatus by Richardson, Wooller & Collins (1986) have shown that at the tip, the upper surface of the tongue is covered for 3–4 mm with keratinised filiform papillae, mean length about 0.224 mm, which give the tongue its brush-tipped appearance (Figs 33.3a & 4). Much of the rest of the upper surface of the tongue is covered with more robust compound

papillae about half of the length of the papillae at the tip (Fig. 33.4). The anterior half of the tongue is triangular in cross section with a ventral keel stiffened by keratinized epithelium. The ventral keel runs in a groove in the floor of the mouth and is guided by the protruding lower incisors.

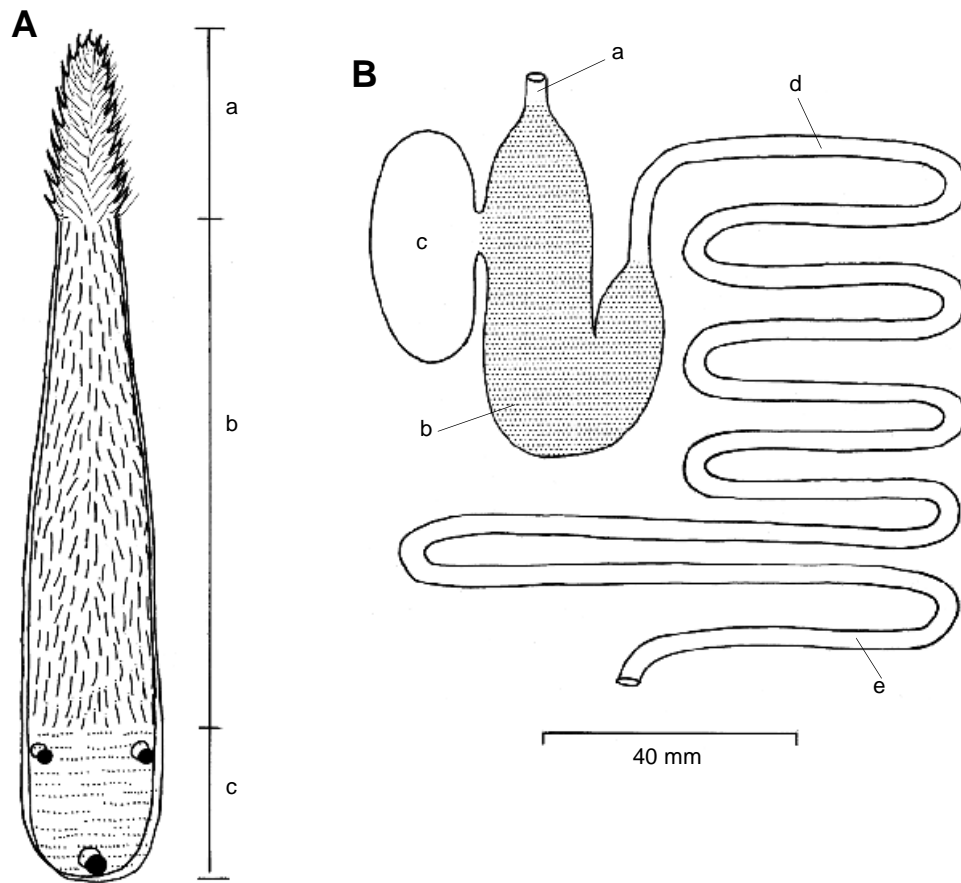
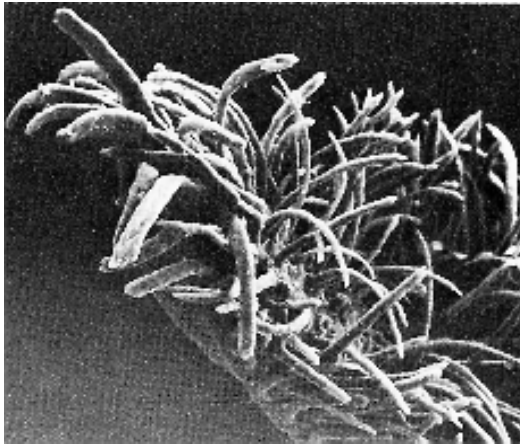


Figure 33.3 **A**, Schematic representation of the dorsal surface of the tongue of *Tarsipes rostratus*; region (a) is the tip of the tongue; region (b) the middle three-fifths and region (c) is the basal fifth. Scale line is 100 μ m. (After Richardson *et al.* 1986). **B**, Schematic representation of the stomach and intestine of *Tarsipes rostratus* showing: a = oesophagus; b = main chamber of stomach; c = diverticulum; d = small intestine; e = colon. A caecum is not present. (After Richardson *et al.* 1986; A, © ABRS) [A, B. Scott]

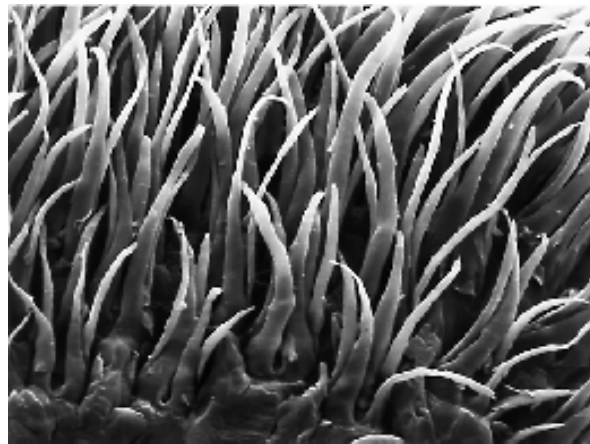
When feeding, the Honey Possum either protrudes and retracts the tongue two to three times a second into the nectar-containing parts of a flower or brushes the upper surface of the tongue across the pollen-bearing parts. The long papillae at the tip probably pick up nectar by capillary action and possibly some pollen, but most pollen probably is collected by the compound papillae in the mid-region of the tongue. When the tongue is retracted and protruded, it is pressed against the roof of the mouth. The load of nectar and pollen is removed by a series of transverse ridges on the hard palate. The four most posterior ridges are like rakes, each with forwardly directed spines which comb through the compound papillae on the mid-region of the tongue as it is drawn past (Fig. 33.4).

From the mouth, food passes through the oesophagus to the stomach. From the stomach there is a diverticulum, about half the size of the main chamber, which may serve as a nectar storage organ (Hume 1982). The intestine is elongate, simple and possesses no caecum (Fig. 33.3b). From the work of Richardson *et al.* (1986), pollen digestion must take place in the small intestine, probably through the germinal apertures in the resistant coats of pollen grains. Pollen grains rarely are found in the diverticulum, while almost all pollen grains in the

A



B



C



Figure 33.4 Scanning Electron Microscope photographs of the surface of the tongue and hard palate of *Tarsipes rostratus*: top = tip of tongue with filiform papillae; centre = compound papillae from middle of tongue; bottom = posterior regions of hard palate showing spine-like projections on palatal ridges.

[© K.C. Richardson]

main stomach chamber retain their contents. As the pollen grains move through the intestine, more and more lose their contents. Passage of pollen through the gut takes about 6 hours (Turner 1984a; Richardson *et al.* 1986). Faecal samples from animals in the wild contain large numbers of pollen grains, 95–100% without their contents.

Pollen appears to be the major source of protein in the diet of *Tarsipes*. Pollen grains typically contain 20% protein and 4% fat, as well as carbohydrates, minerals and vitamins and may supply dietary components that are lacking in nectar. The important nutrients of pollen are contained in a tough outer coat which was once thought to pose problems in digestion. The Honey Possum appears to be able to make use of pollen with an alimentary system which shows little morphological specialisation. Whether there are any biochemical specialisations in the form of enzymes for pollen digestion is not known.

Circulatory System, Respiration and Excretion

There are no particular published studies on circulation, respiration or excretion in the Honey Possum, but from the authors' personal observations these systems are typically mammalian. Due to small body size, blood is difficult to obtain, though the orbital sinus may be used with some success in the conscious animal. Cardiac puncture yields less than 100 µl blood. Lungs and kidneys bear no special characteristics. The urinary bladder, when fully distended, is translucent and may enlarge to approximately 3 x 5 mm.

Sense Organs and Nervous System

The Honey Possum is well endowed with olfactory apparatus (Kratzing 1982) as are other marsupials (Russell 1985). The olfactory sensory epithelium lines the roof of the nasal cavity and extends well forward in the nasal cavity. As in most other mammals, there is a second completely separate chemosensory organ, the vomeronasal organ, located further forward in the nasal cavity than the olfactory epithelium. It lies in the floor of the nasal cavity as a pair of blind tubes partly lined with sensory epithelium extending to the rear from openings into the roof of the mouth towards the tip of the snout. Tongue movements may force material to be sampled into these openings. In other mammals, including the Virginia Opossum, *Didelphis virginiana*, the vomeronasal organ is particularly important for chemoreception related to reproduction (see Russell 1985 for review). Certainly in the Honey Possum, olfactory cues may be important for males and oestrous females to locate each other.

Taste buds are found at the anterior end of the hard palate (Kratzing 1982) and on the surface of the tongue (Richardson *et al.* 1986).

There is no specific information about other sense organs. The auditory region of the skull is conspicuous, suggesting that hearing is an important sense. The eyes are large and look forward and upward, but nothing is known of their capabilities. The size of the brain is what would be expected for a marsupial of its size. No sign of increased relative brain size is found as in some arboreal marsupials such as petaurids (Nelson & Stephan 1982) and the didelphids (Eisenberg & Wilson 1978).

Endocrine and Exocrine Systems

The mammary glands, of which there are four, have a diffuse appearance. Each teat is surrounded by numerous, discrete alveolae whitened with their contained milk. In non-breeding females, the teat is <1 mm in length, but by the end of lactation the teat may have elongated to 10–15 mm. Nothing is known specifically of the control of lactation or of milk composition in the Honey Possum. The long period of lactation and the immaturity of the young at birth suggest that milk composition changes during lactation as in other marsupials. The marsupium is a deep and well-developed pouch containing four teats, two placed to the anterior and two posterior of the opening. The pouch completely encloses the mammary area and as the young grow it becomes deep and bilocular, extending on each side almost onto the flanks of the animal (Russell 1982). The pouch is closed by an efficient pouch sphincter muscle. The pouch lips appear swollen at oestrus as in macropodids.

As in most mammals, the Honey Possum possesses two pairs of paracloacal glands which open into the gut just anterior to the anus. Rotenberg (1928) recorded only one pair, but two pairs appear to be present (Russell 1985). The anus is situated, with the urogenital aperture, in a long groove on the ventral surface of the conical urogenital papilla. The secretions of the paracloacal glands can be deposited passively with the urine or faeces or actively in a specific marking behaviour where the urogenital papilla is touched to or dragged along the substrate. The significance of this behaviour is not clear (Russell 1986).

The Honey Possum has the normal mammalian complement of the overt endocrine organs: hypothalamus, pituitary, pineal, adrenal, ovary, testes and prostate and, presumably, the endocrine tissues of the urinary and digestive systems. Nothing is known of the hormones of this species. The adrenal gland weighs 0.005 g on average and has the usual division into cortex and medulla. Details of the reproductive endocrine organs are given below.

Reproduction

Hill (1900a) and de Bavay (1950) described the female reproductive tract and Rotenberg (1928) that of the male. More recent descriptions of male and female reproduction are detailed below.

The testes and epididymides are suspended in a large, furry scrotum (Fig. 33.5). They represent a significant proportion of the body weight, the testes alone equal 4.2% (Table 33.1) (Renfree, Russell & Wooler 1984). Underlying the scrotal skin, the tunica vaginalis is intensely pigmented (Figs 33.6 & 33.7). Each epididymis is divided grossly into a caput, a long, slender corpus and a distal cauda, which is sequestered into a pouch-like extension of the scrotum (the pyriform sac described by Woolley & Scarlett 1984), and weighs around 50 mg (Table 33.1, Figs 33.6 & 7). The caput contains some ductuli efferentes as well as a zone analogous to the initial segment of eutherian mammals. Within this region the sperm mass undergoes concentration by fluid resorption. Immediately distal to this region is a middle segment in which the spermatozoa complete morphological maturation. The majority are arranged with their heads in intimate contact with the epithelial stereocilia (Cummins, Temple-Smith & Renfree 1986). A single efferent duct drains the testis and six, eight or ten seminiferous tubules may connect to the duct (Woolley & Scarlett 1984). The seminiferous tubules are amongst the largest known in marsupials (average diameter 0.35 mm). A single pair of bulbo-urethral glands lie dorsal to the crus of the penis. The penis is not bifid at the tip. When withdrawn into the body in the non-erect state, it assumes an S-shaped curve (Woolley & Scarlett 1984).

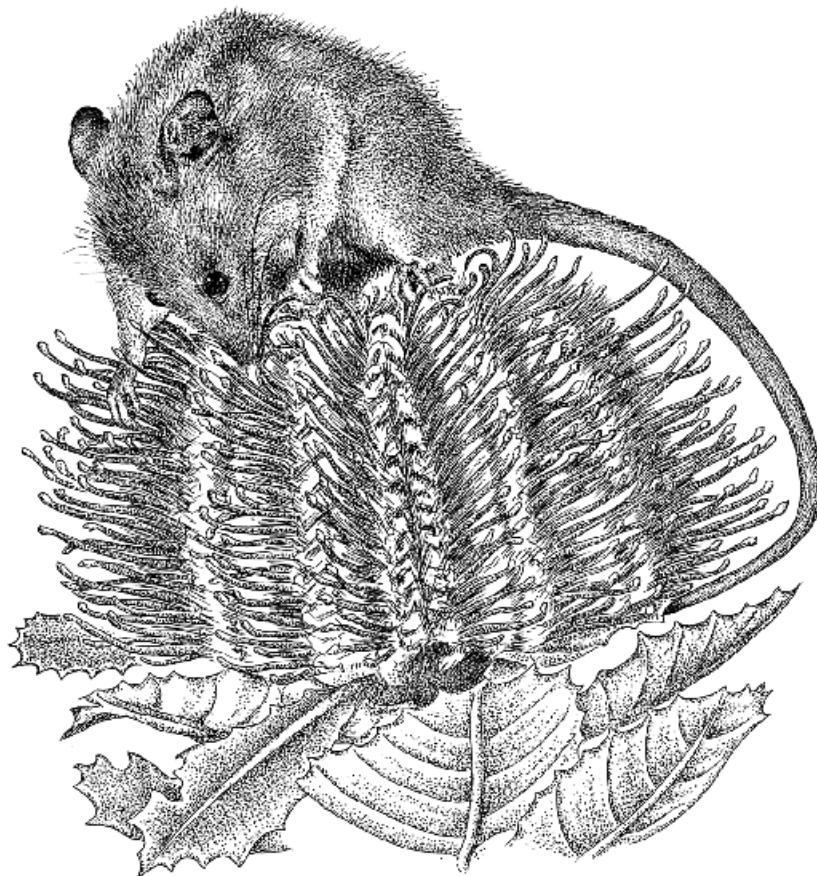


Figure 33.5 A male *Tarsipes* (7.4 g) drinking nectar from the inflorescence of a *Banksia coccinea*. Note the large scrotum. (© ABRS) [K. Hollis]

Table 30.1 Gonad weights of mature *Tarsipes* ($X \pm S.D.$) and percent body weight.

	FEMALES	MALES
Number of animals	23	26
Body weight (g)	12.54 ± 3.32	8.6 ± 1.56
Right ovary/testis (mg)	1.07 ± 0.40	178.8 ± 32.0
Left ovary/testis (mg)	1.10 ± 0.36	177.9 ± 30.0
Right epididymis (mg)	-	56.2 ± 15.7
Left epididymis (mg)	-	51.5 ± 16.0
% Body weight (g)	0.0173	4.2

The spermatozoa acquire the potential for motility by the end of the middle segment of the epididymis and are fully active on removal from the cauda (Cummins, Renfree & Temple-Smith 1981). The spermatozoa are very long, up to 360 μm overall (nucleus 14–15 μm ; midpiece 90 μm ; principal piece 250–260 μm (Cummins *et al.* 1981, Cummins *et al.* 1986; Renfree *et al.* 1984; Woolley & Scarlett 1984). While the sperm are the longest recorded for any mammal and the testes are amongst the largest in relative terms, the ovaries represent only 0.017% of the female body weight (Table 33.1) (Renfree *et al.* 1984). The large size of the testes may reflect a promiscuous mating system (Harcourt *et al.* 1981) and this, together with the large spermatozoa, could be a response to gamete selection.

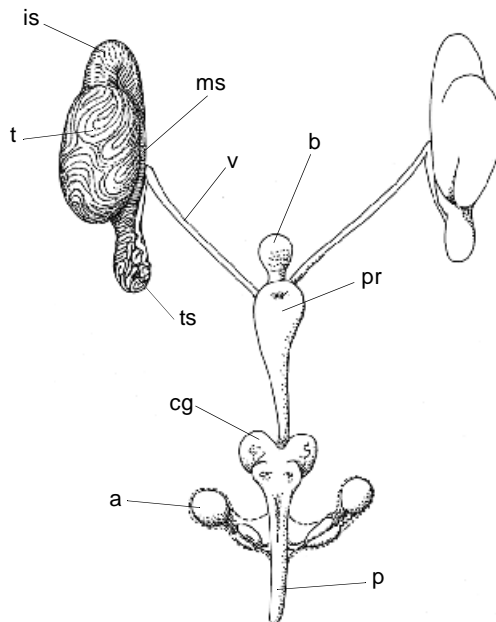


Figure 33.6 Male reproductive tract of *Tarsipes* showing left testis still enclosed within its pigmented tunica vaginalis; the right testis (t) has the tunica removed to show the caput (i.s. = initial segment), corpus (m.s. = middle segment) and cauda (t.s. = terminal segment) of the epididymis. Other structures shown are: a = anal glands; b = bladder; Cg = Cowper's glands; p = penis; pr = prostate; v = vas deferens. (© ABRS) [G. Scott]

During maturation of the spermatozoon, the nucleus rotates on the neck of the flagellum so as to align with it (Cummins *et al.* 1981). The acrosome contracts towards the nucleus during maturation so that when mature it lies within the outline of the nucleus. Contraction of the acrosome, and of the cytoplasmic droplet, is accompanied by exocytosis of membranous vesicles and this process appears to be most active in the lipid-rich initial part of the middle segment (Cummins *et al.* 1981, Cummins *et al.* 1986). As the cytoplasmic droplet shrinks to the neck region and finally drops off, a fibrous sheath appears under the plasmalemma of the middle piece. In the fully mature spermatozoon, this has three main substructural components: a submembranous fibre; an underlying

pair of microtubule-like structures; and an underlying unilaminar membrane (Cummins *et al.* 1986). This three-part form of the mid-piece fibre network is unlike the simpler structure seen in other marsupials (Harding, Carrick & Shorey 1984).

The pattern of sperm maturation is similar to that of other marsupials. The Honey Possum, however, shows an intriguing mosaic of features of sperm structure and development similar to a wide range of marsupial families (Renfree *et al.* 1984; Harding *et al.* 1984). The head structure, and in particular the mode of maturation of the acrosome and the droplet, is reminiscent of macropodids and phalangerids. The shed droplets, however, appear to accumulate in the lumen of the terminal segment rather than being resorbed as in the Common Brushtail Possum, *Trichosurus vulpecula*. The midpiece fibrous sheath is similar to that seen in dasyurids. Details of the structure of the flagellum, in particular the arrangement of the satellite fibrils or longitudinal columns, are more reminiscent of peramelids.

The disseminate prostate is carrot-shaped and varies in weight from <10 mg to a maximum of 110 mg (M.B. Renfree, E.M. Russell & R. D. Wooller, unpublished results). The prostate is divisible macroscopically and histologically into anterior and posterior segments (Woolley & Scarlett 1984). In both segments branching tubules radiate from the urethral canal. A thin coat of smooth muscle surrounds the gland. Scarlett & Woolley (1980) noted a correlation between prostate size and spermatogenesis. Testis weights and sizes vary little from month to month. Peaks in prostate weight and marked hypertrophy and abundance of secretory material, however, are observed at times roughly corresponding to the three peaks in breeding and to active spermatogenesis in the testis (Duncan 1979; Wooller *et al.* 1981; M.B. Renfree & E.M. Russell, unpublished observations). The gross morphology of the prostate in mature males collected in April (during a breeding 'peak') and in July (during a breeding 'trough') are shown (Fig. 33.7b, c).

Scarlett & Woolley (1980) noted that in adults there is no seasonal variation in testis size, but found a proportionally greater maximal scrotal length compared to maximum testis length. They suggested that this may be attributed to the enlargement of the epididymis as it fills with spermatozoa and may reflect testis function more accurately than testis size.

The female reproductive tract consists of the usual arrangement into lateral and median vaginal canals and two separate uteri (Figs 33.8 & 9). The ovaries are very small (Table 33.1) and multiple ovulation appears to occur from both ovaries. Between four and six eggs are shed, although never more than four young are born. Like the macropodids, the birth canal (median vagina) is patent after the first parturition (de Bavay 1950) and becomes lined with cuboidal epithelium merging posteriorly with the stratified squamous epithelium of the urogenital sinus. Females are polyovular and polyoestrous. They have a post-partum oestrus at which pregnancy commences, but embryonic development beyond a 1.2–2.0 mm diameter vesicle either stops or is retarded during most of lactation (Renfree 1980a, 1981).

While the delay in development is associated with concurrent lactation, removal of the pouch young does not result in acceleration of embryonic development (Renfree *et al.* 1984). This implies that the slow development is under some environmental control, possibly associated with the flowering periods of the food plants. Litter size is usually two or three (mean 2.4). The individual birth weight of 3–6 mg is the smallest of any mammal (Renfree 1980a). In captivity, lactation lasts for about 90 days.

In the population studied by Wooller *et al.* (1981), females bred at all times of the year, but the proportion of females carrying pouch young reached peaks in February – March, May – July and September – October (Fig. 33.10). These

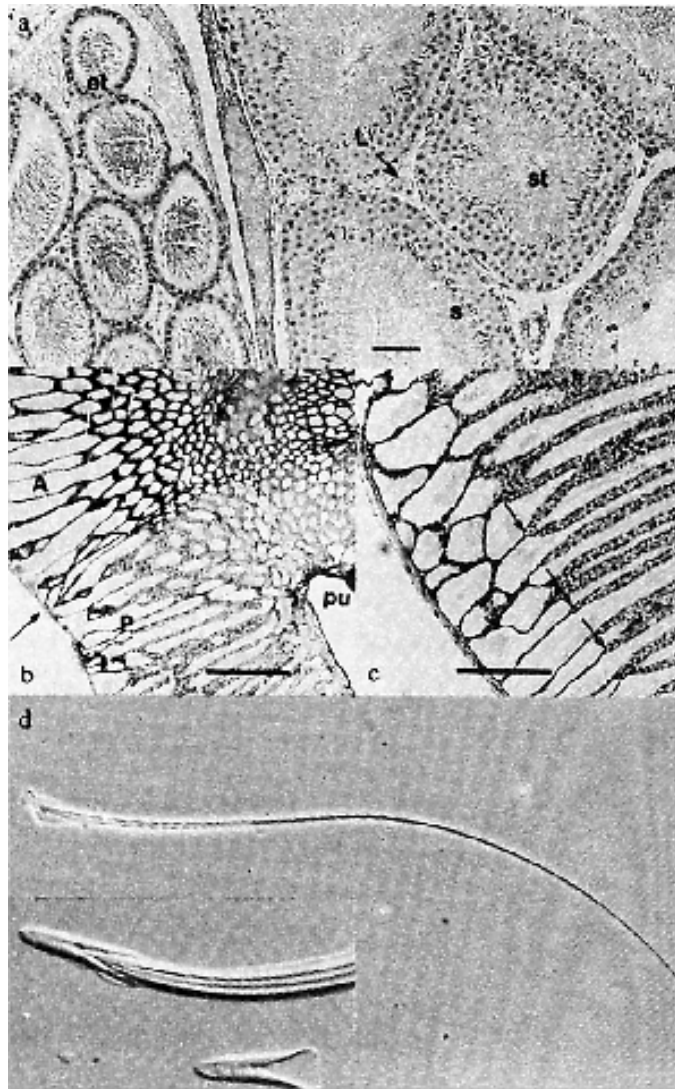


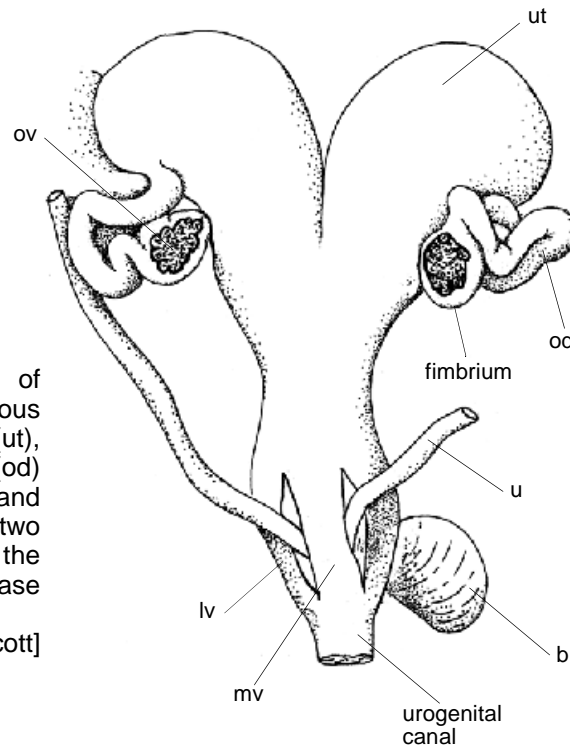
Figure 33.7 Cross section of testis and epididymis of *Tarsipes* showing the epididymal duct (et) and seminiferous tubules (st) both with enclosed sperm (s) and Leydig cells (L) between the tubules; (c) & (d). Longitudinal sections of the prostate, showing anterior (A) and posterior (P) segments and the prostatic urethra (pu). Arrows show the changing cellular structure of the tubules; (e). Spermatozoan measuring 360 μm and detail of the head. All scale bars measure 0.2 mm.

peaks occurred at the same time in two consecutive years and the interval between peaks is approximately the time required for a female to rear a litter. Condition of animals began to improve in February, reaching its highest level in July and declining rapidly to a low level by October. This pattern lead Wooller, Russell & Renfree *et al.* (1984) to suggest that breeding is influenced by food supply. Females may breed at any time of year as their condition allows.

Embryology and Development

The two or three unilaminar blastocysts within each uterus of the Honey Possum are highly variable in size, but all are much larger than the ovum in the follicle (Fig. 33.9). The Honey Possum carries uterine blastocysts while suckling pouch young (Renfree 1980a, 1981). This, together with the occurrence of a post-partum oestrus, is evidence for embryonic diapause. The nature of delay differs from the macropodid pattern of diapause. Growth may be slow but continuous

Figure 33.8 Dorsal view of reproductive tract of an oestrous female showing the two uteri (ut), ovaries (ov) and oviducts (od) and the small lateral (lv) and median (mv) vaginae. The two ureters (u) pass between the lateral vaginae to enter the base of the bladder (b). (© ABRS)
[G. Scott]



during diapause, but the data so far obtained showing apparent increase in blastocyst diameter may reflect individual variation. Variation of blastocyst sizes within one uterus may be greater than between animals supporting young of different sizes (Fig. 33.9). Removal of the sucking pouch young failed to initiate resumption of embryonic development up to 93 days post-lactation (M.B. Renfree, E.M. Russell & R.D. Wooller, unpublished observations). The active gestation period, therefore, has been difficult to determine. Data on captive and retrapped animals suggest it to be 21–28 days, though it may be much less. Organogenesis is apparently of very brief duration. Only six specimens with late term fetuses were recovered from many hundreds of individuals examined.

The information on duration of pouch life and lactation is much better established. Three newborn young of a litter weighed 3, 4 and 6 mg. As in all marsupials, the neonates are altricial with better developed forelimbs than hind. After birth, the pattern of growth is typical of marsupials, but relatively slow. The young leave the pouch when they attain a weight of around 2–2.5 g and by the time of weaning weigh about 5 grams. At present, our best estimate of the time from birth to first pouch exit is 56–63 days, with permanent pouch exit a few days later. When the young first leave the pouch they are well furred, their eyes are open and within a week they are able to climb up and down branches. In captivity, young continued to suckle for approximately 1 month, although they began to eat a little honey 1 week after first pouch exit.

NATURAL HISTORY

Life History

The biology of the Honey Possum in the wild has been studied by Wooller *et al.* (1981, 1983, 1984). Young are found in the pouch in every month of the year. In most years, however, not many births occur in the summer months (November, December and January) when few plants are in flower (Fig. 33.10). The mid-summer trough in births is followed by a synchronised peak of births in late

January – February. There are two further, less synchronised peaks of breeding at about three month intervals, the minimum time from birth to weaning for a litter (Fig. 33.10). Since the Honey Possum exhibits embryonic diapause, a second litter may be born soon after the first is weaned. Similar peaks in breeding occur at the same time from year to year and in different localities. External factors such as food availability or rainfall patterns, therefore, may be involved in determining when reproduction occurs. Males and females reach sexual maturity at about six months. Females born in January – February may produce young within the same year.

In mid-summer, the number of animals is at a low level (Fig. 33.10) and the population contains old and very young animals (as determined by head length). The population builds to a peak in August as the juveniles from the second peak of breeding become independent. A further increase in the population does not follow the September – October peak in breeding. Rather, the population declines rapidly from its spring peak to its summer trough. By October, most animals show a marked decline in condition, reflecting the food shortage which comes with the end of the spring flowering peak. The population crash is not due solely to the death of juveniles. For adults, the maximum interval from first to last capture was 14 months and the mean (from 307 adults) was only 2.9 months, suggesting high adult mortality. Since animals are sexually mature at about 6 months, life span is estimated at 1–2 years. Since females may produce at least two litters in a year, high mortality is balanced by high fecundity. Litter size may be up to four with litters of two and three most common.

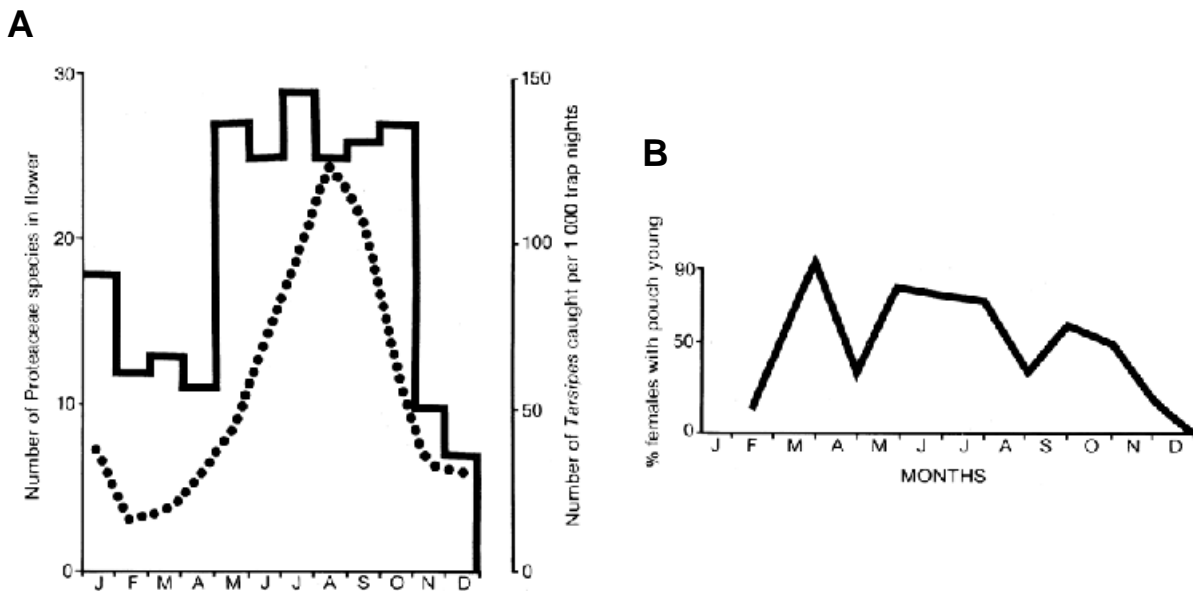


Figure 33.10 **A**, Seasonal fluctuations in a population of *Tarsipes* (estimated by trapping; broken line) shown in relation to the number of species of shrub of the family Proteaceae recorded in flower (After Wooller *et al.* 1984); **B**, seasonal changes in the percentage of females which were carrying pouch young. (After Wooller *et al.* 1981)

The Honey Possum is one of the few small marsupials which may breed continuously throughout the year. For any particular litter, the rate of offspring production, measured as grams offspring per month, is low (Smith & Lee 1984). Litter size is small, growth and development are slower and time to weaning longer than expected for an animal the size of the Honey Possum (Russell 1982). The low rate of production of one litter is compensated for by the possibility of producing a second litter in quick succession. The current belief is that there is a relationship between the slow production of two or three small litters per year and the specialised diet of nectar and pollen.

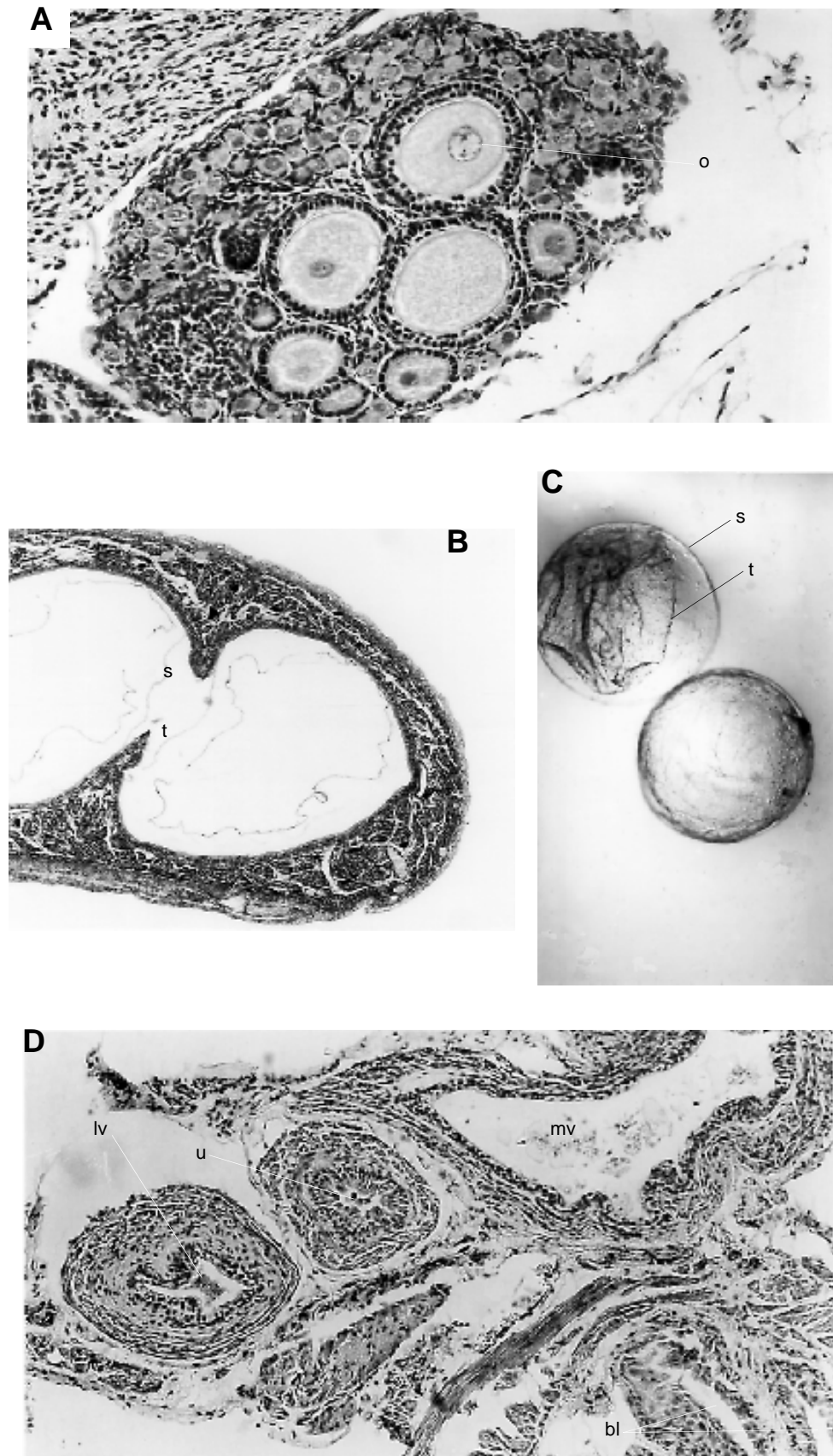


Figure 33.9 A, Cross section of the ovary of a female *Tarsipes* with oocyte (o) within a follicle; B & C, cross section of one uterus, containing two unilaminar blastocysts similar to those shown in C; s = shell membrane; t = trophoblast; D, Cross section of the lower vagina (mv) and its relationship to the ureters (u); lateral vaginae (lv) and bladder (b).

For many mammals, both in Australia and elsewhere, nectar and pollen are a resource used for part of the year, at times of abundance. Rodents, lemurs and marsupials such as the Eastern Pigmy Possum, *Cercartetus nanus*, are known to eat nectar and pollen in addition to insects or seeds (Rourke & Wiens 1977). Few mammals feed exclusively on nectar and pollen. Most of these are tropical bats whose mobility enables them to easily move from one flowering plant to another. Of all non-flying mammals, the Honey Possum is the most specialised to feed on nectar and pollen, although the burramyid, the Feathertail Glider, *Acrobates pygmaeus*, appears to be largely dependent on nectar and pollen, at least in some habitats (Turner 1984b).

The low rate of offspring production and the pattern of holding blastocysts in diapause during lactation found in the Honey Possum seems to be shared with the Feathertail Glider (Smith & Lee 1984; M. Renfree & S. Ward personal observations) adding weight to the suggestion that their life history characteristics may be dictated by the nutritional constraints of a pollen and nectar diet. At the time reproduction occurs, there would appear to be an abundance of food. While energy from nectar is easily and quickly digestible, the rate at which offspring can be produced may be limited by the rate at which the necessary protein can be obtained. The protein balance of the mother will be influenced by the rate at which pollen grains can be collected and digested. From Turner's data on the protein available from *Banksia* inflorescences (Turner 1984a) and the estimated protein requirements of the Honey Possum, a 15 g female with a large litter would have to collect all the pollen from at least 2400 individual flowers each day. Although the flowers may be located on relatively few inflorescences, the actual time taken to collect the pollen will be substantial. *Banksia nutans*, an important component of the Honey Possum's diet, has about 300 flowers per inflorescence, but at any one time only a small proportion are open and some will have been harvested by insects.

Ecology

Animals observed feeding on flowers lick pollen from the pollen presenters and probe deeply for nectar. There is little evidence that insects are a significant component of the diet of the Honey Possum; Wiens, Renfree & Wooller (1979) reported no obvious insect remains in the faeces. There are records of captives eating insects (Vose 1973; sources cited in Troughton 1923), but in all these cases the animals were fed on honey and water with no protein source other than insects. Animals fed honey with added supplementary protein and dried pollen generally ignore insects (Russell 1986).

The species occurs only in the winter rainfall area of the south-western corner of Western Australia. It is most common near the coast in areas of sand plain heath land which are rich in plants of the family Proteaceae, in particular, species of *Banksia*, *Dryandra* and *Adenanthos* (Fig. 33.11a). In these areas, there are always at least some species in flower, providing a year round supply of nectar and pollen. There is a marked peak of flowering in the wetter winter – spring period, at which time the populations reach their highest level.

The quantities of nectar and pollen produced by many of these plants are far in excess of what they would need to attract insect pollinators. The belief is that as the plants have evolved the means to produce sufficient reward to attract vertebrate pollinators, so some vertebrates have evolved the ability to collect these rewards. As an animal such as the Honey Possum probes a flower for nectar, pollen grains adhere to the fur of the snout, head and chin. When the animal visits another plant of the same species, some of the pollen may be transferred, effecting cross-pollination. The plants benefit from a reliable, mobile pollinator and from the advantages of outcrossing. The animals benefit from a food source which is available to only a few species with the necessary

equipment to collect it. Such relationships are well known for birds and bats in many parts of the world (Sussman & Raven 1978), but very few non-flying mammals have adopted this way of life as completely as the Honey Possum.

Identification of pollen grains which accidentally adhere to the fur shows that it visits a range of species at any one time and that the pattern of plants visited changes with the species of plants in flower (Fig. 33.11b). The plants which provide food for the Honey Possum also are visited by large numbers of honeyeater birds, particularly the New Holland Honeyeater, *Phylidonyris novaehollandiae*, and the Western Spinebill, *Acanthorhynchus superciliosus*. There is a broad overlap in the diets of the honeyeaters and the Honey Possum (Wooller *et al.* 1983), although there are some differences. For example, a few prostrate species of *Banksia*, those with flowers hidden within the bush, are visited predominantly by the Honey Possum. The flowers are more accessible to a small mammal approaching from the ground. Since it feeds largely at night and the honeyeaters feed exclusively during the day, competition for nectar between the possum and honey-eating birds may be reduced. Since the honeyeaters obtain their protein largely from insects (Ford & Paton 1977), competition for pollen may not be a serious factor.

The field study of marked Honey Possums carried out near Albany, W.A. by Wooller *et al.* (1981) suggested that a large part of the population is sedentary. The distance between successive captures of marked individuals one or more months apart was less than 50 m for 148 out of 208 animals (71%). Most of the animals which moved longer distances were males or females with no young in the pouch. More than half of all females with young moved less than 10 m over several months. The pattern of recaptures does not suggest that animals normally are dispersed in exclusive individual territories. Rather, home ranges appear to overlap and are probably about 1 ha in area. Females carrying large young in the pouch, however, appear to stay within a very small area. By the time it is ready to leave the pouch, each young weighs about 2.5 g and a litter may consist of three. The pouch is very distended by the large young and the female clearly hampered in her movements (Russell 1986). Such females in captivity are very aggressive towards strangers, especially males. This led Wooller *et al.* (1981) to suggest that in the wild, females with young actually may exclude other animals from a small area when food is plentiful. A good nectar area in spring may produce 5 kJ/m of energy daily. A 15 g Honey Possum requires an estimated 70 kJ/d and at least twice that at the peak of lactation (from calculations in Wooller *et al.* 1984). A female's energy requirements, therefore, could be met within a relatively small area.

Behaviour

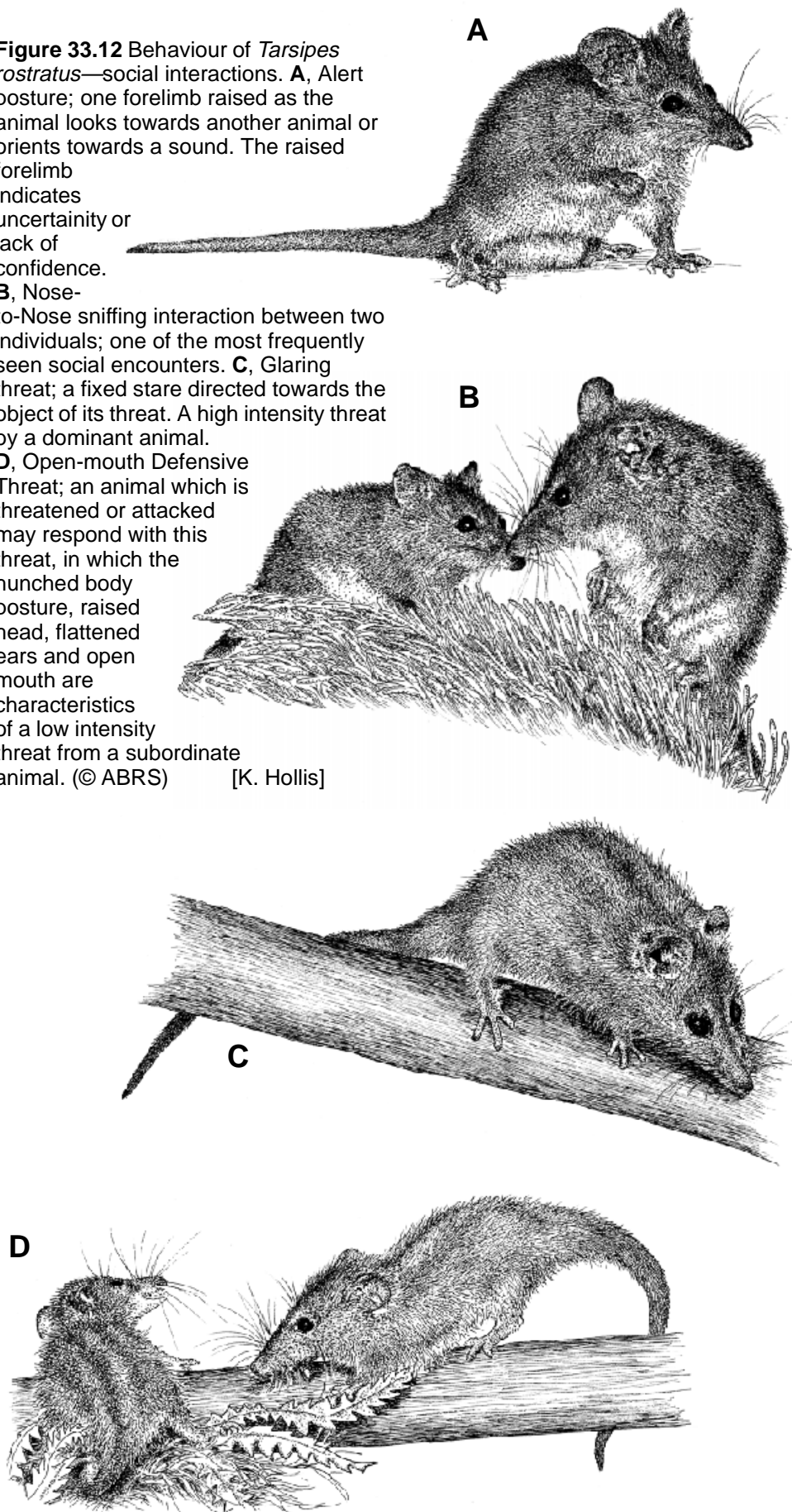
The behaviour of the Honey Possum is similar in many aspects to that of mammals in general (Fig. 33.12). Some behavioural patterns are typical of marsupials and others, such as those related to feeding, are highly specialised. A detailed description of the behaviour of the species in captivity is given by Russell (1986).

In response to a sound or to another animal at a distance, the possums assume an alert posture, with eyes and ears directed towards the stimulus and the snout raised. An animal which is not very confident may stand with one forelimb raised (Fig. 33.12a). Orientation may be followed by approach to the other animal. The most common interaction is Nose-to-Nose Sniffing, behaviour which generally has no obvious aggressive elements (Fig. 33.12b). More intense sniffing of the head, cloaca, pouch or scrotum may follow. After sniffing, one animal may supplant the other passively or no further interaction may occur.

Figure 33.12 Behaviour of *Tarsipes rostratus*—social interactions. **A**, Alert posture; one forelimb raised as the animal looks towards another animal or orients towards a sound. The raised forelimb indicates uncertainty or lack of confidence.

B, Nose-to-Nose sniffing interaction between two individuals; one of the most frequently seen social encounters. **C**, Glaring threat; a fixed stare directed towards the object of its threat. A high intensity threat by a dominant animal.

D, Open-mouth Defensive Threat; an animal which is threatened or attacked may respond with this threat, in which the hunched body posture, raised head, flattened ears and open mouth are characteristics of a low intensity threat from a subordinate animal. (© ABRS) [K. Hollis]



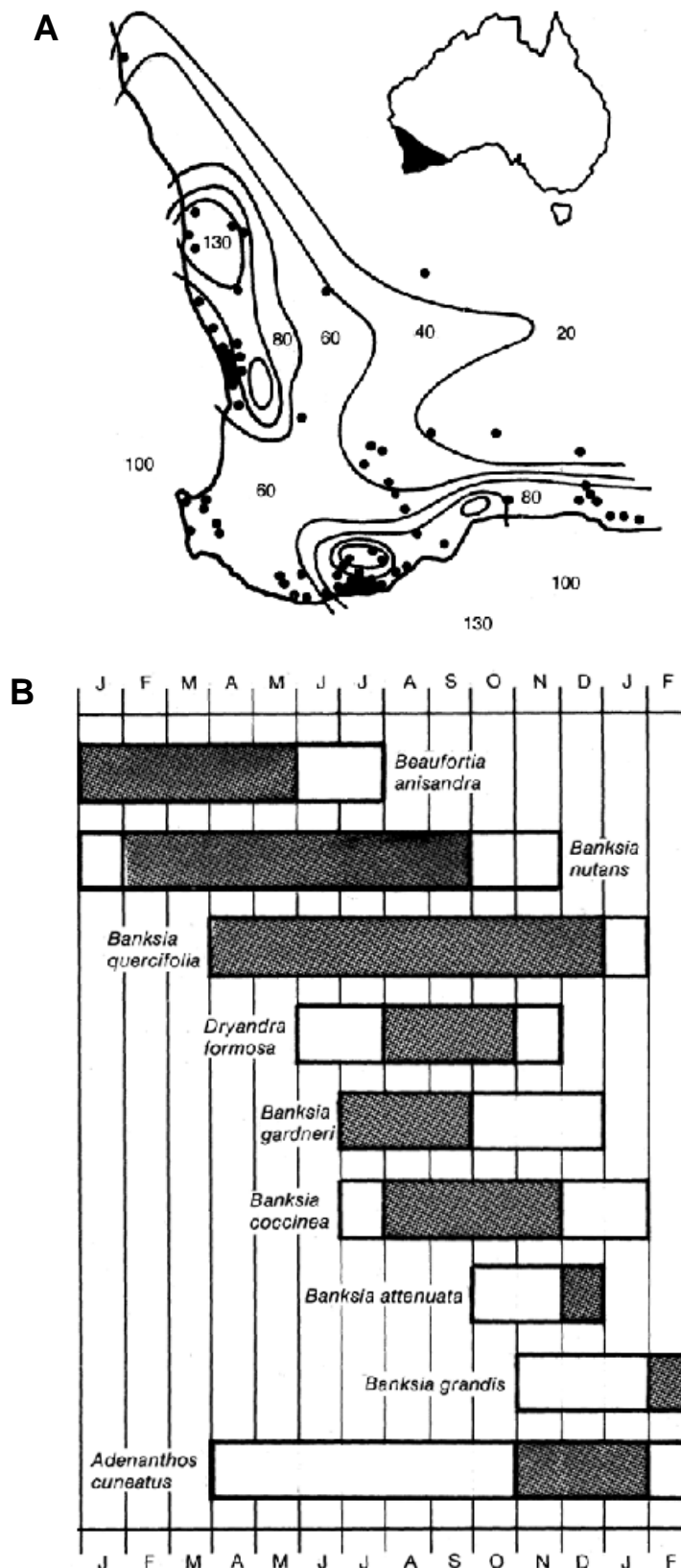


Figure 33.11 **A**, Distribution of *Tarsipes rostratus*. Each dot indicates the location of a specimen in the collection of the Western Australian Museum. The lines join points of equal plant species richness within the family Proteaceae. The numbers of species are shown (Wooller *et al.* 1984). **B**, Seasonal changes in the major types of pollen carried by *Tarsipes*. Each bar represent the time during which animals trapped were carrying pollen of that type. Shaded parts indicate the period when animals were found with heavy loads of a particular pollen. (After Wooller *et al.* 1984)

Sequences of behaviour leading to agonistic interactions include some more stereotyped elements. Initial orientation may be followed by a stereotyped Fixed Stare Threat: the threatening animal may stand and glare at its opponent (Fig. 33.12b) or approach slowly with tail held straight out behind, body elevated, looking fixedly at the subject of the threat. A threatened animal may move away with no further response, give an Open-Mouth Defensive Threat (Fig. 33.12d), often accompanied by a high-pitched hissing vocalisation, or do nothing. Initial threat may be followed by a variety of agonistic acts, increasing in intensity from a push with forelimb or snout to a sudden Jump Attack by the aggressor at its subject who flees, is chased and, if caught, involved in a wrestling fight.

Social interactions are of the general type found across a wide range of mammalian species, particularly the initial contact behaviours of nose-nose and cloacal sniffing and threats which involve looking directly at the opponent (Fig. 33.12c; Eisenberg 1981). The teeth are of no significance as an offensive weapon and threats involving wide open mouth do not occur. The hunched posture and turned away head of a submissive animal are also seen in other species. Forms of attack and fighting are of a type present in an un-ritualised or semi-ritualised form in all conservative mammals. There is no elaborate ritualisation of aggressive displays (Eisenberg 1981).

The nature of social relationships between small, nocturnal animals in the wild is difficult to determine. Observation of captive groups of different size and composition showed a consistent pattern of interactions and gives some indication of what may happen in the wild. One or more females lived together quite amicably. One female, generally the largest, soon became dominant to other females without obvious aggression, supplanting them at food. The same female was aggressive towards males, threatening, chasing and attacking them at every encounter. Adult females are significantly larger than adult males. Their greater size and behaviour towards males in captivity suggests that a female in the wild would be capable of defending a local food resource, if only on a day to day basis.

Olfactory communication seems to be particularly important. Most social interactions begin with simple sniffing. Recognition of individuals and of reproductive state appears to depend on it. Specific marking behaviour occurs which distributes secretions of the paracloacal glands, although the function of the secretions is not known. Some visual signals are evident, chiefly threat postures, which convey information about an animal's intentions at a distance. Vocalisations occur chiefly in agonistic situations. Very high pitched sibilant squeaks are produced, primarily by the object of aggression.

Few observations of reproductive behaviour have been made. Courtship is minimal. A male follows a female approaching oestrus. He sniffs her cloaca, paws her tail and attempts to mount. Only when actually in oestrus does the female allow a male to mount. At other times she moves away or attacks any male approach. Copulation appears to be brief.

Little is known of the actual mating system in the Honey Possum. There is no evidence of a monogamous relationship and a mating system in which several males compete for access to a receptive female is most likely.

The young are carried in the deep pouch for about 9 weeks. During this time they remain almost entirely within the pouch. During the last week or two a limb or tail may project when the pouch is relaxed. The female grooms the pouch and young. She clearly is encumbered by her litter during the last few weeks of pouch life (Fig. 33.13).

After about 9 weeks in the pouch, the young leave the pouch for the first time — very briefly at first. After 2–3 days, they do not return to the pouch. Their eyes are open and they have a good covering of fur, including the dorsal stripes. Each

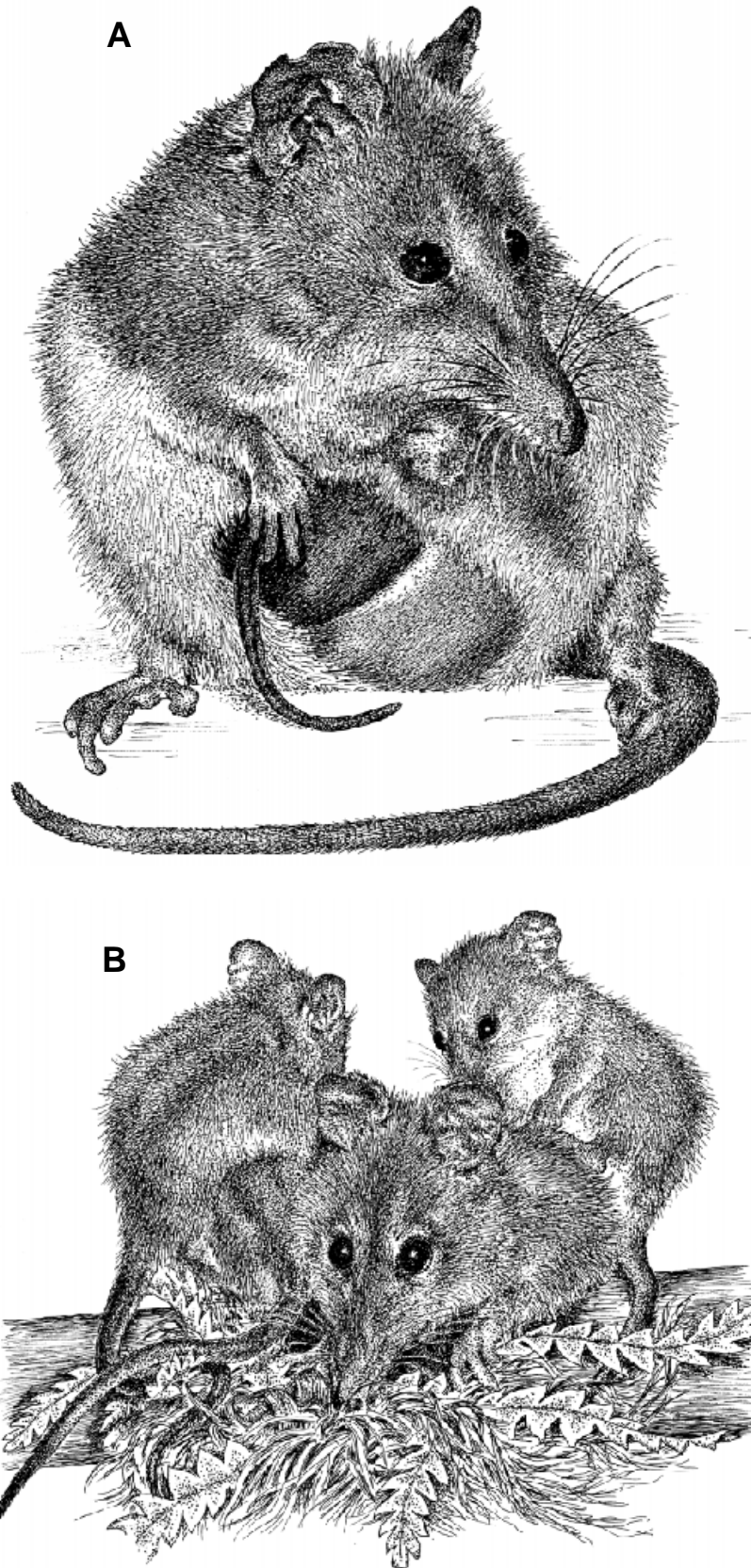


Figure 33.13 Female *Tarsipes* with young. A litter of two or three young in the last stage of pouch life impose a considerable burden on their mother and impede her movements considerably. The large pouch containing young is evident **A**, as is the advanced stage of development of the young which also may be carried on the mother's back **B**. (© ABRS) [K. Hollis]

young weighs about 2.5 g. Initially, the mother leaves them in a nest while she forages, returning from time to time to suckle, groom and huddle with them during her inactive periods. After a few days the young are able to cling to her belly and, soon after, to ride on her back (Fig. 33.1). She appears to try to avoid this, running away from the young as they try to climb on or lowers her body and scrapes the young off her belly. During this stage, mothers do retrieve young which become separated. Vocalisations from the young are inaudible to the human ear, but a female will run to them, push them towards the pouch and stand while they enter her pouch or cling to her belly.

Young are able to run, climb and follow their mother after about one week out of the pouch. They gradually spend less time feeding from the pouch. Suckling ceases at about 13 weeks. Young probably disperse soon after.

Females do not appear to construct a nest, but use existing structures such as an old bird nest, a hollow branch, the crown of a grass tree (*Xanthorrhoea* species) or a fork of branches within a particularly dense shrub. In most respects, maternal behaviour in the Honey Possum is similar to that of other marsupials which normally give birth to litters rather than single young (Russell 1982).

The Honey Possum is mainly nocturnal. Some diurnal activity may occur, especially in cooler, cloudy weather (Hopper & Burbidge 1982). Like many small marsupials, they exhibit torpor and animals are often caught in a torpid state during cold or wet weather. Another energy saving behaviour is huddling, which presumably helps to reduce loss of body heat. In captivity, females with their young, as well as adult males and females, are found huddled in a tight cluster.

Economic Significance

Although the Honey Possum has no known direct economic significance, as the only genus in a family whose phylogenetic affiliations are at present uncertain, the scientific significance is considerable. Its restricted occurrence in Australia and very specific habitat requirements demand special conservation measures. Adequate areas of heathland must be left uncleared and management practices must retain the diversity of food plants which provide a supply of nectar and pollen throughout the year. The Honey Possum is listed as protected fauna in Western Australia and occurs in several large national parks.

BIOGEOGRAPHY AND PHYLOGENY

Distribution

The Honey Possum is confined to south-western Australia, from Kalbarri National Park north of Geraldton to Duke of Orleans Bay east of Esperance (Vose 1972), a distance of 1140 km (Winter 1979). It occupies a winter rainfall area and is most common near the coast. Museum surveys (Kitchener & Chapman 1975, 1976, 1977) show that most records occur in areas of greatest species richness of the family Proteaceae (Fig. 33.9a).

Affinities with other Groups

The dentition, the occurrence of syndactyly and a superficial thymus clearly make the Honey Possum a diprotodont marsupial. The phylogenetic position of the genus, however, remains uncertain. Kirsch (1977a), on the basis of morphological and serological data, considered it the sole representative of the superfamily Tarsipedoidea. This accorded with Hayman & Martin's (1974) observation that the chromosome complement of $2n=24$ (XX, XY) is unusual in comparison with other marsupials. Subsequent analyses of nucleolar organiser

regions and staining characteristics led Hayman & Sharp (1981, 1982) to conclude that chromosomal features ally *Tarsipes* with the superfamily Phalangeroidea and, especially, with macropodids. Baverstock (1984) also placed *Tarsipes* with the phalangeroids, but possibly closer to the petaurids. Using the microcomplement fixation test for antisera raised to a single blood protein, serum albumin, he showed that *T. rostratus* and the Sugar Glider, *Petaurus breviceps* have very similar albumins. *Petaurus*, however, has a chromosome complement of $2n=22$ and all chromosomes are bi-armed rather than the all-acrocentric type of *Tarsipes* (Hayman & Sharp 1982). From basicranial morphology Aplin & Archer (1983) concluded that the Honey Possum is a member of the Phalangeroidea, but not a petaurid.

Reproductive characters fail to clarify the situation. Honey Possum sperm show a blend of dasyurid, peramelid and phalangeroid (but not petaurid) characters, but also have a number of unique features (Cummins *et al.* 1981; Harding, Carrick & Shorey 1981c, 1984). *Tarsipes*, like the macropodids, has embryonic diapause (Renfree 1980a) and retains a patent birth canal after the first birth (Hill 1900a). As in the macropodids, the pouch is deep and well developed, closed by an efficient sphincter muscle and the young are well furred with open eyes when they first leave the pouch (Renfree *et al.* 1984). In summary, the collective evidence does not conclusively contradict Kirsch's placement of *Tarsipes* in a monotypic superfamily with closest affinities to the Phalangeroidea.

Fossil Record

There are no Tertiary fossil records of *Tarsipes* and few in the late Quaternary. Lack of records may be due in part to the small size, fragility of skeletal remains and to the much reduced dentition. A single specimen, probably >30 000 years old, is known from Koala Cave near Yanchep in the coastal heath north of Perth (Archer 1972). In the Cape Leeuwin—Cape Naturaliste region, a single specimen, probably about 5 000 years old, is known from the Skull Cave (Porter 1977). A significant series of fossil *Tarsipes* is known from the Devil's Lair cave in the same region (Balme, Merrilees & Porter 1978). *Tarsipes* is present in greatest abundance in the lowest layers (mean age about 33 000 years), declines relative to other small mammals and finally disappears from the deposit at least 10 000 years ago. The decline probably is correlated with the gradual vegetational change from coastal heath to forest.

COLLECTION AND PRESERVATION

Collection

Honey Possums are difficult to trap by conventional box-trapping methods (Troughton 1923). There had been relatively few captures and, therefore, few studies of the species until the use of pit-fall traps for mammals became widespread in Western Australia. Ecological surveys began to capture occasional Honey Possums (Kitchener & Chapman 1975, 1976, 1977). The study area and techniques used by Wooller *et al.* (1981) were established after discussions with local farmers who frequently found *Tarsipes* at the bottom of newly dug post holes, especially if the holes were in sandy rather than lateritic soil at the perimeter of areas of uncleared bush. A grid of pit-fall traps established in an area of suitable sand plain heath showed that Honey Possums occur patchily at high density, probably determined by the current distribution of available food. The most suitable diameter for pitfall traps is 150–200 mm with a depth of approximately 400 mm. The hole is made readily with a hand auger. A smooth lining, such as PVC piping, is inserted to prevent escape of animals.

Holes are unbaited and captures made when the animals fall in. Permanent traps need to be covered when not in use. When in use they should be left open overnight and checked early next morning. Animals often are found torpid on cold or wet mornings, but become active when warmed.

Preservation and Taxidermy

Standard mammalian techniques apply. Whole specimens may be adequately fixed in buffered formalin. Testes are best preserved in Bouin's Fixative. Due to their small size, dried specimens may be produced from whole animals more successfully by freeze-drying than by the usual skinning techniques. This method also has the advantage that the animal can be prepared in a more natural stance.

Laboratory Culture

Honey Possums may be housed successfully in groups in box cages (1000 x 600 x 600 mm) or individually in smaller cages with mesh lids. Six to eight females and approximately the same number of males can be accommodated together, but best success in raising pouch young is achieved with fewer animals. The floor of the cage is covered in clean sand to a depth of 30–40 mm or with vermiculite. Sand/vermiculite needs replacing only each fortnight or month. Cover can be provided with fresh foliage. Nest boxes with a small entry hole are used if provided. The animals tolerate air conditioning well. At low ambient temperatures they may become torpid. The animals may be transported from the wild to laboratory in plastic rubbish bins with sand in the bottom and water-sprayed fresh foliage. Animals can be earmarked with a 2 mm mouse ear punch. Due to their small size and speed of movement, handling of animals should be carried out in a secure room with all possible escape routes (under doors, drains, sinks, etc.) blocked. Honey Possums rapidly adapt to a glass-fronted cage and can be observed in red light.

A suitable artificial diet is based on that used to feed honeyeater birds and consists of 400 ml honey, 240 ml warm water, 4 g dried pollen, 5 g Sanatogen (Fisons Pty Ltd., Sydney) and 11g Complian (Glaxo Labs., N.Z. Ltd.). This mixture must be stored frozen to prevent fermentation and can be fed at the rate of 3 ml per animal per day in 10 ml syringes fixed upright on a spring clip or inserted through a hole in the cage. Water is provided in a bird cage water holder or in syringes as for the food mixture. Females mate and give birth in captivity on an artificial diet, but successful rearing of pouch young is difficult to achieve. Greatest success is achieved if the lactating females are isolated from other individuals.

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