



FAUNA *of* AUSTRALIA

23. NOTORYCTIDAE

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DEFINITION AND GENERAL DESCRIPTION

The family Notoryctidae (marsupial moles) is represented by a single genus and two extant named species that are endemic to Australia. There is no known fossil record for the family and among the Marsupialia, the Notoryctidae comprises the only wholly fossorial form.

Marsupial Moles exhibit the general characteristics typically associated with fossorial mammals. They are of small size and the extremities are reduced in length. The body form is tubular, the ear pinnae are absent and heavily keratinized, bare skin covers the rostrum and short tail. There is no external evidence of eyes. The body is covered with dense hair that is pale cream to white in colour, usually burnished with gold to ochraceous tips. The pouch opens posteriorly and the epipubic bones are conspicuously reduced. Sand and sand-ridge areas of central and western Australia are the preferred habitats.

HISTORY OF DISCOVERY

The first specimen of *Notoryctes* to reach a scientific institution was collected by W. Colthard on Idracowra Pastoral Lease, a cattle station in the southern part of the Northern Territory. He found some peculiar tracks near his camp at the Finke River and, following them, found the animal lying under a tussock of spinifex (*Triodia* or *Plectrachne* species). The specimen was forwarded, wrapped in a kerosene soaked rag enclosed in a revolver cartridge box, to the South Australian Museum some 1500 km to the south. It was received in an eviscerated and rather decomposed condition by E.C. Stirling, Director of the Museum (Stirling 1888b, 1889, 1891a, 1891b).

Stirling (1888a) announced the discovery in a paper, 'Notes upon a New Australian Mammal', delivered at an Ordinary Meeting of the Royal Society of South Australia on September 4, 1888. About one year later it was recorded in the Abstract of Proceedings of the Society for the Ordinary Meeting of September 10, 1889, that 'Dr Stirling...would shortly submit a full diagnosis of the newly-discovered mammal...to which he gives the name *Psammoryctes typhlops*, gen. et spec'. Stirling (1891a) later recorded, however, that while accompanying an expedition led by the Earle of Kintore into central and northern Australia, during which Stirling visited Idracowra Station and acquired further specimens, he was advised by '...his old friend and teacher, Professor Newton of Cambridge...' that the name had already been appropriated for another group of animals. Stirling (1891a) was required, therefore, to abandon *Psammoryctes* (sand-burrower) in favour of *Notoryctes* (southern-burrower).

Discovery of Marsupial Moles caused great excitement among the scientific community because of its very great likeness to the eutherian Cape moles (Chrysochloridae). The poor state of preservation of the first specimen made it difficult to recognise features that would place it in any one of the major groups and there was, consequently, a great deal of speculation. Stirling (1888a) could find no trace of a marsupium, epipubic bones or a separate urogenital orifice in the poorly preserved specimen. This initially led him to think that the mole was a member of the Monotremata. Intrigued by the dentition, Stirling ventured the opinion that the shape of the mandible and general tooth characteristics bore strong resemblance to those of *Amphitherium*. Jaws of this group had been found associated with the remains of plesiosaurs and pterodactyls and were at that time the earliest known mammal remains. He qualified this opinion by noting that his comments were speculative, but justified because '...the Society

[Royal Society of South Australia]...has been excited by the announcement of the discovery of this very interesting animal, singular even in this land of curious and antique types’.

Ogilby (1892) tentatively placed it with the polyprotodont marsupials, but recognised its apparently close affinities with the monotremes. In the same year, Cope (1892) considered the affinities and concluded that it had arisen from the same stock as the African Chrysochloridae and did not have connections with the monotremes, but in fact connected the marsupials with the eutherians.

Gadow (1892), with the benefit of nine specimens to dissect, supported the placement by Ogilby (1892) of *Notoryctes* in a separate family among the polyprotodont marsupials.

MORPHOLOGY AND PHYSIOLOGY

Thomas (1920) described *Notoryctes caurinus* from north-western Western Australia and among certain characteristics he employed to distinguish *N. caurinus* from the Marsupial Mole, *N. typhlops*, a smaller size was a general feature. Since the original description of *N. caurinus*, there have been few references to it and the information which follows, therefore, is based wholly upon *N. typhlops*.

Probably because of the initial confusion whether the Marsupial Mole was prototherian or marsupial, the two and a half decades following its discovery yielded a variety of detailed anatomical studies of the small animal. Few recent anatomical investigations have been conducted. The information which follows is based largely on those early works, but does not attempt to duplicate their detail or comparative aspects.

External Characteristics and Body Wall

Available information, based on specimens examined by one of the authors (DWW), indicates that the upper limits of size for the Marsupial Mole are a head and body length of about 140 mm and a weight of about 60 g. The ventral deflection of the head and of the posterior portion of the body produces a convex arch of the dorsum. From the dorsal aspect, the cone-shaped head merges directly with the body, so there is no obvious neck region. The limbs are short, powerful and furred to the manus and pes. The manus is folded and digits III and IV bear large spade-like claws. The dorsal surface of the manus is rotated medially. A scoop is formed by the enlarged claws and folding of the manus. The pes is rotated antero-laterally so that digit V is the most anterior digit and the plantar surface faces laterally (Stirling 1891a).

The fur is silky and pale cream in colour. The golden or reddish-brown tint of the fur may be the stain of iron compounds found in the red sand (Howe 1975).

The hair grows in bundles, each comprising a single long guard hair and from nine to 20 small hairs. A line of three to five bundles form a group. Each bundle has its own follicular opening. The bundles reach their greatest density on the chin, the side of the head and on the dorsal surface of the body in the sacral region. In this latter area, termed the ischiotergal patch, the hair may be matted in appearance and more deeply stained than the hair over the rest of the body. Sebaceous glands are well developed, particularly in the patch area and around the cloacal opening (Sweet 1907).

The dorsal surface of the rostrum and the tail lack fur and the bare skin is heavily keratinized. The epidermis is greatly thickened and the dermis thinner than in other parts of the body. On the rostrum, the exposed skin forms a shield. This extends from the external nares, which it surrounds, over the antero-dorsal

surface of the head to about the interorbital region. The exposed, horny skin of the tail forms in annular rings, decreasing in circumference from the base to the knob-like tip (Stirling 1891b; Sweet 1907).

The external ear openings are covered by fur and pinnae are absent. All external evidence of the eyes is obscured and the area is well covered with fur.

The pouch is present in both sexes though better developed in the female. The cloacal opening is surrounded by solitary large hairs with which are associated very well-developed sebaceous glands. The testes are prepenial and do not descend into an obvious scrotum (Stirling 1891b; Sweet 1907).

Myology

Details of the complete myology of the Marsupial Mole are beyond the scope of this account. In what follows, emphasis is placed on peculiarities which contribute to the unique character of this species. For details, see Wilson (1894) upon whose work the following information is based.

The muscle group associated with the skin, the panniculus, is poorly developed. However, a slip arises from the ischium inserting on the skin of the lumbar region, termed the ischiotergal slip. This appears to be unique in the Marsupial Mole. The slip passes below the glandular ischiotergal patch of skin previously noted, but the functional significance of this proximity is unknown.

Among the trapezius group, the spinotrapezius is independent of the other portions at origin and insertion. The rhomboideus is a single thick and extensive sheet of muscle. Part of its origin is from the long neural spines of the first two thoracic vertebrae and the insertion is very extensive over the vertebral border of the scapula, while other fibres extend anteriorly to insert on the preaxial extension of the spine of the scapula.

Among the muscles which traverse the clavicular-sternal-cranial expanse, the cleidomastoid is absent. However, the sternomastoideus is present, arising from the anterior projection of the keel of the manubrium. The clavodeltoid is small and the status of the clavotrapezius is somewhat doubtful. A well-developed, well-anchored clavicle and associated musculature generally are associated with considerable lateral extension of the anterior limbs.

The latissimus dorsi has its origin exclusively from the neural spines of thoracic vertebrae three through 12. It completely lacks a humeral insertion, but instead inserts onto an aponeurosis on the surface of the flexor carpi ulnaris at about the mid-point of the forearm.

The pectoralis is a large, thick muscle divisible into three parts. Arising from the manubrium and body of the sternum, the two anterior portions insert on the ventral surface of the massive deltoid ridge of the humerus. The third, deeper and most posterior portion originates from the ventral costal surfaces and inserts onto the greater tuberosity of the humerus.

Although the teres major is present and independent of the latissimus dorsi, both the teres minor and the coraco-branchialis are absent.

The scapular head of the triceps has a very extensive origin. The origin extends over the entire length of the axillary border of the scapula and the secondary spine formed by that border. The humeral portions of the triceps originate along the entire length of the shaft of the humerus. All parts of the triceps insert on the great convex surface of the olecranon. A portion of the scapular head appears to extend onto the forearm with those of the latissimus dorsi.

Extensive alterations of the musculature of the forearm and manus are seen. The extensor carpi radialis brevis is well developed and has its insertion over the proximal three-fifths of the radius. The pronator teres is well developed, but the pronator quadratus is absent. The flexor carpi ulnaris is powerful, overlain by

the strong aponeurosis into which the latissimus dorsi inserts. The entire inner surface of the curved olecranon and the space inside the curve are taken up by the flexor digitorum profundus. The origin of this muscle continues down the medial half of the ulnar shaft. It inserts on the large sesamoid in the palm of the manus. Of the intrinsic muscles of the manus, only three remain: abductor brevis pollicis, flexor brevis pollicis and the flexor brevis digiti secundi.

There is, unfortunately, no information on the myology of the pelvic region or posterior limbs.

Skeletal System

The information which follows is based on the work of Stirling (1891b, 1891c, 1894), Gadow (1892) and personal observations by one of the authors (DWW). The skeletal components of the Marsupial Mole are modified so greatly for a fossorial existence (see Nevo 1979 for a general discussion of such adaptations), they contribute little to an understanding of its phylogeny. Rather than present a detailed description of each component, a general picture is attempted which reflects the more notable features of the skeleton.

The skull, in dorsal aspect, is conical in outline (Fig. 23.1). On 11 specimens from central Australia (*typhlops*), the greatest length of the skull (mean \pm standard deviation) is 25.2 ± 1.65 mm and on three from Wallal, Western Australia (*caurinus*) the mean of the same measurement is 23.5 mm (D.W. Walton personal observation).

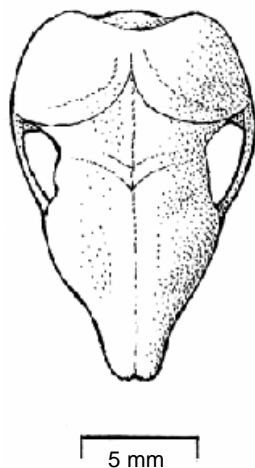


Figure 23.1 Dorsal view of the skull of a Marsupial Mole. (© ABRS) [F. Knight]

From the nuchal line anteriorly to the beginning of the nasals, the dorsal surface of the skull is flat. At the nasals, however, the dorsal surface is directed ventrally at an angle of about 60° . The zygomatic arch is strongly developed, but there is no trace of a postorbital bar; an interorbital constriction is present. The greatest width of the skull occurs in the area where the jugal portion of the zygomatic arch arises. No trace of a sagittal crest is evident, but two low ridges emanate from the posterior apex of the mid-line of the cranium arcing laterally toward the posterior origin of the zygomatic arch. The auditory bullae are conspicuously inflated and best seen with the skull in ventral aspect.

The posterior portion of the skull, the occipital region, is flat and rises vertically to the nuchal line. The foramen magnum is located medially along the postero-ventral margin of the skull and is best viewed from the ventral aspect. No evidence of the optic foramen is visible.

The dentaries flare broadly from the mandibular symphysis. The angular process tapers to a point and curves medially. The condyloid process and coronoid process are joined over the lower half of their length. On the outer surface of this union is the conspicuous masseteric fossa. The coronoid process rises almost vertically, deflected postero-medially only slightly. The condyloid process is deflected posteriorly at an angle of about 60° and rises to a knob-like articular facet which is displaced laterally only slightly from the antero-posterior axis of the tooth row.

The description of the cervical vertebrae by Stirling (1891b) is not very clear. The implications are that the atlas, axis and seventh cervical are mobile. In the specimens examined by one of the authors (DWW), the axis and next four cervicals are fused completely (Fig. 23.2). The atlas is conventional except for a circular articular facet in the dorso-medial region of the posterior face of the neural arch. The odontoid process of the axis is present and conspicuous. The neural arches and spinous processes of the fused five vertebrae rise slightly and bear a short anteriorly directed process which articulates with a facet on the posterior face of the neural arch of the atlas. Although the head may be rotated about the axis and depressed, the dorsal articulation between the atlas and axis effectively prevents raising the head much above the horizontal.

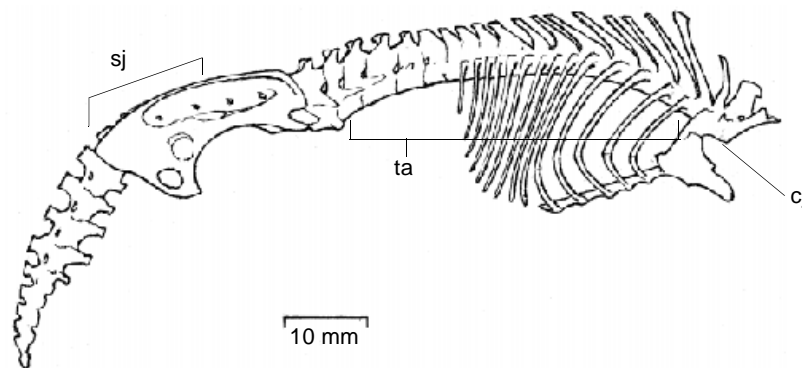


Figure 23.2 Lateral view of the articulated vertebral column of the Marsupial Mole showing the cervico-thoracic junction (cj), thoracolumbar arching (ta) and sacro-caudal junction (sj). (© ABRS) [F. Knight]

The cervical region is deflected postero-ventrally at such an angle that the sixth cervical articulates posteriorly not only with the seventh cervical, but with the first rib. The seventh cervical alters the ventral deflection into a dorsal arch.

Pressure directed posteriorly from the head, therefore, is directed towards the sternum as well as posteriorly down the vertebral column.

The first thoracic bears a very long spinous process and a short, but massive, rib that articulates with the seventh cervical and ventrally with the large manubrium of the sternum. There are 14 additional rib-bearing thoracics. Thoracics one through six bear prominent spinous processes, the longest on the first. The thoracic vertebrae arch dorsally from the articulation with the last cervical to the level of the sixth thoracic. From that point, the vertebral column is horizontal until the sacral region.

There are four lumbar vertebrae. The transverse processes of the last lumbar form a loose articulation with the transverse processes of the first sacral and the ilium. Six fused vertebrae comprise the sacrum. The sacrum arches dorsally,

then is deflected ventrally at the first caudal. The first nine caudal vertebrae are well formed, but beyond the ninth they become knob-like structures which probably vary in number from three to four.

The first seven ribs are joined directly to the sternum. The costal cartilages of the remaining ribs are joined, each to its predecessor. The first rib is short, thoroughly ossified and solidly anchored to the sixth cervical, first thoracic and the manubrium of the sternum.

The manubrium or presternum is a large shield-shaped structure with a prominent anteriorly directed keel. The appearance of the manubrium is reminiscent of that seen in some microchiropterans. The remainder of the sternum is rod-like, although the ziphisternum terminates in an expanded, flat cartilaginous extension.

The clavicle is a slender, curved bone, slightly enlarged at the scapular end. The attachment to the sternum, however, is ligamentous on the antero-lateral border of the manubrium.

The scapula is unique (Fig. 23.3). From the glenoid fossa, the coracoid and axillary borders flare to the vertebral border in such a way as to resemble a v-shape. over the lower two-thirds of the scapula, the spine is greater in height than the scapula is wide. Much of the muscle attachment surface now lies along the spine rather than in the supraspinous and infraspinous fossae. The spine projects distally beyond the level of the glenoid fossa as a long acromial process. The axillary border of the scapula turns up along its edge, the height increasing toward the glenoid fossa, to form a second spine. The infraspinatus, therefore, passes through a deep groove formed by the true spine of the scapula and the upturned axillary border. The tops of the two spines are so closely approximated that the channel for the infraspinatus becomes almost a tube. The vertebral border of the scapula is curved and the bone thickened and slightly raised.

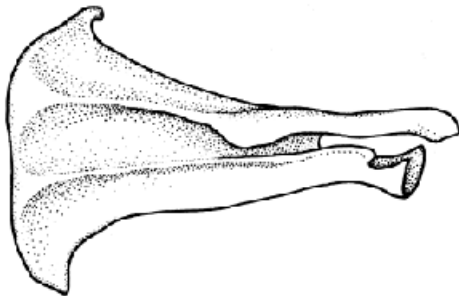


Figure 23.3 Lateral view of the scapula of the Marsupial Mole. (© ABRS) [M. Thompson]

The humerus is a short, massive element (Fig. 23.4). The greater and lesser tuberosities are evident and the great ridge for the insertion of the deltoids and other muscles of the shoulder extends over half the length of the humerus. The medial epicondyle projects from the distal end of the humerus for a distance about equal to half the length of the humerus. The ulna exhibits a long, curved olecranon process which nearly equals the shaft in length. The radius almost equals the shaft portion of the ulna in length.

The manus is folded so that the dorsal surface faces inward. All digits bear claws. The claws of digits I and II are long, slender and tapering. The claws of digits III and IV are greatly enlarged. The claw of digit III is the largest of all, measuring 4 by 15 mm with a blunt tip. The claw of digit IV is wider at the base, but shorter than that of digit III and triangular in shape to terminate in a point. Digit V is represented externally by a broad, short nail-like claw. On the palmar surface there is what appears to be a large sesamoid (see Fig. 23.6a).

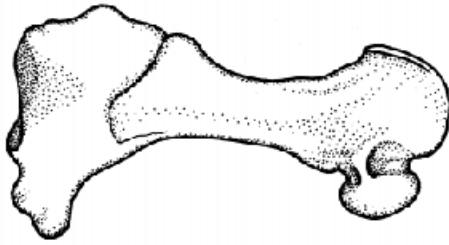


Figure 23.4 Lateral view of the humerus of the Marsupial Mole.
(© ABRS) [M. Thompson]

The innominates lie almost horizontally and parallel to the longitudinal axis of the thoracolumbar portion of the vertebral column. The ilium extends anteriorly to the level of the fourth lumbar. Dorsally, the fusion of the innominates with the spinous processes of the sacral vertebrae is expanded laterally forming an arch of bone. This arch flares ventrolaterally to pass underneath the transverse process of the fourth lumbar. Posteriorly, the arch merges into the ischium to flare postero-laterally to the level of transverse process of the second caudal. In dorsal aspect, the rod-like ilia are completely obscured and a cavernous area lies between the ilium and the dorsal bony arch.

The obturator foramen is round. The acetabulum lies antero-dorsally and is similar in size to the obturator foramen. Although complete, the antero-dorsal wall of the acetabulum is strengthened and raised well above the remaining rim of the socket, directing the face of the acetabulum postero-ventrally.

Epipubic bones are represented by thin, bony filaments which could easily be missed in a dissection or lost in a skeletal preparation, as Stirling (1888a) experienced.

The head of the femur projects from the shaft as an oval with the apex at its top and there is no significant neck. The lesser trochanter is distal to the head and conspicuous. The greater trochanter, however, rises above the level of the head, is antero-posteriorly flatter and extends distally as a prominent ridge over the proximal quarter of the shaft. The distal articular surfaces of the femur are conventional except that the condylar surfaces are expanded anteriorly for articulation with the very large patella. The anterior face of the tibia is dorso-ventrally flattened into a prominent ridge which extends, decreasing in height distally, over the proximal two-thirds of the length of the shaft. Proximally, the ridge forms an extensive articulation with the large patella. The proximal end of the fibula is expanded antero-posteriorly and may articulate loosely with a dorsally directed process from the patella. Though less robust than the tibia, it is of approximate equal length.

The pes is normal in its complement of bony elements. There are five digits, all of which bear claws. As with the manus, there is a large sesamoid on the plantar surface. This sesamoid, along with the expanded fifth metacarpal, produces a trough-like groove for the sole. Whether syndactyly is present has been debated (see Archer 1984b), but the essential embryological studies have not been done.

In summary, the extensive bony buttressing of the cervical and upper thoracic regions and the horny shield on the dorsal surface of the rostrum indicate that the anterior end of the body is employed as a ram. When burrowing, the forelimbs are extended alongside the head and, with each scoop-like manus, draw sand postero-medially underneath the body. The large surface area for muscle attachment on the innominates and the surface areas on the anterior face of the femur, patella and tibia suggest that the power thrust for the ram is generated and braced by extension of the hind limbs. The well-developed spinous processes of the thoracolumbar region suggest that the epaxial musculature is deep and powerful and that forward progress is aided by flexion

of the arches in the spinal column at the cervicothoracic and sacrocaudal junctions. The tail, adpressed to the substratum, probably braces the vertebral flexion.

Locomotion

Above ground, the Marsupial Mole uses the spade-like front claws to drag the body over the surface while simultaneously shoving with the hind limbs. Each forelimb is extended in unison with its rear opposite and the animal proceeds with a rapid sinuous shuffle. In loose sand or soil, a mole leaves a track of three parallel furrows: the outer two made by the legs and the inner one by the tail which is adpressed to the surface.

Jones (1923a) noted that a specimen kept by him moved with its tail held in the air. Of the several live specimens seen by one of us (KAJ) and that reported by Howe (1975), none held their tails in this manner and it seems likely that Jones observed an unusual individual.

Moles move on the surface with much haste, but little speed; the limbs move rapidly, but progress is slow. Jones (1923a) described them as feverishly restless and prone to nervous activity. Captive animals move hurriedly about their cages, intermittently stopping abruptly to change direction or commence digging. Often the individual will burrow into the substratum, then reappear shortly to resume patrolling the cage.

When commencing a burrow, a Marsupial Mole scratches rapidly with the forelimbs while holding the back slightly arched and the hind limbs braced and scarcely mobile. The substratum is shovelled backwards under the ventral surface of the animal. Once the body is about half submerged, the hind limbs are used in unison (in contrast to above ground movement) to push the body forwards and down.

The Marsupial Moles can burrow rapidly from view. Stirling (1891b) relates how one of his collectors placed an individual on loose soil, but upon disappearing from view the work of two men with shovels failed to unearth it. A similar account is given by Russell (1934: 160-163) and verbal corroboration was provided by Walter Smith to R. Kimber (personal communication). Smith, now an elderly resident of Alice Springs, travelled widely in the Simpson and Western Deserts in his youth and saw marsupial moles on various occasions. He likened the moles disappearing into sand to a person jumping into water and found it difficult to get closer than 2—3 m to an individual before it burrowed quickly out of sight.

Once underground, the moles virtually swims through the soil. The sand collapses behind the animal as it progresses and no tunnel is formed. Nevertheless, where one has passed through a soil profile, an oval shaped differentiation in soil texture and colour can be seen.

Feeding and Digestive System

There was considerable early confusion regarding the dental formula of the Marsupial Mole and even the suggestion of asymmetrical distribution of those teeth present. Much of this early controversy and reasons for it are presented by Gadow (1892). There is variation among individuals in the number of teeth present and, as Gadow indicated, the variation in number primarily occurs anterior to M1. The dental formula may be represented as (after Gadow 1892) $I \frac{4}{4} C \frac{1}{1} PM \frac{3}{3} M \frac{4}{4} =$ a maximum of 48. Archer (1984b), to reflect the variation, expressed the dental formula as $I 1-4/1-3 C \frac{1}{1} PM 2-3/1-3 M 2-5/2-5 =$ a maximum of 50. Turnbull (1971) gave the basic marsupial formula as $I \frac{5}{4} C \frac{1}{1} PM \frac{3}{3} M \frac{4}{4} = 50$.

The premolar (PM3) which immediately precedes M1 is the largest of the anterior teeth and the only one which exhibits modifications (Fig. 23.5). The incisors, canines and other premolars do vary in size, but are little more than conical projections.

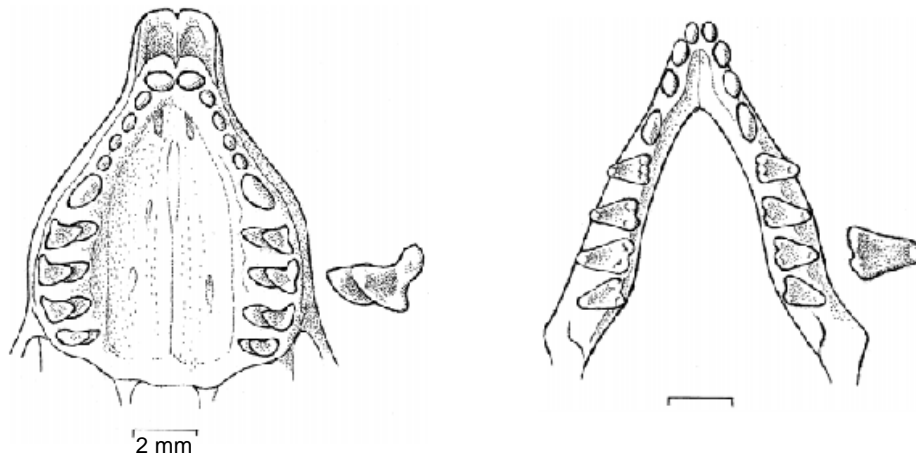


Figure 23.5 Upper (left) and lower tooth rows of the Marsupial Mole. (© ABRS) [F. Knight]

The pattern of the molars is of particular interest. They are zalambdomorphic, a rather unusual pattern among marsupials. There is no satisfactory explanation for the occurrence of this tooth morphology in the Notoryctidae.

Tomes (1897) reported that the molars are only lightly implanted in bone; the root comprises only about one-third of the length. This was taken to indicate that particularly hard substances could not be included in the diet of *Notoryctes*. Peculiarities in the vascular canals within the dentine and enamel are also noted in the same work.

There is surprisingly little information on the viscera except for the reproductive structures. Stirling (1891b) provided brief descriptions and the following information is derived therefrom.

There is no information on the oesophagus other than that the post-diaphragmatic portion is short and that the oesophagus joins the stomach about the middle of the lesser curvature. The stomach is said to be 'considerably compressed and contracted' and to measure 17.5 mm at its greatest length and 12.5 mm at its greatest width. The pancreas is apparently normal in position, along the greater curvature of the stomach and a portion adheres to the small intestine just beyond the pyloric valve.

The length of the intestinal tract, pylorus to cloacal aperture, is given as 29 mm, a not unreasonable figure. The anterior portion is said to have a greater diameter, 5 mm, than the posterior, 3 mm. These two latter dimensions are given as cm (in error) by Stirling (1891b).

No clear boundary exists between the small and large intestines. A sacculaton and what may represent a valve occurs about 100 mm from the cloacal terminus of the intestines. Whether the sacculaton represents a caecum is not clear.

The liver is divided into two large and two small lobes. The large lobes lie ventral to the smaller. There is no apparent gall bladder. The common bile duct enters the small intestine 2.5 mm below the pyloric valve.

Circulatory and Respiratory Systems

The heart lies in its normal position with the rather pointed apex directed to the left. Dorsally, the heart is separated from the diaphragm by a portion of the right lung, but ventrally the pericardium is connected directly to the diaphragm. The right ventricle does not form part of the apex.

The pulmonary artery arises from the right ventricle, is a short, thick vessel and divides almost immediately into the left and right pulmonary arteries. The right branch is shorter and wider than the left.

The aorta arises from the left ventricle at about the same level as the pulmonary artery arises from the right ventricle. Arching anteriorly and to the left, the aorta continues posteriorly in the usual mammalian pattern.

In the region of the arch, however, individual variation occurs with regard to the origins of the carotid and subclavian arteries. Two patterns are seen: the two carotids arise as a common trunk, from the root of which arises the right subclavian, and the left subclavian arises from the aorta further to the left along the arch, and; the right carotid and subclavian arise as the innominate trunk, the left carotid arises independently but close to the base of the innominate trunk and the left subclavian as in the first pattern.

One other peculiarity of the arterial system is that the median sacral artery arises just prior to the division of the abdominal aorta into the two common iliac arteries. The median sacral artery may be represented by one to three small vessels or be absent entirely. In the usual mammalian pattern, the median sacral artery is present as a small continuation of the abdominal aorta.

The two pulmonary veins unite to form a median trunk which equals the pulmonary arterial trunk in thickness, but is about twice its length. Sweet (1904) stated (p. 98) that the pulmonary trunk, as well as the left precava, enters the right auricle. No doubt the left precava does enter the right auricle, as Sweet noted later (p. 103), but the pulmonary trunk must enter the left auricle. The three caval veins, the posterior vena cava and the left and right venae cavae, come in contact prior to entry into the right auricle, but retain separate openings into the chamber.

The remainder of the venous system conforms to the usual mammalian pattern. Both the venous and arterial vessels servicing the anterior limbs are thought to be rather enlarged (Sweet 1904). There is no information on the spleen other than that it is present in the normal position and is a v-shaped organ. Information relating to the vessels which serve them represent the extent of published knowledge of the lungs, so the assumption is made that these organs, at least in gross anatomy, are not especially distinctive.

Excretion

The kidneys are suboval in shape and the external surface is smooth. The adrenal gland lies on the artero-medial surface. The ureters pass from the hilus of each kidney to open on the ventral surface of the bladder very near the opening to the urethra. The urethra opens to the outside by a long, dorsal slit on the penis. In the female, the urethra follows the usual marsupial pattern (Stirling 1891b; Sweet 1904).

Sense Organs and Nervous System

The brain of the Marsupial Mole, like the other portions of the body, is greatly modified (Smith 1895a, 1895b). According to Smith (1895a), the brain exhibits 'extreme simplicity of structure' and represents the 'lowliest marsupial brain' which he had examined. Burkitt (1938) added that it is 'an extremely primitive marsupial brain'.

Anteriorly, the olfactory bulbs and tubercula olfactoria are enormous. Both are discrete, well-defined structures, the olfactory bulbs larger and superior to the tubercula olfactoria. Posterior to these structures, there is a peculiar antero-posterior compression of the midbrain. Here, the axis of the midbrain is vertical and essentially at a right angle to the medulla. The cerebral hemispheres have a large pyriform lobe, a small neopallium and very large amygdaloid tubercles.

The cerebellum is dorso-ventrally flattened and leaf-like, completely covering the posterior bulge of the inferior colliculi. The cerebellum is also compressed antero-posteriorly, as is the medulla, so much so that the brachial plexus appears to be a continuation rather than a part of the spinal cord proper.

Ventrally, the surface of the brain is dominated by the very large roots of cranial nerve V. The pituitary lies in the mid-line between the amygdaloid tubercles. An optic chiasma is lacking. No trace of cranial nerves II, III, IV and VI can be detected. Medially and dorsally, the pineal body lies over the dorsal portion of the third ventricle. No information is available on the pineal (Burkitt, 1938).

Cranial nerves VII, VIII, IX, X, XI and XII are present. Of these, cranial nerve XII is very well developed. The spinal cord measures about 70 mm in length. Definite swellings (plexuses) are present in the brachial and sacral regions.

As noted previously, there is no external evidence of the eye. Internally, the optic nerve and the three cranial nerves which serve the muscles of the eye are absent. A pigment layer, possibly the remnant of the retina, is present, but rods or cones can not be identified. Lachrymal glands are very well developed, as is the conjunctival sac. The relicts of the muscles of the eye are present and innervated by the ophthalmic branch of cranial nerve V. There is no evidence of a lens (Sweet 1906).

Jacobson's organ is well developed and there is extensive associated glandular development and vascularisation. There is a strong possibility that the well-developed lachrymal glands, devoid of any role with the eye, play a significant role in the lubrication of the nasal passages, including the Jacobson's organ (Sweet 1904), but there is no conclusive evidence. Vibrissae are entirely absent.

In the region of the ischiotergal patch, in the skin over the head region and in the pouch region, there are specialised groups of cells. These cells, while overlain by the corneal layer of the skin, give the general appearance of a taste bud. Whether they have any chemical or tactile sensory role is unknown (Sweet 1907).

Endocrine and Exocrine Systems

No information exists on endocrine function nor are there published data which establish the presence of the full mammalian complement of endocrine structures.

More information, however, is available on exocrine structures. Sebaceous glands are associated with hair over the body, though less developed over the shoulders and thighs. The internal lining of the cloaca is highly glandular, especially near the external opening. These glands are probably apocrine in nature.

On either side of the anterior half of the cloaca there is an anal gland. The gland, 2.4 mm in diameter, lies in a fibrous capsule surrounded by striated muscle fibres. The glandular, bulbiform mass has a central lumen into which collect the products of the apocrine glands of the structure. A duct opens from the lumen into the cloaca.

Within the pouch, sebaceous glands are well developed, especially around the two mammae. As noted above, sebaceous glands are especially well developed over the head and ischiotergal patch (Sweet 1907).

Reproduction, Embryology and Development

The anatomy of the reproductive system of the Marsupial Mole conforms to the normal marsupial pattern with one major exception. The testes lie neither in the abdomen nor are they scrotal. Instead, they lie between the skin and the abdominal wall. Oval in shape, the testes lie at about the level of the anterior edge of the pubic bones. They are, therefore, prepenial. The vasa deferentia and the spermatic artery pass through an inguinal ring into the abdomen (Stirling 1891a). The vasa deferentia enter the urethra at about the same level as the ureters empty into the bladder. At about this level is a glandular mass, probably the prostate. Paired bulbourethral glands apparently are present at the base of the penis (Sweet 1907).

Neither copulation, pregnancy nor birth has ever been observed in the Marsupial Mole. Jones (1921a) did obtain a pouch young and the partial remains of a much larger pouch young are held in the Northern Territory Museum. The South Australian Museum contains a specimen with '2 sucklings' collected in 1931 at Sturt Creek in Western Australia.

At what point hair develops is not known. Eye locations are clearly marked by dark pigment patches and the external ear openings are obvious. There is little flexion of the head, but flexion is extensive in the sacral area. The enlargement of the two digits of the manus are seen clearly even though the young examined measured only 10 mm in crown-rump length. Length of gestation, duration of pouch life and details of young-maternal association are unknown.

NATURAL HISTORY

Life History

Very little is known of the life history of the Marsupial Mole because there have been no concerted field studies and few animals have been kept in captivity for an appreciable length of time. Stirling's (1891c) collector kept one for a little over 10 weeks, and Howe (1975) held one for a little over a month. Both animals died in captivity, apparently from hypothermy. One of us (KAJ) kept an individual for more than a month before it died of pneumonia, probably cold-induced. Few live animals reach the hands of biologists and, with few exceptions, specimens are collected opportunistically by Aborigines.

Virtually all information on the marsupial moles has been obtained from preserved specimens. Among these, pouch young apparently are rare and Jones (1921a) found only one individual to use in describing external characteristics of the young. Troughton (1973) expressed the opinion that females make a deep permanent burrow in which they produce their young, but also remarks that nothing definite is known of the breeding biology of the species. In the red sandy deserts of central Australia, the substratum is loose and it seems unlikely that a mole could make a permanent hole under such conditions. Moreover, a female with a furred pouch young was collected at the surface by Aborigines about 250 km north-west of Alice Springs, indicating that not all reproductive females make a permanent burrow.

Ecology

Corbett (1975) summarised the habitats from which moles have been reported. Ten of the 11 original reports include sand ridge and/or sand plain, usually with a spinifex (*Triodia* species and *Plectrachne* species) cover while the eleventh (Shortridge 1909) noted only spinifex. Corbett (1975) considered that river flat country with associated sand ridges may be the typical habitat of the mole on the basis that moles appeared to prefer scarabaeid beetle larvae as food and these are

often associated with ‘river gums’ which fringe the water courses. He also notes that many early records were from station homesteads adjacent to the Finke River in the Northern Territory. Massive sand ridges also adjoin these places.

At Nyirrpi, where several specimens have been taken, the sand ridges are low and separated by swales of approximately 800 m (Fig. 23.6d). Plants recorded from within 100 m of one site where tracks were found and a burrow excavated are listed in Table 23.1.

Table 23.1 Plants found within 100 m of a Marsupial Mole burrow.

<i>Plectrachne schinzii</i>	<i>Bonamia rosea</i>
<i>Triodia pungens</i>	<i>Zornia</i> sp.
<i>Aristida browniana</i>	<i>Acacia dictyophleba</i>
<i>Scaevola parviflora</i>	<i>A. maitlandii</i>
<i>Dicrastylis exsuccosa</i>	<i>A. coriacea</i>
<i>Keraudrenia</i> sp.	<i>A. pruinocarpa</i>
<i>Goodenia mueckeana</i>	<i>Santalum lanceolatum</i>

All information on diet has been obtained by examining the gut contents of preserved specimens or by observing foods accepted by captive animals. The Marsupial Mole appears to be mainly insectivorous, preferring the eggs, larvae and pupae of various insect species. Stirling (1891b) reported that the larvae of ‘Longicorn beetles and Lepidoptera’ were eaten by animals kept by his collector and that ant fragments and other insect debris were found in the intestines. He noted, however, that ants were not eaten by captive individuals. Spencer (1896b) found ants and the hard ‘shells’ of ant eggs in the stomach of one specimen and in captivity, moles seem very partial to ant eggs, larvae and pupae. Adult ants probably are ingested coincidentally.

Jones (1923a) found earthworms (*Lumbricus* species) to be acceptable to captive moles, but neither Howe (1975) nor one of the authors (KAJ) could get captive animals to take fresh earthworms. Corbett (1975) pointed out that only one species of earthworm, *Diplotrema eremia*, has been found in central Australia and it is possible that captive animals need to be trained to new food sources. C.W. Brazenor reported in a letter in 1956 to the then Director of Animal Industry in the Northern Territory that specimens he had been sent contained burrowing sawfly larvae, *Rhytidiponera* species (ants) and legs of chrysomelid beetles. Captive animals enthusiastically take the larvae of scarabaeid beetles and mealworm (*Tenebrio* species) larvae. They seem uninterested in beetles, but M. Gillam (personal communication) reports a captive animal taking centipedes (Fig. 23.6a), spiders and gekkonid lizards (Fig. 23.6b), all of which often live below ground in central Australia.

There is no documentation of moles eating vegetable matter, but W. Smith (personal communication via R. Kimber) was certain they eat truffles, a form of underground desert fungus, and yams (*Vigna* species). No vegetable matter has been documented from the gut of moles, but there have been no more than superficial examinations of a few specimens. No moles have been observed feeding above ground in the field and all available evidence from captive animals and gut content studies indicate a strong preference for subterranean food items. Captive moles will, however, feed above ground if food is placed there for them. They sometimes grasp large beetle larvae in the mouth and burrow underground to consume the food.

A



B



C



D



Figure 23.6 Marsupial Mole: (a) eating a centipede; (b) eating a gekko lizard; (c) tracks and burrowing point; (d) representative habitat.

[© (a) & (b) M. Gillam, (c) & (d) K. Johnson]

Food items are only crudely manipulated using the forelimbs, usually to the extent of holding down the prey while it is grasped in the mouth. Large food items, such as beetle larvae, are chewed progressively via the premolar region and there is no attempt to tear or lacerate the food.

The behaviour of captive animals indicates that they would find it difficult to pursue and catch prey owing to their slow rate of movement. The forelimbs are specialised for digging rather than catching and they lack dentition capable of delivering a quick kill. Olfactory senses seem well developed (Howe 1975). Moles probably are able to detect and follow the tunnels and galleries of underground insects. Consumption of food while underground and without the benefit of an open chamber must inevitably lead to the ingestion of quantities of sand. Greatly accelerated tooth wear would certainly result.

There are no published accounts of moles being taken by predators apart from Aborigines. Species such as varanid lizards (*Varanus* species) are not likely to dig rapidly enough to be a threat. Moles above ground might present a much easier target, especially to raptorial birds which could make a swift and relatively silent approach.

No ectoparasites are known from the Marsupial Mole. Only two species of trichostrongyloid nematodes (Beveridge & Durette-Desset 1985) are known to be endoparasites.

Behaviour

Little is known of the burrowing activities of Marsupial Moles in terms of the depth to which they will dig and the horizontal home range area. Dollman (1932) reported notes of Mrs Daisy Bates who maintained that moles burrow to a depth of more than 18 m. Dollman (1932), however, further comments on inaccuracies in Bates' notes, such as a claim that moles are deaf and dumb, when plainly they have quite proficient auditory senses.

One of us (KAJ) was shown the tracks of a mole by Aborigines living at Nyirrpri about 280 km WNW of Alice Springs. The mole had entered the red sand in the characteristic fashion (Fig. 23.6c) and its passage through the substratum took the form of a tube, oval in cross-section with the long axis horizontal, containing loose sand clearly different from the surrounding mass. This sand tube was followed by digging away the sand with the aid of a shovel. The plan view of the animal's travel is shown in Fig. 23.7. Initially it maintained a fairly even depth of approximately 200 mm below ground level, but then suddenly took a vertical angle. A 2.5 m shaft, sunk when following the vertical sand tube, revealed numerous other sand tubes which intersected the walls of the shaft. These tubes were of varying ages, indicated by the degree to which they had been invaded by fine plant roots. Old sand tubes were encountered for the full 2.5 m depth of the shaft and gave the appearance that moles passed fairly randomly through the sand profile.

Little is known of the social organisation of the Marsupial Mole, but it appears to lead a solitary life. Permanent burrows, where communication would be relatively easy, are not formed. How males find oestrous females is unknown, but with their well-developed olfactory system, a male passing near or through a recent sand tube of such a female would have little difficulty following her trail and making contact. Copulation underground must have its difficulties.

Grooming has not been recorded, but this may simply reflect the few opportunities for observation. Captive animals are energetic, but docile and refuse to bite. Howe (1975) recorded a sitting and a lying posture for resting animals. The mole comes to the surface for what appears to be brief excursions before returning underground. Aborigines testify that it is most commonly seen

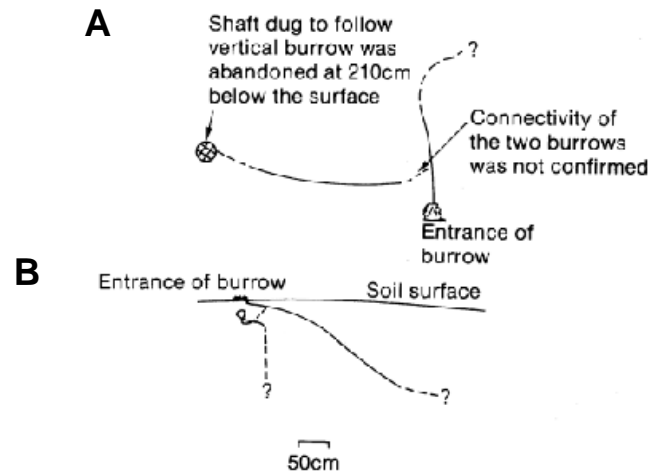


Figure 23.7 Plan showing the burrowing route followed by a Marsupial Mole.

above ground after rain (Russell 1934; Spencer 1896a), but as mole tracks are conspicuous in dry sand, Stirling's (1891b) claim that the animals are easier to procure after rain because they are easier to track is not tenable.

Economic Significance

Marsupial Moles occur mainly in desert country used sparsely, if at all, for pastoral purposes. There is little potential for them to affect the productivity of land in a positive or negative way.

R. Kimber (personal communication) reported information he received from Walter Smith regarding the sale of Marsupial Mole skins by Aborigines to Europeans and Afghan cameleers. The market apparently took place circa 1900 to 1920 and skins were worth 10 shillings (= about \$1) each, a substantial sum for that period. Pelts were purchased mainly at Horseshoe Bend and Bloods Creek at the western edge of the Simpson Desert in the Northern Territory and were sent away to market, whereupon the itinerant purchasers received £2 (= about \$4) for each pelt.

Smith (R. Kimber personal communication) maintained that Aborigines arrived at the buyers' quarters in large numbers and each would carry about five to six pelts on average. About 50 to 70 pelts would be traded at one of these meetings although clothing or food, not cash, was the usual transaction.

Smith (via R. Kimber personal communication) estimated that several thousands pelts were probably traded and that Marsupial Moles must have been reasonably common in the Simpson Desert which adjoins the two major market places. For what purpose the pelts were used is unknown, but as the fur is an attractive pale yellow, has a strong sheen, is short and very dense, it would be attractive for fine leather work such as purses and bags.

Conservation

The early literature commonly includes remarks that the Marsupial Mole is rare. Spencer (1896b) comments that the mole was 'a rare form of marsupial', but his collector, Byrne, was able to secure 40 to 50 specimens within 48 km of Charlotte Waters on the western edge of the Simpson Desert. Smith's comments on the numbers traded (see above) supports Spencer's (1896a) notes which imply that the species was not particularly rare. The current situation remains unclear. Virtually all specimens have been collected by Aborigines who now do

not move extensively over their traditional lands on foot. There have been no documented trapping studies and information on abundance is fragmentary and collected on an *ad hoc* basis. Nevertheless, Aborigines still report seeing moles and specimens are received occasionally by scientific institutions. Apart from the registration of the unusually large number of 87 specimens into the Australian museums in the decade 1911-1920 (most coming as a donation by Baldwin Spencer of his personal collection), the flow of specimens has remained relatively steady at about 5 to 15 every 10 years. Given the burrowing habits and the rare occasions of above-ground travel, the evidence indicates that it is still widespread and not endangered. It is protected by legislation in each State and Territory in which it occurs.

BIOGEOGRAPHY AND PHYLOGENY

Distribution

Corbett (1975) summarised the locality records for Marsupial Moles (Fig. 23.8) to which more recent records have been added. Those marked 1 and 3 are recorded by Finlayson (1961) who, nevertheless, queries their validity as does Parker (1973). The locality of Barrow Creek marked No. 2 is based on a specimen supplied by Baldwin Spencer to the National Museum of Victoria in 1902. None of these places is within sand ridge country, but each is close enough to such habitat that Aborigines could have brought them in.

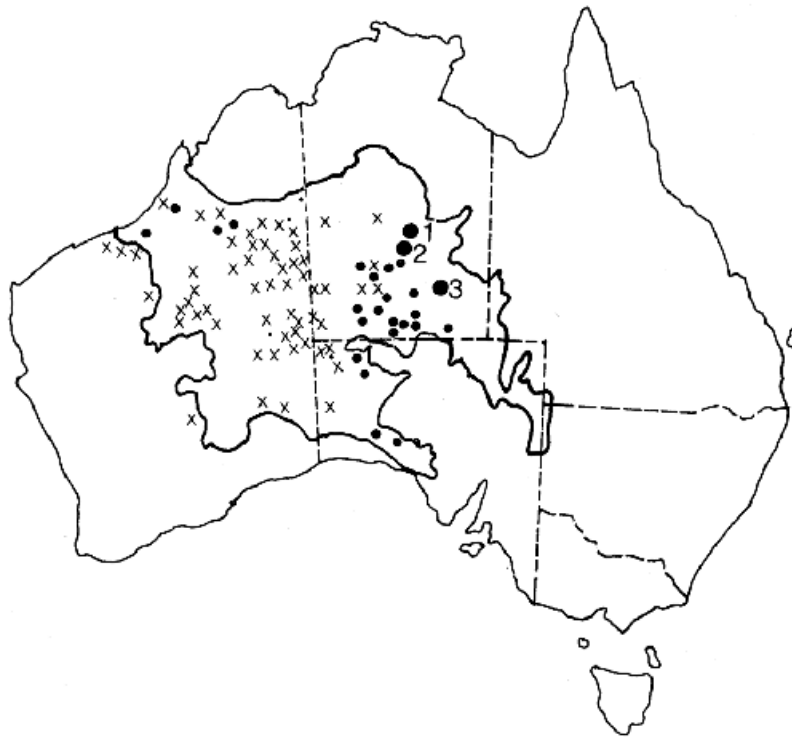


Figure 23.8 Specimen records of Marsupial Moles from Corbett (1975) and records from the Northern Territory Museum, South Australian Museum, Western Australian Museum, Australian Museum and Museum of Victoria [•] with anecdotal records collected from Aborigines [x] (Burbidge *et al.* 1988). Most points are enclosed by a line indicating the extent of the sandy soils (Hubble 1973) of the central desert region. Points 1, 2 and 3 are queried localities, see text.

There are no museum specimen records from Queensland, but Duncan-Kemp (1933) reported sight records from south-western Queensland and her statements are supported by Johnston & Cleland (1943). Finlayson (1961), during 1931, found no knowledge of the mole among Aborigines who had lived 40 years between the Diamantina and Barcoo Rivers in the north-east of South Australia and adjoining States.

The distribution of moles approximately follows the sand dune habitat preferred by them (Fig 23.8). On this basis, the species could be expected to occur in north-eastern South Australia and in south-western Western Australia. Aborigines of the Great Sandy and Gibson Deserts of Western Australia know the species well (Burbidge *et al.* 1988) and it is safe to include this region within the distribution despite the lack of specimen records. Aborigines who have spent a considerable part of their early life in the sand plain areas of the Tanami Desert in the north-west of the Northern Territory know of the mole only from the more southern dune field areas. Extensive fauna surveys (Gibson 1986) in the region have failed to reveal Marsupial Moles. On these two grounds, the region is excluded from the potential range of the species. Aborigines who had lived traditionally in the Lander River flood-out area until about 1930 knew the species and maintained that it used to occupy the massive sand dunes of the region.

Fossil Record and Affinities with other Groups

Discussion of the affinities of the Marsupial Mole to other taxa is greatly hampered by their absence from the fossil record. The rarity of fossil marsupials with zalambdodont molars imposes additional constraints and, consequently, there is no historical context in which to place the Marsupial Moles.

The teeth of the mole, at least for the present, provide little insight into phylogeny (Fig. 23.5). The Marsupial Mole is not an obvious diprotodont, but one might well question if it is in fact a polyprotodont. No doubt, this quandry has carried over into proposed phylogenies (see Archer 1984b for an excellent review of proposed phylogenies of the Marsupialia). Turnbull (1971) emphasised the peculiarities of the dentition by proposing that *Notoryctes*, *Necrolestes* and a host of insectivores with zalambdodont molars be placed in a separate order, the Zalambdodonta, a view that has not been widely accepted. This proposal did, however, serve the purpose of diverting attention away from reproductive patterns.

When Stirling (1888a) initially was unable to find the epipubic bones in Marsupial Moles, speculation was rife: the Marsupial Mole was a monotreme, it was the link between monotremes and marsupials, had its closest affinities with *Chrysochloris*, it was convergent with edentates, it was a polyprotodont diprotodont, and so on. As Calaby *et al.* (1974) pointed out, Gadow (1892) accurately assessed the situation even before most of the detailed studies of comparative anatomy were done: the Marsupial Mole ‘...has some characters in common with almost every other existing marsupial family’.

Largely on the basis of chromosome number ($2n = 20$) and structure, Calaby *et al.* (1974) included the Marsupial Mole in the Australian radiation of the polyprotodonts. Baverstock (1984), however, found no molecular basis for a close relationship with either the polyprotodonts or Diprotodonta and suggested that Marsupial Moles represent a unique lineage. Using albumin as a ‘molecular clock’, the diprotodont / polyprotodont divergence is estimated at about 50 mybp. Marsupial Moles, therefore, must represent a lineage of at least that age (see Chapter 19).

Any higher category placement of the Marsupial Moles is based not on characters shared with other taxa, but rather on the extent of unshared traits. At this point, no clear assessment of the phylogeny of the Marsupial Mole can be made.

Affinities within the Notoryctidae

Two species of Marsupial Mole have been described: *N. typhlops* (Stirling, 1889) and *N. caurinus* Thomas, 1920. The Stirling name was applied to specimens from central Australia. The whereabouts of these early specimens is unknown. From Gadow (1892), we know that at least one of the specimens involved in Stirling's description made its way into the Cambridge Museum. There is no evidence of the designation of a holotype or of syntypes.

Thomas (1920) described *Notoryctes caurinus* from the north-western coast of Western Australia. The skull of the holotype is in the British Museum and the skin is in the Western Australian Museum. Although Troughton & Iredale (1934) list *N. caurinus*, most subsequent authors have ignored the name. Ride (1971) does list the name in the index. No basis for synonymy exists except a passing comment by Matthews (1971) that *caurinus* has been described 'perhaps prematurely'. While available information may indicate that the name lacks biological validity, the rules of nomenclature clearly preclude ignoring the existence of the name.

Archer (1984b) posed an interesting question. Given the extensive geographic distribution and long phylogenetic history, why is there only one species (actually two named forms do exist)? No comparative morphological or biochemical study has been conducted of the characteristics of *Notoryctes typhlops* from the Idracowra area with those from the 80-Mile Beach area (*N. caurinus*) beyond the original description of *caurinus*. One must bear in mind the history of the areas in which *Notoryctes* now occurs. There is evidence that the vegetation, soil and climate profiles for coastal Western Australia, central Australia and the western edge of the Great Australian Bight differ significantly (Bridgewater 1987) and certainly have done so during the Cainozoic (Frakes *et al.* 1987). Sand ridge habitat is continuous throughout the known range of *Notoryctes* and the association appears clear. Burrowing is not the speediest means of locomotion and suitable substratum is critical. Limited observations on captive *Notoryctes* indicate high vulnerability to alterations in environment, yet the preferred habitat (sand) is affected greatly by both wind and water. Nothing is known of the population biology of this fossorial marsupial and no comparison, therefore, can be made with the available information on fossorial eutherians.

The Marsupial Mole has no known extant close relatives. The specialised and unique morphological features which characterise the mole support the biochemical evidence that the lineage of Marsupial Moles has been separate from other Australian marsupials for a considerable period.

Despite the fact that a rather large number of specimens of Marsupial Moles (most are fluid-preserved) is in the various museums of Australia and elsewhere, no detailed study of the genus has been done since the description of *caurinus*.

COLLECTION AND PRESERVATION

There is no documented success of breeding Marsupial Moles in captivity. Few captive moles survive longer than one month and most succumb to respiratory ailments, mainly pneumonia.

Virtually all specimens of Marsupial Mole brought into captivity are collected above ground and it is possible that many which pass to the surface are already in a debilitated condition. Capture is wholly opportunistic. Those which are collected alive usually spend one or more days in a container of sand before reaching a scientific institution and are probably already in shock from lack of food, disturbance and uneven or low temperature conditions.

Once in captivity, moles apparently must be provided with a heat source on one side of the container. A suitable substratum seems important. Howe (1975) recommends red sand from the central Australian sand plain or dune complexes kept in a container measuring about 1 x 1 x 0.3 m deep. This substratum should be changed approximately monthly to prevent fouling. Water is not required.

An initial prophylactic course of antibiotics might help prevent the development of pneumonia if it has not already been contracted. Animals may be provided with the foods noted above in the section on diet. Howe (1975) reported egg, milk, lambs' (*Ovis aries*) brain and fat were taken, but proved unsatisfactory due to fouling of the animal's fur.

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