

20. THYLACINIDAE

JOAN M. DIXON

DEFINITION AND GENERAL DESCRIPTION

The single member of the family Thylacinidae, *Thylacinus cynocephalus*, known as the Thylacine, Tasmanian Tiger or Wolf, is a large carnivorous marsupial (Fig. 20.1). Generally sandy yellow in colour, it has 15 to 20 distinct transverse dark stripes across the back from shoulders to tail. While the large head is reminiscent of the dog and wolf, the tail is long and characteristically stiff and the legs are relatively short. Body hair is dense, short and soft, to 15 mm in length. Body proportions are similar to those of *Sarcophilus harrisii*, *Dasyurus viverrinus* and *Dasyurus maculatus*. *Thylacinus* is digitigrade. There are five digital pads on the forefoot and four on the hind foot.

The face is fox-like in young animals, wolf- or dog-like in adults. Hairs on the cheeks, above the eyes and base of the ears are whitish-brown. Facial vibrissae are relatively shorter, finer and fewer than in *Sarcophilus* and *Dasyurus* spp. The short ears are about 80 mm long, erect, rounded and covered with short fur. Sexual dimorphism occurs, adult males being larger on average. Jaws are long and powerful and the teeth number 46. In the vertebral column there are only two sacra instead of the usual three and from 23 to 25 caudal vertebrae rather than 20 to 21. Clavicles are reduced, marsupial bones rudimentary and unossified.

The pouch opens posteriorly and contains four mammae. The litter size is up to four. Young are dependent on the mother until at least half-grown.

Though mainly nocturnal or semi-nocturnal, they also are seen during the day. The pace is slow and the animal generally stiff in its movements. Hunting is done singly or in pairs and mainly at night. Food preferences are kangaroos and other marsupials, small rodents and birds. *Thylacinus* is known to have preyed upon sheep and poultry following colonization by European man.

Harris (1808) comments: "It from time to time uttered a short guttural cry". Usually they are mute, but when anxious or excited they make a series of husky, coughing barks. They are relatively quiet and nervous in comparison to *Sarcophilus harrisii* and shy and secretive in their habits, avoiding contact with humans.

HISTORY OF DISCOVERY

Thylacinus cynocephalus is probably one of the most widely known of Australian mammals, even though it has not been collected for fifty years. In all probability, it is now extinct in its former haunts in the island State, Tasmania.

The first European reference to *Thylacinus* was by the Dutch explorer Abel Tasman when, in 1642, he reported that a crewman had found "footprints not ill-resembling the claws of a tiger" on the shores of Van Diemen's Land.

In 1805, the first account of the animal appeared in the Sydney Gazette and New South Wales Advertiser.

"An animal of a truly singular and novel description was killed by dogs the 30th of March on a hill immediately contiguous to the settlement at Yorkton Port Dalrymple; from the following minute description of which, by Lieu-

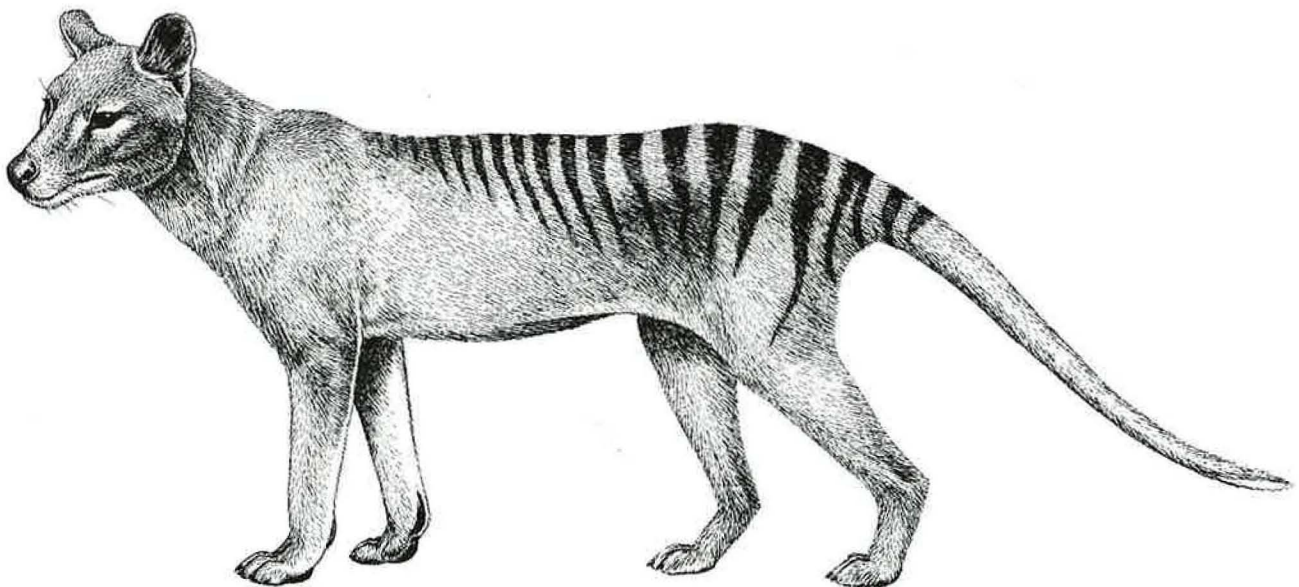


Figure 20.1 *Thylacinus cynocephalus*, side view of the whole animal.

[D. Kirshner]

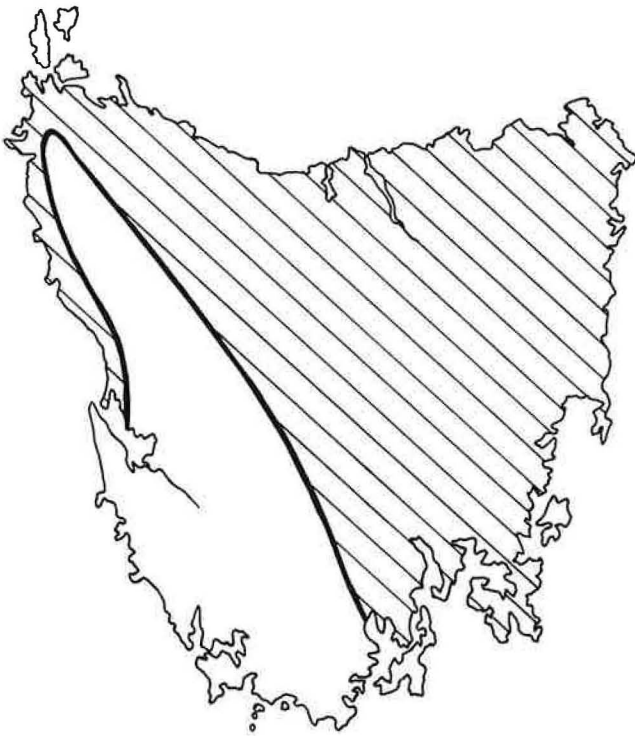


Figure 20.2 Possible former range of *Thylacinus* in Tasmania based on bounty records and sightings.

tenant Governor Paterson, it must be considered of a species perfectly distinct from any of the animal creation hitherto known and certainly the only powerful and terrific of the carnivorous and voracious tribe yet discovered on any part of New Holland or its adjacent Islands."

George Prideaux Harris, Deputy Surveyor-General of the colony, provided the first scientific description of the animal to the Linnaean Society of London in 1807. The two male *Thylacinus* which he caught in a kangaroo meat baited trap, probably near Hobart, were described (Harris, 1808).

Apparently widespread (Fig. 20.2) from the "sea coast to the summits of the mountains 4000 feet above the sea level" (Gunn, 1863), the species was seen rarely in the early days of settlement. Colonists were fascinated by this strange animal and applied a variety of common names to it. Its marsupial affinities were recognized by Harris, but there were other opinions on its relationships.

In 1803, sheep were introduced to Tasmania when the first soldiers and settlers arrived in Tasmania. Sheep formed the basis of a new industry and were of considerable importance to colonists, but problems soon arose. They were introduced to the fertile midlands, also habitat for *Thylacinus*, and sheep losses occurred which were attributed to it. These increased as sheep were introduced further into the Tasmanian wilderness. Reference to the taking of sheep by *Thylacinus* goes back as far as 1824 (Lycett, 1824). Mudie (1829) says:

"It is also found in the inland parts of Van Diemen's Land, and often commits depredations upon the lands at the sheep farms, and sometimes too upon the poultry yards though it is a solitary animal, and does not approach the thickly settled parts of the country."

In 1830, the Van Diemen's Land Co. introduced a bounty scheme to control *Thylacinus* on its North West sheep properties, at Hampstead and Surrey Hills. Conflicting opinions

on the numbers of thylacines were reported, but in 1888 a Government Bounty Scheme was introduced: £1 for an adult 10 shillings for a sub-adult. In 1909, the Government bounty scheme finished; 2,184 bounties had been paid over 21 years. In 1910, two were sold to London Zoo for £28 each by Mrs Roberts' Beaumaris Zoo and in 1926 the London Zoo bought its last specimen from Tasmania for £150. It was in 1930 that the last *Thylacinus* was killed in the wild in Tasmania and in 1931 the last animal died in the London Zoo. The Hobart Zoo received a specimen snared in the Florentine Valley in 1933. In 1936, the species was added to a list of wholly protected animals and in the same year the last *Thylacinus* died in the Hobart Zoo.

Now, 50 years have elapsed and no further specimens have been collected, despite considerable effort, time and money spent in this endeavour. Undoubtedly, the most persistent person involved in this search is Eric Guiler, formerly Reader in Zoology at the University of Tasmania, who recently published the results of his work (Guiler, 1985).

The location of most learned institutions, museums and universities in Europe and the United Kingdom until the second half of the 19th Century meant that most scholarly studies were undertaken there. Few of these researchers visited Australia and the appropriate journals for publication of their work were in their home countries. So it is with much of the early research on *Thylacinus*. The published information is related to the actual material which was dispatched from Australia. A surprisingly detailed amount of morphological information exists. The system of trading in zoological material throughout Europe resulted in specimens being lodged in many of the major institutions of Europe. Most of these were skulls or mounted display specimens. These can still be located together with the source data.

The systematists of the period, Étienne Geoffroy St Hilaire, Desmarest, Temminck, Lesson, Owen, Waterhouse and others, contributed much to knowledge of the species (Thomas, 1888). Likewise, anatomical studies were conducted outside Australia and the results published in overseas journals. Numerous observations were made by Ronald Gunn, Tasmanian resident and botanist (Gunn, 1850; 1863). John Gould (1863) makes detailed notes on the species in *The Mammals of Australia*.

There is little preserved anatomical material in existence. Crisp (1855) comments "This animal (a male) died at the Society's Gardens, where it had been for several years. I believe that it is the only one that has been dissected in this country". Cunningham (1882) published a detailed account of the anatomy of the species based on preserved specimens. Pocock (1914; 1926) used available material for his studies on the external features of the species.

Australia's increased involvement in anatomical studies of marsupials in the 20th Century provided considerable information on the species. The work of Boardman on pouch young morphology is significant. His resource material was limited, but was based on collections preserved in Australian institutes (Boardman, 1945). The first account of the female urogenital system was made by Pearson & de Bavay (1953), which, as with Boardman's work, was published in an Australian journal.

Moeller (1968; 1970) carried out comparative studies of the brains of marsupials and provided valuable information on the behaviour of *Thylacinus*.

By the 1960's, following the research of Guiler (1961), interest turned mostly to the distribution and abundance of the species. This theme still persists, although there is also considerable interest in the phylogeny and palaeontology of *Thylacinus*.

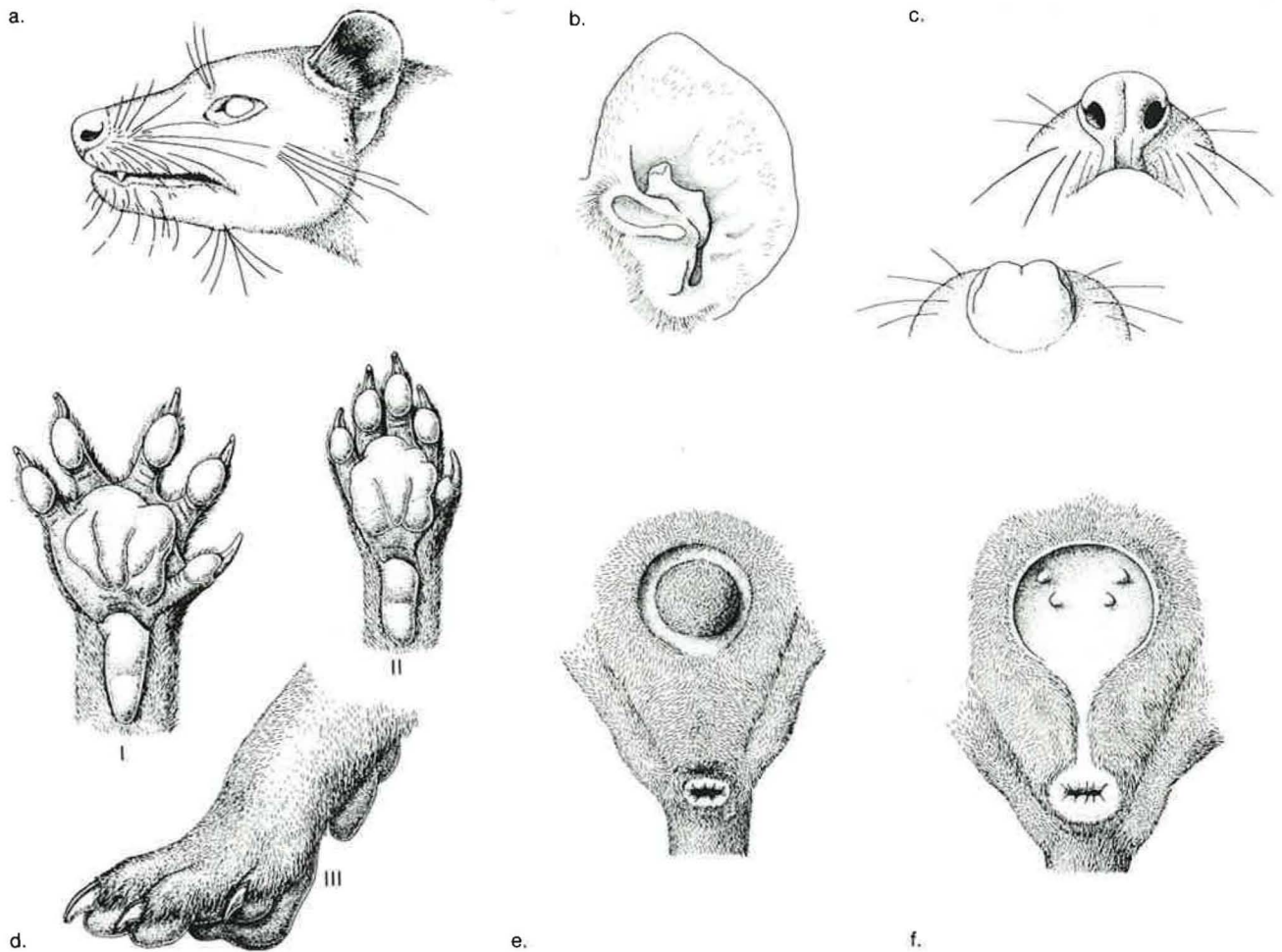


Figure 20.3 a. Side view of head of *Thylacinus* showing vibrissae; b. ear of *Thylacinus* expanded with the supratragus raised; c. rhinarium of *Thylacinus*; d. (i) ventral view of right forefoot of *Thylacinus* with digits spread, (ii) the same the digits not spread, (iii) the same from the inner side; e. anal and genital area of male *Thylacinus* showing the scrotal pouch; f. pouch and mammary area of a female *Thylacinus*. (After Pocock, 1926) [D. Kirshner]

MORPHOLOGY AND PHYSIOLOGY

External Characteristics

Thylacinus shows a remarkable external similarity to the Wolf and Dog. (Fig. 20.1 & 20.3). It typically has a large head, with a large coriaceous, entirely naked rhinarium. In both sexes, the head widens and becomes less wolf-like, with age. The ear is moderately large and attached to the head by a broad base. There is an evenly balanced backbone, legs are of approximately equal length and in the hind legs, the femoral segment points forwards. Like the dog, it has a deep chest and non-retractile claws; it runs on its toes rather than on the whole foot.

Measurements of *Thylacinus* and data on its weight are few. Moeller (1968) collates much of this information, using museum specimens as well as sources from older literature. The head and body length range from 851 to 1181 mm (mean = 1086 mm), tail length 331 to 610 mm (mean = 534 mm) and height at the shoulder about 560 mm. The whole animal weighs about 25 kg. As there are reported sightings of much larger animals, larger specimens possibly existed that were never sent to museums, universities or zoos.

Of all its distinctive features, the most characteristic are the 15 to 20 dark-coloured bands running from the posterior thoracic region onto the butt of the tail. They contrast with the brown or sandy colour of the body. Those at the anterior end extend only a short distance from the midline, while the longest bands occur on the rump and extend laterally as far as the upper thigh. Posterior rump bands are short and extend onto the base of the tail.

There is a variation in the number of bands from individual to individual and the coloured bands are more prominent in younger animals. The disruptive colour pattern may relate to its need for camouflage in woodland conditions.

Short, dense body hair covers the body. Usually, it is fawn to yellow-brown with some, usually younger individuals, being a darker brown. Ventral belly fur is of a creamy hue. The hair of *Thylacinus* has a distinctive cuticular scale pattern (Lyne & McMahon, 1951). Unlike that of the dog, the tail of *Thylacinus* cannot be wagged laterally. It appears clumsy and has close, tight fur. Even the continuation of the body stripes onto the thick butt of the tail gives the impression that the tail is a continuation of the body.

In the female, there is a backward-opening, nearly circular pouch which contains four nipples (Fig. 20.3f). *Thylacinus* males are unique among marsupials in that the testes are

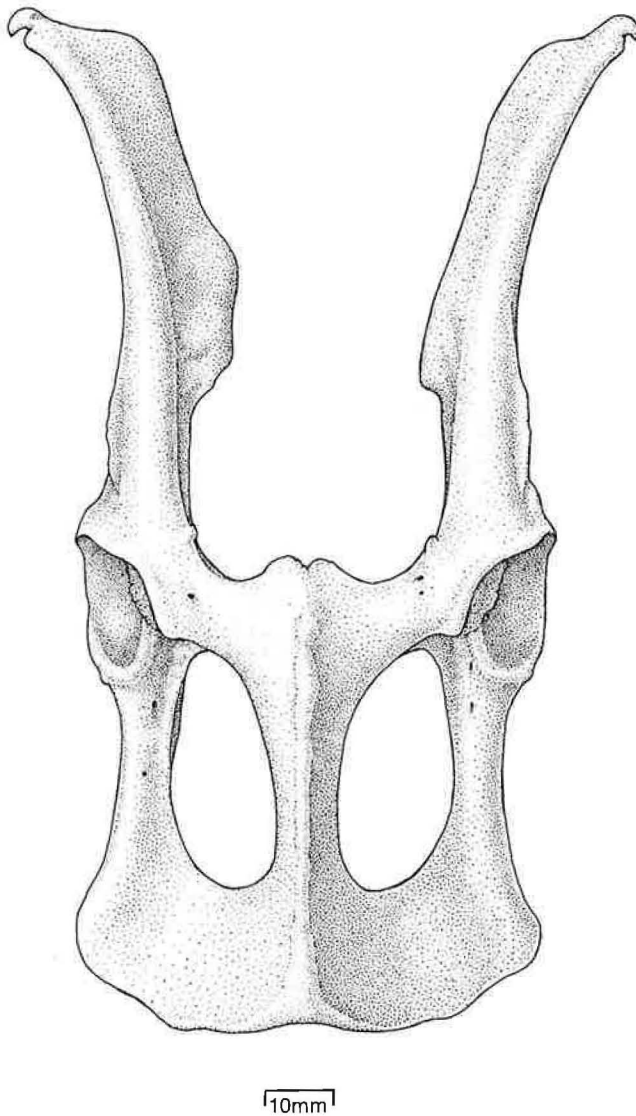


Figure 20.4 The pelvic girdle of *Thylacinus*. Museum of Victoria specimen C5742. [D. Kirshner]

carried in a partial pouch (Fig. 20.3e), (Beddard, 1891; Pocock, 1926; Hickman, 1955). This peculiar feature of the species is retained throughout life.

Body Wall

Cunningham (1882) studied numerous aspects of *Thylacinus* musculature, making interesting observations on the foot. Whereas the dog has coalesced flexores breves and adductors of the pes, those of *Thylacinus* are typical. This may bear relation to the movements of the animal. There is no rigidity of the wrist and Cunningham thus inferred that it had a low, skulking habit. This observation has been confirmed by those who have seen *Thylacinus* hunting.

Skeletal System

While showing most of the skeletal characteristics of other marsupials, *Thylacinus* exhibits some differences. There are only two sacral vertebrae and the normal 20 to 21 caudal

vertebrae are replaced by 23 to 25. The clavicles are reduced (Cunningham, 1882) and the marsupial bones of the pelvic girdle are rudimentary and unossified (Fig. 20.4)

The epipubic bones are reduced to "two small oblong, flattened fibro-cartilages embedded in the internal pillars of the abdominal rings, and appear each as a thickened part of the tendon of the external oblique abdominal muscle, which forms the above pillars. This was the condition of the rudimentary marsupial bones in two full-grown females and one male specimen of the *Thylacinus*; in a fourth large and old male a few particles of the bone salts were deposited in the centre of the fibro-cartilage, occasioning a gritty feeling when cut across by the knife" (Owen, 1843). The reasons for their rudimentary nature are speculative.

There are a number of diagnostic features of the skull and teeth. The dental formula is $I \frac{4}{3} C \frac{1}{1} PM \frac{3}{3} M \frac{4}{4}$. Detailed information on the teeth is given by Owen (1841), Thomas (1888) and Bensley (1903). Moeller (1968) notes that the lower incisors of *Thylacinus* are distinguished by transverse grooves and show a typical wearing pattern. It is possible to separate the sexes of *Thylacinus* by special tooth measurements.

Marsupial features of the skull are well developed (Fig. 20.5) and enable ready separation of the species from the domestic dog. The lacrymal foramen opens at the anterior surface of the lacrymal bone at the anterior of the orbit and not on the inner surface as in eutherian mammals. There are two large foramina on the palate compared with the complete palate in the skulls of eutherian mammals.

The inner posterior surface of the lower jaw has a reflected angle. The fairly comprehensive literature to 1888 on the skeletal system is presented by Thomas (1888).

Locomotion

The feet of *Thylacinus* are described in detail by Pocock (1914). They have often been likened to those of the dog, but the resemblance is superficial only (Fig. 20.3d). The animal is digitigrade, the feet resting on the anterior part of the plantar pad and the digital pads, with the carpal and metacarpal pads raised from the ground. Plantar and digital pads are covered thickly with fine pointed papillae. The five digits on the manus are short, naked beneath and free from webbing as far as the plantar pad. The carpal vibrissae are suppressed. Cunningham (1882) studied numerous aspects of *Thylacinus* musculature, making interesting observations on the foot.

The hind foot resembles the forefoot in most respects (Fig. 20.3), but digit I is entirely suppressed. Digits II to V are a little longer and form a straighter line proximally where they project beyond the distal margin of the plantar pad, which is less strongly curved. Field identification of prints of the forefoot is difficult because of the arrangement of the toes. The plantar surface of the pes is easier to identify because of the larger space separating the digits and main pad. The tarsal segment of the leg has a granulated surface and on occasions may be applied to the ground.

The distance between consecutive prints of any one foot in an adult *Thylacinus* is about 800 mm or more. This feature can be used in identification of the species from tracks.

Locomotion has been noted by a number of observers. Gunn (1863) watched a female spring six to eight feet (1.8 to 2.4 m) from the floor of the cage to the top of the wall and from cross-beam to cross-beam with great agility. From early film, Moeller (1968) notes that the animal has two modes of locomotion. The first of these is the plantar walk common to most mammals and the second is a bipedal hop. The latter movement is remarkably like that of a kangaroo.

Feeding and Digestive System

Crisp (1855) describes the alimentary tract of *Thylacinus*, noting the shortness of the canal and the absence of a caecum. The stomach is very muscular and capable of considerable distension. This relates to the animal's habit of taking in a large amount of food, probably at irregular intervals.

The distended stomach has a close resemblance to that of man. Curvatures are more pronounced and transition from the wide cardiac portion to the narrow pyloric part is more abrupt. The fundus rises high above the cardiac opening; the lining mucous membrane, though not of uniform appearance, is highly rugose and the rugae almost entirely disappear on distension. A marked pyloric constriction separates the stomach from the small intestine.

The intestinal canal proceeds backwards as a uniform tube and at the pelvis becomes continuous with the rectum. It is remarkably short and there are no indications of its division into a small and large intestine. While diminishing in diameter towards the pelvis, it assumes a diameter equal to or greater than the upper duodenal part.

The intestinal villi are very long. Anteriorly, they are filamentous and slender, but posteriorly they become stouter and club shaped. They become sparser, stunted and conical posteriorly, finally arranged in parallel longitudinal rows before disappearing about 400 mm above the anal orifice.

There is a very large Peyer's patch which begins about 400 mm above the anus. In addition, there are several others placed further forwards in the gut.

The rectum has a perfectly smooth mucous membrane and is perforated with minute orifices of Lieberkühn's glands which are visible to the naked eye. A simple mesentery suspends the intestinal canal from the upper abdominal wall.

Examination of the gut by Mitchell (1916) confirmed Crisp's findings. He noted that the gut had the same internal diameter throughout.

There is an elongated tongue-like spleen totally invested by peritoneum and placed obliquely in the abdominal cavity. From the outer border, a splenic process projects towards the kidney. Splenic nerves and vessels enter the organ on the inner surface along the line of the mesenteric attachment. The pancreas is well developed and consists of a thickened massive right extremity or head from which an elongated process of the gland projects towards the spleen. The pancreatic duct joins the bile duct before entering the duodenum.

The liver of *Thylacinus* has a small left segment in comparison with the right segment and shows no tendency whatsoever to subdivision into lateral and central lobes. The right segment is divided into two equal sections by a well-marked cleft and the right central lobe shows a deep and broad deficiency in its sharp free margin for the reception of the gall bladder.

The caudate lobe is long and prismatic in form, the Spigelian lobe small and attached by a broad base, partly to the left segment and partly to the right segment of the liver. The gall bladder is very small and has a globular shape when distended. The cystic duct emerges from the upper end of the gall bladder and runs upwards to the portal fissure where it is joined by three or four hepatic ducts which issue from the various lobes and enter it by separate orifices. The common bile duct thus formed is joined by the pancreatic duct before it opens into the duodenum.

Lydekker (1894) comments:

"Before the introduction of flocks into the country, the Thylacine doubtless subsisted mainly on the smaller Kangaroos and Wallabies, together with other Marsupials; the first known specimen, captured by Harris, having portions of a spiny Anteater in its stomach".

Circulatory System

The thoracic visceral descriptions by Cunningham (1882) offer some information on the circulatory system.

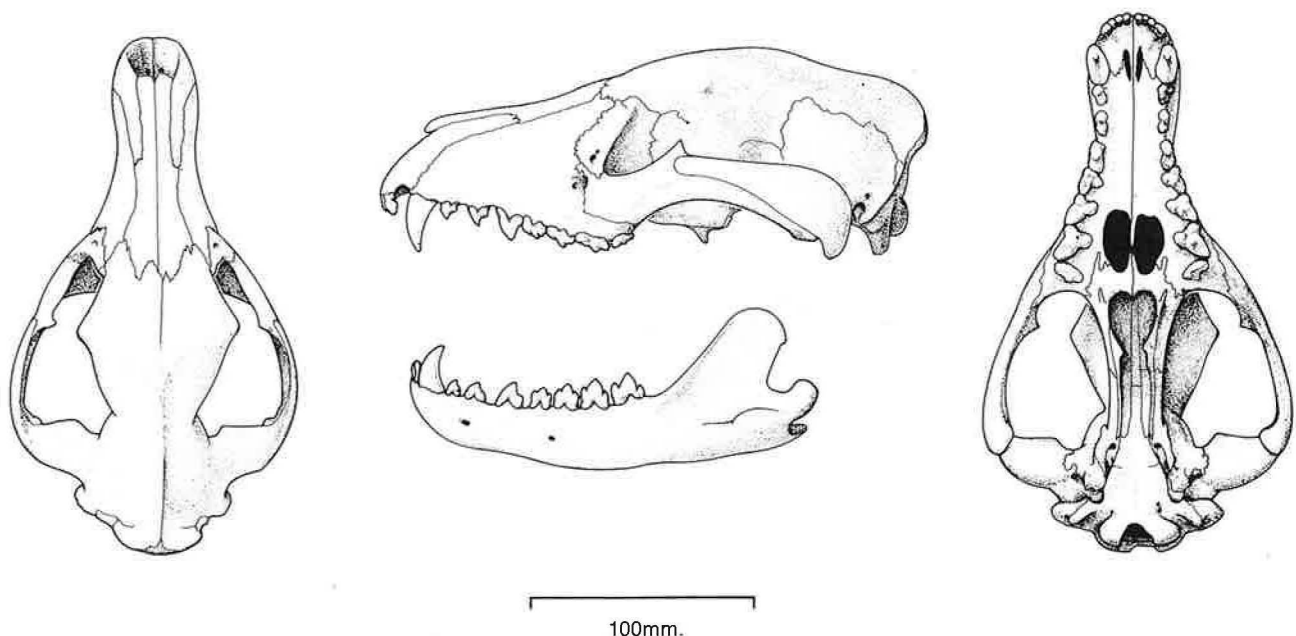


Figure 20.5 *Thylacinus* a. cranium dorsal aspect; b. ventral aspect; c. cranium and mandible lateral aspect.

[G. Milledge]

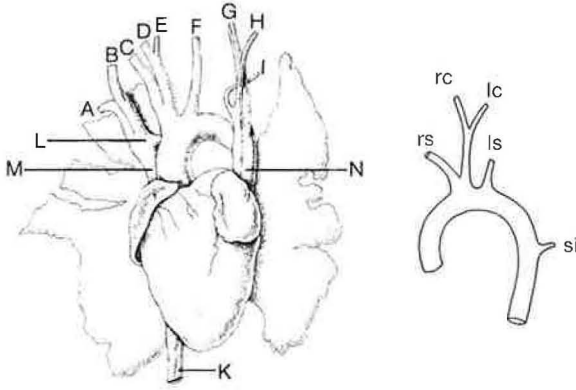


Figure 20.6 Left: heart and lungs of *Thylacinus*; (a) subclavian vein (right); (b) internal jugular vein (right); (c) right subclavian artery; (d) right common carotid artery; (e) left common carotid artery; (f) left subclavian artery; (g) left internal jugular vein; (h) left subclavian vein; (i) superior intercostal vein; (k) posterior vena cava; (l) azygos vein; (m) posterior vena cava; (n) left anterior vena cava. Right: aortic arch in *Thylacinus*; rs = right subclavian; rc = right carotid; si = superior intercostal; lc = left common carotid; ls = left subclavian. (After Cunningham, 1882)

The pericardium is oval or fusiform in shape, considerably narrower behind than in front. Posteriorly, the fibrous layer presents a slight attachment to the diaphragm, whilst anteriorly it is lost upon the coats of the aorta and great vessels.

The heart (Fig. 20.6) is narrow, elongated and pointed, with a capacious right auricle and a wide appendix. The cavity of the right ventricle falls short of the apex of the heart by fully 38 mm. The conus arteriosus is very pronounced. The right auriculo-ventricular opening is guarded by a valve formed of five triangular membranous cusps and the orifice of the pulmonary artery is guarded by the usual three semi-lunar valves. The cardiac veins are divided into an anterior and a posterior group. The great cardiac vein takes its origin near the apex of the heart. Instead of winding around the left margin of the heart to join the left anterior vena cava, it deviates to the right, passes behind the pulmonary artery and the aorta and opens into the upper part of the right auricle near to the entrance of the right anterior vena cava.

Respiration

Tracheal rings are deficient superiorly throughout the entire length of the tube. The left lung is undivided by any marked fissure, but the margin is deeply crenated. The right lung has a well-marked azygous lobe separated from it by the posterior vena cava. The right lung is divided into three ill-defined lobes.

Excretory System

Only a detailed account of the urogenital apparatus of the male is available (fig. 20.7). The kidneys present the usual reniform outline, the sinus being very small and having a constricted outlet. A uniform medulla is coated by a thin cortex. Uriniferous tubules open onto the surface of a single prominent papilla which projects into the surface of the kidney. Where they are attached to the kidney, the ureters show only a slight expansion. The bladder, in a contracted state, is only the size of a small walnut, ovoid in shape and

compressed with exceedingly thick, muscular walls. Completely invested by the peritoneum, it is connected to the upper aspect of the lower abdominal wall. The ureters pierce the inner aspect of the neck of the bladder, one on each side of the mesial plane and about 6 mm apart (Cunningham, 1882).

Immediately behind these, the vasa deferentia pierce the commencement of the urethra. The contracted bladder has a very rugose mucous lining membrane, but where the neck merges into the urethra it is quite smooth. The ureters pursue a "curious course through the vesical wall" before each terminates at a prominent papilla at the neck of the bladder.

Sense Organs and Nervous System

Compared with other marsupials, *Thylacinus* exhibits specialization in the nature and number of its facial vibrissae. There are only facial and supraorbital vibrissae plus the interramal between the rami of the lower jaw and the submental on the lower lip. Both supraorbital and mystacial vibrissae are very long (Fig. 20.3).

The brain of *Thylacinus* is described by Flower (1865), Beddard (1891) and in comparative detail by Moeller (1968; 1970). It is larger both in relative and absolute terms than that of *Dasyurus* spp. or *Sarcophilus*.

Flower (1865) notes that *Thylacinus*, which is so divergent in external characters from both kangaroos and wombats, shows the same general peculiarities of cerebral organization, but has a smaller development of the superior transverse commissure, especially the anterior part, and a greater reduction of the thickness of the interventricular septum. Moeller (1970) determined the brain weight of *Thylacinus* and showed that it had a greater brain capacity than expected.

The reduced olfactory lobes in the brain of *Thylacinus* indicate that olfaction is not a prime sense in hunting. Unlike the scavenging *Sarcophilus*, for example, *Thylacinus* is tall enough to see over grass and bushes. It is probable, therefore, that the sense of smell is replaced by vision and sound as the more important hunting senses. The increased intelligence required for hunting by *Thylacinus* is reflected in the ridges on the surface of the neocortex.

Reproduction

The body of the testis is small and spherical; the epididymis is exceedingly large. The vas deferens is a slender and uniform tube some 180 mm in length. There is no tendency towards dilatation at the neck of the bladder and no associated diverticulum or seminal vesicle. It sinks into the urethral wall close to the base of the prostate, immediately behind the point where the ureter disappears into the vesical wall. The prostate is large and pyriform, commencing at the neck of the bladder and gradually terminating along the urethra. There are four Cowper's glands, the anterior glands are of uniform shape and about twice the size of the posterior set, overlapping them slightly. The body of the penis is 150 mm long from crural junction to the extremity of the glans. At its extremity, the corpus spongiosum bifurcates to form a forked glans penis (Cunningham, 1882).

The pouch in the female (Fig. 20.3 & 20.8) opens backwards and possesses four mammae (Owen, 1868). In a young, possibly non-parous, female, the marsupium is oval and exceedingly shallow. The antero-posteriorly directed long axis measures 50 mm with a transverse diameter of 28 mm. There is little demarcation between the pouch and the surrounding skin of the abdomen, but laterally there are prominent overhanging folds of integument. Apart from some sparse, white,

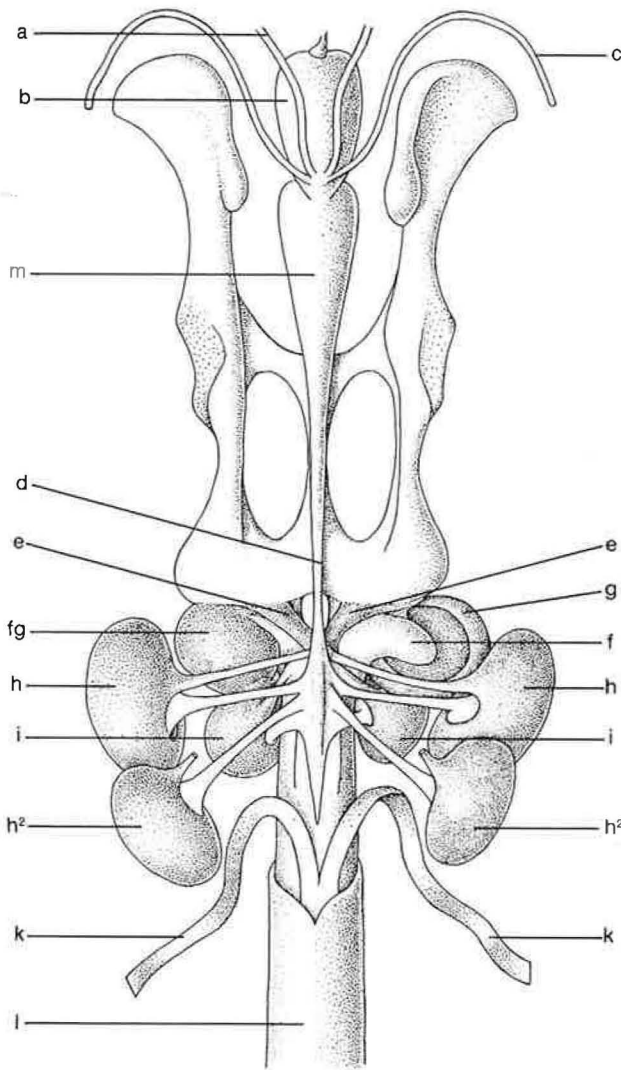


Figure 20.7 Genito-urinary organs of male *Thylacinus* — shown by removal of sacrum; (a) ureter; (b) bladder; (c) vas deferens; (d) membranous portion of urethra; (e) levator penis; (f) crus penis; (g) erector penis; (fg) crus penis clothed by the erector penis; (h & h²) Cowper's glands enveloped in their muscular capsules; (i) bulb of the penis enveloped by the bulbo-cavernosus muscle; (k) retractor penis; (l) penis; (m) prostrate. (After Cunningham, 1882) [D. Kirshner]

downy hair, it is bare. On the pouch floor are four small conical elevations, slightly raised above the general surface and located in the centre of the pouch. A minute aperture barely visible to the naked eye perforates the summit of each elevation and within it is a teat (Cunningham, 1882).

Beddard (1903) describes structures seen in transverse sections of the ovary, noting the immigration of follicular cells into the ova. The arrangement of the uterus, uterine neck and medial vaginal cul-de-sac bears a close resemblance to that seen in *Sarcophilus*. A very long urogenital sinus occurs in *Thylacinus* (Pearson & de Bavay, 1953).

More recent observations are based on the reproductive system of a mature *Thylacinus* found in the Hill collection at Hubrecht Laboratory in the Netherlands. The distinctive aspects of the reproductive tract include a disproportionate enlargement of the corpus uteri, unparalleled in other marsu-

pial species. The cervical canals enter the vaginal complex via a thick median vaginal septum. The greatly elongated caudal component of the vaginal cul-de-sac lacks a median vaginal septum (Hughes, 1981; 1982).

By 1860, *Thylacinus* was reported to retire to the mountains and rough inaccessible places to breed (Gould, 1863). In 1929, a closed season was declared for December which was believed to be the month of mating. Lord (1927) states that *Thylacinus* lays a scent trail across country during the breeding period, but there is no positive evidence for this in the literature. Guiler (1985) comments that as far as he is aware, mating of *Thylacinus* has not been observed in captivity or in the wild.

Claims have been made that *Thylacinus* has a lair such as a hollow log, tree, cave or other retreat. There is no evidence that it establishes a den in which it brings up young.

Thylacinus appears to be polyovular, but the number of eggs produced by the ovary in one season is unknown. The gestation period is not known, but should be about thirty five days (normal dasyurid pattern). The young spend about three months in the pouch (Le Souef & Burrell, 1926). Old records indicate that two to three young are reared.

From all accounts, *Thylacinus* is assumed to breed once a year. The species is monoestrous and there is no evidence of embryonic diapause. The breeding biology of *Thylacinus* is unlikely to differ much from that of *Sarcophilus* in its main features, with a restricted breeding season and some out-of-

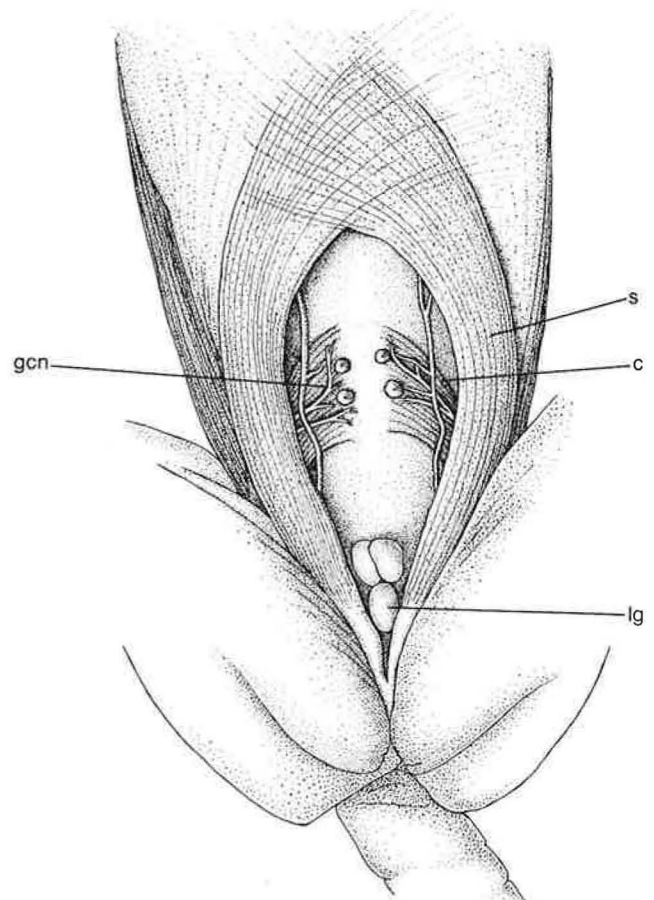


Figure 20.8 Dissection of marsupium of female *Thylacinus*; gcn = genito-crural nerve; lg = lymphatic glands; s = sphincter marsupii; c = cremaster muscle. (Modified after Cunningham, 1882)

[D. Kirshner]

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phase breeding. Mating probably takes place in or about December, the young being born in January to reach a half-grown stage between June and September. Guiler received reports that the young ran with the parents for some time and that "packs" of up to six individuals had been seen. It is unusual for young to be seen with both parents, implying absence of a pair bond between the parents.

Embryology and Development

Several opinions have been made on the duration of pouch life. Le Souef & Burrell (1926) indicate that it is about three months, Guiler (1985), 130 to 140 days, assuming a similarity to the cycle of *Sarcophilus*.

Boardman (1945) describes a pouch young of 7.5 mm crown-rump length as naked, devoid of colour pattern and showing no development of fur. A larger young, 288 mm long, was furred and had its eyes open. Data on breeding have been gleaned from the Tasmanian Lands Department account books by Guiler (1985). Some breeding appears to take place throughout the year and young can be found in the pouch at all times of the year.

NATURAL HISTORY

Life History

An animal purchased by the London Zoo in 1884 lived in captivity for eight years and five months, the longest known time for *Thylacinus* in captivity in an overseas zoo. As it was probably about a year old when purchased from a dealer, a life span of nine and a half years is suggested. The longest known life span is that of one of the cubs of a specimen obtained by Beaumaris Zoo, Hobart in 1924, some twelve years. In the wild, longevity of 12 to 14 years can be anticipated. There is no information on the growth of juveniles or the age of maturity.

Ecology

Guiler (1985) comments that he knows of no written descriptions of the methods used by *Thylacinus* to kill prey. Trappers have reported that the animals lie in wait and then jump on prey. They seem to have a liking for vascular tissues, as well as eating the tail to within 50 mm of the anus, to provide roughage. While the heart, lungs, kidneys and liver are consumed together with some of the meat from the inside of the "ham", the remainder of the carcass is left. In captivity, *Thylacinus* accepted almost any food presented. Although they are usually considered to have been major sheep predators, in actual fact the numbers scared by them far exceed the numbers taken.

From early records, *Thylacinus* apparently was widespread from the seashore to the mountains (Fig. 20.2) and found in nearly all newly settled areas, especially where they bordered onto densely forested, mountainous tracts of land. Their preferred habitat seems to be hilly, dense, dry sclerophyll or mixed sclerophyll – rainforest communities, often with rocky outcrops. Feeding occurs on the neighbouring grassy plains and lightly timbered woodland in the evening, at night and in the early morning. Most distribution data arise from records of Government and private bounty payments from 1880 to 1909.

That the species is hardy and adaptable has been shown by its long survival in captivity in zoos in England, northern Europe and eastern United States. Although three parasites, a flea, tapeworm and roundworm have been recorded from

Thylacinus, only one of these was found on animals resident in Tasmania. This is the flea, *Uropsylla tasmanica*, which infests members of the family Dasyuridae.

Behaviour

Observations on the behaviour of *Thylacinus* are limited to the notes made by the early colonists, explorers, hunters and those who kept animals in captivity in zoos. Most of these observations were made during the day, although the species is nocturnal or semi-nocturnal.

Two *Thylacinus* were sent to London Zoological Gardens by Gunn (1850). A further consignment of a female and three young was sent in 1863. Gould observed the former animals in the Gardens and comments on the species:

"In confinement it is excessively shy, and on being alarmed dashes and leaps about its cage in the most violent manner, uttering at the same time a short guttural cry resembling a bark, but whether this sound is also emitted in a state of nature has not been observed".

Thylacinus in the New York Zoo spent most of the time basking in the sun and apparently had poor vision in sunlight (Renshaw, 1938). Moeller (1968) made observations on behaviour using a film of the last surviving captive animal.

Aggressive behaviour must be normal for the species. The savage nature of their fighting is exemplified by the mode of attack and savage killing of a bull terrier recorded by Le Souef & Burrell (1926). Only two records of attacks on humans in the wild are on record (Smith, 1982).

The wide gape of *Thylacinus* has been depicted in numerous photographs. It could be compared with the yawn-like threat of *Sarcophilus*.

Although native macropodids undoubtedly were eaten by the species, there is no description of an individual hunt. Lord (1927) considers that they covered large areas of ground when hunting, returning to the lair by day. "During the breeding season a male Thylacine has been known to follow the same route across many miles of country..." He also states that packs of four or five had been noted, although normally animals were solitary. This pack may refer to a female and almost mature young.

There is no direct evidence to indicate whether the animals were sedentary, had a territory or home range or whether they were vagrants. There are indications, however, that they had a home range, if not a territory and that this may have been extensive.

Parental behaviour has received little attention. Gunn (1863) observed three young so big that they could only just fit into the pouch. The female would lie on her side like a dog with the skin of the pouch thrown back to allow the young access to the teats. When alarmed, the young entered the pouch with their backs downwards and were assisted by the mother who placed her rump against the side of the cage.

Economic Significance

Economic considerations in Tasmania in the 1800's were responsible for the culling of thousands of *Thylacinus* and undoubtedly contributed to the likely extinction of the species. From the very early days of colonization and the earliest account of *Thylacinus* in the Sydney Gazette and New South Wales Advertiser (1805), the species obviously was unusual, significant and potentially destructive.

Even in very early days of settlement, it was not believed to be a common animal. In 1824, sheep were introduced to open grasslands, mainly in the eastern part of the State. When large flocks were run near mountains, *Thylacinus* killed lambs; raids on poultry also were experienced.

From 1878 to 1893, some 3,482 skins were exported to London to be made into waistcoats. "Tiger" shoots for visitors were offered as recently as 1909. The bounty system, based on the belief that *Thylacinus* was a major predator on sheep in the colony, was introduced in 1830 by the Van Diemen's Land Company to control *Thylacinus* on its northwest properties and by the Government in 1888.

The Tasmanian Government received scalps of 2,040 adults and 144 juveniles and the Van Diemen's Land Company, in the northwest of the island 84. Similar numbers no doubt were taken by individual farmers. There were few scalps from the dense rainforest of the west coast. Although the Government bounty was dropped in 1910 and the Company bounty in 1914, a rapid decline set in after 1900. Apparently, this decline was not due to hunting pressure and seems to have occurred simultaneously through the island.

Unsubstantiated reports refer to the fact that in 1910 many marsupial carnivores died of a disease resembling distemper. Management of the populations was poor in the 1920's and the animals were still being exported to zoos overseas. The last confirmed wild *Thylacinus* was shot at Mawbanna in 1930.

BIOGEOGRAPHY AND PHYLOGENY

Distribution

Thylacinus was once widespread over continental Australia, extending north to New Guinea and south to Tasmania. Now, it is confined to Tasmania where its presence has not been established conclusively for 50 years. Fossils have been reported from Victoria by Gill (1953; 1964), South Australia (Archer, 1971), Western Australia (Glauert, 1914) and from far northwestern Australia (Kendrick & Porter, 1973). Van Deusen (1963) reports the species from New Guinea.

While the precise reasons for extinction of *Thylacinus* on the Australian mainland are not known, its decline and possible extinction in Tasmania was hastened (apart from the importance placed on it as a food item by the Aborigines) by the introduction of dogs and by the active persecution of the species. An irreversible decline in population appears to have resulted.

Reports of the occurrence of the species have continued over the years. They have been documented by Smith (1981; 1982) and Guiler (1985). Despite the irregular sightings by a number of credible persons, no live or dead animals have been displayed in 50 years.

In Tasmania, the species is best known from the north and east coast and midlands plains regions rather than from the mountains. Although the captures of most animals were made in the farmed flat areas, it seems likely that the coastal and plains regions were the preferred habitat of the species.

Affinities with Other Groups

The question of the relationships of *Thylacinus* has received much attention. Bensley (1903) suggests that it could be a foreign element in the Australian fauna. He notes that it

seemed to show a striking similarity to the South American carnivorous borhyaenids. While Sinclair (1906) agreed, Simpson (1941) opposes the theory and considers that these similarities arose from parallelism. He views *Thylacinus* as a specialized dasyurid. This is supported by Tate (1947) and Marshall (1977).

Archer (1976a;b) supports a thylacinid-borhyaenid relationship. Sarich *et al.* (1982), using albumin, measured the genetic relationship as the immunological distances separating *Thylacinus* from various dasyurid genera. Their studies indicate that *Thylacinus* belongs within the Dasyuridae as a distinct genus and that *Thylacinus* diverged from other dasyurids some six to 10 million years ago.

Affinities within the Thylacinidae

There are several forms in the fossil record which are considered to be related very closely to the present day *Thylacinus cynocephalus*. Several fossil species have been named from Australian mainland deposits. Owen (1845) describes *Thylacinus spelaeus* from material probably collected in the Wellington Caves, New South Wales. He later named *T. major* as a result of his examination of further specimens from the Wellington Caves (Owen, 1877). De Vis (1894) describes *T. rostralis* from Queensland. Woodburne (1967) describes a Tertiary species, *T. potens*, from the Late Miocene Alcoota fauna. Ride (1964) compares dental and mandibular features of western and eastern Australian fossil thylacinids. The statistical evidence does not support separation of *T. spelaeus* from *T. cynocephalus*. Recent taxonomic studies of fossil thylacinids indicate that there is no valid reason to warrant the specific separation of *T. spelaeus* and *T. cynocephalus* (Dawson, 1982). *T. rostralis* and *T. major* are regarded as junior synonyms of *T. cynocephalus*.

Fossil Record

The oldest known occurrence of *Thylacinus* is an isolated premolar from the Miocene Kutjamarpu fauna estimated at 12 mybp, which is older than the date of divergence of *Thylacinus* from *Dasyurus* estimated using immunological techniques (Sarich *et al.*, 1982). A species from the Late Miocene Alcoota fauna, *T. potens*, shows a great many similarities with the modern species and *T. rostralis* from the Early Pliocene Chinchilla fauna of Queensland is considered a junior synonym of the latter. From the few available records, thylacinids have been anatomically conservative since at least the Late Miocene. A review of Miocene thylacinids is given by Archer (1982). The Pleistocene record of the thylacinids is poor. *Thylacinus spelaeus* from this period is almost indistinguishable from *T. cynocephalus*.

Dated fossil records indicate that the modern species was present in the southwest Australian mainland until some 3090 years ago. In the Kimberley region of Western Australia, a deposit containing thylacinid remains has been dated at 0 ± 180 years bp (Archer, 1974). In the same region, Aboriginal rock-paintings of thylacine-like animals are recognized. They have also been found on walls or overhangs on exposed rock surfaces in the Upper East Alligator region, Deaf Adder Creek and Cadell River crossing in the Northern Territory (Smith, 1982).

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