

Dasyus novemcinctus. By Karen McBee and Robert J. Baker

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***Dasyus* Linnaeus, 1758**

- Dasyus* Linnaeus, 1758:50. Type species *Dasyus novemcinctus* Linnaeus, by tautonymy (Hall, 1981) or *Dasyus septemcinctus* Linnaeus (according to Wetzel and Mondolfi, 1979).
Tatus Fermin, 1765:3. Type species *Tatus cucurbitalis*.
Tatu Blumenbach, 1779:74. Type species *Dasyus novemcinctus* Linnaeus.
Cataphractus Storr, 1780:40. Based on "Armadillo," and six other names.
Loricatus Desmarest, 1804:28. No type designated; included eight names.
Tatusia Cuvier, 1827:309. No type designated; included seven names.
Cachicamus McMurtrie, 1831:163. Included *Dasyus novemcinctus* Linnaeus and *D. septemcinctus* Schreber.
Cachicama Geoffroy St.-Hilaire, 1835:53. An emendation of *Cachicamus* McMurtrie.
Zonoplitis Gloger, 1841:114. No type designated; based on the armadillos with 4 toes on forefeet, the two middle being longer than the others.
Praopus Burmeister, 1854:295. Type species *Dasyus longicaudus* Wied-Neuwied.
Cryptophractus Fitzinger, 1856:123. Type species *Cryptophractus pilosus* Fitzinger.
Hyperoambon Peters, 1864:180. Included *Dasyus pentadactylus* Peters (= *Dasyus kappleri* Krauss) and *Dasyus peba* Desmarest (= *Dasyus novemcinctus* Linnaeus).
Muletia Gray, 1874:244. Type species *Dasyus septemcinctus* Linnaeus.

CONTEXT AND CONTENT. Order Edentata, Suborder Xenarthra, Superfamily Dasypodoidea, Family Dasypodidae, Subfamily Dasypodinae. Within the genus *Dasyus*, Wetzel and Mondolfi (1979) recognized six living species: *Dasyus novemcinctus*, which occurs both in the Nearctic and Neotropics; and five Neotropical species, *Dasyus hybridus*, *D. kappleri*, *D. pilosus*, *D. sabanicola*, and *D. septemcinctus*.

***Dasyus novemcinctus* Linnaeus, 1758**

Nine-banded Armadillo

- Dasyus novemcinctus* Linnaeus, 1758:51. Type locality "America"; restricted to Pernambuco, Brazil by Cabrera (1958).
Tatus minor Fermin, 1769:111. Type locality unknown.
Loricatus niger Desmarest, 1804:28. No type designated.
Dasyus longicaudus Wied, 1826:531. Type locality Morro d'Arara; restricted to Rio Mucuri, Bahia, Brazil by Avila-Pires (1965).
Dasyus uroceras Lund, 1841:65. Type locality unknown.
Hyperoambon peba Peters, 1864:179. Included *D. pentadactylus* Peters (= *D. kappleri* Krauss) and *D. peba* Desmarest (= *D. novemcinctus* Linnaeus).
Dasyus fenestratus Peters, 1864:180. Type locality Costa Rica, San Jose.
Tatusia platycercus Hensel, 1873:105. Type locality Rio Grande do Sul.
Tatusia granadiana Gray, 1873:14. Type locality Antioquia, Concordia.
Tatusia mexicana Gray, 1873:14. Type locality Mexico.
Tatusia brevirostris Gray, 1873:15. Type locality Brazil, Rio de Janeiro.
Tatusia leptorhynchus Gray, 1873:15. Type locality Guatemala.
Tatusia boliviensis Gray, 1873:16. Type locality Bolivia.
Tatusia leptcephala Gray, 1873:16. Type locality Brazil.
Tatusia leptorhinus Gray, 1874:246. A misspelling of *T. leptorhynchus*.
Dasyus mazzai Yepes, 1933:226. Type specimen only; the paratype was a species distinct from *D. novemcinctus*. Type lo-

cality Salta, Argentina; considered a composite of *D. novemcinctus* and other species by Wetzel and Mondolfi (1979).

Cabrera (1958) listed some other species names as synonyms. These names were not assigned in the review by Wetzel and Mondolfi (1979) and still need critical assessment.

CONTEXT AND CONTENT. Context as noted above in generic summary. Three subspecies were recognized by Cabrera (1958) in South America and Hall (1981) recognized four others in North America. Wetzel and Mondolfi (1979) seem to have recognized no subspecies; at least they did not use subspecies names. They did discuss geographic differences within the species, however.

- D. n. novemcinctus* Linnaeus, 1758:51, see above (*longicaudus* Wied, *platycercus* Hensel, *brevirostris* Gray, *boliviensis* Gray, *leptocephala* Gray, *mexicana* Hagmann, and *mazzai* Yepes are synonyms, as presumably are *minor* Fermin, *niger* Desmarest, *uroceras* Lund, and *peba* Peters).
D. n. mexicanus Peters, 1864:60. Type locality Matamoros, Tamaulipas, Mexico (see Hollister, 1925; *texanum* Bailey, *mexicana* Gray, *leptorhynchus* Gray, and *cucurbitinus* Gaumer are synonyms).
D. n. fenestratus Peters, 1864:180, see above.
D. n. hoplites Allen, 1911:195. Type locality hills back of Gouyave, Grenada, Lesser Antilles.
D. n. aequatorialis Lönnberg, 1913:34. Type locality Peruchu, Pichincha, Ecuador (*granadiana* Gray probably a synonym).
D. n. davisii Russell, 1953:21. Type locality Huitzilac, Morelos, Mexico.

DIAGNOSIS. Armadillos differ from all other living mammals in having ossified dermal scutes. The subfamily Dasypodinae differs from the other members of the family by the presence of four toes on the forefeet (other subfamilies have five), the middle pair being largest. The cephalic shield is trapezoidal. The combination of an asymmetrical pattern of bony dermal scutes and a carapace characterized by 7 to 11 transverse movable bands also is unique to the subfamily Dasypodinae.

Dasyus novemcinctus is characterized by having 8 to 11 (usually 9) movable bands, 54 to 65 scutes on fourth movable band, ears 40% to 50% of length of head, long tail (70% or more of length of head and body), and teeth usually 8/8 (Hamlett, 1939; Talmage and Buchanan, 1954; Wetzel and Mondolfi, 1979). It differs from *D. hybridus* and *D. septemcinctus* in that these two species normally have 6 or 7 movable bands; both rarely have 8 bands. *Dasyus hybridus* and *D. sabanicola* have shorter ears, 25% to 33% of head length, and *D. septemcinctus* has only 6 upper teeth in each jaw. *Dasyus kappleri* has two or three rows of bony projecting scutes on the knee, whereas *D. novemcinctus* has no such projections. Rostral and palatal lengths are proportionally smaller than in *D. kappleri* and *D. pilosus*, and *D. pilosus* generally has 11 movable bands. Individuals of *D. novemcinctus* are difficult to identify to subspecies without assessment of cranial characteristics.

GENERAL CHARACTERISTICS. The sides, back, tail, and top of the head are covered with ossified dermal plates (Fig. 1) which are covered by a leathery skin, producing a turtle-like carapace that accounts for approximately 16% of body weight (Szabuniewicz and McGrady, 1969). This dorsal carapace is divided into three main regions (Kalmbach, 1943): a scapular shield across the shoulders and a pelvic shield covering the hips, each composed of 18 to 20 rows of ossified scutes (Hall, 1955), and a series of 9 (8 to 11, the latter rarely) transverse, telescoping bands between the two shields. Each band is composed of 50 to 75 scutes (Storrs, 1971), and is connected to the adjacent band by a fold of soft, hairless skin. The anterior margin of each band is overlapped by the preceding band. The top of the head is covered with heavy scales that are closely attached to the skull. The scutes closely abut the skeleton at two points in the pelvic region

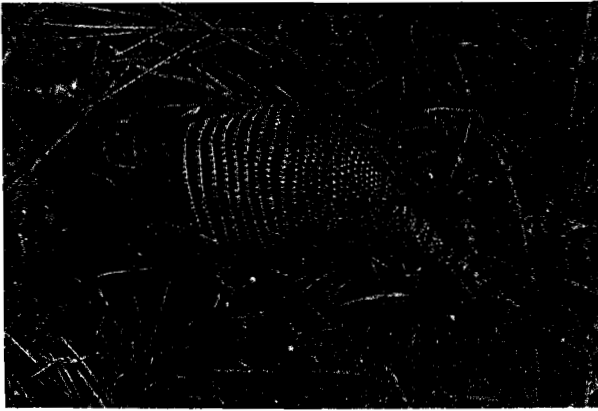


FIGURE 1. Photograph of a live nine-banded armadillo in characteristic pose from Junction, Texas.

and at numerous points in the tail. The tail is covered by a series of 12 to 15 rings, which decrease in size to a tapered terminal portion that is covered with irregular scutes. Each ring abuts five vertebral processes (Kalmbach, 1943).

Between the large head scutes and the scapular shield, and between the pelvic shield and the first tail ring, are folds of soft, hairless skin. The under parts of the body and the protected parts of the legs and head also are covered with soft skin. Groups of coarse greyish hairs arise from regularly spaced papillae on the under surface. The carapace has sparse hairs at the posterior borders of individual scutes.

The ears are large, greyish to black, and covered with tough, pebbly skin (Fig. 1). The head tapers to a soft, pinkish, pig-like snout; the eyes are small. The legs are short, stout, and well adapted for digging. There are four toes on the forefeet and five on the hindfeet. These toes, particularly the medial ones, are equipped with large, sharp, slightly curved claws (Fig. 1).

Canines and incisors are absent (Fig. 2). All teeth are peg-like and single-rooted. Enamel is absent in adult dentition. The skull has smooth lines and the rostrum and frontal portion of the skull are attenuated (Fig. 2).

Male armadillos tend to be slightly larger than females (Hall, 1955; Kalmbach, 1943). Anderson and Benirschke (1966) and Storrs (1971) reported average adult weights ranging between 3 and 5 kg, whereas Hall (1955) reported weights of 3.6 to 6.0 kg for females and 5.5 to 7.7 kg for males. Selected measurements (in mm) included: total length, 615 to 800; length of tail, 245 to 370; length of hindfoot, 75 to 107; length of ear from notch, 40; greatest length of skull, 85.5 to 100 (Hall, 1955); height at shoulder, 155 to 230 (Walker et al., 1968).

Females have four mammae, two pectoral and two inguinal (Kalmbach, 1943). The uterus is simplex and a true vagina is replaced by a urogenital sinus serving both as vagina and urethra (Talmage and Buchanan, 1954). In the male the testes descend no further than the pelvis. There is no scrotum (Talmage and Buchanan, 1954).

DISTRIBUTION. *Dasypus novemcinctus* has a wider distribution than any other edentate (Fig. 3). The southern limit of distribution of the nine-banded armadillo extends into northwestern Argentina and Uruguay, as well as the islands of Trinidad, Tobago and Granada (Borrero, 1967; Clark, 1914; Hamlett, 1939). It also is common throughout Central America and most of Mexico.

The armadillo first was recorded in the United States by Audubon and Bachman (1854) along the shores of the Rio Grande in southern Texas. Cope (1880) noted that the species had reached as far east as the Nueces River. Bailey (1905) mapped the armadillo's range in the Pecos Valley and as far west as northeastern New Mexico, but Anthony (1928) showed it extending no further than Devil's River. The species now occurs throughout Texas except for the Trans Pecos and panhandle areas; however, nonfossilized shells and bones are recorded from San Simon Sink, New Mexico, indicating a recent distribution that far west (Buchanan and Talmage, 1954).

Strecker (1926) reported that the armadillo entered Louisiana sometime prior to 1925, advancing along the Sabine and Red River valleys (Strecker, 1928). By 1936 (Lowery, 1936), it occupied all of Louisiana west of the Mississippi. In 1943, Lowery

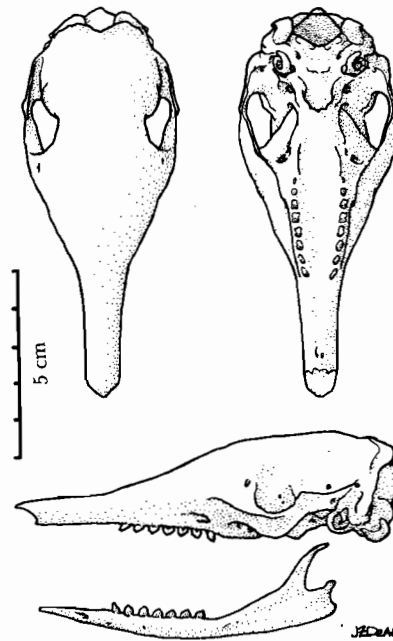


FIGURE 2. Views of skull: dorsal (top left), ventral (top right), and side view including dentary (bottom) of *Dasypus novemcinctus* (TTU-34119) from Junction, Texas. Drawing by J. Z. Deal.

reported the armadillo east of the Mississippi. The distribution now includes two-thirds of Mississippi (Humphrey, 1974).

The armadillo's expansion in Oklahoma has been documented by Blair (1936), Gardner (1948) and Taber (1939). Armadillos are now common in southeastern Oklahoma and west-central Arkansas, throughout the Ouachita Mountains, and eastward past Little Rock (Humphrey, 1974). Black (1944) and Dellinger and Black (1940) reported the expansion northward almost to the northwestern border of Arkansas.

The first Alabama armadillo was reported by Taber (1939) but an established colony was not reported until 1952 by Fitch et al. Woolfe (1968) reported armadillos as locally abundant and widespread in southern Alabama as far north as Wilcox County.

The distribution of the armadillo in the U.S. is further complicated by its introduction into southern Florida during World War I (Bailey, 1924), and at Cocoa, Florida in 1924 (Sherman, 1936). Neill (1952) reported armadillos observed on Merrit Island and several other off-shore islands, and recorded the animals as occurring throughout the state except in the swampy portions of the south and the extreme western portion of the panhandle. Woolfe (1968) reported armadillos on both sides of Mobile Bay and considered the animals common in western Florida.

The armadillo is reported from Kansas (Hall, 1955; Hibbard, 1943; Smith and Lawlor, 1964), Missouri (Anon., 1947), southeastern Georgia (Fitch et al., 1952), Tennessee (Humphrey, 1974), South Carolina (Humphrey, 1974), Colorado (Hahn, 1966) and southern Nebraska (Hoffmann and Jones, 1970). Fig. 4 shows the pattern of range extension of the nine-banded armadillo for the past hundred years.

Possible reasons for the armadillo's northward expansion since the 19th century have included progressive climatic changes (Humphrey, 1974; Price and Gunter, 1943), man's encroaching civilization including overgrazing and removal of large carnivores (Buchanan and Talmage, 1954; Strecker, 1926). Drought and cold, however, are postulated as conditions most limiting to the expansion of *D. novemcinctus* (Humphrey, 1974).

The currently recognized subspecific distributions are as follows: *D. n. hoplites* is known from Trinidad, Tobago and Grenada (Clark, 1914), and has been recorded from Costa Rica (Calvert and Calvert, 1917) and Barro Colorado Island in the Panama Canal (Enders, 1930); *D. n. mexicanus* extends from the southern U.S. into southern Mexico (Kalmbach, 1943); *D. n. aequatorialis* is reported from western Ecuador and possibly into Colombia in the north and Peru in the south (Cabrera, 1958); *D. n. novemcinctus* occurs east of the Andes from Colombia and Venezuela to Paraguay and northern Argentina (Cabrera, 1958); *D. n. fenestratus* is reported from Oaxaca (Hooper, 1947) and Panama



FIGURE 3. Current distribution of *Dasypus novemcinctus* (adapted from Borrero, 1967; Humphrey, 1974; Wetzel and Mondolfi, 1979). Scale is in kilometers.

(Kalmbach, 1943) and possibly across northern South America; *D. n. davisii* is known from the Balsas Basin to the mountains of northern Morelos, Mexico (Talmage and Buchanan, 1954).

FOSSIL RECORD. *Dasypus bellus*, an extinct species which is osteologically identical to *D. novemcinctus* except for greater overall size (Holmes and Simpson, 1931; Slaughter, 1961), is considered the fossil counterpart of *D. novemcinctus*. *D. bellus* was described from Seminole Field, Florida (Simpson, 1929), was common in Florida throughout the Pleistocene (Simpson, 1929; Webb, 1974), and is also recorded from Texas, Missouri (Simpson, 1949), Oklahoma (Slaughter, 1961), and Kansas (Hibbard, 1958; Hibbard and Taylor, 1960). Texas localities date to the Sangamon (last interglacial), Wisconsin and a transition between Sangamon and Wisconsin (Dalquest, 1962; Slaughter, 1959, 1961).

FORM. Because of its peculiar structure the integument of *D. novemcinctus* has received considerable attention. Leydig (1859) first described the structure of the bony plates. Wilson (1914) thoroughly studied the development and histology of the integument. Cooper (1930) reported on sudoriferous and sebaceous glands as well as hair structure. In addition to glands of the integument, *D. novemcinctus* also possesses a pair of evertable anal glands that produce a characteristic musty scent (Talmage and Buchanan, 1954). Campo-Aasen and Convit (1975) discussed histochemistry of armadillo skin, emphasizing the extremely large dendritic cells.

Talmage and Buchanan (1954) compiled a comprehensive bibliography on the skeletal system of *Dasypus* and Kalmbach (1943) discussed the skeletal system in general. Specialized modifications of the ribs have been suggested as an adaptation for the armadillo's semifossorial habits requiring unusual trunk stability (Jenkins, 1970).

The muscle system is especially well developed in the limbs. The shoulder anatomy was described by Miles (1941). Zeiger (1929) studied the musculature of the trunk and Edgeworth (1923) discussed cranial musculature.

Reports on the neuroanatomy of *D. novemcinctus* consist of a description of the brain morphology (Smith, 1899), cerebellar morphology (Larsell, 1970), mid-brain and isthmus morphology (Crosby and Woodburn, 1943), and corticospinal tract patterns (Fisher et al., 1969). The thalamic nuclei of the diencephalon and rostral mesencephalon were described (Papez, 1932) and correspond to those of the Insectivora. Neocortical projections of the mesencephalon have been studied (Harting, 1969; Harting and Martin, 1970a), especially those to the pons and medulla (Harting and Martin, 1970b).

Hayes (1968, 1970) studied the spleen of *D. novemcinctus* using both light and electron microscopy, and concluded that spleen morphology was similar to the sinusoidal class of mammalian spleens possessing ellipsoid sheaths. It is invested by a smooth muscle capsule and shows a typically mammalian follicular ar-

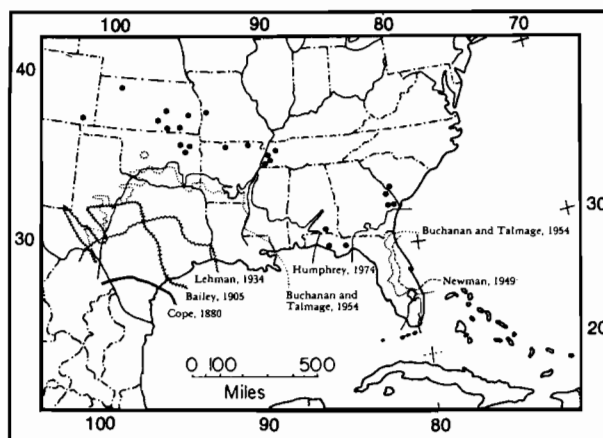


FIGURE 4. Patterns of range extension of *Dasypus novemcinctus* during the past 100 years. Dots represent individual sightings.

rangement. Relative weights for edentate spleens are within the same range as for most other mammals (Storrs, 1971).

The anterior and neural lobes of the pituitary are of equal size, whereas the intermediate lobe is missing (Wislocki, 1938). Oldham (1938) discussed the anatomy and embryology of the pituitary with special emphasis on the neural lobe and Drager (1947) examined the innervation and histology of the anterior lobe.

Dasypus novemcinctus is unique in having a salivary bladder surrounded by skeletal muscle (Ruby and Allen, 1976; Shackleford, 1963; Shackleford and Wilborn, 1968). This bladder stores large amounts of highly viscous saliva. It empties by one efferent duct leading to the oral cavity, and may be used in feeding for rapid coating of the tongue.

The parotid gland is similar in location and structure to that of other mammals (Shackleford, 1963) except secretory granules of the acinar cells contain a wide variety of substructures (Ruby, 1978). These acinar cells are seromucous in nature (Shackleford and Wilborn, 1968). The submaxillary gland is composed of two lobes which differ histochemically (Shackleford, 1963) and ultrastructurally (Ruby and Canning, 1978), and possess specialized afferent ducts terminating in the salivary bladder (Shackleford, 1963). The sublingual gland is absent in *Dasypus* (Shackleford, 1963). Azzali and Di Dio (1972) have described the lymphatic system of this armadillo.

The female reproductive tract with its blend of archaic and highly specialized characteristics has been described by Newfang (1947) and Enders and Buchanan (1959). The two kidney-shaped ovaries lie in the typical mammalian position. The uterus is simplex, and appears similar to a primate uterus. A urogenital sinus serves both as vagina and urethra.

The male reproductive system is typically mammalian. The testes descend only to the entrance of the inguinal canal. There is no scrotum (Talmage and Buchanan, 1954). Nagy and Edmunds (1973a) described the morphology of the spermatogonia. The epididymis is similar to that of other mammals except that there are large accumulations of rough endoplasmic reticulum and smooth endoplasmic reticulum in separate segments of the epididymis (Edmunds and Nagy, 1974). Nagy and Edmunds (1973b) reported the spermatozoa resemble those of several other mammals. The sperm head is paddle-shaped, the sagittal profile ensiform and the acrosome exhibits three distinct regions. They also reported a short "bilaminar plate" not seen in other mammalian sperm. Glover (1963) described the penis, epididymis, prostate gland, and pelvic urethra and noted the absence of a prepuce and a retractor penis muscle. Weaker (1977a) discussed the cycle of the seminiferous tubules and spermatogenesis. The process of spermatogenesis occurs in thirteen steps. Four generations of spermatogonia are described. *D. novemcinctus* belongs to the first category of interstitial tissues (i.e., few Leydig cells and extensive lymphatic sinusoids) (Weaker, 1977b).

FUNCTION. Lewis and Doyle (1964) found the cellular elements of *Dasypus* blood to differ only slightly from those of humans. Total plasma protein and fibrinogen concentrations were higher than human levels. Blood clotted effectively and clotting factors showed greater activity than human counterparts. Hemoglobin is relatively insoluble in the oxygenated state but becomes soluble when reduced. A high potassium, low sodium concentra-

tion was noted. Compared to other mammals, the armadillo has a disproportionately high rate of erythropoiesis for its basal metabolic rate (Ebaugh and Benson, 1964). Strozier et al. (1971) reported serum chemistry values for 10 variables and noted that cholesterol levels differed significantly between sexes. Giacometti et al. (1972) reported blood chemistry values, noting that lactate dehydrogenase and serum glutamic oxaloacetic transaminase were higher than in other mammals. Dementi and Burke (1972) found a high oxyhemoglobin affinity and a small Bohr effect for *Dasypus*. A major and a more slowly moving minor hemoglobin fraction were confirmed by starch-gel electrophoresis.

A morphological study of the immune system of *Dasypus* revealed that neutrophils predominate among leucocytes. The thymus gland is well developed and thymus-dependent areas in lymph nodes and spleen contain abundant lymphoid cells (Purtilo et al., 1975).

The rectal temperature of *D. novemcinctus* ranges from 30° to 36°C when the ambient temperature is 25°C (De Almeida and Fialho, 1924; Enders and Davis, 1936; Wislocki and Enders, 1935). Males have an average body temperature of 33.4°C, whereas females average 31.3°C (Burns and Waldrip, 1971). Johansen (1961) looked at responses to temperature stress in *D. novemcinctus*. Either an increase or decrease in ambient temperature can result in an elevated core temperature indicative of the primitive thermoregulatory capabilities of *Dasypus*.

Both Wilber (1964) and Burns and Waldrip (1971) gave electrocardiographic data for *D. novemcinctus*. Females show a consistently lower heart rate than males.

Scholander et al. (1943) noted that the normal oxygen consumption of a resting animal is well below that found for other mammals of a similar size. Under stress, *Dasypus* is able to build up a large oxygen debt and can exercise on the order of 10 to 15 times resting metabolism without access to oxygen for up to 4 min. Recovery periods last 3 to 4 h. The respiratory quotient averages 0.74. Average blood-oxygen capacities for four armadillos measured by Dhindsa et al. (1971) were found to be higher than expected. These studies suggest respiratory adaptations of *D. novemcinctus* to its semifossorial lifestyle. Findings regarding armadillo lactate dehydrogenase and its role in anaerobiosis (Burns et al., 1975) and the high myoglobin content of armadillo tissues (Seab and Burns, 1976) show further evidence of the armadillo's tolerance to hypoxia.

The size of dermal bone marrow and marrow cavities in the scutes of *D. novemcinctus* fluctuate seasonally. Skeletal bone marrow shows no seasonal variation (Weiss and Wislocki, 1956).

Dasypus novemcinctus sleeps up to 17 h a day, 18% of which is paradoxical sleep. The animal shows four categories of rapid eye movement (Prudom and Klemm, 1973; Van Twyver and Allison, 1974).

Walsh et al. (1975) and Weiser (1975) reported a leprosy-like disease naturally occurring in wild armadillos from Louisiana, but studies by Filice et al. (1977) failed to document association between armadillo contact and leprosy in humans.

Dasypus novemcinctus has also been the subject of skin transplant experiments (Anderson and Benirschke, 1962), organ transplants, teratogenesis, and drug metabolism experiments (Storrs, 1971).

REPRODUCTION AND ONTOGENY. Reproduction in *D. novemcinctus* is marked by two unique phenomena: the blastocyst shows a long period of quiescence before implantation, and specific polyembryony results in the formation of identical quadruplets.

Hamlett (1932a) and Talmage and Buchanan (1954) described the reproductive cycle of *D. novemcinctus*. The nine-banded armadillo first breeds at about one year of age, with ovulation occurring from June to August (Asdell, 1964). July 15 is the average date of mating (Hamlett, 1935). At five to seven days the ovum forms a blastocyst and passes into the uterus. At this point, development appears to cease. The vesicle remains free in the uterine lumen. Enders (1962) described the blastocyst and found no evidence of four centers of development at that stage.

By November the blastocyst becomes implanted. This delayed implantation was first reported by Patterson (1913). The fetal villi penetrate the maternal blood system in the formation of a villous haemochorial placenta (Enders et al., 1958). Implantation is fundic and placental development occurs in three stages: 1) initial attachment and inverted yolk sac formation; 2) formation of cell columns and invasion of maternal blood supply; and 3) placental invasion throughout the uterus (Enders, 1960a). Enders (1960b) also examined placental structure using electron microscopy.

Talmage et al. (1954) suggested that implantation is preceded by increased activity of the corpus luteum. Possibly the pituitary caused the corpus luteum to produce a high titer of progesterin and either too little or too much estrogen. Just before implantation the amount of progesterin being produced is altered until proper levels allowing implantation are reached and maintained. Buchanan et al. (1956) showed that implantation occurred in animals ovariectomized in month four of the delay period, suggesting that the uterus is maintained by a non-ovarian source. Effects of other hormonal injections on placentation have also been studied (Brinck-Johnsen, 1970; Enders and Buchanan, 1959; Labhsetwar and Enders, 1968).

Changes in the uterus during delayed implantation and placentation were outlined by Enders (1967). Enders and Schilafke (1969) discussed interactions between trophoblast and uterus during implantation.

Specific polyembryony first was observed by Lane (1909) who reported that four amnia united, dividing the single chorionic chamber into four longitudinal chambers, each with a separate umbilical cord attached to its wall. The process of implantation leading to specific polyembryony was described by Patterson (1913). Hamlett (1929) discussed the relationship between polyembryony and delayed implantation. Patterns of cleavage and cytoplasmic elimination were observed by Hamlett (1932b). Hamlett (1933) also discussed genetic and physiological implications of polyembryony.

The development of the nine-banded armadillo has been thoroughly described by Newman and Patterson (1910). Vanne-man (1917) followed the migration of the germinal epithelium showing that the germ cells of the four embryos do not have a common origin in the sense of arising from a prespecialized region of the blastocyst. The gonads begin to differentiate into ovaries or testes at a fetal length of 17.5 mm, and the fetal ovary encloses a rudimentary testis with a well-developed rete apparatus (Newfang, 1947).

The adrenal gland is remarkably large in the fetus (Newfang, 1947; Szabuniewicz and McGrady, 1969). Postnatal involution of the adrenal fetal zone is similar to that in man (Moser and Benirschke, 1962). Steroid synthesis in the fetal armadillo increases with advancing age (Bloch, 1969; Bloch and Benirschke, 1965). Fetal circulation (Anderson and Benirschke, 1963) and development of the hypothalamohypophysial neurosecretory system (Wurster and Benirschke, 1964) were also described.

Variation from the normal four young per litter has been reported by Newman (1913). In 300 cases he found four sets of triplets, four sets of quintuplets and one set of twins. Buchanan (1957) reported six well-developed embryos and a rudimentary seventh from one female and the presence of two conceptuses in the uterus of another armadillo (Buchanan, 1967).

Young are born fully formed and with eyes open in March or April. Within a few hours they are walking and they begin to accompany the mother on foraging expeditions within a few weeks (Neck, 1976; Talmage and Buchanan, 1954).

ECOLOGY. Food habits of *D. novemcinctus* have been thoroughly documented by Kalmbach (1943). From analysis of 169 stomachs he concluded that 93.3% of stomach contents were animal in nature. Insects constituted 77.6% (41.6% Coleoptera, 14.0% Hymenoptera, 7.8% Lepidoptera and 14.2% other insects). Other invertebrates, including millipedes, centipedes, earthworms and snails, made up 14.4% of contents, while 1.2% were amphibians and reptiles, and 0.4% included birds and their eggs and unidentified carrion. The remaining 6.7% comprised vegetable matter, primarily berries, fruit, and debris.

Analysis of food habits of armadillos from Louisiana supported Kalmbach's findings and also revealed seasonal variation in the diet (Fitch et al., 1952). Newman and Baker (1942) observed an armadillo eating three young cottontail rabbits (*Sylvilagus*). Clark (1951) observed a captive armadillo eating the carcass of a robin (*Turdus migratorius*). Examination of eight armadillo stomachs from Bexar County, Texas, revealed that 80% of the contents comprised fruit and seeds of the black persimmon (Hamilton, 1946).

The armadillo's only serious predator appears to be man. Sperry (1941) examined stomach contents of 566 coyotes (*Canis latrans*) and found no armadillo remains. Kalmbach (1943) reported armadillo remains from stomach contents of one cougar (*Felis concolor*).

During rainy periods there is a marked movement to higher ground. A return to the original area generally occurs as soon as the wet season has passed. During dry seasons a similar local

movement occurs toward streams and creeks where foraging is facilitated by the moist soil (Taber, 1945).

Armadillos forage immediately upon leaving the burrow each evening. Movements are made from areas with dense underbrush to open pastures as the night progresses (Fitch et al., 1952; Taber, 1945). Clark (1951) discussed the armadillo's ability to orient when removed from familiar surroundings.

Population density estimates range from 0.05/ha to 3.04/ha (Kalmbach, 1943; Taylor, 1946). Thirteen animals were tagged and their movements followed for 4.5 months in Natchitoches Parish, Louisiana. An average home range of 20.3 ha was calculated (Fitch et al., 1952). A similar study in central Texas based on three adult animals yielded an average home range of 3.45 ha (Clark, 1951), but the author stated that extreme drought conditions might have been responsible for the small size. He also reported a large degree of overlap between home ranges. In Highlands County, Florida, Layne and Glover (1977) found minimum home ranges from 1.6 ha to 13.8 ha. A straight line movement of 1,896 m was recorded for one young female.

Armadillos share burrow systems with cottontail rabbits (Clark, 1951), cotton rats (*Sigmodon hispidus*), opossums (*Didelphis virginiana*), and skunks (*Mephitis mephitis*). Insect occupants include camel crickets (*Ceuthophilus* sp.), mosquitoes (*Psorophora ferox*), and ants (*Monomorium* sp.). Mites and spiders have also been found in armadillo burrows (Taber, 1945).

In central Texas, the average burrow length was 125 cm ($n = 26$). Thirteen burrows led to enlarged nest chambers filled with vegetable debris. The average vertical depth to the nest chamber was 50 cm, although an extreme of 151 cm was measured. Burrows averaged 17 cm in diameter, and nest chambers averaged 34 cm in diameter (Clark, 1951). In central Texas, Taber (1945) estimated one armadillo to 4.5 burrows; on the coastal prairies he estimated one animal to 8.5 burrows.

Compared to opossums, raccoons, and skunks, armadillos have relatively few parasites (Chandler, 1946). Talmage and Buchanan (1954) give a detailed account of *Dasypus* parasites. All ticks reported on armadillos are of the genus *Amblyomma*, and *A. concolor* and *A. pseudocolor* are considered true *D. novemcinctus* parasites (Storrs, 1971). Although rare, fleas found on the nine-banded armadillo include *Tunga travassosi*, *Juxtapulex echidnophagoides*, *Echidnophaga gallenacea*, *Polygenis roberti*, and *P. occidentalis* (Hightower et al., 1953; Storrs, 1971).

Dasypus has long been known to be a carrier of *Trypanosoma cruzi*, the infective organism of Chagas' disease. Armadillos probably become infected by ingesting infected insects or their feces (Talmage and Buchanan, 1954). Helminths reported from *D. novemcinctus* include *Brachylaemus virginianus*, *Oncicola canis*, *Hamanniella* sp., *Aspidodera fasciata*, *Physocephalus* sp., *Ascariops* sp. (Chandler, 1946), *Travassosia carinii*, *Oochoristica* sp., and *Mazzia mazzia* (Talmage and Buchanan, 1954). Armadillos are hosts for several Strongyloidea, including *Macielia macieli*, *M. flagellata*, *Delicata ransomi*, *D. uncinata*, *D. cameroni*, *Pulchrostrongylus complexus*, *Dasypostrongylus filamentosus*, *Moennigia moennigi*, *Pintonema intrusa*, *P. pulchra*, *P. pseudopulchra* and *P. pintoii* (Storrs, 1971). Kuntz et al. (1975) reported that *D. novemcinctus* is moderately susceptible to infection by *Schistosoma haematobium* but that no significant pathology develops and no parasites or eggs are found in the urogenital system.

Kirchheimer and Storrs (1971) and Kirchheimer et al. (1972) chose the armadillo as a possible model for the study of leprosy because of its low body temperature and because replication of experiments on genetically identical individuals would be possible. Armadillos were injected with leprosy bacilli prepared from humans. One armadillo developed lepromatid leprosy 14 months after infection, showing over a 1,000 fold increase in bacilli count in injection sites and also showing infection at sites remote from the site of inoculation. Eighteen of 20 armadillos in later studies developed severe disseminated leprotic disease, involving skin, bone marrow, liver, spleen, lymph nodes, lung meninges, and eye (Storrs et al., 1973). Comparison of bacteria isolated from lesions of lepromatid leprosy in the armadillo with *Mycobacterium leprae* isolated from human lesions showed that the bacteria were identical (Convit and Pinaridi, 1974). Lepromatous leprosy, in armadillos, involves visceral organs as well as extremities because of cooler body temperature. Purtilo et al. (1974) suggested that cellular immunity to leprosy may be modified by cool temperatures.

Sixty-eight per cent of animals examined by Stuart et al. (1977) showed spontaneous renal disease. Jackson et al. (1972) reported strong accumulations of strontium-90 in the exoskeletal

scutes of *D. novemcinctus* from radioactive fallout via the normal food chain.

BEHAVIOR. *Dasypus novemcinctus* is described as nocturnal or crepuscular (Kalmbach, 1943; Newman, 1913). Bider (1962) recorded active armadillos from 1700 h to 0900 h with a peak between 2100 h and 2200 h. Clark (1951) observed armadillos foraging as early as 1430 h, but stated the extended activity could have been due to conditions of extreme drought. Rainy and cloudy weather as well as cold weather tend to induce armadillos to become active earlier in the day (Kalmbach, 1943; Taber, 1945). Talmage and Buchanan (1954) felt that the armadillo oriented with respect to temperature rather than light. Foraging patterns may be erratic and random (Clark, 1951; Kalmbach, 1943; Taber, 1945; Talmage and Buchanan, 1954), but Bailey (1905) and Neck (1976) reported armadillos following crude trails in foraging activity.

The armadillo relies heavily on a keen sense of smell when searching for food. It shuffles along, nose to the ground, stopping to root with its nose, and digs a small conical hole with its forefeet when a food item is found. A muffled grunting often accompanies the rooting and digging activity (Kalmbach, 1943).

Newman and Baker (1942) observed an armadillo feeding on young cottontail rabbits (*Sylvilagus*) by using the forefeet to hold the carcass down while chunks of flesh were chewed off. Armadillos have also been seen using the forefeet to crack bird eggs (Kalmbach, 1943). Water is a requisite part of an armadillo's diet and drinking is accomplished much in the same manner as in dogs (Kalmbach, 1943).

During periods of foraging or traveling, an armadillo will periodically rear up on its hind legs, using its tail for a brace, and turn its head slowly from side to side, sniffing the air (Clark, 1951; Kalmbach, 1943).

There are several accounts of armadillos outrunning hunters and dogs (Kalmbach, 1943; Roosevelt, 1919; Talmage and Buchanan, 1954). Clark (1951) reported a buzzing sound made when an animal was running as hard as possible. Contrary to some reports (Audubon and Bachman, 1854; Borrero, 1967), *D. novemcinctus* does not curl up into a tight ball to avoid danger, although the three-banded armadillos, *Tolypeutes* spp., assume this protective posture if threatened (Kalmbach, 1943). *D. novemcinctus* does exhibit a characteristic nervous reflex when alarmed; it jumps straight up and arches the back (Talmage and Buchanan, 1954). When chased into a burrow an armadillo will arch its back, wedging the armor-like scales into the dirt of the roof, making it almost impossible to pull the animal from the burrow (Talmage and Buchanan, 1954).

Armadillos are believed to pair for each breeding season (Newman, 1913) and a male and a female may share a burrow during the season (Kalmbach, 1943). Because of the bony carapace and ventral position of the genitalia, copulation occurs with the female lying on her back (Newman, 1913; Walker et al., 1968). The young may remain with the mother even after weaning until they are several months old (Taber, 1945).

Dasypus novemcinctus apparently shows no tendency toward territoriality. Clark (1951) observed three animals of both sexes feeding very closely with no sign of intraspecific aggression. Greatly overlapping home ranges offer further evidence of non-territoriality (Clark, 1951). Taber's (1945) work with captive armadillos showed a complete lack of concern about the presence of other armadillos, with several individuals of both sexes sharing a common nest box. Wampler (1969), however, reported that a sick or injured animal in a colony may become subject to mutilation or cannibalism.

Burrow and nest construction is unique. The nose and forefeet are utilized in loosening soil, which is then pushed with the forefeet into a small pile beneath the abdomen. The armadillo then balances momentarily on forefeet and tail while bringing the hindfeet forward over the pile of dirt. The animal arches its back and then suddenly straightens out by thrusting back and upward with the hindlimbs, throwing dirt several feet to the rear (Taber, 1945).

Nest material (leaves, dead grass, twigs) is brought to the burrow by raking a pile of vegetation beneath the body with the forefeet so that the pile rests on top of the hind feet. While balancing with the tail, the forefeet are then lowered to the ground, clamping the pile of vegetation under the body. The animal then shuffles backwards on a zigzag course to its burrow. The tail is extended backward and may serve a tactile function. Once the burrow is reached the animal backs into it, raking the vegetation into the hole with its forefeet and nose (Clark, 1951; Taber, 1945).

A controversial aspect of *Dasypus* behavior has been its abil-

ity to swim and/or walk under water. Although not a regular practice, when the water is shallow and the distance short, *D. novemcinctus* may walk across the bottom of a body of water rather than swimming (Kalmbach, 1943; Taber, 1945). This is possible for two reasons: first, the armadillo has a normal specific gravity of 1.06; and second, the armadillo can accumulate a considerable oxygen debt, as discussed above (Kalmbach, 1943; Talmage and Buchanan, 1954). *D. novemcinctus* is also capable of swimming for considerable distances, using a style similar to that of dogs (Talmage and Buchanan, 1954). When an armadillo first enters the water it is almost totally submerged. By repeatedly gasping, the animal ingests air into the digestive tract increasing buoyancy. The longer it is in the water the higher it rides (Kalmbach, 1943). Kalmbach (1943) and Taber (1945) discussed experiments involving the distance and duration of swimming in *D. novemcinctus*.

GENETICS. Beath et al. (1962) found the diploid chromosome count to be 64. The autosomes separate into five groups: two pairs of large metacentrics, four pairs of large acrocentrics, six pairs of medium metacentrics, 14 pairs of medium acrocentrics, and five pairs of small acrocentrics. One pair of medium metacentrics exhibits a well-defined satellite. The X chromosome is a large metacentric, which can be distinguished from either of the two chromosomes with which it shares its length by having a slightly more medial centromere. The Y chromosome is a small acrocentric. Benirschke et al. (1969) compared the karyotype of *D. novemcinctus* with that of other armadillos.

Storrs and Williams (1968) explored cytoplasmic influences on inheritance in these monozygous quadruplets and discovered that the four individuals from one egg are not identical. They suggested that the variation may be due to slight differences in the cytoplasmic makeup of the four primordial buds, such as differences in migration of mitochondria in the original egg.

REMARKS. The generic name is derived from the Greek *dasypodis* (a hare or rabbit) and is based on the translation of the Aztec name *Azotochli*, meaning tortoise-rabbit (Anderson and Benirschke, 1966). The specific name is a combination of the Latin *novem* (nine) and *cinctus* (banded or girdled). Linnaeus apparently found the Aztec name as reported by the conquistador Hernandez unacceptable for latinization and translated the meaning of "rabbit-turtle" into the Greek *Dasypos* (tautonym) (Anderson and Benirschke, 1966; Thomas, 1911).

The nine-banded armadillo is also known in the vernacular as the long-nosed armadillo, cachicamo, and tatu-hú.

Summaries of the literature subsequent to Kalmbach (1943) and Talmage and Buchanan (1954) include Storrs (1971) and Wetzel and Mondolfi (1979).

Armadillos are frequently used as food in parts of the southern United States and in Latin America. They are customarily roasted or barbequed in the "shell." Their hides have been manufactured into baskets and handbags for the tourist trade and they serve as mascots for bands and beer drinkers in much of the southern United States. Armadillos eat many harmful insects, but they also often are responsible for some crop damage and occasionally attack ground-nesting birds (Kalmbach, 1943); although often accused of preying on turkey and quail eggs, there is no evidence to support these accusations (Taber, 1945). As the only animal besides man that naturally suffers from lepromatid leprosy, the armadillo provides an invaluable medical research tool.

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