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THE ARMADILLO
(Dasyphus novemcinctus)

A REVIEW OF ITS NATURAL HISTORY, ECOLOGY, ANATOMY AND REPRODUCTIVE PHYSIOLOGY

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PREFACE

BEFORE having driven many miles over the highways of east Texas, one is sure to pass the body of an odd looking animal, lying on the side of the highway. This victim of the speeding car is an armadillo, a quaint and reportedly archaic animal, but a newcomer to the United States, and one which is very likely someday to become one of the most common types of mammalian wild-life in the South.

Some time ago one of the daily feature columns in a local Houston newspaper carried two articles on the armadillo. One of these was a scathing treatise on the evils of the little beast in the destruction of garden plants and in the damage to valuable shrubs. The other was an answer to the query of some New England school boys who were seeking an armadillo. This column ended with a remark on this order: "And why would anyone want an armadillo?" This last incident brought an immediate reply from us which appeared shortly in the same column in which we stated that we very much would like to procure some armadillos, and suggested likewise that the armadillo was being maligned by the column. For, in fact, we argued, the armadillo actually aided man by devouring the very insect pests that man was trying so hard to destroy, but that unfortunately, in his devotion to this duty, he occasionally exposed the roots of a shrub or completely dug up a tomato plant.

From that time, armadillos have been plentifully supplied to our laboratory. As physiologists, our interest in these animals has been due to the fact that the process of reproduction includes as part of its regular pattern two very striking and unusual phenomena: one a long delay in the implantation of the blastocyst, and the other the phenomenon of
specific polyembryony which causes each litter to be composed of four young of the same sex. As the result of our lengthening acquaintance with these animals our interest has broadened to include a general study of their habits, their associations and their remarkable advance through the southern United States.

This review is the result of these studies. Its bibliography is intended to be comprehensive and as complete as the authors were able to make it. The subject matter ranges from a general discussion of the natural history of the armadillo to a scientific description of finite parts of its anatomy. It is not expected that the interest of any one individual can be held throughout the review. The Natural History section, we feel, will be of interest to all who are interested in the wild life around them. The other and more technical sections are an attempt to bring together the greater part of the accumulated scientific knowledge concerning this animal. We hope that, by this book, the scientist and layman alike can become acquainted with what we consider one of the strangest and most interesting mammals invading our land today.

We wish to express our particular appreciation to Dr. A. C. Chandler for editing the section on Parasites, to Mrs. Frances W. Kraintz for her aid and work on all parts of the manuscript, and to Miss Pat Bowman for the drawing used as the frontispiece of the monograph.

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Houston, Texas
April 1, 1954
THE NATURAL HISTORY OF THE NINE-BANDED ARMA DILLO IN THE UNITED STATES

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In his recent book, *Possums*, Hartman (1952) mentions the armadillo as being, along with the opossum, one of the “strange beasts” of this country. Although the possum is better known than the armadillo, it is probable that the latter would win any contest conducted among North American mammals to determine the strangest of them. The local armadillo, *Dasypus novemcinctus mexicanus*, Peters, though not fabled in song and story as are some of our long indigenous creatures, is not completely without a legendary portfolio; and one of his cousins, *Chaetophractus villosus*, the peludo armadillo of Argentina, is to the children of the Pampas what “Br’er Rabbit” is to children of the Southern United States (Hudson, 1922). The Mayan Indians had a legend that the black headed vulture, when it became old, crawled into a hole and became an armadillo (Nelson, 1918). The majority of the “tall tales” regarding the armadillo, however, are to be found in several scientific works which ascribe to the animal numerous physically impossible powers. These will be discussed under later headings.

**Appearance**

Being quite singular in appearance, the armadillo is nonetheless exceedingly difficult to describe simply. It is variously pictured as resembling a pig in a turtle’s shell (Audubon and Bachman, 1854), a small tank (Maslowski, 1948), tortoise-rabbit (translation of the Aztec name for *D. novemcinctus*) (Gadaw, 1908) or a knight in armor (Breland, 1953). Dressed out, the animal looks much like a rabbit with a malformed head, or somewhat like an opossum. The animal is comparable in size to an opossum, but is considerably heavier,
due to the sturdy build and shell. Perhaps the most expressive, if not the most scientific, description of an armadillo is that given to Strecker (1928), by a Negro resident of Louisiana. He called it a “dry-lan’ varmint, wid er turpin shell.”

**Daily Habits**

The nine-banded armadillo inhabits many diverse ecological communities over its tremendous range. But, with minor variations in burrowing habits and items in diet necessitated by strictly local conditions, its habits are generally constant. Usually described as nocturnal or crepuscular (Kalmbach, 1943; Newman, 1913a; Nelson, 1918), the armadillo seems to be oriented not so much with respect to light, as with respect to temperature. Cold greatly hampers the animal’s movements (see section on environmental relationships) and it does not go abroad at all in very cold weather. In the summer the armadillo seems to avoid the hottest part of the day, coming out near sundown, or immediately following rains or extreme cloudiness, if the temperature falls. (Taber, 1945).

Upon leaving its den the armadillo immediately begins to forage. When not foraging, the animal walks with a shuffling gait or trots like a pig, and is likely to shift from one gait to another for no apparent reason (Newman, 1949; Taber, 1945; Clark, 1951).

The feeding armadillo is a perfect picture of devotion to duty, for when so occupied it is almost oblivious to its surroundings. An actively feeding animal progresses at a rate of perhaps one third of a mile per hour (Lehmann, 1934) and appears to follow a completely random route. The observed fact that the number of burrows exceeds by far the
number of armadillos has led to speculation as to whether or not these supplementary burrows serve as food traps. Certainly, insects suitable as food are found in these non-home burrows. It is safe to assume that the armadillo which enters one of them will enjoy a repast. However, visits to these secondary burrows are apparently chance occurrences. (Kalmbach, 1943; Taber, 1945; Clark, 1951).

The armadillo locates food exclusively by the sense of smell. When foraging, the nose is held just off the ground, often ploughing a furrow in the litter of the forest floor, which constitutes one of its favorite haunts. The animal can locate grubs beneath five or six inches of earth, and when food is found, immediately digs a steep conical hole, using both the forepaws and the nose (Taber, 1945). When ant or termite nests are attacked, the animal may become nearly buried in the litter in its search for these choice morsels (Ingles, 1953).

The only confirmed use of the vocal cords made by the armadillo is a wheezy grunting sound emitted while feeding (Kalmbach, 1943; Clark, 1951). However, Clark also describes a buzzing noise made by the armadillo when thoroughly alarmed.

The olfactory senses are not only utilized in food-getting, but serve also as the first line of defense for the animal. While foraging or just traveling, the animal stops at intervals, rears on its haunches, and tests the air (Kalmbach, 1943; Clark, 1951).

The animal’s hearing is probably of average acuteness though this is open to some argument. Newman (1913a) described the hearing as not at all keen since the animal could be approached without disturbing his activity. However, Clark (1914) reported the hearing as satisfactory. In this connection, it might be observed that the animal appears
to have great powers of concentration when occupied with the search for food.

The eyes are very small for an animal of its size, and are usually described as rudimentary (Newman, 1913a). Certainly, the armadillo does not rely heavily on its eyesight. This is not surprising when one considers that the animal, when actually probing for food, often has the eyes covered.

There is probably more longstanding misinformation about the armadillo’s defense against enemies than any other subject. Early workers (Audubon and Bachman, 1854; Baird, 1857) said the armadillo was unable to run fast and thus could be easily caught; this fallacy is still found in more recent works (Nelson, 1918; Hamilton, 1943). The clumsy appearance and awkward gait of the armadillo are very deceiving, for when alarmed it is capable of astonishing speed and agility (Kalmbach, 1943). It is quite as fast as a man in open country. While it is unable to outdistance a grown dog, it is able to twist and dodge so effectively that, coupled with the fact that only the tail offers a mouth hold, it usually eludes the pursuer. Roosevelt (1919) graphically described an encounter between two nine-banded armadillos and a pack of hunting dogs in Brazil.

While actively feeding, an armadillo is not easily induced to flee. However, they do exhibit a nervous reflex to sudden noises. The reflex consists of jumping straight upward like a bucking horse. They usually resume their probing, or whatever they were doing, and only after being so startled several times do they take flight. This reflex probably causes them more harm than good in their encounters with automobiles, for there are indications that they are often killed, not by being run over by a wheel, but rather by being struck by some under part of the car when they jump upward (Kalmbach, 1933, 1943).
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The armored skin of the armadillo serves him well as a means of defense, but not in the manner usually supposed. Early workers (Baird, 1857; Audubon and Bachman, 1854; Elliot, 1904) and unfortunately, present day reports as well (Nelson, 1918; Hamilton, 1943; Writer’s Program, W.P.A., N.Y., 1940) describe the armadillo as “rolling up into an iron clad ball” when attacked, and some even claim that it will roll down hill to escape enemies. In the first place, it is physically impossible for the nine-banded armadillo to roll up in a ball. The authors have tried to curl freshly dead animals into balls; this simply could not be done, unless one wished to break several bones. In the second place, the bony shell of the armadillo is not so sturdy as to be an adequate passive defense (Newman, 1913a; Kalmbach, 1943). One species of armadillo (Tolypuetes tricinctus) found in South America does curl up in a ball when attacked, (Krieg, 1941; Scott, 1929; and Sanborn, 1930a), and, owing to a heavier armor, the edges of which are sculptured so as to fit together perfectly, it is relatively safe from attack. Sanborn (1930a) has described its habits, and points out that dogs will not even bother with T. tricinctus, but will pursue the six- or nine-banded armadillos which occur in the same area.

The armadillo’s shell serves the armadillo much as do the chaps of the cattleman. It enables the animal to plunge headlong into tangled and thorny brush, which is impenetrable to other animals. The anterior part of the pectoral girdle extends slightly forward on each side. By ducking its head down so that these projections protect the eyes and the unarmored side of the head, the animal can push through an indescribably thick tangle, with only the ears exposed. That this is done often is apparent by the fact that most adults have nicks and tears in the ears. The armor also serves to allow the armadillo to search into such areas for food.
Clark (1951) has stated that in his observations armadillos always seemed perfectly oriented, heading for the "home" burrow when pursued, passing up others on the way. If one assumes, as seems reasonable, that the armadillo's eyes are poor, it is likely that it locates its burrow by using the sense of smell in such circumstances. Those burrows not used frequently will not have sufficient spoor trails leading toward them to allow them to be located. Thus a retreating armadillo might pass several burrows simply because it does not detect them, and enter the "home" burrow because it is the only one found. Further experiments on this point and on that concerning the visual acuity of the animal would be desirable.

Once inside a burrow, the armadillo can again employ its armor, for by arching its back against the roof, it can resist extraction most effectively. The animal can, however, be induced to release its hold by tickling the stomach (Maslowski, 1948). The authors have employed this technique and found it effective. The tickling causes the armadillo to kick with its powerful hind quarters; the traction broken, the animal may be extracted in a great shower of dirt and confusion. The claw marks invariably obtained heal nicely in a few days.

Swimming

One of the less credible stories about the armadillo concerns its reputed ability to walk under water. More amazing than the story is the fact that this is true. This is not to say that this is the normal procedure employed by the armadillo in crossing streams, but at least it has been experimentally observed. (Kalmbach, 1933, 1943; Taber, 1945). The armadillo can accomplish this for two reasons: first, due to its heavy build, the animal has a normal specific gravity of
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more than one. Kalmbach (1943) determined, for an animal he captured, a specific gravity of 1.06. Second, as discussed in the section on physiology, the armadillo can accumulate a considerable oxygen debt. Scholander et al. (1943) observed that an armadillo can struggle violently for some six minutes without being able to breathe. Armadillos can swim, dog fashion, and most often when placed in water this is how they manage their exit. A number of workers (Aldous, 1943; Kalmbach, 1933, 1943; Maslowski, 1948) have observed that after an armadillo had been swimming some time, its girth increased appreciably. This was found to be due to the ingestion of air which distends the stomach and small intestine. Lehmann (1934) probably observed the armadillo swallowing air when in the water, but thought the animal was gasping for air. Taber (1945) reported that he was unable to confirm Kalmbach's observations regarding air ingestion. It is not known under what conditions the armadillo walks under water instead of swimming, since this walking has apparently been observed only experimentally. Kalmbach feels that the animal walks only when the distance is short and the water shallow; however, Hardberger (1950) reports that a Louisiana schoolboy claimed to have caught one in a seine in six feet of water.

Burrows and Nests

The location, type and extent of armadillo burrows depends upon the character of the soil. A typical home (nesting) burrow consists of a tunnel of 7-8" diameter some four to twenty-four feet in length, at the end of which is a slight enlargement for the nest. Whether or not tunnels are straight seems to depend on obstacles met in tunneling. Home burrows often have two and occasionally more tunnels leading
to the outside; however, only one is regularly used. The expression "home burrow" is necessary because there are usually more burrows than armadillos in any given area. The function of these accessory burrows is somewhat problematical. They may serve either as food traps, or temporary shelters (see section on Daily Habits). Burrow entrances are usually situated in the side of a bank or mound of earth, but this is not invariably true (Kalmbach, 1933, 1943; Taber, 1945; Clark, 1951). Further discussion of the number and types of burrows will be found in the section on environmental relationships.

The nest consists of a mass of leaves or grass which the armadillo stuffs in the nesting chamber, and into which the animal forces its way to sleep. The nesting material may be half a bushel in volume. The manner of carrying the nesting material to the nest was a puzzle for some time. Lehmann (1934) thought the animals must push the material into the burrow. Kalmbach (1943), observing armadillos in holding pens, saw them pile up corn shucks, which had been put into the pen, and then squat down over the pile and back slowly to and into the burrow. Clark (1951) observed this same procedure by armadillos in the wild. He said that they hopped backwards toward the burrow. Both Kalmbach and Clark thought the tail was used in a tactile manner when moving material into the nest. The authors at one time kept armadillos in a large pen with a concrete floor. Wooden boxes with short enclosed tunnel entrances were provided for nests, and nesting material was placed within. It was noted that within several days the animals became very dirty and feces were smeared over the carapace. This was puzzling, since no animal will ordinarily defecate within its nest unless it is prevented from leaving. One day an armadillo was seen to move backward into its box, pulling several balls of feces
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with its forepaws, apparently instinctively trying to make a nest.

Armadillos change the nesting material occasionally and piles of wet and rotting leaves are often found near the entrances of burrows, especially after rains or floods. Such a pile of debris was near the burrow entrance of the animal observed by Clark (1951). Before leaving the subject of burrows it would be well to mention the armadillo’s digging ability. Armadillos are admittedly excellent excavators, and are reputed to be able to bury themselves entirely in one or two minutes. Taber (1945) reports seeing an armadillo actually do this in soil so hard it required a pick for a man to dig.

Armadillo Trails and Signs

The armadillo leaves an easily recognized trail wherever it goes, for the dragging tail leaves an imprint not unlike a rope (Newman, 1913a). Since the trail is so plain and distinctive, the armadillo has often received the blame for the misdeeds of other animals which preceded it to a given spot. (Kalmbach, 1943).

Armadillo feces are spherical and about \( \frac{3}{8} \)–1 inch in diameter. They appear to be made up of mud, but are actually composed principally of the hard indigestible parts of the insects they eat, with some soil presumably accidentally ingested, acting as a binder (Taber, 1945). Taber describes mud streaming from the anus of an armadillo he caught. He ascribed this as being due to the animal’s having ingested mud while feeding at the edge of some nearby ponds. The authors have seen this phenomenon several times in armadillos which were not near ponds at all. As noted in the section on food habits, the amount of dirt found in the armadillo stomach is small. It is to be wondered if what is seen
in these cases is really not mud, but thousands of small insect body parts which have not yet formed into boluses. Unfortunately, this material was not examined closely. Should it prove to be composed largely of mud, then the possibility exists that the armadillo may be less discriminate in eating than supposed, or that, perhaps, under certain circumstances, moist earth is ingested to secure its water content.

Feces are not found in the nest, although they have occasionally been found in the tunnels (Taber, 1945). In this connection it may be possible that these pellets were raked inside in the manner described for our caged animals. Usually fecal pellets are found singly or, less frequently, several close together, along the trails used by armadillos. One animal, which Taber (1945) had partially tamed, was observed to dig a hole in an ant bed and cover its feces in the manner of cats.

References to Habits of Other Armadillos

There are several accounts of the habits of some of the other species of armadillos. Gray (1873e) described the habits of a specimen of *Cabassous unicinctus* which was in the zoological gardens at London. Hensel (1872) discussed the habits of this species in Brazil. Cully (1939) described the diet and daily habits of a *Priodontes giganteus* on exhibition in the New York Zoological Society's gardens. Krieg (1941) gives an account of the daily habits of *Tolypuotes* in Brazil. The articles of Peard (1899), Aplin (1908) and Holzapfel (1939) described some of the habits of *Chaetophractus villosus*. Leybold (1865) discusses the habits of *Zaedypus pichiy*.

In 1880, White described some of the daily habits and the usual habitat of *Chlamyphorus truncatus*. Miniprio (1945) has an excellent and extensive work on this species. His
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studies cover range, habits, and taxonomy of the animal. Hensel (1872) discusses the habits of *Dasypus hybridus* and *D. novemcinctus* in Brazil. Dugès (1902) also describes some of the habits of *D. novemcinctus*.

Several articles of a popular nature have appeared in recent years which deal with the habits of *D. novemcinctus* in the United States (Trester, 1950; Breland, 1953). Other articles of this type are mentioned elsewhere in this monograph.

**Environmental Relationships**

*Climate*

As will be discussed in the section on the range of the armadillo, *Dasypus novemcinctus* occurs over a large part of South America, Central Mexico, and the Southern United States. It is obvious that the animal is able to live in a number of diverse ecological situations. Its entire range can be characterized, however, as having neither extreme cold nor extended periods of cold weather. The armadillo has very poor temperature control. At 72°F. it is uncomfortably cool and shivers continually. At colder temperatures it cannot long survive unless provided with adequate nesting material into which it can crawl. Two factors, probably, have allowed the armadillo to reach its present northern range. First, its nest is of such a construction that the animal literally packs itself in insulation. While in the nest it can survive for some time unless the ground is frozen down to that level. Second, in the northern part of the area now inhabited, although it may get quite cold at times, the periods of cold weather are not normally protracted and the interim periods of relatively mild weather allow the animals to forage for food. The animal does not hibernate, and while able to go for relatively long periods without eating, must seek food
Natural History during all seasons of the year. At the other extreme, hot weather does not markedly effect the nine-banded armadillo, other than to limit its activities to the cooler part of the day or to the night (see section on habits).

The amount of rainfall apparently limits the armadillo quite sharply by its effect on the food supply. In spite of the fact that some workers have described the armadillo as a denizen of the semi-arid regions (Bailey, 1905; Newman, 1913a; Lehmann, 1934), this is not so. However, it does occur at the edge of the semi-arid areas, and during especially favorable times may push into almost barren sections (see section on Range). The lack of rainfall in West Texas appears to be the limiting factor in the westward extension of its range.

Armadillos seem to prefer wooded areas such as occur in East Texas, and although Strecker (1928) predicted otherwise, they have also taken to the swamps of Louisiana. With rainfall limiting further permanent migration of the armadillo to the west, and the severe winters preventing the animal from going further north, it appears that its primary future expansion will be eastward.

Soil

Taber (1945) points out that it is difficult to note any influence of the type of soil on the armadillo. It is likely that aside from causing alterations in the architecture of the burrow, there is little direct effect exerted in this regard. Dasypus novemcinctus occurs in areas consisting of all types of soil and as a general rule, it may be stated that the easier the soil is to dig, the more elaborate and complex will be the burrows. In addition, there will be more burrows per animal under these conditions.

A few references (Taber, 1940; Kalmbach, 1943; Taylor,
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1946; Clark, 1951) give information as to the population density of armadillos under various soil conditions in Texas. Very dry, hard-packed soil limits the armadillo's probing activity as well as its burrowing efforts; however, this is a condition referable to the climate and not to the soil per se. Further, it is possible that in this circumstance a shortage of food for which to probe would be more critical than the difficulty in securing it.

Water

Although armadillos occur in habitats ranging from swampy to relatively dry, within a given area they will usually be found relatively close to the supply of water. Two circumstances appear to account for this. First, the food supply will usually be more abundant in the more moist area; second, armadillos by preference burrow into an inclined surface such as the side of a stream bank; but so far as burrowing is concerned, it seems to have no really direct relation to the water, since burrows occur just as frequently along the banks of intermittent or dry stream beds. During flood periods there is a migration away from the streams. Conversely, in periods of drought, there is a movement toward the remaining water. It is not known whether or not this movement is caused by a need of water or is related to the food supply (Taber, 1945).

Plant Associations

Plants serve armadillos as cover (Taber, 1945). Burrow entrances are located whenever possible at the base of a tree or bush. Hence, there is no relationship with any particular plant species, the only requirement being an extensive root system. Armadillos occur in greatest numbers in areas of dense growth (Clark, 1951). This again is probably cor-
related with the fact that such areas would support a better food supply. There is also the fact that the armadillo can move with impunity in dense and thorny brush, where a would-be predator would experience much difficulty, thus this may be a protective measure.

Animal Associations

Those animals upon which the armadillo preys are discussed under the heading of food habits, and will not be referred to here. Only the larger carnivores, such as wolves, coyotes, cougars, etc., are likely candidates for the position of predator upon the armadillo. It is mentioned in the range section that the general opinion holds that the decimation of these carnivorous animals was in part, at least, responsible for the expansion of the armadillo's range. So far as the record is concerned, this opinion seems hardly justified, since little proof of predation upon armadillos is offered. Sperry (1941) examined the stomach contents of 566 coyotes and found no armadillo remains. Kalmbach (1943) reported remains of an armadillo in the stomach of a cougar; however, there seems to be little other evidence regarding armadillo predation. Regardless of the past situation, the only enemy which the armadillo seems to have now is man, his dog, and his car (Dickerson, 1939; Kalmbach, 1943; Siegler, 1944). In parts of Texas and Louisiana the armadillo is hunted for food, and it is generally considered fair game by the hunter and farmer, who feel that it must be guilty of many crimes against game birds and crops (see food habits). The nine-banded armadillo comprises a major food item to many rural families, and in fact, at one time, several 4-H clubs in Texas carried out a project of canning the meat (Kalmbach, 1943).

Use as food is not confined to this country, for several authors (Darwin, 1933; Prichard, 1902a; Hudson, 1917) record that
they are roasted in the shell by the Argentinean gauchos.

The extensive burrowing activities of the armadillo lead to the establishment of a sort of commensalism with several other animals. Taber (1941) discusses the possible value of the armadillo to fur-bearing animals. Lay and Baker (1938) and Lay (1942) have found possums and wood rats utilizing armadillo dens. Taber (1945) reports finding rabbits, rats, skunks, opossums, and burrowing owls in unused armadillo dens. He also mentions observing quail and rabbits using armadillo dens to escape hunters. Clark (1951) reports a case of an armadillo apparently evicting a skunk from its burrow. Nelson (1918) reports a rabbit and a rattlesnake found in different side chambers of the same den occupied by an armadillo. Clark also lists a number of arthropods found in armadillo burrows. Crickets and several spiders were found. These animals were apparently only incidental inhabitants, although it is probable that at least the crickets were eaten when found. A number of mites were found in the nesting material but their relationship to the armadillo is not known.

Two phases of the armadillo's ecology, food habits and parasites, are treated in separate sections.

Range of the Nine-Banded Armadillo in the United States

Introduction

Speaking of Dasypus novemcinctus, Hamlett (1939) said: "This species has an amazing distribution. It ranges south into northern Argentina, spreads over all the countries east of the Andes, reaches the Pacific slope in Ecuador, extends throughout Central America and most of Mexico, and at present is spreading north and east in the United States. It has already reached Oklahoma and Louisiana, at least one has been killed in Kansas, and Florida has been partly
collected..." *Dasypus novemcinctus* has a wider distribution than any other species of *Dasypodidae* and it is still extending its range. Relative to this continued expansion, there are several questions unanswered: 1) What started this range expansion and how long has it been occurring? and 2) How far will it go and what will stop it? The indications are that as yet the second question cannot be answered. Three times in the past, workers have postulated a particular range as being the furthest the animal would be able to move northward (Bailey, 1905; Newman, 1913a; and Taber 1945) and each time these limits have been surpassed. As for how long this expansion has been continuing, it is likely that it will never be known. The records of the armadillo's range go back only about a century and during all that time the animal has been spreading north and east in the United States.

Some workers feel that the armadillo began to expand its range during the latter half of the nineteenth century (Strecker, 1926; Price and Gunter, 1943). They cite the encroachment of civilization and the corresponding destruction of the large carnivores, wolves, coyotes, cougars, etc., as a probable mechanism for allowing the armadillo to increase its numbers and expand its range. Certainly, the area concerned (Texas) was being settled during this period (1850-1900), and the larger carnivorous animals were being decimated on a wholesale scale, and the records do indicate a concurrent appreciable advance in range by the armadillo. It has not been proved, however, that the animal was not already extending its range at this time. If it were, it might have continued to advance even if the country had not been settled.

It is possible also, that the early records indicating that the armadillo was extending its range were in reality merely
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the recording of the animal in its existing range, by men who were extending their observations to new territory. While the decimation of the ranks of the large predators may not have led to an actual extension of the armadillo's range, it is probable that their absence allowed the armadillo to become abundant in areas where it was formerly scarce, perhaps giving the impression of a range extension which in reality would be a range exploitation.

On the other hand, if the armadillo did have a stable range prior to the latter part of the nineteenth century, it would be most interesting to determine what causative agents initiated the advance of the animal. The previously mentioned factor of predators, if a factor, was probably only a minor one (see section on Animal Associations). Since these predators have occurred within, as well as without, the range of the armadillo for as long as records are available, it would seem illogical to assume that they prevented its northern spread while at the same time coexisting in its southern habitat.

While the extermination of the predators may have assisted in the rate of expansion, it appears a more fundamental cause is needed for its initiation. Price and Gunter (1943) discuss changes in topography of South Texas as well as the range changes of the armadillo, coati mundi and the chaparral brush which have occurred in the last century. They feel that some fundamental climactic change, occurring in the latter 1880s, triggered the march north of the several species which they discuss. While more study is needed, on the whole it would seem that this line of approach would be most profitable.

**U.S. Range of the Armadillo prior to 1900**

It appears that the earliest reference to the armadillo in the United States is in Audubon and Bachman, *Quadrupeds*
They describe it as existing in the “southern portion of Texas . . . along the lower shores of the Rio Grande.” Baird, in 1857, gave essentially the same range. In 1859, he delineated the range further by saying that the animal occurred no higher (north) than Ringgold Barracks and not too far east of the Rio Grande. Cope (1880) described the armadillo as being found as far east as the Nueces River and north to latitude 29°. His range is shown on the accompanying map (Figure 1) taken from Buchanan and Talmage (1954). Mearns (1907) listed a U.S. range which was very similar to that of Cope. Strecker (1926) appears to have been the only one to attempt to determine whether or not the armadillo was in Texas prior to the time of the studies listed above. He consulted old journals of travel and life in early Texas history and found a few references to the armadillo which indicated that it was confined to the Rio Grande region.

The Advance of the Armadillo through Texas

In 1905, Bailey in his Biological Survey of Texas published the first range map for the armadillo. As shown by his map (included in Figure 1) the armadillo had pushed north and west, had ascended the Pecos Valley, and entered the southeastern corner of New Mexico.

Subsequently, the animals moved eastward and to the north. Strecker (1926) was the first to note this continuous range expansion and commented on its rate and the direction it was expanding. In 1928, the Field Book of North American Mammals (Anthony, 1928) gave the armadillo’s distribution as north to latitude 33° and west to Devils River. This range excluded the Pecos Valley Portion of Bailey’s 1905 map. Since this was but a brief range reference, with no authority given, it is not known whether this retraction of the western extension was an error or was based on an actual survey. However, Lehmann (1934) reported a similar westward distri-
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Distribution in a range map which he stated was as of 1914. For this year he excludes all of Bailey's range north and west of a line drawn between Val Verde and Hamilton counties and to the east noted that the animal had crossed the Brazos and moved to the Trinity, and along the coast had already reached the Louisiana line (see Lehmann's 1914 Range given in Figure 1). In this connection, Peterson (1946) claimed that the armadillo had reached into Brazos county by 1910. Lehmann (1934) also gave the range as of 1920. The portion west of Brownwood was the same as in 1914. The eastern portion showed a northward movement to approximately latitude 33°.

Four range maps published since those of Lehmann (Taber, 1939; Kalmbach, 1943; Texas Game, Fish and Oyster Commission, 1945; and Fitch et al., 1952) all indicate the western boundary as that of Bailey (1905) extending the range up into a corner of New Mexico. The discrepancy is not easy to explain. The present range of the armadillo as shown by Buchanan and Talmage (1954) indicates that the armadillo is no longer found in the Pecos valley. These authors note that game wardens in some of the west Texas counties claim that the armadillo has been gone from there for many years. The continued eastward and northward march of the armadillo through Texas is shown in the successive range maps cited above.

The Armadillo in New Mexico

As noted above, Bailey, in 1905, indicated that the arma-

Figure 1. The Range of the Armadillo in the United States
(Taken from Buchanan and Talmage, 1954)

Figure 1-A—Western Portion of Range containing the original and main population of armadillos.
dillo had entered New Mexico via the Pecos River valley. He also listed it as a rare resident of the southeastern part of the state as late as 1931. Buchanan and Talmage (1954) report that armadillos are no longer found in New Mexico, and according to the older residents of the southeastern area have been absent from the state for at least twenty years. However, armadillo shells are occasionally found around San Simon Sink indicating their presence there at one time.

**The Armadillo in Louisiana**

According to Strecker (1926), there were reports of armadillos in Louisiana for several years prior to 1926. This is in good accordance with the data of Lehmann (1934) for his Texas range of 1914 in which he states that the animal had reached the Louisiana border. However, official notice of its presence in Louisiana seems not to have been made until Strecker's 1926 record of the capture of one near Gayle. In 1928, he recorded its presence at Ruston. The numerous sites listed by Lowery (1936) show that by 1936 it was fairly well distributed over the state west of the Mississippi, and by 1943 it was found not infrequently on the east side of the river (Lowery, 1943). In 1950 Hardberger described the armadillo range as covering essentially all of Louisiana and

Figure 1-B—Eastern Portion of Range showing the separation between the Western and Florida colonies with the small isolated Alabama colony between.

**Key:**

--- Edward Cope, 1880

---------- Fig. 1-A Vernon Bailey, 1905

----- Fig. 1-B, C. Newman, 1949

--- V. Lehmann, 1914

----------- Tex. Game, Fish and Oyster Comm. 1945

--- Buchanan and Talmage, 1954
parts of southwest Mississippi. Buchanan and Talmage (1954) include the entire state in their range though this state was not surveyed. Their basis for this inclusion was the work of Hardberger (1950) and the fact that their 1954 survey showed it in all states surrounding Louisiana.

*The Armadillo in Oklahoma*

Blair (1936) recorded the armadillo's presence near Tulsa, and cited reasons for believing the animal had reached there by natural progression. Taber (1939), Kalmbach (1943), Gardner (1948) and Fitch *et al.* (1952) all gave additional records of the animal in Oklahoma. The armadillo apparently entered Oklahoma from Arkansas, moving along the Canadian-Arkansas-Red River systems. At the present time (Buchanan and Talmage, 1954) it appears to be firmly entrenched in the southern part of the state with an isolated colony in north central Oklahoma.

*The Armadillo in Arkansas*

The armadillo was reported near the northern part of the state of Arkansas as early as 1921 (Dellinger and Black, 1940). These may be reports of animals, brought in by man, in which the armadillo failed to become established. By 1944 (Black, 1944) it was fairly well established in the southwestern section entering probably both from Texas and from Louisiana. At present (Buchanan and Talmage, 1954) it occurs in southern Arkansas in an area extending approximately 100 miles north of the Louisiana line.

*The Armadillo in Mississippi*

The armadillo has recently been reported in western Mississippi by both Hardberger (1950) and by Fitch *et al.* (1952). In their 1954 survey, Buchanan and Talmage list western
Mississippi as a questionable inclusion in the armadillo range since the State Game and Fish Commission stated that they were not convinced that the armadillo was established there, though individuals are captured frequently.

**The Armadillo in Alabama**

The armadillo was first reported in Alabama in 1939 by Taber. This animal was captured near Auburn. Due to the distance from the main body in Louisiana it must have been brought in by human agency. This is further borne out by the fact that a colony was not established and armadillos are not reported from this locality now. The first colony to be established in Alabama was near Foley as reported by Fitch *et al.* (1952). This colony is still thriving as are several smaller colonies further up the Mobile River (Buchanan and Talmage, 1954). There is little doubt that all these colonies were started by animals transported to these localities by man.

**The Armadillo in Florida**

A classic example of the successful introduction of an animal into an area is furnished by the colony of armadillos in Florida. The state received three apparently successful inoculations of armadillos on its east coast. During the First World War, a marine brought a pair from Texas to Hileah where they escaped and at least temporarily became established for several were found in the vicinity in the early twenties (Bailey, 1924). A private zoo near Cocoa was destroyed by storm in 1924, liberating several armadillos. These became permanently established in this area (Sherman, 1936) and were strengthened by additional armadillos which escaped from a circus truck which overturned near Titusville in 1936. The colony near Miami apparently died out but
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from the other two loci the animals spread along the east coast and westward as indicated by the reports of Sherman (1943), Moore (1946) and Pournelle (1950). The first range map for Florida was that of Newman (1949) which was also used later by Fitch et al. (1952). This range is indicated in Figure 1. The present range indicates a further increase both northward and westward covering almost a third of the entire state (Buchanan and Talmage, 1954).

Reports of Armadillos in Other States

The armadillo has been reported from Kansas (Hibbard, 1943; Hall, 1944; and Lutz, 1950) and once from Missouri (Mo. Cons., 1947). It is probable that these isolated reports are of animals which had escaped or been freed by travelers or by inhabitants of these areas. There has even been one unpublished report of an armadillo killed by a car in Illinois.

The Present Range of the Armadillo in the United States

(Taken from Buchanan and Talmage, 1954). The present range of the armadillo, *Dasypus novemcinctus mexicanus*, in the United States has been shown to have as its western limits an arc running from Langtrey, Texas on the Mexican border to Lawton, Oklahoma. Its present northern limits vary between the 35th latitude in central Oklahoma and the 34th latitude in eastern Arkansas. The eastern limit of the main population is the Mississippi River except for southern Louisiana where it has become established east of the river. The frequency of the reports of these animals in western Mississippi make it problematical as to whether that area should be included in its range.

In addition to this main population, smaller but expanding colonies have become established in Baldwin County, east
of Mobile, Alabama and in Florida. In the latter state, armadillos now range on the eastern seaboard from Jacksonville south almost to Palm Springs, and have pushed westward across the state to within thirty miles of Tampa (see Figure 1).

Problems of Range Determinations

At the beginning of this section, some questions were raised regarding the range extension of the armadillo. Also, some of the problems of determining whether such a phenomenon is occurring were discussed. Another problem in mapping an animal's range is that of deciding where to draw the line marking the range limits. The periphery of an animal's range is not a sharp demarcation but rather a gradual thinning of the population. As a result there will be some individuals which will occur well ahead of what can logically be called the proper range for the animal. There are numerous examples of this in the literature cited above. For example, in 1884 (Forest and Stream, 1884, cited by Hall, 1944) an armadillo was reported from Denton, Texas. This was only four years after Cope had stated the range of the animal to be south of a line between Eagle Pass and Refugio. In addition, there are cases of animals being transported by human agency to places far removed from their natural range. Such reports as these make interpretation of range lines difficult, since they cannot be logically classed as part of the animal's range. If, however, as in the case of Florida and Alabama, the transplanted animals become established and begin to flourish, they must be recognized as constituting part of the proper range of the animal. The final decision as to where to place the limits of an animal's range must therefore be somewhat subjective and rest with the individual investigator.
A question of some importance is the one regarding the ultimate limit of dispersal of the armadillo in the United States. As mentioned, Bailey (1905), Newman (1913a) and Taber (1945) postulated northern limits that have been long since surpassed. With the animal now at the 35th latitude, it would be incautious to predict another northern limit. Certainly nothing stands in its way to the Atlantic coast. If the present rate of march holds, some of us may see, in our lifetime, the link-up between the Florida and Alabama populations and the main population now in Louisiana.

Hall (1944) in a review of Kalmbach's work, stated that the limit of an animal's range may surge and fall back just as do the tides. If this is so, then we may infer that the animals recorded by Blair (1936) and Taber (1939) represented a crest of a high tide as did the Arkansas animals of Black (1944) and Dellinger and Black (1940). Such would also be true of the temporary advance of the armadillo up the Pecos valley into New Mexico.

Regardless of the factors that have allowed the armadillo to extend its range, it seems that cold and lack of suitable food will finally draw a halt to what is probably the most amazing migration in the animal kingdom, save perhaps the march of the lemmings to the sea. As indicated in the section on anatomy, the armadillo has imperfect temperature control and since it does not hibernate, this factor will limit, indeed may already have limited, its northern movement. The arid west where the supply of insects is insufficient appears to have precluded its further advance in that direction. However, the clumsy archaic-looking, and even, perhaps, stupid armadillo has in the past so blithely surmounted insurmountable obstacles that one hesitates to predict what the future holds.
Notes on the Range of Other Armadillos

Considerably less is known about the range of the South American armadillos, than is known about *Dasypus novemcinctus* in the United States. This is not surprising when one considers that much of that continent is rather remote. In addition, no particular economic importance is attached to the animals, nor do they fall into the category of a novelty as in the case of our own armadillo. As noted below, the range of five species has been fairly well worked out but the rest of the data consists mostly of individual reports of captives at particular locations. These references are included partly for the sake of completeness and also to gather them in one spot so as to facilitate the evaluation of future reports.

Two works discuss the range of edentates in general (Palacky, 1901; Grevé, 1902), and the work of Bartholemew *et al.* (1911) gives a range map for the family Dasypodidae.

Hamlett (1939) adequately described the range of *Dasypus novemcinctus* outside the United States. *D. novemcinctus* is known to occur from sea level to an altitude of 10,000 feet (Gadaw, 1908), *Dasypus novemcinctus hoplites* is found on several islands in the West Indies; Tobago and Trinidad (Clark, 1914), Costa Rica (Frantzius, 1869; Calvert and Calvert, 1917), as well as on Barro Colorado Island in the Canal Zone (Enders, 1930). Tate (1931) reported *Dasypus novemcinctus* to be common in western Ecuador and Hooper (1947) lists the nine-banded armadillo found near Oaxaca, Mexico, as *Dasypus novemcinctus fenestratus*. *Dasypus novemcinctus* was recorded from Guatemala by Moore (1859) and was found at Vera Cruz, Mexico in 1890 (Thomas, 1890).

The entire range of five armadillos, excluding *Dasypus novemcinctus* has been studied. Miniprio (1945) gives the range of *Chlamyphorus truncatus*, which species is confined to Argentina.
The Armadillo

Yepes (1929) discusses the geographic distribution of *Chlamyphorus truncatus* and *Chaetophractus vellerosus*. Yepes (1944a) gives the distribution of *Zaedyus pichiy*. Sanborn (1930a, 1930b) gave the known captures of the various sub-species of *Tolypuetes tricinctus* and discussed their probable ranges. Several works (Krieg, 1929; Yepes, 1938, Yepes, 1944b) have dealt with the distribution of Argentinean armadillos.

Thomas (1880) reported *Dasypus novemcinctus*, *Dasypus kappleri* and *Priodontes giganteus* from Ecuador. Aplin (1894) reported *Dasypus novemcinctus*, *D. sexcinctus* and *D. hybridus* from Uruguay.

*Chaetophractus nationi* was recently recorded for the first time in Chile (Mann, 1945), and Crespo (1944) gives several new localities for the related *Chaetophractus vellerosus pannosus* in Argentina.

*Priodontes giganteus* was reported from southern Matto Grosso in Brazil by Miller (1930).

*Cabassous unicinctus* was reported to occur in Costa Rica by Frantzius (1869), and *Cabassous centralis* was recently found on Barro Colorado Island by Ingles (1953).

*Zaedyus pichiy* has been reported from Chile (Schneider, 1935). This same species was recorded from Guatemala in 1861 by Tomes under the name "*Dasypus minutus*." It is probable that the animal referred to here is not really the “piche” armadillo.

Several early authors (Hudson, 1922; Prichard, 1902a, 1902b;) have recorded *Dasypus minutus* as occurring on the north banks of the Rio Santa Cruz north of Rio Negro in Argentina. The animal is not, however, found on the south bank of the river. Such a phenomenon at first seems curious but this same thing is seen with the nine-banded armadillo in the United States. The authors (1954) have found several
instances where the limits of the armadillo’s range exactly parallel rivers, the animals being present on one bank but not the other. This brings up the point discussed in the section on habits about the armadillo’s swimming ability. The armadillo probably does not swim voluntarily except to cross very small streams. Crossings of major streams is probably accomplished by transportation by humans or by being accidentally swept into a stream and deposited on the other bank somewhere downstream (Fitch et al., 1952).

FOOD HABITS OF THE ARMADILLO

Introduction

The food habits and the range expansion of the nine-banded armadillo are the two best known factors in the animal’s ecology. As a matter of fact, the two, in many cases, have been studied together, and not without reason, for these are the subjects which are most likely to be of economic importance to man. Most of the attention to the armadillo’s food habits has been directed toward determining whether or not the armadillo is a factor in the destruction of the eggs of game birds, principally quail.

There is a decided difference between what an armadillo is capable of eating and what it does eat in its natural habitat. It is now well known that the armadillo is primarily entomophagous; however, in captivity it has proven to be essentially omnivorous. Its vegetable diet is exceedingly small, most common vegetables remaining untouched, even when the animal is hungry (Taber, 1945). In our laboratories armadillos were fed raw chopped horse meat which was consumed with gusto. Taber (1945) fed captive animals on bone and fish meal mixed with mash and sour milk. His animals also ate dead chickens, especially if they were maggot infested. In the latter case, of course, it would seem that the
animals were attracted to the meal by the maggots, which is the type of food they normally consume. The occasional reports of armadillos eating carrion (Kalmbach, 1943; Fitch et al., 1952), do not mention the state of the meat, and it is possible that in these cases also the animals were after maggots rather than the meat itself.

Kalmbach (1943) has a most extensive section devoted to the natural food of the armadillo, and other workers (Bailey, 1931; Baker, 1943; Aldous, Williams and Kalmbach, ms.) have published shorter accounts of the animal's diet, giving similar results. The combined data of these workers is presented in Table I. A tabulation of the food of some Louisiana armadillos is in Fitch et al. (1952).

Insects

As can be seen from the Table, some 90% of the armadillo's diet consists of animal life, of which over 80%, or about 75% of the total diet, consists of insects. Krumbiegel (1940), reporting on several South American species, found a high insect content in stomachs examined.

The Order Coleoptera comprises the largest single group of insects found, amounting to about one half of the total animal material ingested (ca. 40% of the total diet). Within the Coleoptera, the chief item on the menu was the Scarabidae, a goodly number being coprophagous and phytophagous species. Since many of the phytophagous beetles are important as crop pests, it seems that in this respect the armadillo is of benefit to the farmer. Aldous (1943) reported that east Texas sugar cane farmers felt that the armadillo was of value in controlling the sugar-cane beetle (Eutheola rugiceps). Kalmbach (1943) also reports that the armadillo is recognized as an ally of the farmer in this respect.

The Carabidae (ground beetles), both larvae and adults,
### Table I

**The Diet of the Armadillo**

All figures represent % of volume of total food unless otherwise indicated.

<table>
<thead>
<tr>
<th>Food</th>
<th>Kalmbach (1943)</th>
<th>Baker (1943)</th>
<th>Aldous et al.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>ANIMAL</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Insecta</td>
<td>93.3</td>
<td>9.0</td>
<td>87.8</td>
</tr>
<tr>
<td>Coleoptera</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Scarabidae</td>
<td>27.0</td>
<td>28.0†</td>
<td>13.0</td>
</tr>
<tr>
<td>Carabidae</td>
<td>9.4</td>
<td>20.0†</td>
<td>9.2</td>
</tr>
<tr>
<td>Elateridae and other</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coleoptera</td>
<td>4.3</td>
<td>13.0†</td>
<td>4.5</td>
</tr>
<tr>
<td><strong>Hymenoptera</strong></td>
<td>14.0</td>
<td>10.0†</td>
<td>16.0†</td>
</tr>
<tr>
<td><strong>Lepidoptera</strong></td>
<td>7.8</td>
<td>13.0†</td>
<td>7.2</td>
</tr>
<tr>
<td><strong>Orthoptera</strong></td>
<td>6.2</td>
<td>13.0†</td>
<td>8.2</td>
</tr>
<tr>
<td><strong>Isoptera</strong></td>
<td>4.5</td>
<td>1.0</td>
<td>8.0</td>
</tr>
<tr>
<td><strong>Hemiptera</strong></td>
<td>2.0</td>
<td>none</td>
<td>0.5</td>
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<tr>
<td><strong>Diptera</strong></td>
<td>1.5</td>
<td>1.0†</td>
<td>2.7</td>
</tr>
<tr>
<td>Arachnida</td>
<td>1.7</td>
<td>trace</td>
<td>4.1</td>
</tr>
<tr>
<td>Myriopoda</td>
<td>6.2</td>
<td>1.0</td>
<td>trace</td>
</tr>
<tr>
<td>Isopoda</td>
<td>6.2†</td>
<td>trace</td>
<td>4.5†</td>
</tr>
<tr>
<td>Crustaceans</td>
<td>6.2†</td>
<td>trace</td>
<td>4.5†</td>
</tr>
<tr>
<td><strong>Annelida</strong></td>
<td>6.2†</td>
<td>13.6</td>
<td>4.5†</td>
</tr>
<tr>
<td>Mollusca</td>
<td>6.2†</td>
<td>0.2</td>
<td>4.5†</td>
</tr>
<tr>
<td>Amphibians and Reptiles</td>
<td>1.2</td>
<td>0.9</td>
<td>2.4</td>
</tr>
<tr>
<td>(including eggs)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mammals and Birds</td>
<td>0.4</td>
<td>none</td>
<td>4.5†</td>
</tr>
<tr>
<td>(including eggs)</td>
<td></td>
<td></td>
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<tr>
<td><strong>VEGETABLE MATTER</strong></td>
<td>6.7</td>
<td>2.6</td>
<td>12.2</td>
</tr>
<tr>
<td>Food</td>
<td>2.1</td>
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</tr>
<tr>
<td>Debris</td>
<td>4.6</td>
<td>trace</td>
<td>12.2</td>
</tr>
</tbody>
</table>

* Total for Isopoda, Crustacea, Annelida, and Mollusca.
† Total for Isopoda, Crustacea, Annelida, Mollusca, and Reptile Eggs.
‡ Indicates frequency in 25 stomachs examined.

...comprise the other large group of beetles consumed by armadillos. Together with the scarabs they account for 90% of the Coleoptera eaten. Here too, the armadillo may be considered a beneficial creature, since several species of these animals are detrimental to man. The remaining families of
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beetles make up a small percent of the diet, less than 5% of the total. Of some interest among these latter is the incident cited by Kalmbach (1943). In the stomach contents examined by him were found an excellent series of the small and rare hister beetle, *Echinodes setiger*. These animals, whose collection would have required perhaps years of search by an entomologist, now enhance the collections at the United States Museum and the Fish and Wildlife Service.

The second largest order of insects composing the armadillo's diet is the Hymenoptera, which comprise some 15-20% of the total diet. This percentage figure is surprisingly low when it is considered that earlier workers (Newman, 1913a; Audubon and Bachman, 1854; Bailey, 1905; Nelson, 1918) described them as being chiefly, if not exclusively myrmecophagous. Audubon and Bachman (1854) describe them as being kept as house pets for that very purpose. Ants occasionally constitute nearly the total contents of an armadillo's stomach and are said to be present in at least trace amounts in nearly all (Kalmbach, 1943). Since the family Dasypodidae is adjacent to the family Myrmecophagadae one would expect that the armadillos might have a preference for ants, and indeed, it is claimed that certain Central and South American species do eat mostly ants (Hudson, 1922; Ingles, 1953). No study seems to have been done to determine the contents of the armadillo's diet in relation to the availability of the forms concerned. It is possible that the relatively low percentage of ants consumed by United States armadillos is a reflection of their abundance. There might also be some selectivity of species since the armadillo is known to dislike one species, *Pogonomyrmex comanche*, the large red ant. The other Hymenoptera make up a small part of the diet and consist chiefly of wasps.

Between five and ten percent of the armadillo's food con-
sists of Lepidoptera, almost exclusively larvae and pupae, although on some fortuitous occasions a much larger proportion may be found (Bailey, 1931; Kalmbach, 1943). Most notable of the caterpillars taken by the armadillo are the Noctuidae (cut worms), which are occasionally eaten in great number. While this destruction of cut-worms tends to make the armadillo better liked by the farmer, the benefit is occasionally offset, in the farmer’s mind, at least, by some damage to crops resulting from a too energetic search for the grubs.

The Orthopoda make up a portion of the armadillo’s diet only slightly less large than the Lepidoptera, but are of considerably less economic value. The chief orthopterans taken are the wood roaches. Fewer numbers of grasshoppers and crickets are consumed. Termites (Isoptera) form a fairly small portion of the diet for the armadillo; however, this is likely due to lack of opportunity to eat them, since the nine-banded armadillo is reported to eat them with as much relish as it eats ants. The nine-banded armadillo is reported to eat many termites in South America, where they are extremely abundant, and some other species of armadillos are reported to eat them extensively (Ingles, 1953).

Other insects are eaten by the armadillo in small quantities. These consist chiefly of flies, mostly larvae and pupae, and several hemipterans. While these items of food have little, if any, economic significance, the ingestion of hemipterans of the family Triatomidae is of some potential medical importance. These insects are the transmitters of Trypanosoma cruzi, the infective agent of Chaga’s disease. As discussed in the section on parasitology, infection may be acquired by ingestion of these bugs, and infected armadillos of several species have been found in Brazil and elsewhere. On at least one occasion, D. novemcinctus has been found infected in the United States.
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Other Arthropods

According to Kalmbach (1943), myriapods constitute one of the most frequently found items in the armadillo’s diet. They constitute some 5% of the diet, although the volume varies with the seasons. Millipedes appear in the diet more frequently than do centipedes, probably because they are captured more easily.

Among the other miscellaneous arthropods eaten by armadillos, are spiders, scorpions, pillbugs, and occasionally crayfish. Lehmann (1934) reported that captive animals showed a decided liking for crayfish. Nothing appears to be known regarding their method of capturing such food.

Other Invertebrates

Of the other invertebrates, the chief item of diet for the armadillo is the earthworm. They ordinarily comprise not more than 5% of the diet, but on occasion they are taken in large numbers (Bailey, 1931; Kalmbach, 1943).

Vertebrates

Approximately 1.5% of the animal food eaten by armadillos is vertebrate, and three quarters of this amount is composed of amphibians, lizards, snakes, and the eggs of the latter. Several observers have reported seeing armadillos eating eggs of various reptiles (Lehmann, 1934; Kalmbach, 1943), but there is no information regarding the method by which the animals locate such food. The few reptiles and amphibians which are eaten are taken mostly in the cold months when they are least active. The nine-banded armadillo has occasionally been reported to be a snake killer but there is little concrete evidence to support this contention (Lehmann, 1934; Hardberger, 1950). Hudson (1922) describes Chaeto-
phractus villosus as killing a snake by squatting on it and sawing it apart with the sharp edges of the shell.

Most of the remaining percentage of vertebrate food is carrion. It was pointed out earlier in this section that the armadillo will eat carrion and probably does so on occasion in the wild. There are few instances recorded of armadillos eating mammals. The only one reported for D. novemcinctus, aside from Newman’s (1913a) report of apparent cannibalism, is one of Newman and Baker (1942), which is a description of an armadillo devouring new born rabbits. Earlier reports (Baird, 1857) claimed that the armadillo ate flesh which it concealed in large holes; however, evidence has failed to support this contention. South American species have been reported as eating carrion (Hudson, 1922) and the Peludo armadillo (Chaetophractus villosus) is described by Hudson (1922) as capturing mice and snakes. Krumbiegel (1940) reports Cabassous sp. eating mice. Darwin (1933) also says they eat snakes.

The only report of armadillos eating birds is contained in Lehmann’s Armadillo Investigations (1934). The birds reported eaten were young chicks and young quail. Lehmann (1934) experimentally induced armadillos to eat chicks. There are also a few instances, cited by Kalmbach (1943), of armadillos destroying wild turkey nests.

The armadillo is thoroughly condemned by farmer and sportsman alike as a destroyer of the nests, eggs, and young of quail, turkeys, and to some extent domestic poultry. The evidence above seems to be the only eye witness data to support this contention. As previously mentioned, most of the research into food habits of Dasypus novemcinctus was conducted in an attempt to elucidate this problem. Work by Kalmbach (1933), Lehmann (1934), Aldous (1936), and work conducted by Kalmbach and Lehmann in 1935 are sum-
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marized by Kalmbach (1943). Some four hundred dummy quail nests containing quail eggs in half and hen eggs in half were “planted” and observed by these investigators. In addition, a number of natural nests were kept under observation. In only slightly over five percent of all the nests observed was there any evidence of destruction by armadillos, and in many cases there is the possibility that the armadillo visited the nest after some other animal had destroyed it. Examination by Kalmbach (1943) of the stomachs of 281 armadillos revealed the presence of bird eggs in only five. One of these contained hen eggs from a dummy nest, another contained quail eggs, and the other three could not be identified. Lehmann showed that the armadillo must break an egg with its foot before eating it, and that this trait is learned rather than instinctive. Taber (1945) found the armadillos captured by him to be completely oblivious to hen eggs placed in their pen.

The meager evidence presented above is all that has been produced to justify the relentless persecution of the armadillo which occurs generally throughout its range. While an occasional armadillo does destroy nests of ground nesting birds, the amount of harm is relatively insignificant compared to that perpetrated by such animals as skunks, possums, snakes, and the like.

Vegetable Matter

The remaining portion of the armadillo’s diet consists of vegetable matter and amounts to approximately 7%. Of this amount only two percent represents food, the remainder being debris ingested along with other food items, chiefly insects. Some succulent berries and fruits, such as blackberries, mulberries, plums (Kalmbach, 1943), and persimmons (Hamilton, 1946) are eaten by armadillos. Some mush-
rooms and fungi, especially puffballs, are taken (Kalmbach, 1943; Cahalane, 1947). Another bone of contention between the farmer and the armadillo is its reputed habit of eating melons and cantaloupes. They will eat such food if it is previously opened (Kalmbach, 1933), and while there is likely some primary damage by armadillos to these crops, it is probable that the armadillo, by leaving a conspicuous trail, takes the blame for many deeds of other predators which precede him in the melon patch.

REFERENCES TO THE NATURAL HISTORY OF THE NINE-BANDED ARMADILLO
Aldous, S. E. 1936. Quail vs. Armadillos. MSS in files of Fish and Wild Life Service, Austin, Texas.
The Armadillo

Darwin, C. 1933. Journal of researches into the natural history and geology of the countries visited during the voyage round the world of H. M. S. "Beagle" under command of Captain FitzRoy, R. N. Edited by Nora Barlow. London.


———. 1946. The black persimmon as a summer food of the Texas Armadillo. J. Mamm. 27:175.


———. 1943. The Armadillo: Its Relation to Agriculture and Game. Game, Fish and Oyster Commission, Austin, Texas.


The Armadillo


——. 1902b. Field notes upon some of the larger mammals of
Roosevelt, T. 1919. Through the Brazilian wilderness. C. Scribner's Sons.
——. 1943. The armadillo in Florida. Florida Entomologist 26:54.
——. 1928. The nine-banded armadillo in northeastern Louisiana. J. Mamm. 9:69.
Texas Game, Fish, and Oyster Commission. 1945. Principal Game Birds and Mammals of Texas. Austin.
——. 1890. On a collection of mammals from central Vera Cruz, Mexico. P. Z. S. 1890:71.
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INTRODUCTION

ANIMALS like men are usually known by the company they keep. And the company they keep can often be deduced by the parasites they harbor. The armadillo lives in the same general environment as the opossum, raccoon and the skunk, but, compared to these neighbors of his, is strikingly free of parasites. The high arthropod content of the armadillo's diet would appear to make it a primary target of parasites requiring an arthropod intermediate host, but here again this is not the case (Chandler, 1946). Taber (1945) re-
marked that in his studies he had found no endoparasites or ectoparasites.

As noted below, the nature of the integument probably accounts for the lack of ectoparasites. The lack of endoparasites presents somewhat of a problem, for it would seem that the armadillo is in a most "favorable" position to accumulate parasitic infections. While no explanation of this phenomenon can be offered here, it seems not inappropriate to draw attention to two very striking features of the armadillo's physiology. The Dasypodidae have low body temperatures, ranging from $32^\circ$-$34^\circ$ C., and in addition are somewhat poikilothermous (see Physiology section). It is to be wondered whether the relatively cool and unstable environment presented by the armadillo is not unfavorable to many potential armadillo parasites. This is a difficult point since numerous mammals, notably bats, having a variable body temperature are well parasitized, as are the reptiles, etc. However, there appears to have been no work done to determine the effect of host body temperature on the endoparasitic fauna and until some proof is forthcoming the possibility that this factor does in part explain the armadillo's lack of parasites must be considered.

The armadillo is not without parasites, however; and several of these are of some importance. But on the whole this animal offers a meager field of endeavor for the descriptive parasitologist.

However, with the emphasis in parasitology shifting toward the more intimate, physico-chemical relationships between parasite and host, it may be that the armadillo will become of peculiar value to the physiological parasitologist for the very reason that it is not so attractive to his taxonomically-inclined colleagues.
In one aspect of its parasitology the armadillo does follow a logical pattern—it has few ectoparasites. The bony shell excludes them from the dorsal surfaces and tail and the extremely scanty hair discourages fleas and lice from setting up housekeeping on the ventral surface or legs of the animal. It is surprising, however, that the armadillo does not become the festive board of ticks more often than is reported. The literature reveals few reports of ticks having been found on the nine-banded armadillo. This paucity of acarine parasites is the more surprising when one considers that the armadillo's haunts abound in ticks. One of the writers, in poking in an armadillo's burrow, once became covered with seed ticks which were in the burrow and around the entrance, yet from over 150 armadillos examined in 1952 not one was observed to harbor ticks. A long-time resident of Hufsmith in north-east Harris County, Texas, once remarked to the writers that though her family had hunted armadillos for as long as she could remember, she recalled only once finding a tick on one.

On the other hand, some of the South American armadillos of the sub-family Euphractinae are rather hirsute, and one would expect to find them bearing a more extensive ectoparasitic fauna. That this is not borne out by the literature cited below is perhaps due to the fact that less work has been done on these species. It is interesting to note that in such records as we do have for these armadillos, there are proportionately more fleas and mites than ticks.

Ticks

All of the ticks reported on armadillos are of the genus Amblyomma, and the species encountered most often is A. concolor; this and the closely related A. pseudoconcolor are
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the only ones that can be considered true armadillo parasites; the others are accidental (Nuttall et al., 1926). Three species of ticks are reported from armadillos identified only as Dasypus sp. They are Amblyomma cajennense (Rohr, 1909), A. concolor (Neumann, 1901), and A. pseudoconcolor (de Beaurepaire Aragao, 1908). The first named species is quite indiscriminate as to hosts, attaching itself to most domestic animals as well as man.

From Dasypus novemcinctus the following ticks have been reported: Amblyomma cajennense (Fiasson, 1943), A. concolor (Fiasson, 1943, Osorno-Mesa, 1940), A. parvum (de Beaurepaire Aragao, 1938), and A. crassum (Fiasson, 1943). Amblyomma parvum is found principally on horses and A. crassum was originally described from a specimen from a tortoise.

Amblyomma concolor is the only tick reported from any of the other species of armadillos. Those which have been found carrying A. concolor are: Dasypus hybridus (Boero, 1945), Tolypuetes tricinctus conurus (de Beaurepaire Aragao, 1936), Tolypuetes tricinctus matacos (de Beaurepaire Aragao, 1938), Chaetophractus vellerosus (Lahille, 1920), and Chaetophractus villosus (Lahille, 1920; Neuman, 1911).

The finding of relapsing fever spirochaetes in two of thirty-two armadillos in Panama may be considered strong evidence that these armadillos are sometimes bitten by ticks of the genus Ornithodoros.

Fleas

As noted, the hirsute euphractine armadillos have been found to have fleas more often than ticks. Euphractus sexcinctus has been reported to harbor Malacopsylla grossiventris by Jordan and Rothschild (1906) and del Ponte and Riesel (1939). This flea was also reported from Tolypuetes tricinctus conurus by Jordan and Rothschild (1906). The only
Parasites

Parasites which have been listed from the Euphractine armadillo, *Zaedyus pichiy*, are the fleas *Malacopsylla agenoris* (Jordan, 1934), *Ctenocephalides felis* (Wolffhugel, 1920), and *Hectopsylla broscus* (= *mazzai*) (de Costa Lima, 1935). Curiously, the literature contains no reference to fleas from the genus *Chaetophractus* which is more hairy than the genera listed above.

Five species of fleas have been recorded from *Dasypus novemcinctus*: *Tunga travassosi* (Pinto and Dreyfus, 1927), *Juxtapulex echiophagoides* (Wagner, 1933), *Echidnophaga gallinacea* (Hightower, et al., 1953), *Polygenis roberti* (Guimaraes, 1941), *Polygenis occidentalis* (Guimaraes, 1941, de Almeida Cunha, 1914).

From the related armadillo, *Dasypus hybridus*, there have been reported *Rhopalopsyllus lutzi oleophontis* (del Ponte and Riesel, 1939) and *Malacopsylla agenoris* (Baker, 1905). *Rhopalopsyllus cacius saevus* was reported from *Dasypus sp.* by Fuller (1942).

The only ectoparasite which has been reported from *Cabassous unicinctus* is *Tunga terasma* (Jordan, 193).

Of the fleas mentioned above all are primarily parasites of other animals and only accidental on armadillos except *Tunga travassosi T. terasma* and *Polygenis occidentalis*.

**Miscellaneous Arthropod Parasites**

Only two species of mites seem to have been found on armadillos. *Dasyponyssus neivae* from *Euphractus sexcinctus* (de Fonseca, 1940), apparently a true armadillo parasite, not having been found on any other animals; and the mange mite, *Sarcoptes scabiei*, on *Dasypus hybridus* (Wolffhugel, 1920). Clark (1938) described a case of *Dermatobia hominis* infestation in *Dasypus novemcinctus*. This bot is transported by mosquitoes principally.

Larvae of the pentastomid, *Porocephalus crotali*, have
been reported on three occasions from the nine-banded armadillo, *Dasypus novemcinctus* (Stiles and Hassall, 1894; Shipley, 1898; and Sambon, 1912). Since the adults are known to occur only in the lungs of snakes, it is unlikely that the presence of *Porocephalus* in the armadillo is other than accidental, as snakes have not been reported to eat armadillos.

**Spirochaetes and Miscellaneous Protozoan Parasites**

*Spirochaetes and Rickettsia*

In 1931 Graham reported several cases of relapsing fever in Texas and listed several widely scattered sites (caves) in the state in which ticks, *Orinthodoros turicata*, were found to be infected (Graham, 1931). Due to the wide dispersal of these locations he felt that some animal reservoir might be involved. Among other possible carriers he mentioned armadillos. Just a year later Dunn and Clark (1933) reported spirochaetal infections in two of thirty-two Panamanian armadillos, *Dasypus novemcinctus fenestratus*, which they examined. They said that these spirochaetes were identical morphologically with the infective organism of human relapsing fever. Two armadillos were inoculated with a known human strain and both animals became infected, one dying after nine days and the other being positive until sacrificed a month later. Since armadillos harbor ticks so infrequently and have not yet been observed harboring species of *Orinthodoros* there is no reason to believe that the armadillo is a reservoir of any importance in the spread of relapsing fever.

Magalhães and Rocha (1944) reported an experimental infection of *Dasypus novemcinctus* with exanthematic typhus rickettsiae (strain VB). The infected animals died of the infection. Varela and Mazotti (1947) report *D. novemcinctus* susceptible to murine typhus infection.
Protozoa

With the exception of *Trypanosoma cruzi*, to be discussed below, there has been little work done on the protozoan parasites of the armadillos.

Three species of coccidia of the genus *Eimeria* and one species of the genus *Globidium* have been described from armadillos in Brazil. *Eimeria travassosi* was recorded from the intestine of *Dasypus hybridus* and *Euphractus sexcinctus* by da Cunha and Muniz (1928). Carini (1933) described two new species of *Eimeria*, *E. tatusi* and *E. cabassusi*, from oocysts in the feces of a young armadillo, *Cabassous sp*. In 1924, da Cunha and de Magarinos Torres described encysted forms of a sporozoan of the genus *Globidium* from the small intestine of *D. novemcinctus* (1924, 1926). They proposed the name *Globidium tatusi* for this form.

*Balantidium coli* has been found in six-banded armadillos, *Euphractus sexcinctus*, which were kept in close proximity to infected pigs (Pinto, 1944).

O. O. R. da Fonseca (1915) described a flagellate, *Trichomonas tatusi*, from the large intestine of *D. novemcinctus* in Brazil. F. O. R. da Fonseca (1939) described *Chilomastix olympiai* from "*Dasypus aguti*." *D. aguti* appears to be a synonym and it is not certain from which species of armadillo *C. olympiai* was actually taken.

**Trypanosoma Cruzi**

The only disease of clinical importance known to occur in armadillos is American human trypanosomiasis, Chagas' disease.

The infective organism itself, *Trypanosoma cruzi*, is not unduly host specific, being found in several rodents, dogs, cats, and marsupials besides man and armadillos.

The disease is transmitted by hematophagous arthropods,
principally hemipterans of the sub-family Triatominae, although infected bedbugs and ticks have been found. No less than thirty-six species of triatomes found from Argentina northward to the United States have been recorded as vectors of *T. cruzi*. Reinfection of mammalian hosts is accomplished by way of fecal material from infected triatomes. The fecal material may be introduced into the body via cuts in the skin, the conjunctiva of the eye or ingestion of infected bugs or their feces. This latter route is probably the common pathway by which armadillos are infected. Chagas (1912) first reported *T. cruzi* in armadillos, finding it in *Dasypus novemcinctus* in Brazil. Magarinos Torres (1915) reported Brazilian specimens of *Euphractus sexcinctus* and *Cabassous unicinctus* as well as *D. novemcinctus* to be 40-60% infected.

A number of Argentinian armadillos have been found infected with *T. cruzi* by Mazza and his workers. Listed are *Dasypus novemcinctus* (Mazza and Romana, 1936; Mazza, 1939), *Chaetophractus vellerosus vellerosus* (Mazza, 1930, 1940), *Chaetophractus vellerosus pannosus* (Mazza and Driollet, 1935; Mazza, 1940), *Zaedyus pichiy caurinus* (Mazza and Miyara, 1935) and *Tolypuetes tricinctus matacos* (Mazza, and Romana, 1936).

Torrealba (1937) reported *T. cruzi* from *Dasypus novemcinctus pentadactylus* and *D. paraguayense* from Venezuela. *D. paraguayense* is not a valid species name of an armadillo and it is not known which animal is meant by this designation.

Clark and Dunn (1932) demonstrated *T. cruzi* infections in Panamanian armadillos, *Dasypus novemcinctus fenesstratus*, and Brumpt *et al.* (1939) found an infected specimen of *D. novemcinctus mexicanus* in Colima, Mexico. Finally, Packchanian (1942) found a specimen of the latter species in Texas which was infected with *T. cruzi*. 
Parasites

Although *Trypanosoma cruzi* is found in many different host animals, it is generally assumed that there is only one species. There is, however, a differential infectivity to be seen in *T. cruzi* from different hosts. For example: Villela *et al.* (1924, 1926, 1933) report that *T. cruzi* from *Dasypus novemcinctus* (in Brazil) was highly virulent in dogs. On the other hand, Clark and Dunn (1932) were unable to infect guinea pigs with *T. cruzi* from *D. novemcinctus* in Panama. The variation in virulence in different hosts may indicate that the importance of reservoir hosts for Chagas’ disease is less than might be expected but in absence of definite proof the armadillo must be considered a possible factor in the spread of the disease.

**Helminths of Armadillos**

As previously mentioned, Chandler (1946) noted that the armadillo is peculiarly free of helminths, especially those requiring arthropod intermediate hosts. This statement appears to hold for parasites in general, as we have seen.

Of the helminths found in the armadillos, nematodes are in the majority both as regards species and actual numbers of individuals. Some 43 species of nematodes have been recorded, whereas there are reports of only four species of flukes, one species of tapeworm, and four species of acanthocephalans.

**Flukes**

Two dicrocoeliid flukes have been described for *D. novemcinctus*. The first, *Dictyonograptus dictyonograptus* was found by Travassos (1920) in the pancreas of a specimen of *D. novemcinctus* in Brazil. Ribeiro described a second species from the pancreas of a specimen of *Dasypus novemcinctus* at Minas Gerais, Brazil, which he named *Eurytrema*
minensis (Ribeiro, 1941). Cesar Pinto (1944) was able to infect six-banded armadillos, Euphractus sexcinctus, with Schistosoma mansoni. In later publications, Magarinos Torres and Pinto (1945a and 1945b) described the technique of infection used in the previous work. They placed cercariae on the skin of the abdomen of the armadillo and secured ova in the feces 53 days later. Autopsy revealed numerous schistosomal tubercles in the intestinal tract, liver, and hemolymph nodes.

Chandler (1946) reported the presence of Brachylaemus virginianus in three of eight Texas specimens of D. novemcinctus examined by him. This fluke reaches the infective stage in land snails and had been previously recorded only from the opossum.

Cestodes

The literature on cestodes in armadillos consists of a half-dozen publications. All these worms are of the genus Oochoristica, with the possible exception of the “Taenia sp.” of Stiles and Hassall (1894); those that have been identifiable to species have proved to be O. surinamensis. The genus Oochoristica is a large and cosmopolitan group, being found in mammals, birds, and reptiles. On the other hand the individual species are quite host specific. So far as is known, these cestodes pass through a beetle intermediate host.

Parona (1901) described a cestode from Dasypus sp. as Oochoristica (Taenia) tetrangocephala. Janicki (1904) in redescribing Parona’s specimen felt that it could not be identified to species and listed it as Oochoristica sp. In the same paper, Janicki recorded O. surinamensis from Dasypus novemcinctus. Oochoristica surinamensis had been described a year previously by Cohn from Priodontes giganteus (1903). Baer (1927) reported O. surinamensis from Dasypus sp. and
Cameron (1939) recorded *Oochoristica sp.* from *Dasypus novemcinctus* in Trinidad (1939).

The authors examined sixteen armadillos in the winter of 1952 and secured from one a tapeworm which appears to be of the genus *Oochoristica*. Specific identification may be impossible, but this cestode might provide a new range record for *Oochoristica* in armadillos. Except for the questionable "*Taenia sp.*" (reported from Texas, Stiles and Hassall, 1894) it is the only tapeworm found in armadillos in the United States. The authors also found larval tapeworms encysted in the mesenteries of one armadillo. It is hoped that time will be available in the near future to examine properly this and other material from armadillos so that the results may be published.

**Acanthocephala**

With the Acanthocephala as with the flukes, there appear to be four species recorded from various armadillos. One, *Travassosia carinii* is found only in armadillos. *Travassosia (Hamanniella) carinii* was described from *Dasypus novemcinctus* in Brazil by Travassos (1917a). Lent and Texeira de Freitas (1938) also recorded *T. carinii* from *D. novemcinctus*. Meyer (1933) recorded *Travassosia carinii* taken from *Tolypopetes tricinctus conurus* by Eisentraut on his Bolivian expedition of 1930. This acanthocephalan, the two species of discrocoeliid flukes, the tapeworm *Oochoristica* and one of the spiruroids, *Mazzia mazzia*, are the only adult helminths requiring an arthropod mid-host which are reported from armadillos.

Chandler (1946) recovered immature intestinal forms of acanthocephalans of the genus *Hamanniella* from one of the armadillos examined by him. The author stated that the
worns were probably *H. tortuosa* which has otherwise been recorded only from the opossum.

In this connection it might be mentioned that the authors found an acanthocephalan in the intestine of a specimen of *Dasypus novemcinctus* which they examined. These are the only two instances of intestinal forms of acanthocephalans being found in armadillos in North America.

Two species of *Oncicola*, *O. oncicola* and *O. canis*, occur as encysted forms in the mesenteries of armadillos of the genus *Dasypus*. Travassos (1917b) recorded *Oncicola oncicola* from the connective tissue and muscles of *Dasypus (=Tatus) sp.* in Brazil. The adult forms occur in the stomach and intestine of *Felis onca* and *Felis jaguarundi*. Travassos claimed that armadillos ingested the eggs of *O. oncicola* but as Van Cleave (1921) pointed out, it would be unwise to assume armadillos as the primary host lacking proof of direct infestation.

*Oncicola canis*, normally parasitic in dogs and coyotes, has been found encysted in the mesenteries of *D. novemcinctus*. Due to the rather interesting relationship postulated between the nine-banded armadillo and *Oncicola canis* it might be profitable to deal with this parasite in some detail. *Oncicola canis* was described by Kaupp in 1909 from a dog from San Antonio, Texas. All infections of adult forms were found in Texas dogs or coyotes except the case discussed by Van Cleave (1921) from Nebraska. The identification of four groups of larval encysted acanthocephalans from armadillos as *O. canis* led Van Cleave to propose the armadillo as the intermediate host of this parasite. Included in the above groups of larvae is the *Echinorhynchus sp.* listed by Stiles and Hassall (1894) from *D. novemcinctus*. Price (1926) felt this explained the apparent occurrence of this parasite only within the range of the armadillo.
Chandler (1946) noted high percentage of dead and calcifying cysts in his specimens, and suggested that the armadillo might represent a dead-end rather than a link in the life cycle of the parasite. Several other bits of evidence point to the unlikelihood of the armadillo serving as a mid-host for *O. canis*. As pointed out in the section on ecology, there is no proof of any considerable predation on the armadillo by any animal, dogs and coyotes included. Other species of *Oncicola* occur in carnivores well outside the range of any armadillos. Finally, the listing by Van Cleave (1953) of *Oncicola canis* infections from *Canis latrans* in Wyoming, *Lynx rufus* in Arizona, and domestic cats in several places including Washington, D.C., preclude that possibility of *D. novemcinctus* being a necessary part of the life cycle of the parasite.

Van Cleave (1953) re-examined some of the encysted material from armadillos and found indications that some of the forms might be of the genus *Echinopardalis*. Confirmation of this view would provide another larval acanthocephalan species from the Dasypodidae.

**Nematodes**

*Trichuroidea*. A single trichurid, *Trichuris subspiralis*, has been recorded from feral armadillos. Linstow’s Compendium (1878) lists *Dasypus hybridus, Tolypuotes tricinctus* and *Cabassous uncinctus* as hosts for *Trichuris (Trichocephalus) subspiralis*. Linstow cites Diesing (1861) as his source for the above data.

Although it has not been reported in *Dasypus novemcinctus*, Fitch et al. (1952) discuss the possibility of this armadillo serving as host of *Trichinella* in those areas where pigs and armadillos range together, and feed upon the carcasses of one another, as they report in the case of Louisiana.
In this connection it is interesting to note that Niño (1937a) secured an experimental case of trichinois in *Chaetophractus villosus*.

**Strongyloidea.** The Dasypodidae serve as hosts for a number of Strongyloidea and except for two of the hookworms all of this group of worms are host specific.

The human hookworm, *Necator americanus*, has been reported from two sub-species of *Tolypuetes tricinctus*, *T.t. conurus* (Vogelsang, 1930), and *T.t. matacos* (Vogelsang, 1932a). Ancylostoma caninum, the dog hookworm, was found in *Chaetophractus villosus* by Vogelsang (1932b) and in *Euphractus sexcinctus* by Pinto (1944). Another species of Ancylostoma, Ancylostoma (=Diploodon) mucronatum had been described from *Euphractus sexcinctus* gilvipes by Molin (1860). This hookworm is a specific parasite of the armadillo.

The remaining parasites in this group are all in the family Trichostongylidae and may all be considered specific parasites of armadillos.

*Macielia (=Cooperia) macieli* was described by Travassos (1915) from *Dasypus novemcinctus*. Subsequently Travassos found *M. macieli* in *Dasypus hybridus* and *Euphractus sexcinctus* (1937). Two additional species, *Macielia chagasi* from *Euphractus sexcinctus* (1935) and *M. flagellata* from *D. novemcinctus* (1937) have been described by Travassos.

Six species of the genus *Delicata* are known from armadillos. *Delicata (=Ostertagia) delicata* and *Delicata (=Ostertagia) ransomi* were described by Travassos from *Cabassous unicinctus* and *Dasypus novemcinctus* respectively (Travassos, 1921). Four other species from armadillos were described by the same author in 1935. They are: *Delicata similis* from *E. sexcinctus*, *D. uncinata* from *Cabassous unicinctus*, *D. variabilis* from *D. novemcinctus*, and *D. cameroni* from *Dasypus hybridus* and *D. novemcinctus*. 

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Parasites

*Pulchrostrongylus complexus* and *Dasypostrongylus filamentosus* were both described by Travassos (1935). They were found in *Dasypus novemcinctus* as well as *Euphractus sexcinctus*.

*Moennigia moennigi* has been described from *Dasypus novemcinctus* only (Travassos, 1935).

*Adolpholutzia lutzi* has been found in *Dasypus hybridus*, from which it was described (Travassos, 1935).

*Trichohelix tuberculata* was first described from *Chaetophractus villosus* by Parona and Stossich as *Oesophagostomum tuberculatum* (1901). It has since been found in *C. villosus* and *Dasypus hybridus* (Vogelsang, 1932a) as well as *Euphractus sexcinctus*, and *Cabassous unicinctus*. *Longistriata ninoi* described by Vogelsang (1937) from *Tolypuetes tricinctus matacos* is probably a synonym of *Trichohelix tuberculata* (Travassos, 1937).

The genus *Pintonema* consists of four species, *P. intrusa*, *P. pulchra*, *P. pseudopulchra*, and *P. pintoi*, all of which were described from *Dasypus novemcinctus* by Travassos (1935). The latter species was also listed by Travassos as occurring in *Euphractus sexcinctus*.

Travassos in 1921 described a trichostrongylid from *Cabassous unicinctus* as *Viannaia incognita*, but in a later publication (1937) he concluded that this was not a valid species as the diagnostic features were too general in nature. Some unidentified parasites listed as *Trichostrongylidae sp.* were reported by Travassos *et al.* (1939).

*Oxyuroidea*. Five species of *Aspidodera* have been listed from the Dasypodidae, and these all may be considered specific parasites of the group. *Aspidodera ansirupta* and *A. vasi*, both described by Cavalcanti Proenca (1937) are known only from *D. novemcinctus* (Cavalcanti Proenca, *l.c.*; Travassos, Texeira de Freitas and Lent, 1939). *Aspidodera*
The Armadillo

*binansata*, described by Railliet and Henry (1914) from *Chaetophractus villosus*, has been additionally reported from *D. novemcinctus* (Cavalcanti Proenca, 1937), and *Toypuetes tricinctus conurus* (Sprehn, 1932).

*Aspidodera fasciata* is the only oxyurid reported from the armadillo in North America, having been found by Chandler (1946). *A. fasciata* was described from *Toypuetes tricinctus* by Travassos (1913). Other South American species from which it is reported are *Chaetophractus villosus* (Khalil and Vogelsang, 1932a), *Toypuetes tricinctus conurus* (Cavalcanti Proenca, 1937) and *Euphractus sexcinctus tucumanus* (Teixeira de Freitas and Lent, 1939) and *D. novemcinctus* (Railliet and Henry, 1914).

*Aspidodera scoleciformis* may also be considered a specific parasite of armadillos although it has been recorded from *Didelphys* as well. *A. scoleciformis* was first described by Diesing from *Cabassous unicinctus* and *Toypuetes tricinctus* (1851). Travassos (1913) recorded *A. scoleciformis* from these same two species as well as from *Dasypus novemcinctus*, *Chaetophractus villosus*, and *Euphractus sexcinctus*. Travassos, Teixeira de Freitas and Lent (1939) found *A. scoleciformis* in *Euphractus sexcinctus tucumanus*.

Ruiz’ revision (1947) of the genus *Cruxia* lists four species which have been found in armadillos. *Cruzia mazza* was described from *Dasypus novemcinctus* (Khalil and Vogelsang, 1932a) and *C. boliviana* was described from *Toypuetes tricinctus conurus* (Sprehn, 1932). *Cruzia travassosi* was recorded from *T. tricinctus conurus* by Khalil and Vogelsang (1932a), but it is also found in *Tupinambus*. *Cruzia tentaculata* is most widely distributed, being found in marsupials, pigs, turtles and frogs. It was listed from *Euphractus sexcinctus tucumanus* by Ruiz (1947).

*Lauroia travassosi* was described from *Dasypus novem-
Parasites

cinctus and Euphractus sexcinctus by Cavalcanti Proenca (1938). A second species, also specific for armadillos, was described a year later from Dasypus novemcinctus by Cameron (1939).

Schneider in 1866 described Heterakis fasciata from a specimen of D. novemcinctus. This is the only parasite of this genus recorded from the Dasypodidae.

The first parasite recorded from armadillos was Schneider-nema retusa which was described by Rudolphi in 1819 from Dasypus novemcinctus and Euphractus sexcinctus. This parasite has also been found in Cabassous unicinctus by Araujo (1940) and in Dasypus sp. (Travassos, 1926).

Embryonated oxyurid eggs of unknown species were removed from the gut of a specimen of Chaetophractus villosus by Niño (1937b).

Ascaroidea. Two species of the genus Ascaris have been reported from armadillos. Ascaris dasypodina was described from Cabassous unicinctus by Baylis (1922). This species has been reported in no other animal. The ascarid so common in men, monkeys and pigs, Ascaris lumbricoides, has been reported from Euphractus sexcinctus by Pinto (1944) and from “armadillos” by Machado (1941).

Spiruroidea. Four spiruroids, which require arthropod intermediate hosts, have been reported from armadillos and three of these only as larvae, the armadillo serving as a transport host. Three of the spiruroids are from Dasypus novemcinctus. Cameron (1939) reported larval Physaloptera from a specimen in Trinidad. This genus occurs in mammals, birds, reptiles, and occasionally in amphibians. The only known arthropod hosts are cockroaches.

Encysted larvae of Physocephalus sp. and Ascarops sp. were found by Chandler (1946). These parasites normally occur in pigs, donkeys, etc. One species of the former occurs
in an edentate, $\textit{Bradypus tridactylus}$. Dung beetles act as arthropod hosts for both genera. The armadillos examined by Chandler came from hog pastures.

Khalil and Vogelsang (1932b) described $\textit{Mazzia mazzia}$ from the stomach of $\textit{Chaetophractus vellerosus vellerosus}$.

$\textit{Filaroidea}$. $\textit{Filaria acuticauda}$ was reported from $\textit{Dasypus novemcinctus}$ and $\textit{D. hybridus}$ by Molin (1858). Since that time it appears that this filaria has not again been found. $\textit{Dipetalonema anticlava}$ has been found in several species of Dasypodidae. It was recorded from $\textit{Dasypus novemcinctus}$ by Lent, Texiera de Freitas (1942), $\textit{D. hybridus}$ by Mazza and Anderson (1925), $\textit{Euphractus sexcinctus}$ by Stossich (1897), $\textit{E. sexcinctus tucumanus}$ by Mazza, Romana and Fiora (1932) and Travassos et al. (1939), and $\textit{E. sexcinctus gilvipes}$ by Lent and Texeira de Freitas (1942).

There are two records of microfilariae from armadillos, Léger (1918) reported $\textit{Microfilaria sovoura}$ from $\textit{Dasypus sp.}$ and di Primio (1936) reported microfilaria from $\textit{Dasypus novemcinctus}$.

REFERENCES TO THE PARASITES OF ARMADILLOS

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Lahille, F. 1920. Enumeración sistemática de los pediculídos, malófagos, pulicídos, linguátílidos y ácaros (la parte) encontrados en la República Argentina, con una nota sobre una especie de piojo de las ovejas. Buenos Aires.

Machado, O. 1941. Os mamiferos domesticos e silvestre como reservat-


Magarinus Torres & Pinto, C. 1945a. Lesoes produzidas pelo Schisto-


Mazza S. and Anderson, C. 1925. Filarideos en el peritoneo (Acan-

Mazza S. and Anderson, C. 1925. Filarideos en el peritoneo (Acan-

Mazza S. and Anderson, C. 1925. Filaridades en el peritoneo (Acan-


The Armadillo

——. 1860. Il sottoraine degli Acrofalli (Venezia). Memoria del’Institut. Veneto, IX.
Stossich, M. 1897. Filarie e spiroptere. Lavoro monografico. Trieste 1897.


THE CLASSIFICATION AND TAXONOMIC RELATIONSHIPS OF THE NINE-BANDED ARMADILLO

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CLASSIFICATION OF THE NORTH AMERICAN NINE-BANDED ARMADILLO

Class—Mammalia
Subclass—Eutheria
Order—Xenarthra
Suborder—Hicanodonta
Family—Dasypodidae
Subfamily—Dasypodinae
Genus—*Dasypus* *novemcinctus mexicanus*

INTRODUCTION TO THE ORDER XENARTHRA

At least one example of every curse which has beset the systematists seems to occur in the Edentata. From the often amusing and maddening dialogues regarding priority and propriety of typographical errors, to the gross misassociation of animal types; they are all present.

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The order Edentata has served in the past as a sort of taxonomic grab-bag. The group was first called Bruta by Linnaeus, but he included the elephant and walrus in the order. Cuvier considered the monotremes to belong to the Edentata. When these obvious misfits were removed, the order was still left with five distinct groups, the sloths, ant bears, armadillos, scaly anteater (Manis), and the Aard-Vark (Beddard, 1909). The latter two groups are old world forms and they differ from the first three groups considerably. It was subsequently proposed to split the Edentata into two groups; the Xenarthra, new world forms; and the Nomarthra, old world forms. In addition to the three groups named, the Xenarthra consisted of some extinct forms, the Glyptodontidae and the Megatheridae (ground sloths). Cope (1889a) gave a classification of the Edentata and showed the proposed pedigree of the groups.

As the wide difference between the Nomarthra and the Xenarthra became more apparent they were given ordinal status. The classification of Lane (1909c) is shown here to illustrate this point.

Super order: EDENTATA
Order: TAENIODONTA—The Ganodonts (two families)
Order: XENARTHRA—Suborder: PILOSA
   Bradypodidae
   †Megalonychidae
   †Megatheridae
   Myrmecophagidae
   †Orophodontidae

BRADYPODIDAE MYRMECOPHAGIDAE DASYPODIDAE MANIDAE ORYCTEROPIDIDAE
   †MEGATHERIDAE †GLYPTODONTIDAE
   †PIRIMITIVE XENARTHRA
   †PIRIMITIVE NOMARTHRA

†extinct forms
Suborder: LORICATA (called Hicano-
donta below)
Dasypodidae
†Glyptodontidae

Order: PHOLIDOTA—Manidae
Order: TUBULIDENTATA—Orycteropodidae
† extinct forms.

The first order, Taeniodonta, is thought to be an ancestral
Edentate group, but as Scott (1929) points out, they are
imperfectly known and the points of resemblance to the Eden-
tates are very complex. As a matter of fact except for the
tentative relationship of the Taeniodonta to the Xenarthra,
there is no reason why any of the orders listed need to be
grouped as a super-order. The scales of Manis are composed
of modified hair and are not at all comparable to the dermal
scutes of the armadillos. The food habits of the old world
forms are similar to that of the ant bears and some armadillos,
but such a character has little if any diagnostic value. The
dentition which would appear to be a prime factor for the
grouping of the forms, if anything, would lend support to the
idea that they should be separated. Orycteropodus has a com-
plex dentition unlike anything in the Xenarthra, whereas
Manis has no teeth but on other grounds cannot be aligned
with Myrmecophagidae, the only edentolous Xenarthra.

Finally, it should be mentioned that of the living families of
Xenarthra, only Dasypodidae is known to contain extinct
genera.

THE WORK OF MATTHEW (1912) ILLUSTRATES WHAT MAY BE THE
EVOLUTIONARY TREE OF XENARTHRA
The Armadillo

Classification of the Living Xenarthra

Order: XENARTHRA, Gill (1872)
        syn: Bruta, Linnaeus (1758)
        Edentata, Cuvier (1798)
        Edentati, Vicq-D'Azyr (1792)
Suborder: PILOSA (This suborder will not be discussed here, and
          is included only to show the relationship to the armadillos.)
          Family: Bradypodidae (Sloths)
          Family: Myrmecophagidae (Ant Eaters)
Suborder: HICANODONTA, Ameghino (1889)
        syn: Loricata, Owen (1845) (Cockrell (1931) pointed out
            that Loricata was preoccupied by Loricata, Merriam, for
            a group of crocodilian reptiles.)
        Family: Dasypodidae (Armadillos)

Introduction to the Family Dasypodidae

This family comprises the armadillos. They may be distinguished from all other mammals by the presence of ossified dermal scutes (Miller and Gidley, 1931; and Frechkop, 1949). Some of the whales have remnants of bony plates along the back (Beddard, 1909). The armadillos are all new world inhabitants and except for *Dasypus novemcinctus*, all are neo-tropical. There are some nine or ten valid genera of living armadillos, and as many extinct genera. The living forms fall into six natural groups and in the following taxonomic scheme are placed in the six sub-families employed by Yepes (1828). Whether or not all these groups rate subfamilial status is not certain, just as the problem of the correct affinities of the order is still unsettled. However, taxonomic schemes are all arbitrary and since this particular one adequately indicates the degree of affinity among the genera, it is employed. The reader is invited to make such changes in the familial and ordinal groupings as may to him seem appropriate.

Two genera are omitted from the family because of the very dubious nature of their validity. The first, *Tolypoides*
Taxonomy

(Nevoe-Lemaire et Grandidier, 1905) contains only one species, *bicinctus*, and is likely an anomalous specimen of *Tolypuetes tricinctus matacos*. If such a genus should prove to be valid it would belong to the subfamily Tolypuetinae. Secondly, in 1871, A. Milne-Edwards described an armadillo from Peru which he called *Scleropleura bruneti* (1871, 1872). Milne-Edward’s description was made from an incomplete tanned hide purchased from a dealer. The hide was without hair and contained dermal ossicles of no particular size or conformation. Except for the absence of hair, the description is reminiscent of the skin of a supposed ground sloth found in a cave in Argentina. The reader is referred to Prichard (1902) for a complete description of this latter skin and the circumstances surrounding its discovery.

Except for the Dasypodinae, the synonymies are treated in condensed form. References to taxonomic work treating the particular forms is given following each group. For further synonymies of many general names see Palmer (1904), also see Yepes (1928) for additional references to names used below.

*Description:* Several works by Flower and Lydekker (1891) and Frechkop and Yepes (1949b) give adequate descriptions of the family Dasypodidae. Magne de la Croix (1938) provides a brief popular description of the principal genera.

*Vernacular names:* Simpson (1941) gives the vernacular names of the more common armadillos. Hamlett (1939) and Yepes (1928) give several common names for the armadillos they discuss.

**Classification of the Family Dasypodidae**

Family: DASYPODIDAE, Bonaparte (1838)
syn: Armadillidae, Redfield (1858)
Chlamyphoridae, Gray (1869)
Dasypidae, Gray (1821)
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Praopidae, Ameghino (1889)
Scleropleuridae, Lahille (1895)
Tatusidae, Burnett (1830)
Tolypuetaeidae, Gray (1869)

The subfamilies are considered in detail in succeeding sections.

Subfamily: Chlamyphorinae
 Genera: Chlamyphorus
 Burmeisteria

Subfamily: Tolypuetaeinae
 Genus: Tolypus

Subfamily: Priodontinae
 Genus: Priodontes

Subfamily: Cabassoinae
 Genus: Cabassous

Subfamily: Euphractinae
 Genera: Euphractus
 Chaetophractus
 Zaedyus

Subfamily: Dasypodinae
 Genus: Dasypus

THE SUBFAMILY CHLAMYPHORINAE

Subfamily: CHLAMYPHORINAE, Bonaparte (1850)
 syn: Chlamydophorina, Bonaparte (1850)

For further notes on synononies see Palmer (1904).

Description: Dorsal shield composed of 24 transverse bands of scutes. Pelvic shield bony, attached to pelvis, tail short, feet strong, toes united, claws large, external surface of body covered with extremely fine hair.

Chlamyphorus, Harlan (1825)
 Genotype: Chlamyphorus truncatus, Harlan.
 syn: Chlamyphorus, Lenz (1831)
 Chlamyphorus, Wagler (1830)

See Yepes (1928) for further synononies.

Chlamyphorus truncatus, Harlan (1825)
 Type Specimen: C. truncatus, Harlan.
 syn: Chlamydophorus truncatus (Wagler, 1830)

Yepes (1932b) described the geographic forms of C. trun-
Several authors deal with the classification of \textit{C. truncatus}, Burmeister (1867).

\textit{Description}: Slade's article (1891) furnishes an excellent description of this animal. The dorsal shield is attached down the mid-dorsal line, the sides are free.

\textit{Range}: Western Argentina.

\textit{Burmeisteria}, Gray (1865)

Genotype: \textit{Chlamydophorus retusus}, Burmeister

syn: \textit{Calyptophractus}, Fitzinger (1871)

The species was put in a separate genus by Gray in 1865. It differs from \textit{C. truncatus} in that it is larger and the armored shell is attached at the edges to the body. The pelvic plate and tail are partly covered with tesserae.

\textit{Burmeisteria retusa}, Burmeister (1863)

Type specimen: \textit{Chlamydophorus retusus}, Burm.

syn: \textit{Calyptophractus retusus}, Fitzinger (1871).

\textit{Chlamydophorus retusus}, Burmeister (1863)

See Yepes (1928) for further synonomies.

Yepes (1939) described a new subspecies of \textit{Burmeisteria} and gave its probable range limits.

\textit{Description}: Burmeister (1863) described the specimens from which the speciation was made.

\textit{Range}: Bolivia and northwest Argentina.

\textbf{THE SUBFAMILY TOLYPUETINAE}

Subfamily: TOLYPUETINAE, Gray (1865)

\textit{Description}: Carapace hard and very convex, scapular shield oval with two or three movable bands, able to roll up into ball.

\textit{Tolypoides bicinctus}, Neveu-Lemaire et Grandidier (1905), probably an anomolous \textit{T. c. matacos}.

\textit{Tolypueto}, Illiger (1811a)

Genotype: \textit{Dasypus tricinctus}, Linnaeus

syn: \textit{Apar}, Geoffrey (1847)
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Apara, McMurtrie (1831)
Sphaerocormus, Fitzinger (1871)
Matacus, Rafinesque (1815)
Cheloniscus, Gray (1865)

See Yepes (1928) for further synonemies.

The shell of this genus is very hard. The animal curls up into a ball when attacked, the shell giving adequate protection from predators.

*Tolypuetes tricinctus tricinctus*, Linnaeus (1758)
Type specimen: *Dasypus tricinctus*, Linn.
syn: *Dasypus tricinctus*, Linnaeus (1758)
*Dasypus quadricinctus*, Linnaeus (1758)
*Tolypuetes tricinctus*, Illiger (1811b)

*Description*: See Sanborn (1930a).

*Range*: Northeastern Brazil.

*Tolypuetes tricinctus matacos*, Desmarest (1804)
Type specimen: *Tatou huitieme*, Azara (1802)
syn: *Dasypus conurus*, Geoffroy (1847)
*Dasypus tricinctus*, Rapp (1852)
*Tatou huitieme ou Tatou mataco*, Azara (1802)
*Tolypuetes conurus*, Gray (1865)
*Tolypuetes globulus*, Illiger (1811b)
*Tolypuetes matacos*, Desmarest (1804)
*Tolypuetes tricinctus*, Gray (1869)

For further synonemies see Yepes (1928) and Osgood (1919).

*Description*: See Sanborn (1930a). This is the commonest 3-banded armadillo.

*Range*: Bolivia, Brazil, Paraguay, Argentina.

*Tolypuetes tricinctus muriei*, Garrod (1878)
Type specimen: *Tolypuetes muriei*, Garrod
syn: *Tolypuetes conurus*, Murie (1875)
*Tolypuetes muriei*, Garrod (1878)

*Description*: See Sanborn (1930a). Possibly not distinct from *matacos*.

*Range*: Patagonia, possibly north to Buenos Aires.
Taxonomy

The Subfamily Priodontinae

Priodontina, Gray (1873a)

Description: See description below of *P. giganteus*.

Priodontes, Owen (1845)

Genotype: *Dasypus gigas*, Cuvier (1822) = *D. giganteus*, Geoffrey (1803)

syn: *Cheloniscus*, Wagler (1830)

*Dasyypus*, Geoffrey (1803)

*Loricatus*, Desmarest (1804)

*Polygomphius*, Gloger (1841)

*Priodon*, McMurtrie (1831)

*Priodonta*, Gray (1843)

*Priodonte*, McMurtrie (1831)

*Prionodon*, Gray (1843)

*Prionodontes*, Burmeister (1879)

*Prionodotes*, Gray (1865)

Contains a single species.

Description: See description of *P. giganteus*.

*Priodontes giganteus*, Geoffrey (1803)

Type specimen: *El Maximo*, Azara (1802)

syn: *Cheloniscus gigas*, Lahille (1914)

*Dasyypus giganteus*, Geoffrey (1803)

*Dasyypus gigas*, Cuvier (1822)

*Loricatus giganteus*, Desmarest (1804)

*Polygomphius giganteus?*, Gloger (1841)

*Priodon giganteus*, McMurtrie (1831)

*Priodon maximo*, Allen (1890)?—Lahille (1899)

*Priodonta gigas*, Gray (1843)

*Priodonte giganteus*, McMurtrie (1831)

*Priodontes giganteus*, Cuvier (1827)

*Priodontes gigas*, Owen (1845)

This species is the largest of the present day armadillos. It is known to reach a length of four feet exclusive of the tail. The scutes of the carapace are of a uniform size and shape and this fact together with the close apposition of the movable bands, of which there are some 11 or 12, makes the bands inconspicuous. The manus is greatly modified for digging. The third digit bears a large sickle shaped claw.
The Armadillo

(see Scott, 1929, for illustration). Kuhlhorn's work (1938) gives a general account of the giant armadillo. This work and that of Cully (1939) have pictures of the animal. See also Lönnberg (1942), for description and discussion of dentition. Mohr (1939) has a description and several good photographs of a *D. giganteus* which was kept in a zoo in Germany.

*Distribution*: Brazil, Paraguay and northern Argentina.

**The Subfamily Cabassoinae**

*Description*: Carapace slightly convex, cephalic shield oval, small; separated from scapular shield by three widely spaced cervical rings; eleven movable bands; five toes on fore foot, claws on third and fourth toe well developed and curved.

*Cabassous*, McMurtrie (1831)

Genotype: *Dasypus unincinctus*, Linnaeus

syn: *Arixostus*, Cogger (1841)

*Cabassous*, McMurtrie (1831)

*Cachicama*, McMurtrie (1831)

*Lysiurus*, Ameghino (1891)

*Tatoua*, Gray (1865)

*Tatusia*, Cuvier (1827)

*Xenurus*, Wagler (1830)

*Ziphila*, Gray (1873a)

*Description*: that of the subfamily. See Yepes (1935).

*Cabassous unincinctus*, Linnaeus (1758)

Type specimen: *Dasypus unincinctus*, Linnaeus

syn: *Arizostus gymnurus*, Cogger (1841)

*Cabassous unincinctus*, Cuvier (1822)

*Dasypus duodecimcosatus*, Schreber (1835)

*Dasypus gymnurus*, Illiger (1811b)

*Dasypus undecimcincintus*, Illiger (1811b)

*Dasypus unincinctus*, Linnaeus (1758)

*Dasypus verrucosus*, Wagler (1854)?—Yepes (1928)

*Dasypus xenurus*, Krauss (1862)
Description: See Yepes (1928), Miller (1899), Palmer (1899).
Range: Peru, Brazil, Paraguay, Argentina.

*Cabassous hispidus*, Burmeister (1854)
Type specimen: *Dasypus hispidus*, Burmeister.
syn: *Tatoua (Tatoua) hispida*, Miller (1899)
*Xenurus latirostris*, Gray (1873a)

Description: See Miller and Miller (1899).
Range: Brazil.

*Cabassous lugubris*, Gray (1873a)
Type specimen: *Ziphila lugubris*, Gray
syn: *Tatoua (Ziphila) lugubris*, Miller and Miller (1899)
*Ziphila lugubris*, Gray (1873a)

True (1896) thought this species as well as *X. latirostris* was synonymous with *C. hispidus*.

Description: See Miller and Miller (1899).
Range: Guiana, Paraguay, Brazil.

*Cabassous centralis*, Miller and Miller (1899)
Type specimen: *Tatoua (Ziphila) centralis*, Miller
syn: *Tatoua (Ziphila) centralis*, Miller and Miller (1899)

Description: See Miller and Miller (1899).

*Cabassous loricatus*, Pelzeln (1883)

**The Subfamily Euphractinae**

Description: Six to eleven movable bands, margin of carapace generally serrated. Cephalic shield well defined and triangular; relatively hirsute. Three genera.

*Euphractus* Wagler (1830)
Genotype: *Dasypus sexcinctus*, Linnaeus
syn: *Cryptophractus*, Fitzinger (1856)
*Dasyphractus*, Fitzinger (1871)
*Dasypus*, Linnaeus (1758)
*Encoubertus*, McMurtrie (1831)
*Pseudotroctes*, Gloger (1841)

One species with five subspecies (Thomas, 1907).
The Armadillo

**Description:** That of subfamily but with six bands; not very hairy.

_Euphractus sexcinctus sexcinctus_, Linnaeus (1758)
- Type specimen: _Dasypus sexcinctus_, Linnaeus
- syn: _Dasypus sexcinctus_, Linnaeus (1758)
- _Dasypus encoubert_, Desmarest (1822)

**Description:** See Thomas (1907).

_Euphractus sexcinctus setosus_, Wied (1826)

**Description:** See Thomas (1907).

_Euphractus sexcinctus gilvipes_, Illiger (1811b)
- Type specimen: _El poyou_, Azara
- syn: _Dasypus encoubert_, Desmarest (1822)
- _Dasypus gilvipes_, Illiger (1811b)
- _Dasypus sexcinctus_, Ameghino (1889)
- _El Poyou_, Azara (1802)
- _Loricatus flavimanus_, Desmarest (1804)

For further synonomies see Yepes (1928) and Osgood (1919).

**Description:** See Yepes (1928) and Thomas (1907).

**Range:** Brazil, Paraguay and Northeast Argentina.

_Euphractus sexcinctus boliviae_, Thomas (1907)
- Type specimen: _Dasypus sexcinctus boliviae_, Thomas
- syn: _Dasypus sexcinctus_, Trouessart (1898)
- _Dasypus sexcinctus boliviae_, Thomas (1907)

**Description:** See Thomas (1907), Lonnberg (1942).

**Range:** Bolivia and Northwest Argentina.

_Euphractus sexcinctus tucamanus_, Thomas (1907)
- Type specimen: _Dasypus sexcinctus tucamanus_, Thomas
- syn: _Dasypus setosus_, Holmberg (1878)
- _Dasypus sexcinctus tucamanus_, Thomas (1907)

**Description:** See Thomas (1907) and Yepes (1928).

**Range:** Western Argentina.

_Chaetophractus_, Fitzinger (1871)
- Genotype: _Dasypus villosus_, Desmarest
- syn: _Chaetophractus_, Fitzinger (1871)
- _Cryptophractus_, Fitzinger (1856)
Taxonomy

*Dasypractus*, Fitzinger (1871)
*Dasypus*, Illiger (1811b)
*Loricatus*, Desmarest (1804)
*Tatusia*, Fischer (1828)

**Description:** Rather hirsute, sometimes almost hiding plates. Seven to nine or more bands. See Yepes (1928).

*Chaetophractus villosus*, Desmarest (1804)
  Type specimen: *El Peludo*, Azara
  syn: *Chaetophractus villosus*, Fitzinger (1871)
  *Dasypus villosus*, Illiger (1811b)
  *El Peludo*, Azara (1802)
  *Euphractus villosus*, Gray (1865)
  *Loricatus villosus*, Desmarest (1804)

**Description:** See Yepes (1928).

**Range:** Argentina.

*Chaetophractus nationi*, Thomas (1894)
  Type specimen: *Dasypus nationi*, Thomas
  syn: *Dasypus* (*Chaetophractus*) *nationi*, Trouessart (1905)
  *Dasypus nationi*, Thomas (1894)
  *Dasypus villosus*, Holmberg (1878)

**Description:** See Yepes (1928).

**Range:** Bolivia and Northwest Argentina.

*Chaetophractus vellerosus vellerosus*, Gray (1865)
  Type specimen: *Dasypus vellerosus*, Gray
  syn: *Cryptophractus brevirostris*, Fitzinger (1856)
  *Dasypus brevirostris*, Fitzinger (1871)
  *Dasypus vellerosus*, Gray (1865)

**Description:** See Yepes (1928).

**Range:** Bolivia and Northwest Argentina.

*Chaetophractus vellerosus pannosus*, Thomas (1902)
  Type specimen: *Dasypus vellerosus pannosus*, Thomas
  syn: *Dasypus vellerosus pannosus*, Thomas (1902)

**Description:** See Thomas (1902) and Yepes (1928).

**Range:** Central Argentina.

*Zaedyus*, Ameghino (1889)
  Genotype: *Dasypus minutus*, Desmarest.
  syn: *Zaëdipus*, Ameghino (1889)
The Armadillo

Description: Similar to but much smaller than Chaetophractus; tail relatively free of hair except at base.

*Zaedyus pichiy*, Desmarest (1804)

Type specimen: *El Pichy, Azara*

syn: *Chaetophractus minutus*, Fitzinger (1871)
*Dasypus patagonicus*, Desmarest (1819)
*Dasypus ciliatus*, Fischer (1814)
*Dasypus minutus*, Desmarest (1822)
*El Pichy, Azara* (1802)
*Euphractus minutus*, Gray (1835)
*Loricatus pichiy*, Desmarest (1804)
*Tatusia minuta*, Cuvier (1827)
*Zaedyus minutus*, Ameghino (1889)
*Zaedyus ciliatus*, Allen (1901)
*Zaedyus minutus*, Ameghino (1889)

For further synonomies see Yepes (1928) and Osgood (1919).

The Subfamily Dasypodinae

Description: Carapace quite complex, dermal and osseous scutes not symmetrically placed (See anatomy section). Seven to nine movable bands. Cephalic shield trapezoidal, ears large, four toes on fore feet.

The Genus Dasypus

*Dasypus*, Linnaeus (1758)

Genotype: *Dasypus novemcinctus*, Linnaeus.

syn: *Cachicama*, Geoffroy (1835)
*Cachicama*, Gervais (1855)
*Cachicamus*, McMurtrie (1831)
*Cachicamus*, Degland (1854)
*Cachicamus*, Cuvier (1822)
*Cataphractus*, Brisson (1762)
*Cataphractus*, Storr (1780)
*Dasypus*, Linnaeus (1758)
*Hyperambon*, Peters (1864)
*Mamiatusiusus*, Herrera (1899)
*Loricatus*, Desmarest (1804)
*Mulietia*, Gray (1874)
*Mulietia*, Rhoads (1894)
Taxonomy

Praopus, Burmeister (1854)
Praopus, Burmeister (1879)
Tatu, Frisch (1775)
Tatu, Blumenbach (1779)
Tatu, Liais (1872)
Tatu, Palmer (1897)
Tatu, Elliott (1904)
Tatu, Neveu-Lemaire et Grandidier (1911)
Tatus, Trouessart (1898)
Tatus, Fermin (1769)
Tatusia, Cuvier (1827)
Tatusia, Gray (1869)
Tatusia, Trouessart (1898)
Zonoples, Cloger (1841)

Since this genus contains the best known and most widely distributed of the armadillos, it is not surprising that there has been more confusion regarding it than the other genera. Hamlett (1939) separated *Dasypus septemcinctus* from *D. hybridus*, clarifying a century old confusion. In this paper he recognized five valid species and indicated that *Dasypus (Cryptophractus?) pilosus*, the hairy armadillo, might belong to the genus.

Species other than novemcinctus

*Dasypus septemcinctus*. Linnaeus (1758)

Type specimen: *Dasypus septemcinctus*, Linn.
syn: Cachicama hybridus, Gervais (1855)
Dasypus septemcinctus, Linnaeus (1758)
Dasypus septemcinctus, Erxleben (1767)
Dasypus septemcinctus, Schreber (1775)
Erinaceus loricatus, Balk (1749)
Praopus hybridus, von Pelzeln (1883)
Praopus hybridus, von Ihering (1894)
Tatu megaleolepis, Thomas (1903)
Tatusia hybrida, Goeldi and Hagmann (1904)
Tatusia megaleolepis, Cope (1889b)
Tatusia (Muletia) propalatum, Rhoads (1894)

This species and *Dasypus hybridus* have been confused for an inordinate period of time due to the fact that they have the same number of bands. Hamlett (1939) clears up
The Armadillo

this problem and gives a very lucid early taxonomic history of the animal.

Description: Four toes on fore foot. Six or seven (rarely eight) movable bands. Small, less than three kilos in adult. Ears 40-50% of head length. Tail 80-100% of body length. Teeth 6/8.

Range: Brazil, mostly south of the Amazon River.

_Dasypus hybridus_ Desmarest (1804)
Type specimen: _Loricatus hybridus_, Desm.
syn: _Cachicamus septemcinctus_, Degland (1854)
_Dasypus_ (Cachicamus) _septemcinctus_, McMurtrie (1831)
_Dasypus hybridus_, Desmarest (1804)
_Dasypus hybridus_, Waterhouse (1839)
_Dasypus hybridus_, Philippi (1893)
_Dasypus hybridus_, Cabrera (1925)
_Dasypus septemcinctus_, Schreber (1775)
_Dasypus septemcinctus_, Gmelin (1789)
_Dasypus septemcinctus_, Lümbberg (1928)
_La mulita_, Azara (1802)
_Muletia septemcincta_, Gray (1874)
_Praopus hybridus_, Burmeister (1861)
_Praopus hybridus_, Burmeister (1869)
_Praopus hybridus_, Burmeister (1879)
_Tatu hybridus_, Neveu-Lemaire et Grandidier (1911)
_Tatu hybridus_, Palmer (1897)
_Tatu hybridus_, Lahille (1899)
_Tatu hybridus_, Elliott (1904)
_Tatu hybridus_, Allen (1905)
_Tatus hybridus_, Troussart (1905)
_Tatus hybridus_, Lahille (1914)
_Tatus hybridus_, Marelli (1924)
_Tatusia hybrida_, Martin (1837)
_Tatusia hybrida_, Gray (1865)
_Tatusia hybrida_, Gray (1869)
_Tatusia hybrida_, Ameghino (1889)
_Tatusia hybrida_, Lahille (1895)
_Tatusia hybrida_, Trouessart (1898)
_Tatusia hybridus_, Cuvier (1827)
Taxonomy

This animal is distinguished from the foregoing species by the shorter tail and ears. Osgood and Osgood (1921) pointed out that species should be cited from Desmarest (1804) and not Fischer (1814). This species and *D. novemcinctus* are the only vertebrates known to exhibit specific polyembryony.

**Description:** Four toes on the fore foot. Six or seven (rarely eight) movable bands. Small, less than three kilos when adult. Ears 25-33% of head. Tail 67-70% of body. Teeth usually 6/8.

**Range:** Paraguay, Argentina, Uruguay, southern Brazil.

*Dasypus kappleri*, Krauss (1862)

Type specimen: *Dasypus peba*, Cabanis (1848)

syn: *Dasypus kappleri*, Krauss (1862)

*Dasypus kappleri peruvianus*, Lönnberg (1928)

*Dasypus peba*, Cabanis (1848)

*Dasypus (Praopus) peba*, Burmeister (1854)

*Dasypus pentadactylus*, Peters (1864)

*Tatu pastasae*, Thomas (1901)

Hamlett (1939) considers that the sub-species which Lönnberg described is not valid being based probably on characters which are individual variations. He likewise makes Thomas’ *pastasae* a synonym, but Thomas (1901) listed numerous skull and armor differences from *kappleri* when he removed the specimen from *D. kappleri*. Sanborn (1929) described three more specimens of *D. pastasae* and pointed out that at that time there were only seven specimens of *kappleri* known. Lönnberg (1928) has described two sub species of *D. kappleri* as *D. kappleri peruvianus* and *D.k. beniensis* (1942). He discussed them and gives comparative figures in this 1942 article.

**Description:** Usually five toes on fore foot. Large, weighing eight kilos or more, ears short, tail about body length. Seven or eight movable bands, two or three rows of bony, projecting scutes on knee. Teeth 8-9/8.
The Armadillo

**Range:** Amazonian and Caribbean regions.

*Dasypus “mazzai,”* Yepes (1933)

Type specimen: *Dasypus novemcinctus*, Linnaeus
Paratype: *Dasypus mazzai*, Yepes (1933)
syn: *Dasypus mazzai*, Yepes (1933)

Described by Yepes from two specimens from Salta, Argentina. The two specimens appear quite different and according to Hamlett (1939) are *D. novemcinctus*. The paratype shows several distinct characters and will have to be redesignated (Hamlett, 1939).

**Description:** Four toes on fore foot. Small. Ears 40% of head length. Tail 40% of body length. Teeth 8/8-9. Cephalic shield without occipital lobe. Scales in middle third of scapular and pelvic shields equal sized.

**Range:** Salta Argentina.

*Dasypus (Cryptophractus) pilosus*, Fitzinger
syn: *Cryptophractus pilosus*, Fitzinger (1856)

*Praophys hirsutus*, Burmeister (1861)

This is the hairy armadillo. Flower (1886) described an armadillo which he said closely resembled *D. novemcinctus* and which he concluded was *D. (C.) pilosus*. Flower (1894) and Thomas (1927) record additional specimens of the species. There is some question regarding the correct affinities of this animal. It is very rare (Hamlett, 1939), the above reference comprising its entire bibliography.

**Range:** Bolivian and Peruvian Plateau.

*Dasypus novemcinctus*, Linnaeus (1758)

Type specimen: *D. novemcinctus*, Linn.
syn: *Cachicamus novemcinctus*, Degland (1854)
*Dasypus (Cachicamus) novemcinctus*, McMurtrie (1831)
*Dasypus fenestricatus*, Peters (1864)
*Dasypus leptorhyncha*, Gray (1873a)
*Dasypus longicaudatus*, Kerr (1792)
*Dasypus longicaudus*, Wied (1826)
This species has the largest range of any of the armadillos and not unexpectedly several sub-species have been described. The northern-most sub-species is *D. n. mexicanus*, Peters (1864). The type specimen is *D. n. texanum*, Bailey (1905) but Hollister (1925) pointed out that *D. n. mexicanus*, Peters has priority. Russell (1953) has described a new sub-species, *D. n. davisi*, from the Balsas Basin, Mexico. This appears to merge with *D. n. mexicanus* in the mountains of northern Morelos, Mexico. The southern sub-species is *D. n. fenestratus*, Peters (1864). According to Hollister (1925) this is the *D. n. mexicana* of Gray (1873b), and the *D. n. mexicanus* of Bailey (1905). Hollister calls the South American nine-
banded armadillo *Dasypus longicaudatus*. The sub-species *D. n. hoplites* of Allen (1911), described from the West Indies, comprises the fourth sub-species.

A dwarf armadillo reported from Tobago by Clark (1914) was referred by him to *D. n. hoplites*. The authors are grateful to Dr. Clark for foregoing this opportunity to erect a new sub-group. A fifth sub-species, *D. n. aequatorialis* from Ecuador, was described by Lönnberg (1913). Lönnberg (1928) discusses the nomenclature and varieties of *D. novemcinctus*. Hagmann (1908) describes a sub-species of the nine-banded armadillo of Brazil as *Tatusia (Dasypus) novemcinctus mexiane*. This sub-species occurs in the island of Mexiane in the Amazon estuary.

*Description:* Four toes on front foot, eight to eleven movable bands, usually eight to nine. Adult weight 3-8 kilos, northern specimens larger. Ears 40-50% length of head. Tail equaling or exceeding body length. Teeth normally 8/8.

*Range:* Southern United States, south to Northern Argentina.

REFERENCES ON THE TAXONOMY OF THE ARMADILLOS


Ameghino, F. (1889). Contribución al conocimiento de los mamíferos fósiles de la República Argentina. Actas de la Acad. nacional de ciencias de Córdoba VI.


Taxonomy

Blumenbach, Johann Friedrich (1779). Handbuch der Naturgeschichte
1:74, Göttingen.
Blumenbach, Johann Friedrich (1779). Handbuch der Naturgeschichte
1:74, Göttingen.
Burmeister, H. C. (1854). Sistematische Uebersicht der Thiere
Brasiliens, Welche Während einer Reise durch die Provinzen von
——— (1863). Beschreibung eines behaarten Gürtelthieres, Praopus
Halle 6:145.
——— (1867). Notes on skeleton of Dasypus gigas; and notes on
——— (1869). Cátálogo de los mamíferos argentinos con las especies
exóticas que se conservan en el Museo publico de Buenos Aires.
An. Mus. B. Aires. 1:446.
——— (1879a). Description physique de la République Argentine
Burnett, Gilbert T. (1830). Illustrations of the Quadrupeda, or
Quadrupeds, being the arrangement of the true four-footed beasts
Cabanis, Jean (1848). Schomburgk’s Reisen in British Guiana in den
Cabrero, Angel (1917). Mamíferos del viaje al Pacífico verificado en
1862 a 1865 por una comisión de naturalistas enviada por el
gobierno español. Museo nacional de ciencias naturales. Series
zoológicas # 31:3. Madrid.
Clark, Austin H. (1914). Two interesting Mammals from the Island of
23:657.
——— (1889b). On the Mammalia Obtained by the Naturalist Explor-
ing Expedition to Southern Brazil. Am. Nat. 23:128.
Cuvier, Georges (1798). Tableau élémentaire de l’histoire naturelle des
——— (1822a). Recherches sur les Ossements Fossiles de Quadrupèdes,
The Armadillo


——— (1874). On the Short-tailed Armadillo (Muletia septemcincta) P.Z.S. 1874:244.
Hollister, Ned (1925). The Systemic Name of the Texas Armadillo. J. Mamm. 6:60.
The Armadillo


International Comm. on Zoological Nomenclature. Opinion #90 (1925) Smithsonian Miscellaneous Coll. v. 73, opin. 90.

Kerr, Robert (1792). The animal kingdom, or zoological system, of the celebrated Sir Charles Linnaeus. London.


Taxonomy


Prichard, H. (1902b). Field notes upon some of the larger mammals
The Armadillo

of Patagonia, made between September 1900 and June 1901.
P.Z.S. 1902 i:272.
Rapp, Wilhelm van (1852). Anatomische Untersuchungen über die
Redfield, Anna Maria (1858). Zoological Science, or Nature in Living
Form. New York.
Rhoads, S. N. (1894). Description of a new armadillo, with remarks on
Russell, Robt. J. (1953). Description of a new armadillo (Dasypus
novemcinctus) from Mexico with remarks on geographic variation
J. Mamm. 10:258.
— (1930a). Distribution and Habits of the 3-banded Armadillo
Schreber, J. C. D. (1775). Die Säugethiere in Abbildungen nach der
Scott, William B. (1929). A History of Land Mammals in the Western
Hemisphere. McMillan and Co. 2nd ed.
Simpson, George G. (1941). Vernacular Names of South American
XXV:541.
Storr, Gottlieg C. C. (1780). Prodromus Methodi Mammalium p. 40,
Tab. B. Tübingen.
— (1901). New sp. of Sarcopteryx, Sciurus, Rhipidomys, and Tatu
— (1902). On Mammals Collected at Cruz del Eje, Central
— (1903). On the Mammals Collected by Mr. A. Robert at
— (1907). On Neotropical Mammals of the genera Callicebus,
— (1927). The Godman-Thomas expedition to Peru. VI. On
mammals from the Upper Huallagas and Neighboring highlands.
Trouessart, E. L. (1898). Catalogus mammalium tam viventium quam
fossilium. Berlin.
— (1905). Catalogus Mammalium tam viventium quam fossilium,
supplement. Berlin.


Wagner, Johann. (1841). Supplement Schreber’s Säugethiere. Vol. II. Leipzig. (?)


—— (1932b). Las formas geográficas del “pichi ciego” menor (Chlamydophorus truncatus Harl.). Physis B. Aires. 11 # 38:9.


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MORPHOLOGY AND ANATOMY

MUCH of the work published prior to 1900 concerning either Dasypus novemcinctus or other South American armadillos dealt with aspects of the anatomical structure. However, some of this work was extremely fragmentary and was published in journals which are not easily available. As a result, a few of these earlier works dealing with the anatomy of the armadillo are not included in this review,
and some of those which are included must necessarily be
based on short abstracts.

It would be both impossible and pointless to discuss all
the aspects of the anatomy of the armadillo. Primary em-
phasis will therefore be given to those anatomical characteris-
tics which are peculiar to this animal, or which, by the
modification thereof, adapt it to its particular mode of life.
The general appearance of the armadillo (*D. novemcinctus*)
has been described in a previous section.

*The Integument*

Due to the unusual character and structure of the integu-
ment, this aspect of the anatomy was the first to receive the
attention of scientists. As early as 1859, Leydig described the
components forming the integument. In 1877, Kerbert de-
scribed the formation of the bands; and Romer (1892) fol-
lowed this with the first detailed histological description of
the carapace. The most complete descriptions of the integu-
ment are given by Wilson (1914), Pocock (1924) and Cooper
(1930). Prior to this, partial descriptions were given by New-
man and Patterson (1911) and Newman (1915, 1916), in works
which were written in connection with genetic variations as
related to specific polyembryony. Other work on the integu-
ment has been done by Fernandez (1921b, 1922a, 1922b) and
by Pocock (1913).

For a general description of the integument the following
is quoted from Kalmbach (1943):

The scale-like skin forms a carapace covering the body
proper. This is divided into three sections, a shell that
protects the shoulders, another that covers the pelvic region
and a series of nine somewhat telescoping bands connecting
the other two parts. The upper parts of the head and the
exposed portions of the legs are well protected with heavy
scales and the tail covering consists of 14 rings of decreasing
size in addition to a terminal portion that is covered with irregularly placed scales.

The under parts of the body and the protected portions of the legs and head are devoid of heavy scales but much of this tough skin is studded with scale-like nuclei from which arise groups of coarse hairs. The insides of the fore and hind legs and the sides of the abdomen protected by the edges of the body shell often are well supplied with long coarse hair, usually more profuse in the males than in the females. Even the upper surface and the edges of the carapace itself have a sparse growth of hair arising largely from the posterior borders of individual scales.

The primary scientific argument concerning the integument was relative to the existence of epidermal scales somewhat similar to those found in reptiles, and to their relationship in embryonic origin to hair follicles. Fernandez (1931) described the structure and development of the integument of *D. villosus* with particular reference to the relationship of glands and hair development. For *D. novemcinctus*, a detailed description of the development of the integument is given by Cooper (1930) with a discussion of this and related phylogenetic problems. The reader is referred to this article for details. Due to its importance, the summary is quoted here verbatim:

In the earlier stages of its development the integument of the armadillo consists of a single layer of cuboidal epithelial cells and the underlying mesenchyme cells. In the midregion of the body bands are formed by the infolding of the dermis and the epidermis, and the integument is thus divided into four general regions: anterior and posterior shields, band region and ventral surface. Development in these four regions proceeds at different rates. This difference is particularly evident in the hair follicles.

The large hairs found on the ventral surface of the animal are the first to develop. During the earlier embryologic stages the follicles in the anterior and posterior shields develop at about the same rate as the primary follicles of the band region. The latter then begin to develop more rapidly, and the secondary hairs of the band region and those of the
anterior and posterior shields become more nearly comparable in size and stage of development. One sudoriparous and one or two sebaceous glands are found in conjunction with each hair follicle. This is probably the typical primitive arrangement of these structures. The epidermal scales are formed by the accumulation of cell remnants above the stratum granulosum. The scales appear much later in embryologic development than do the hair follicles. The dermal plates ossify late in fetal life, and ossification is not complete at birth. This study affords no support for theories which relate the phylogenetic development of hairs and scales.

In addition to the glands of the integument discussed above, the armadillo possesses a pair of anal glands which can be everted or retracted at will. These are scent glands and give the animal its characteristic musty odor, which when concentrated may become pungent and very disagreeable.

**Armadillo Dentition**

In the adult armadillo, there are normally sixteen teeth in each jaw, all are molars and without enamel. These protrude only slightly above the gum line and are relatively flat. The eight teeth on either side do not articulate directly with the eight teeth on the corresponding side of the other jaw. They are so arranged that the first front tooth of the lower jaw has no corresponding tooth on the upper jaw, the second front tooth of the lower jaw articulating with the first on the upper jaw. Accordingly, the last back tooth of the lower jaw articulates with the next to the last of the upper jaw, leaving the last tooth in the upper jaw without a corresponding member in the lower jaw. The premaxillary bone of the upper jaw and the anterior portion of the maxilla are toothless, as are the corresponding portions of the mandible.
The adult condition is obviously a degenerate one, and careful embryological study of tooth formation has shown not only the presence of incisor buds, but also development of single and double cuspid molars. A detailed description of tooth formation in *D. novemcinctus* has been given by Martin (1916), based on a series of embryos from the 30 mm. stage through the post-embryonic animal. In addition to the molars which persist, there develops in embryonic life five to six incisor buds, in the lower jaw, which degenerate in late foetal life, with rarely any persisting at the time of birth. In the upper jaw, in the premaxilla, there have been found three to five epithelial cysts, which may represent front teeth in the last stages of degeneration.

While enamel is absent in the adult teeth, a functional enamel organ is present in the foetus, and at birth the molars are covered with enamel. The enamel organ was noted by Tomes (1874), Tauber (1876), Reinhardt (1876), Gervais (1876) and Pouchet and Chabry (1884) for *D. novemcinctus*, and by Röse (1891, 1892) for *D. hybridus*. It was further studied by Leche (1895, 1896), Kukenthal (1891), Ballowitz (1892) and Spurgin (1904). Martin (1916) showed its early function to be similar to that of other mammals and that the armadillo teeth are coated with enamel at birth. In addition, Martin (1916) showed that the molars which are flat and enamelless in the adult are cusped at least some time during embryonic development. In fact, all but the 1st, 2nd, and 8th teeth of the lower jaw start out with two cusps, while in the upper jaw, all but the first and last are so equipped. Of the eight functional back teeth, seven are replaced by permanent successors; the eighth, which appears late, is not replaced. Flower (1868) first noted the milk dentition in armadillos and it has recently been reviewed by Yepes
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Yepes (1949a) also compared the dentition of various species of armadillos found in Argentina.

Skeletal System of the Armadillo

The skeletal system is typically mammalian in character. It is, however, closely associated with the integument at the top of the skull, and at the lateral edges of the pelvis. The vertebrae of the tail are in contact with the bony rings of the dermal coverings by means of all their major processes. The skeleton of the *D. novemcinctus*, has, in itself, not received too much attention. However, comparisons of parts of the skeleton of various armadillos have been made with other edentates and with other mammals in general. Since it is impossible to take up each of these separately, an annotated bibliography is given below:

1. Skeleton of Edentates with special reference to Armadillos.
   a. The Skull—Bucciante and Muggia (1935), Parker (1884)
   b. The Vertebral Column—Rosenberg (1884)
   c. The Jaws—Sousa (1939), Kühlhorn (1939)
   d. The Pelvis—Albrecht (1883)
   e. The Legs—Burmeister (1871a, 1871b), Gervais (1877), Nauck (1928)
   f. The Feet—von Bardeleben (1894)

2. Skeleton of Mammals with special reference to Armadillos.
   a. The Mastoid Process—Forster (1931)
   b. The Skull—Class (1951) “a key”
   c. The Pelvis—Ruth (1932)
   d. Embryology of Limbs—Schmidt-Ehrenberg (1942)
   e. Nasal Bones—Wegner (1922)
   f. Pelvisternum—Anderson (1886)

3. Skeletal Studies of Armadillos other than *D. novemcinctus*.
   a. *Priodontes giganteus*—Burmeister (1867, 1879), Giebel (1887), Kraus (1866) and Kühlhorn (1938b)
   b. *Euphractus sexcinctus*—Ardouin (1937)
   c. *Tolypuetes conurus*—Gray (1873c, 1873d), Owen (1832a)
   d. *Dasypus kappleri*—Anthony and Logotala (1922)
   e. *Chlamyphorus truncatus*—Atkinson (1870); Gray (1857,
The Musculature of the Armadillo

The muscular system of the armadillo is extremely well developed and makes up the greater portion of the bulk of the animal. The muscles associated with both the fore and hind legs are very powerful and are especially adapted for digging. This large muscle mass has permitted the use of the animal as a source of food. The primary technical works in regard to the development of the musculature of the appendages are those of Miles (1940, 1941) which are limited, however, to the region of the shoulder. Zeiger has described the musculature of the trunk both for D. novemcinctus (1929) and for Tolypuetes (1927). The cranial musculature is discussed by Edgeworth (1923), who gives additional references, not included here, to the description of specific muscles in the cranial region of the armadillo. Fawcett (1921) also describes the development of the cranial primordial musculature. Locchi (1934, 1940) discussed the diaphragm of the genus Dasypus and in 1932 described the innervation of the platysma for the same genus.

In other armadillos, Galton (1869) has described the limb musculature of Euphractus sexcinctus and Tavani (1939) has discussed the vocal muscles of Tolypuetes. Burne (1901) and Chaine and Kunstler (1902) both studied the general myology of Chlamyphorus truncatus. Von Bardeleben (1894) dis-
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cussed the musculature of the foot of *Euphractus sexcinctus*
and *Zaedyus pichiy*.

Other work on the musculature of the armadillos is con-
tained in works covering members of the order Xenarthra,
and include the following: Zeiger (1925, 1927), Ueckermann
(1912), Vuori (1931), Windle and Parsons (1899), and Windle
(1899a, 1899b).

The Central Nervous System of the Armadillo

The central nervous system has been described in only a
few detailed papers. Shuddemagen (1907) gives a detailed
macroscopic study of both the brain and spinal cord with
particular emphasis on the appearance of the brain and its
primary commissures, ventricles, and nerves. She notes the
similarity to that of lower mammals. In this regard, Papez
(1932b), in discussing the thalamic nuclei, indicates that the
armadillo brain resembles that of Insectivora more closely
than it does other Edentata. In addition, two other recent
works describe portions of the brain of the armadillo in some
detail: Howe (1933), on the basal diencephalon, and Crosby
and Woodburne (1943), on portions of the midbrain and
isthmus. An abnormality of the choroid plexus was reported
by Mettler (1932).

In reference to other armadillos, Hubschmann (1903) de-
scribed the medulla oblongata of *Chaetophractus villosus*;
Hyrtl (1855) compared the nervous system, particularly the
brain, of *Chlamyphorus truncatus* and *Cabassous unicinctus*
and Turner described the brain of *Euphractus sexcinctus*
(1867).

The following general works on the nervous system of
edentates make specific reference to the armadillo: Smith
(1899), Gervais (1869), Pouchet (1868a), Rapp (1852), Dräseke
(1913), Krabbe (1942); and Sonntag (1922).
General Anatomy and Miscellaneous Anatomical Studies

In addition to the works mentioned in the preceding sections dealing with special systems or organs, there has been a fair amount of work written dealing with the general anatomy of the armadillo, much of which is in connection with general studies of the edentates. The earliest of these, and one of the earliest mentions of the armadillo, *D. novemcinctus*, was that by Owen (1831a) which contains, as the title implies, notes on the anatomy of one specimen studied by the author. The same year (1831b) he reported on the anatomy of *Euphractus sexcinctus*. In 1878 Garrod reported on the armadillo *Tolypuetes tricinctus*, comparing the external anatomy of five different armadillos, one of which was *D. novemcinctus*. Other armadillos for which notes on the general anatomy have been reported include *Chlamyphorus*, by McAlister (1875) and Burne (1901); *Zaedyus pichiy*, by Lönnberg (1898); *Chaetophractus villosus*, by Dietrich (1911) and Fauvel (1895); and a recent work by Frechkop (1950) on armadillos in general.

A few miscellaneous studies have been made on specialized structures or organs of the armadillo. These are of interest not only for their subject matter, but also because, for the most part, they represent relatively recent work in comparison with the greater portion of the anatomical studies, which were reported in the earlier part of this century, or before.

Five different reports have been made on the pituitary of *D. novemcinctus*. The first of these, by Wislocki (1938), was concerned with the topography of the pituitary. The anterior and neural lobes are about equal in size, and the intermediate lobe is absent. In 1938, Oldham discussed the anatomy and embryology of the pituitary, with special reference to the
neural lobe. In 1940 Oldham et al. reported the presence of intermedin (melanophore dispersing hormone) in the absence of an intermediate lobe. In 1941, Oldham described the embryonic development of the pituitary in some detail. The fifth report by Drager (1947) reviews the histology of the gland, but is primarily concerned with the innervation of the anterior lobe.

Other recent work includes a study by Wislocki and Straus (1932) on the blood vascular bundles in the limbs of armadillos and other edentates; a study of the development of portions of the gut of Dit. novemcinctus by Corti (1923); and a study of the palatine tonsil of Euphractus sexcinctus and Chaetophractus villosus by Hett (1928).

Anatomical Bibliography not Specifically Mentioned in this Section

2. Beddard (1902)—on the vibrissa of the wrist of Chaetophractus villosus.
3. Beddard (1907, 1909)—concerning certain veins of mammals including armadillos.
4. Cabrera (1929)—a reference to the general biology of the Xenarthra.
5. Eggeling (1899)—the mammary glands of edentates and monotremes.
6. Giancomini (1913)—concerning the embryology of nasal components of Dit. novemcinctus.
7. Hochstetter (1897)—the venous system of edentates.
8. Kawano (1924)—concerning the ear of armadillos.
9. Klinkowstrom (1895)—concerning the anatomy of edentates.
10. Krabbe (1929)—relative to the vestigial parietal eye.
11. Kuhlhorn (1940)—melanism in an armadillo.
12. Martin (1837)—one of the first descriptions of Dasypus novemcinctus.
14. Ochoterena and Samano (1937)—relative to the use of the snout in digging.
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15. Owen (1832b)—a description of the genital organs and mammary gland of two armadillos.
16. Papez (1932a)—concerning the mammillary peduncle of the mid-brain.
17. Pouchet (1868b)—concerning the salivary glands of the edentates.
18. Ritterer and Neuville (1916)—on the spleen of edentates.
19. Sonntag (1923, 1925)—describes the tongue of armadillos and certain other vertebrates.
20. Strecker (1927)—concerning an albino armadillo.
21. Veroni (1913)—concerning the development of the brain of *D. novemcinctus*.
22. Yepes (1932a)—concerning the head scutes of *Chlamyphorus truncatus*.

**PHYSIOLOGY AND GENETICS**

Due to the problems connected with securing and maintaining live animals, physiological studies on armadillos are relatively few. These have mostly been reported since 1930 and appear to be casual experiments, performed when happenstance provided the test animal. The genetic studies on the other hand, were done as a result of the discovery of the phenomenon of polyembryony and are for the most part detailed studies of the variations in the integumental characteristics of litter mates. With only one exception, the genetic studies were carried out by H. H. Newman.

**Body Temperature**

The temperature regulation of the armadillo has received considerable attention. Even under normal conditions with environmental temperature varying between 16° and 28° C, the body temperature of armadillos is relatively low for mammals. Eisentraut (1932) reported a relatively constant 32° within these bounds for *Tolypuetes tricinctus conurus*; Wislocki (1933) reports a more variable 32° to 35° for *Dasypus novemcinctus* for the same environmental range. At lower temperatures, the armadillo is unable to maintain a constant high body temperature, this having been recorded
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as low as 29° C with an environmental temperature of 11° C (Wislocki, 1933). Other reports on the body temperature of armadillos include those of Brown (1909) De Almeida and Fialho (1924), Enders and Davis (1936), Gilmore (1943), and Wislocki and Enders (1935). It is quite probable that the poor control of body temperature in the armadillo is directly correlated with its integumental modifications. However, regardless of the cause, this factor will probably be one of the limiting factors in its ecological spread northward. Since the armadillo does not hibernate, it cannot stay in a burrow throughout the winter protected from the weather, and is thereby unable to survive long protracted cold periods.

Respiration

The armadillo's respiration has been of interest in two regards: first in connection with its burrowing habits, and secondly, due to the experimental evidence that it is able to stay under water for long periods of time. (Kalmbach, 1943; Taber, 1945).

Scholander et al. (1943) studied the respiration of the armadillo under normal resting conditions, and under stress during which time breathing was prevented for periods of up to ten minutes. They noted that the normal oxygen consumption of the resting animal was considerably below that found for animals of similar size such as cats, rabbits, etc., but was approximately that of the sloth. Under stress, the animal was able to build up a considerable oxygen debt, and could struggle violently without access to oxygen for periods up to six minutes. This was compensated for by recovery periods of several hours during which the oxygen intake was above normal. They suggest that this phenomenon is directly related to the burrowing habits of the animal, particularly in their ability to dig burrows in a matter of minutes during
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which time the nostrils and mouth are for the most part covered with dirt or debris.

Since all the reliable evidence of the ability of the armadillo to remain under water for exceptionally long periods is experimental, it can not be confirmed as to whether this ability to contract a large oxygen debt is utilized in crossing bodies of water. However, when forced into the water, it would certainly prove a marked advantage to the animal in his fight for survival.

Scholander et al. (1943) reported the respiratory quotient of the armadillo to average 0.74. This confirmed the earlier work of De Almeida (1930) who had reported the R.Q. for this animal as 0.74.

Miscellaneous Physiological Studies

Other than the above studies, the physiological studies using the armadillo bear little relationship to each other and deal with such subjects as blood components, respiratory quotients, specialized reflexes, and assay of endocrine glands.

Peters (1932) included the armadillo in a report on the erythrocyte size in 42 different species of mammals. Knoll (1932) did likewise in giving the differential leucocyte counts of 55 different species. Gulliver reported the erythrocyte size of *Euphractus sexcinctus* (1844a) and of *Chaetophractus villosus* (1844b). Oria (1929) reported the presence of free histocytes in the blood of *Dasypus novemcinctus* and *Tolypuetes tricinctus*. De Almeida (1930) studied a respiratory reflex which occurred on sudden forced expansion of the carapace. Oldham (1938) and Oldham et al. (1940), in two studies primarily concerned with the anatomy of the pituitary, noted that the anti-diuretic and pressor principles of the posterior lobe of the armadillo pituitary assayed per mg. approximately that of standard powder, while the oxytocic
principle and intermedian assay about one-tenth that of standard powder.

In two articles on the protein metabolism of armadillos, Berg (1932) determined protein storage in the liver by histochemical methods; and Braier (1935) compared the protein metabolism with that of the rat and dog, using four armadillos. In studies on the response of the central nervous system, Clarke (1926) electrically stimulated various parts of the brain to elicit responses in various voluntary muscular systems such as the eyelid, the limbs, etc.

**Genetics**

Shortly after the discovery of the phenomenon of polyembryony, Newman, collaborating with Patterson, initiated a series of studies on the hereditary control of specific traits. The armadillo, because of the formation of identical quadruplets, was an excellent experimental animal for this study. Further, the fact that the bands of the integument are well-established comparatively early in the embryonic development, permitted these structures to be used in establishing a basis for the inheritance of traits, as against the organic variability produced in embryonic development. These articles include detailed statistical studies of scute (integumental) variations, with a discussion of the problems of twinning. Since a complete review of these articles is impossible, the interested reader is referred to them directly. They are listed here chronologically. Newman and Patterson (1909 and 1911); Newman (1913b, 1915, and 1916); Newman, texts on twinning (1917 and 1923). Hamlett and Wislocki (1934) also discuss the armadillo relative to the problem of twinning.

The only other work in this regard is the later work by Langmann (1931), who compared the number of plates in the armor bands of *Dasypus hybridus* which exhibits specific
polyembryony and Chaetophractus villosus without specific polyembryony. The coefficient of variability in regard to this characteristic was the same in both species.

**REPRODUCTION IN THE NINE-BANDED ARMADILLO**

Reproduction in the armadillo is of special interest because of two distinct and apparently unrelated phenomena; the long period of arrested development of the blastocyst prior to implantation; and the phenomenon of specific polyembryony which results in the normal formation of identical quadruplets. The problems concerned with these two phenomena will be discussed in some detail. However, as a background for this it seems advantageous to first review briefly the reproductive cycle of the armadillo in the light of all the data accumulated at the present time.

The nine-banded armadillo, as found in Texas, exhibits an annual reproductive cycle which can be divided into three approximately equal parts; the pre-ovulatory period, the period of delayed implantation, and the period of foetal development. The pre-ovulatory period includes the period of lactation in the post-partum female and the anestrus period of the nonmated animal. In the multiparous animal, this period starts in the spring and is terminated by the spontaneous ovulation of a single follicle sometime during the summer months. The exact relationship of sexual receptivity to the time of ovulation is not known, and it can only be assumed that mating occurs at or about the same time.

Following ovulation a single corpus luteum is formed which by ten days has grown until it occupies between 75 and 90% of the volume of the ovary. This ovary is in size approximately twice that of its non-ovulated mate. The fertilized egg descends the fallopian tube while undergoing its early development and reaches the uterus in about seven
days as a monodermic vesicle. Here it becomes located in the fundus of the uterus where it is closely associated with the endometrium which in this region is extremely glandular. It appears to be constantly bathed in fluid secreted by these glands and is thereby supplied with sufficient nutrition and oxygen for survival. The blastocyst remains quiescent for a period of three to four months. Due to the variation in the time of ovulation and to the length of the period of delayed nidation, normal blastocysts have been found from June of one year through January of the following year.

At the conclusion of the period of arrested development, uterine changes take place which in turn appear to start the process of implantation of the blastocyst. During this process the inner cell mass of the blastocyst breaks free of the träger area of the trophoblast, sinks into the yolk sac and divides into two growth centers, each of which very shortly redivide producing four embryonic shields, attached by a common placenta to the uterine mucosa. Development of each of the embryos then proceeds normally and the four young are born approximately four months later. Mothers have been noted with new litters as early as February and as late as the latter part of May. Since the young are fairly well-developed at birth, and growth is rapid, the nursing period is probably less than two months. It appears possible that young born early in one year may mate in the fall of the same year. However, normally, the young born in one year mature during the winter and mate for the first time in the early summer of the following year.

The Female Reproductive Tract

The anatomy of the female reproductive system of the armadillo was described by Altmann (1924). However, the best anatomical work relative to the female is Newfang's
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(1947) detailed study of the embryonic development of the female reproductive tract. Despite the phylogenetic position of this animal as one of the more primitive animals (Fry, 1846), the structure of the tract contains a mixture of supposedly archaic and specialized recent characteristics.

The ovary remains undifferentiated until a relatively late stage in its embryonic development. Apparently as a result of this late differentiation various constituents of the testis appear in the cortex of the ovary, rudiments of which remain throughout the foetal life of the female. The two kidney shaped ovaries in the immature animal lie in their typical mammalian position posterior and lateral to the kidneys. They are approximately of equal size in the nulliparous animal and during the anestrus phase of the mature multiparous female (Newman and Patterson, 1910).

The uterus is simplex in form, appearing grossly similar to the highly specialized primate uterus rather than to the primitive bicornuate type which one might expect to find in a supposedly archaic mammal. Evidence that this is a secondary adaptation has been given by Newfang (1947), who traces the development of the uterus through what she believes to be a bicornuate stage.

Definite evidence of the primitive nature of this animal is the absence of a vagina. This is replaced by the urogenital sinus which persists throughout life serving both as the vagina and as the urethra. This sinus opens to the outside through a long vestibular cleft. The absence of a true vagina makes it impossible to determine stages of the cycle by vaginal smears.

Newfang describes adreno-cortical-like cells appearing in the early embryonic development of the ovary. The animals killed in our laboratory frequently showed clusters of tissue closely associated with the ovary, and sometimes embedded
into the cortex. Histological examinations showed this to be a tissue similar to the tissue of the adrenal cortex, and preliminary histochemical tests indicate it to be secretory. It is probable that these cell clusters are the structures mentioned by Newman and Patterson (1910) who considered them degenerate corpora lutea.

A second type of accessory tissue on the ovary has been reported by Hamlett (1935c) who reports a relatively high frequency of extra-ovarial sex cords protruding from the surface of the ovary.

The Development of the Follicle

While no work has been done yet on the pituitary-ovarian relationship, there is no reason to assume that the ovary is not under similar pituitary control as has been determined for other mammals. During the preovulatory period, there is a gradual growth of the follicles in both ovaries producing half a dozen large thin-walled follicles in each ovary. The maturation of the follicle and ovum has been followed in detail by Newman (1912) who concludes that the ovo-genesis of the armadillo reveals little that is unique. Newman’s work disproved the earlier assumption of Rosner (1901) who believed that polyembryony in the armadillo was due to a peculiar growth of the ovarian follicles such that four adjacent follicles fused into a single follicular cavity subsequently rupturing four eggs simultaneously.

Just prior to ovulation, the maturation of all but one follicle of the two ovaries stops and atresia sets in. The process of the initial atresia and the growth of the single remaining follicle has been described by Newman (1912). The rapid growth of the single follicle culminates in spontaneous ovulation and release of a single ovum. That ovulation was spontaneous and not produced by mating was determined by
Talmage and his co-workers (1954) by biopsy examination of several females maintained two or more months in the laboratory, examined before ovulation and again after a corpus luteum was formed. Further proof was added when a normal corpus luteum was found in a single non-mated female raised in the laboratory from an age of approximately three months until well past sexual maturity.

**Time of Ovulation**

The only thorough study of the correlation of the stages of the sexual cycle of the female with the time of year was done by Hamlett (1932a, 1935a). On the basis of several hundred animals gathered over a period of years, he concluded that ovulation occurred about the 15th of July, and that the young were born during the following February. He tabulates the spread over the summer months, showing relative numbers of animals found in the preovulatory phases and with a corpus luteum. He further mentions that the time-table was thrown off somewhat by abnormal dry seasons.

During the course of examination of over two hundred females in our laboratories over the past three years, it appeared that abnormal conditions were more numerous than the normal. Apparently, the reproductive cycle is easily affected by adverse environmental conditions, particularly drought conditions. This is probably due to the shortage of ground insects or the difficulty of obtaining these in the sandy or hard dried soil of East Texas. In addition, the years 1950 through 1953 have all been abnormally dry. The influence of the climate on the time of ovulation has been further emphasized by the observation that the animals brought in to us from regions of perpetual dampness, such as some of the swampy regions of East Texas, ovulated...
earlier than did those brought in from regions lacking in water.

Because of the variation in the climatic conditions from year to year and from location to location, it is our opinion that no close date can be given for the time of ovulation; we suggest that the broad dates including the three summer months be given as the ovulatory period. Apparently variations in temperature play little part in causing this spread in time of ovulation.

The Corpus Luteum

The work of Newman and Patterson (1910) and Newman (1912) established without doubt that the armadillo normally ovulates but a single egg during each reproductive cycle. The ruptured follicle transforms immediately into a corpus luteum, which undergoes rapid hyperplasia, and within a few days has taken over most of the ovary. Due to the extra growth of the corpus and the parallel degeneration of the follicles of both ovaries, the ovary containing the corpus soon reaches an average size of approximately twice the other ovary, with as much as 90% of the volume being composed of luteal tissue. Plate I (Figures 1 and 2) taken from Talmage et al. (1954) shows the relative size of the corpus and the characteristic luteal tissue.

Because of the arrested development of the blastocyst which remains quiescent in the uterus for at least fourteen weeks, the corpus luteum has received considerable attention, particularly as to whether or not it was functional during this “delayed” period. As the result of his extensive work with the armadillo, Hamlett (1932a, 1933, 1935a, 1935b) concluded that it was non-secretory for the approximate three months of the “delayed” period, and at the end of that time became functional to support the developing foetuses. His
conclusions were based primarily on histological study. As further evidence of the inactivity of the corpus luteum, he reported negative effects on the blastocyst following removal of the corpus luteum, in contrast to the production of abortion if it was removed after implantation. Unfortunately, his results are summarized in his review (1935a) and the actual data of the experiments involving removal of the corpus luteum were not published.

As the result of our own work (1954) we find ourselves in disagreement with Hamlett and are convinced that the corpus luteum is functional and secretory immediately on its formation. The data on which our conclusions are based are summarized in Table II (taken from Talmage et al., 1954). The titer of progestin in the serum of the armadillo during the periods prior to and following ovulation are strikingly similar to that of the corresponding periods in other mammals studied, such as the rabbit, sheep and man. The increase in progestin activity prior to ovulation indicates that the armadillo follicle, as is true in other mammals studied, secretes some progesterone. The progestin level during the quiescent period is as high as is seen in the early part of any mammalian pregnancy. Removal of the ovaries during the quiescent period drops the serum progestin value to pre-ovulation level. There appears to be a marked increase after implantation, indicating increased activity of the corpus luteum at this time. This is further borne out by the increased oxygen utilization of the luteal tissue. Attempts to increase the activity of the corpus luteum during the “delayed” period by injections of endocrine products have not as yet been successful (Hamlett, 1935a).

Uterine Changes during the Reproductive Cycle

The gross anatomy of the uterus has been described in some detail by Newman and Patterson (1910) and the
changes in the uterus during the reproductive cycle have been discussed by Hamlett (1932a, 1935a). The uterus of the immature animal has been described as being broadly kite-shaped. During the period immediately prior to ovulation it enlarges in overall size but does not alter its shape significantly. Neither ovulation nor the formation of a corpus luteum appears to have any gross effect on the uterus, and during the time in which it contains the dormant vesicle, it appears to remain in its pre-ovulatory condition. At the time of implantation the uterus, however, undergoes marked changes in size and shape. The entire uterus enlarges and becomes extremely vascular and the vertex changes from its flattened shape to become rounded and almost spherical. On the basis of two animals in which normal appearing blastocysts were found in uteri in which these changes were already occurring, we conclude that they precede and probably induce implantation. These two animals also showed higher serum progestin activity and increased oxygen utilization by the corpus luteum. (See Table II) (Talmage et al., 1954).

**PLATE I**
Taken from Talmage et al., 1954

Figure 1—Enlargement of a cross-section of an ovary showing the comparison of the size of the single corpus luteum to the remainder of the ovary. (×12)

Figure 2—Enlargement of a small section of a corpus luteum and the adjoining part of the ovary. The corpora lutea taken from armadillos in the various parts of the luteal phase of the reproductive cycle were histologically similar. (×120)

Figure 3—Enlargement of a transverse section of the uterus of an immature armadillo showing the lumen surrounded by numerous endometrial glands. (×72)

Figure 4—Enlargement of a small section of a uterus taken from an animal in which the embryos were approximately 3 cm. long. Note the similarity between this uterus and the uterus of the immature armadillo (Figure 3), and the failure to develop convoluted glands. (×72)
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Unfortunately, histological details have not been worked out. The endometrium of the immature uterus contains numerous glands at the vertex of the uterus, which decrease in number posteriorly so that the greater part of the endometrium in the immature uterus has few glands. The epi-

<table>
<thead>
<tr>
<th>Table II</th>
<th>Relation of Oxygen Consumption of Ovary to Progestin Titer of Serum</th>
<th>(Taken from Talmage et al, 1954)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stage of Cycle</td>
<td>$\text{O}_2$ $\mu$L/mg dry wt. tissue/hr.</td>
<td>Progestin $\mu$g/ml Serum</td>
</tr>
<tr>
<td></td>
<td># of animals</td>
<td>Value range in parentheses</td>
</tr>
<tr>
<td>Immature</td>
<td></td>
<td></td>
</tr>
<tr>
<td>no follicles apparent on macroscopic examination</td>
<td>8</td>
<td>0.54 (0.2-1.0)</td>
</tr>
<tr>
<td>Pre-Ovulatory</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Definite follicular growth</td>
<td>9</td>
<td>1.3 (0.6-1.6)</td>
</tr>
<tr>
<td>Non-Mated</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Corpus luteum present without blastocyst</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Free Vesicle Stage</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Quiescent blastocyst in uterus</td>
<td>7</td>
<td>2.5 (2.1-2.9)</td>
</tr>
<tr>
<td>Transitional Stage</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Uterus in transitional phase—blastocyst still present</td>
<td>1</td>
<td>4.1</td>
</tr>
<tr>
<td>Implanted</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Definite embryonic development</td>
<td>4</td>
<td>3.7 (3.0-4.2)</td>
</tr>
</tbody>
</table>
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The epithelium lining the uterus is for the most part non-convoluted and columnar. The uterus grows markedly during the pre-ovulatory stage. However, except for the hyperplasia, the histological make-up is altered very little. The endometrial glands increase in number, and while still concentrated at the vertex, are found in increasing numbers posteriorly. The endometrial epithelium is still columnar and non-convoluted (Talmage et al., 1954).

Following ovulation there are no marked histological changes. This has probably added to the belief that the corpus luteum was non-secretory. However, progestational changes such as described for the rabbit and monkey, are never seen in the armadillo. At the time of implantation, the glandular endometrium enlarges noticeably and appears to separate easily from its supporting tissue, but even at this time marked “progestational” changes are not apparent. Plate I (Figure 3 and 4) shows the similarity between sections of the immature uterus and the uterus taken from a pregnant animal.

The Period of Delayed Implantation

The phenomenon of delayed implantation in the armadillo was first reported by Patterson (1912) and was discovered in the course of his work on specific polyembryony. Since he was endeavoring to secure early stages after implantation, his periods of collection were limited to late October and November. He concluded therefore, that the period of “quiescence” in which the blastocyst remained free in the uterus was of about three weeks’ duration. However, data accumulated over the years after this first report indicated that this period was considerably longer than had first been suspected and was the basis of the work of Hamlett (1932a) who
first reported the complete reproductive cycle of the armadillo.

After ovulation, the ovum proceeds down the fallopian tube, being fertilized high in the tube and forming a blastodermic vesicle before reaching the uterus. Mating is assumed to occur at the time of, or immediately preceding ovulation. Up until the vesicle reaches the uterus, development is normal and similar to that of other mammals (Hamlett, 1932a). During the entire "quiescent" period the blastocyst, which contains a distinct but relatively small inner cell mass (Hamlett, 1935a), remains in the pocket formed by the vertex of the uterus. While not attached, it is in constant contact with the epithelium and is bathed in the glandular secretions.

The length of the period of arrested development has been determined by Hamlett (1932a) to be approximately 14 weeks. This figure is certainly acceptable, since no evidence to the contrary has been forthcoming. Since, however, we have found non-ovulated females into September, and free blastocysts in January, we suggest the more variable limits of three to four months for the duration of the quiescent period.

Discussion of the Cause and Control of Phenomenon of Delayed Implantation

It has been almost twenty years since Hamlett's review (1935a) on discontinuous development in mammals appeared. Since that time, knowledge of the structure, function, and control of the hormones of the ovary has accumulated. However, the hormonal control of normal implantation of the blastocyst and the factors causing a delay in this process have not as yet been elucidated. This phenomenon is far more wide spread than was at first thought and it is possible
that a delay in the implantation of the blastocyst may occur in all mammalian species, though in most cases this would be as the result of an unusual set of circumstances rather than a part of each pregnancy cycle.

Progesterone has become established as the hormone of pregnancy. Without a source of this hormone, no pregnancy can be maintained. However, the importance of estrogens in the maintenance of pregnancy is also becoming appreciated. The dependence of these two hormones on each other has recently been stressed by Courrier (*Vitamins and Hormones*, Vol. 8; p. 179, 1950). And, it is possible that the maintenance of a proper ratio as well as proper titers of these hormones may be the answer to the problem of implantation as well as to the success of pregnancy. Obviously, in the normal animal, the key to the proper ratio of these two ovarian steroids lies in pituitary function. With this in mind, we feel that the best hypothesis explaining this phenomenon in the armadillo is to place the cause of the "delay" and the process of implantation on pituitary action. At first, the pituitary causes the corpus to produce a relatively high titer of progesterone, but possibly either too little or too large an amount of estrogen. At the proper time and by a genetically controlled stimulus, the pituitary increases its own gonadotropic activity, raising slightly the progesterone output and changing the estrogen output until the proper ratio between the two hormones is reached and maintained, and implantation and embryonic development proceed normally.

We cannot leave the subject of the period of arrested development of the blastocyst without some discussion of the advantage of this phenomenon to the animal. As has been pointed out in a previous chapter, this species of armadillo (*D. novemcinctus*) is a migrant from the tropics. We can see no reason why this delay in embryonic development
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would be of advantage to animals living in perpetual warmth. However, the existence of this phenomenon could be one factor in permitting its spread northward into colder regions. Without the arrested development, the young would be born in early or mid-winter when the source of insect food is at a minimum. By arresting the process for three to four months, the young are born in the spring under the best food conditions for both the nursing mother and the fast growing young.

*Specific Polyembryony*

Following the period of arrested development, the blastocyst implants in the uterine wall. During this process the inner cell mass of the blastocyst becomes free and drops into the yolk sac where it becomes at least partially surrounded by endoderm. This mass of cells hollows out to become the amniotic vesicle. This becomes elliptical and the floor of the cavity thickens at the two ends, thinning out in the center. These two thickened areas are the primary buds, each of which gives rise to two secondary buds by a shifting of the cells. These four secondary buds have a definite position with respect to the original bilateral symmetry of the amniotic vesicle. The thickened ectoderm of the four secondary buds becomes the four embryonic shields and gives rise to the four embryos within the single amniotic vesicle. (Summary of implantation taken from Hamlett, 1933).

This process of implantation leading to specific polyembryony has been described in detail by Patterson (1912, 1913). Speculation as to the cause of this phenomenon has given rise to some lengthy and argumentative dissertations. The first explanation for this phenomenon was the fused follicle theory of Rosner (1901), mentioned above, who unfortunately based his conclusions on limited and abnormal tissue. This theory was discussed and refuted by Cuenot
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(1903). In 1909, Newman and Patterson related the phenomenon to the problem of twinning. The limits of hereditary control in the armadillo quadruplets were discussed in detail by Newman and Patterson (1911), who showed that the variations between the four embryos was on the same order as that between the right and left sides of any single embryo. Despite this evidence, Newman soon became convinced that the phenomenon was a direct result of physiological changes brought about by the arrested development of the blastocyst. This theory is discussed at length in his two books (1917 and 1923) and by Stockard (1921a and 1921b). These two men disagreed primarily on who was to get credit for the theory and on the terminology involved in its expression.

The return to a simple genetic basis for this phenomenon was heralded by Hamlett (1929, 1932b, and 1935a) who showed quite adequately the fallacies of the Newman-Stockard theory. In the light of present knowledge there seems to be no correlation between the two phenomena, other than their occurrence in the same animal. Both the phenomenon of arrested development and that of specific polyembryony appear to be normal and unrelated parts of the genetically controlled reproductive pattern of the armadillo.

Embryonic Development of the Armadillo Quadruplets

The foetal development of the armadillo has been described in some detail by Newman and Patterson (1910) and reviewed by Newman (1917, 1923). The problems related to specific polyembryony have been discussed above. Once the four embryonic growth centers are established the development of the four embryos is with minor exceptions similar to that seen in other mammals. For details of this development, the reader is referred to Newman and Patterson (1910).

There are a few points concerning this development that
should be reviewed. The first of these is in regard to the germ layer inversion referred to by Newman and Patterson. This supposed phenomenon was said to occur not only in the armadillo but in certain rodents. This error has long since been corrected and was apparently made due to the depth to which the embryonic knob moved into the blastocyst with the result that the endoderm extended well up on either side. After implantation the outer layer of the trophoblast was overlooked and the endoderm appeared to be the first layer, giving rise to the misconception of germ-layer inversion.

It has been pointed out above that embryonic development of all four growth centers starts in a single amnionic vesicle. This is only a temporary situation, for as the yolk sac gradually increases in size the embryos are drawn away from the common amnion. Eventually, even the connecting canals are lost and each embryo develops its own amniotic cavity.

A common primary placenta, the träger, forms the first connection between the blastocyst and the uterine mucosa. Later, however, each embryo develops its own nutritive connection with the maternal mucosa. Later the four placentae intermix to form a single placental ring. However, there is no fusion of the placentae and no mixing of blood of the four foetuses.

Additional Bibliography on the Embryology of Armadillos

In addition to the works discussed above there has been considerable other work on the placentation and embryonic development of armadillos both in this country and in South America. In regard to *D. novemcinctus*, Lane (1909a, 1909b) in this country reported on the phenomenon of specific polyembryony almost simultaneously with the first reports of Newman and Patterson. In the second of these reports he describes in some detail the placenta of late pregnancy.
Four very early reports on the peculiarity of the placenta and early development of the armadillos were those of Dugès in 1879 and Milne-Edwards in 1878 on *D. novemcinctus*, of Turner (1874) on armadillos in general, and of Chapman in 1901 on *Euphractus sexcinctus*. Somewhat later, Strahl (1913 and 1914), and Vanneman (1917) reported further on the embryology of *D. novemcinctus*. Two early reports by von Jhering discussed reproduction in armadillos (1885, 1886a) and the embryology of *Praopus* (1886b).

One of the most prolific writers on armadillos was Fernandez, who between 1909 and 1938 published at least ten articles. Of these, six were concerned with the problem of specific polyembryony and embryology, but only one was based on *D. novemcinctus*. Of his two reports on specific polyembryony in *D. hybridus* (1909 and 1914b), the first appeared about the same time as that of Newman and Patterson for *D. novemcinctus*. His only report on this latter species (1914a) dealt with the arrangement of the embryos and the form of the placenta. His other works include a general study of the embryology of the *Mulita* (now genus *Dasypus*) (1915); specific polyembryony in *D. villosus* (1921a) and two studies in 1938 and 1939 on the reabsorption of embryos in *Tatusia* (*D. hybridus*).

**Late Development of the Armadillo**

The gestation period from the time of implantation of the blastocyst until parturition, has been determined by Hamlett (1932a) to be approximately four and one-half months in length. At the end of that period the young are born in a comparatively advanced state of development. Physical maturity is attained in about six months. While it is possible that females born early in the year may breed the same year, the animals are normally approximately two years of age when they give birth to their first litter.
The Male Armadillo

Almost no work has been done in reference to the development and function of the male reproductive system. An early work by Watson (1878) discussed the male reproductive system of *Chlamyphorus truncatus* and *Euphractus sexcinctus* and compared these briefly to other genera of the Dasypodidae. Kaudern (1915) reported on the male reproductive system of the Xenarthra. Newfang (1947) has traced the embryology of both male and female systems. Ballowitz (1906) described the sperm of armadillos. The male system is essentially typically mammalian. The testes descend, but only to the pelvis, and become located at the entrance to the inguinal canal. There is no scrotum. The pituitary-testis relationship has not been checked in the armadillo but there is no reason to assume that it is not similar to other mammals.

REFERENCES TO THE MORPHOLOGICAL AND PHYSIOLOGICAL STUDIES OF THE NINE-BANDED ARMADILLO


The Armadillo


——. 1914b. Die Entstehung der Einzelembryonen aus dem einheit-
Morphology and Physiology


Giancomini, E. 1913. Sullo sviluppo dell’organo di Jacobson (organo


Morphology and Physiology 129


Kalmbach, E. R. 1943. The Armadillo: Its Relation to Agriculture and Game. Game, Fish, and Oyster Commission, Austin, Texas.


Langmann, E. R. 1931. Estudios biométricos sobre la variabilidad de
The Armadillo

la coraza en desdentados con y sin poliembriona específica. Bol. Acad. nacion Córdoba 31:185.


———. 1931b. The modes of inheritance of aggregates of meristic
(integral) variates in the polyembryonic offspring of the nine-banded armadillo. J. Exp. Zool. 15:145.


——. 1917. The Biology of Twins (Mammals). The Univ. of Chi. Press. Chicago, Ill.

——. 1923. The Physiology of Twinning. The Univ. of Chi. Press. Chicago, Ill.


——. 1832b. Description of the genital and mammary organs of Dasypus peba and Dasypus 6-cinctus. P.Z.S. 1832:130.


132 The Armadillo

Shuddemagen, L. C. 1907. On the anatomy of the central nervous
Morphology and Physiology
system of the Nine-banded Armadillo (T. novemcinctu Linn.).
7:277.
Sonntag, C. F. 1922. On the vagus and sympathetic nerves of the
——. 1923. The comparative anatomy of the tongue of the maml
IX Edentata, Dermaptera, and Insectivora. P.Z.S. 1923:
515.
——. 1925. The comparative anatomy of the tongue of the maml
XII Summary, Classification and Phylogeny. P.Z.S. 1925:
701.
Sousa, O. M. de. 1939. Estudo sobre a arquitetura da mandibula dos
Spurgin, A. M. 1904. Enamel in the teeth of an embryo Edentate
(Dasypus novemcinctus Linn.). Am. J. Anat. 3:75.
——. 1914. Uber den Bau der Plazenta von D. novemcinctus II.
Stockard, C. R. 1921a. A probable explanation of polyembryony in
——. 1921b. Developmental rate and structural expression: An
experimental study of twins, “double monsters” and single de-
formities, etc. Am. J. of Anat. 28:115.
Taber, F. W. 1945. Contribution on the life history and ecology of
the Nine-banded Armadillo. J. Mamm. 26:211.
Talmage, R. V., Buchanan, G. D., Kraintz, F. W., Lazo-Wasem, E. A.,
and Zarrow, M. X. 1954. The Presence of a Functional Corpus
Luteum during Delayed Implantation in the Armadillo. J. of
Endocrinology 10: in press.
Tauber, P. 1876. The conformation and development of the teeth of
the vertebrates. Nat. Tids. J. Zool. 6:45.
Tavani, E. 1939. Ulteriore contributo allo studio dell'inserzione del M.
tiro-aritenoides sul legamento vocale. Recerche nell'Armadillo e
n Nel Riccio. Monit. zool. italiano Firenze. 50:60.
Tomes, C. S. 1874. On the existence of an enamel organ in the dental
and Physiol. 1867:313.
——. 1874. “General observations” on the placentation of Edentata.
Tr. R. Soc. Edinb. 8:362.
The Armadillo


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