



# *Priodontes maximus* (Cingulata: Chlamyphoridae)

TRACY S. CARTER, MARIELLA SUPERINA, AND DAVID M. LESLIE, JR.

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Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, OK 74078-3051, USA; [tracy.carter@okstate.edu](mailto:tracy.carter@okstate.edu) (TSC)

Instituto de Medicina y Biología Experimental de Cuyo, Centro Científico Tecnológico (CCT), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), 5500 Mendoza, Argentina; [msuperina@mendoza-conicet.gov.ar](mailto:msuperina@mendoza-conicet.gov.ar) (MS)

United States Geological Survey, Oklahoma Cooperative Fish and Wildlife Research Unit and Department of Natural Resource Ecology and Management, 007 Ag Hall, Oklahoma State University, Stillwater, OK 74078-3051, USA; [cleslie@usgs.gov](mailto:cleslie@usgs.gov) (DML)

**Abstract:** *Priodontes maximus* (Kerr, 1792), called the giant armadillo, is monotypic and by far the largest extant armadillo. Average adult weight is about 30 kg (in captivity, as high as 80 kg). Its carapace extends about halfway down its sides, making it impossible to curl up tightly. It is dark brown to black dorsally, with a broad light band around the lower part of its carapace. It primarily digs to escape, enhanced by its 20-cm, sickle-shaped nail on its 3rd forefingers. *P. maximus* is widely distributed in South America but nowhere abundant. It is affected by habitat loss and fragmentation, agriculture, hunting, collection for museum specimens, and illegal animal trafficking. *P. maximus* is listed as “Vulnerable” by the International Union for Conservation of Nature and Natural Resources.

**Key words:** giant armadillo, habitat generalist, insect specialist, largest extant armadillo, solitary, South America

Synonymy completed 27 May 2015

DOI:10.1093/mspecies/sew002

Version of Record, first published online May 05, 2016, with fixed content and layout in compliance with Art. 8.1.3.2 ICZN.

Nomenclatural statement.—A life science identifier (LSID) number was obtained for this publication: urn:lsid:zoobank.org:pub:FBBC6725-97B3-4BB4-BF8D-4B13DDD94A9D

## *Priodontes* F. Cuvier, 1825

*Dasypus*: Kerr, 1792:112. Part; not *Dasypus* Linnaeus, 1758.

*Loricatus* Desmarest, 1804:28. Part (see “Nomenclatural Notes”).

*Tatus* Olfers, 1818:220. Part; incorrect subsequent spelling of *Tatu* Blumenbach, 1779.

*Priodontes* F. Cuvier, 1825:257. Type species *Dasypus gigas* G. Cuvier, 1817, by monotypy.

*Cheloniscus* Wagler, 1830:35. Types species *Dasypus gigas* G. Cuvier, 1817, by monotypy.

*Priodon* McMurtrie, 1831:164. Type species *Dasypus gigas* G. Cuvier, 1817, by monotypy; proposed as a subgenus of *Dasypus*; preoccupied by *Priodon* Quay and Gaimard, 1824 (Pisces, Osteichthyes).

*Polygomphius* Gloger, 1841:114. Type species *Dasypus gigas* G. Cuvier, 1817, by monotypy.

*Prionodon* Gray, 1843:xxvii. Nomen nudum.

*Priodonta* Gray, 1843:xxvii. Incorrect subsequent spelling of *Priodontes* F. Cuvier, 1825.



**Fig. 1.**—Mature *Priodontes maximus* at Bioparque Los Ocarros, Villavicencio, Colombia. Photograph by Fernando Trujillo used with permission.

*Priodontes* Schinz, 1845:312. Incorrect subsequent spelling of *Priodontes* F. Cuvier, 1825.

*Prionodos* Gray, 1865:374. Replacement name for *Priodontes* F. Cuvier, 1825.

*Periodontes* Altrichter, 2006:2729. Incorrect subsequent spelling of *Priodontes* F. Cuvier, 1825.

CONTEXT AND CONTENT. Order Cingulata, family Chlamyphoridae, subfamily Tolypeutinae, tribe Priodontini. *Priodontes* is monotypic; synonymy was reformatted from Wetzel et al. (2008).

### *Priodontes maximus* (Kerr, 1792)

#### Giant Armadillo

*Dasyopus maximus* Kerr, 1792:112. Type locality “Cayenne,” French Guiana.

*Dasyopus giganteus* É. Geoffroy Saint-Hilaire, 1803:207. Type locality “Le Paraguay” with reference to “*Le Grand Tatou* d’Azara, t. 2, p. 132;” but based on specimen “N°. CCCCXIV. Individu qui servi de sujet pour la description précédente.”

*Dasyopus gigas* G. Cuvier, 1817:221. No type locality given; based on plate “xlv” [error for “xli”], the “*Autre Kabassou*” of volume 10 of Buffon (Daubenton in Buffon 1763); Buffon wrote that “*Le Kabassou*” was the largest tatou and came from Cayenne, which is the type locality.

*D[asyopus]. gigans* Schmid, 1818:164. No type locality given.

*T[atopus]. grandis* Olfers, 1818:219. Type locality “Paraguay.”

*Priodontes giganteus*: Lesson, 1827:309. Name combination.

*D[asyopus]. (P[riodontes].) Gigas*: Voigt, 1831:261. Name combination.

*Priodontes gigas*: Gray, 1843:120. Name combination.

*Priodon gigas*: Owen, 1845:21. Name combination.

*Prionodontes gigas*: Schinz, 1845:316. Name combination.

*Prionodos gigas*: Gray, 1865:374. Name combination.

*Prionodon gigas*: Gray, 1869:380. Name combination.

*Cheloniscus gigas*: Fitzinger, 1871:227. Name combination.

*Priodontes maximus*: O. Thomas, 1880:402. First use of current name combination.

*Priodon maximus*: J. A. Allen, 1895:187. Name combination.

*D[asyopus]. maximus* Larrañaga, 1923:343. Type locality “nemo-ribus septentrionalibus paraquarensibus;” based on Azara’s (1802:110) “*Maximo*;” a junior homonym and synonym of *Dasyopus maximus* Kerr, 1792.

*Periodontes maximus*: Altrichter, 2006:2729. Name combination.

CONTEXT AND CONTENT. Context as for genus. *Priodontes maximus* is monotypic; synonymy was reformatted from Wetzel et al. (2008).

NOMENCLATURE NOTES. As noted by Wetzel et al. (2008), Kretzoi and Kretzoi (2000:204) designated *Dasyopus giganteus* É. Geoffroy Saint-Hilaire, 1803, as the type species of *Loricatus Desmarest, 1804*, which relegated *Priodontes* F. Cuvier, 1825, to

a synonym of *Loricatus*. Nevertheless, we followed Wetzel et al. (2008:153) who concluded that *Loricatus niger Desmarest, 1804* (= *Dasyopus novemcinctus Linnaeus, 1758*) was the valid type species of *Loricatus*, thus “retain[ing] *Priodontes* as the valid generic name for *P. maximus*.”

Common names of *P. maximus* include giant armadillo and giant South American armadillo (English); tatú carreta and tatú gigante (Spanish); tatu-açú and tatu canastra (Portuguese); gran tatú de los bosques, priodonte, priodonte gigante (in Argentina); pejiche and pejichi (Bolivia); ja’ta (Yucuna tribe), jusa trueno and ocarro (Colombia); armadillo gigante, armadillo trueno, cutimbo, and tatú gigante (Ecuador); carachupa gigante, carachupa maman, kintéro, and yungunturu (Peru); cachicamo grande, cuspa, cuspa gigante, cuspa grande, and cuspón (Venezuela); tatou-géant (French Guiana); tatu-guazú (Guarani); mowoorímah (Guiana); granman-kapasi (Suriname); and el máximo napnalu, tatu-assú, etopicnic laté, carreta madre, and carachupa guazu (e.g., Superina and Aguiar 2006; Smith 2007; Trujillo and Superina 2013).

## DIAGNOSIS

*Priodontes maximus* is by far the largest species of extant armadillos (Emmons and Feer 1997; Nowak 1991; Fig. 1). Its carapace extends only about halfway down its sides—seemingly draped on its back—whereas carapaces of other armadillos appear to wrap around their sides and flanks (Smith 2007). Head of *P. maximus* is relatively small compared with other species of armadillos and is somewhat domed with a long snout, narrow but blunt on the end, and with widely separated, small, and short ears (Fitzinger 1871; Kühlhorn 1939).

*Priodontes maximus* and 4 species of naked-tailed armadillos (*Cabassous*) are in the tribe Priodontini (Wetzel et al. 2008), and only a naked-tailed armadillo could be confused for an immature *P. maximus* (Meritt 1985, 2006; Smith 2007; Trujillo and Superina 2013). Adult size is diagnostic: *P. maximus*, head–body length > 700 mm, greatest length of skull > 170 mm and *Cabassous*, head–body length < 495 mm, greatest length of skull < 125 mm (Wetzel 1985a). As the common name of species of *Cabassous* implies, their tails lack scutes and “may or may not have visible scales,” whereas the tail of *P. maximus* is “armored with articulating bony scutes” (Wetzel 1985a:15). *P. maximus* has more upper and lower teeth (about 18/19) that are more laterally flattened and broader than those in species of *Cabassous* (about 9/8—Wetzel 1985a, 1985b).

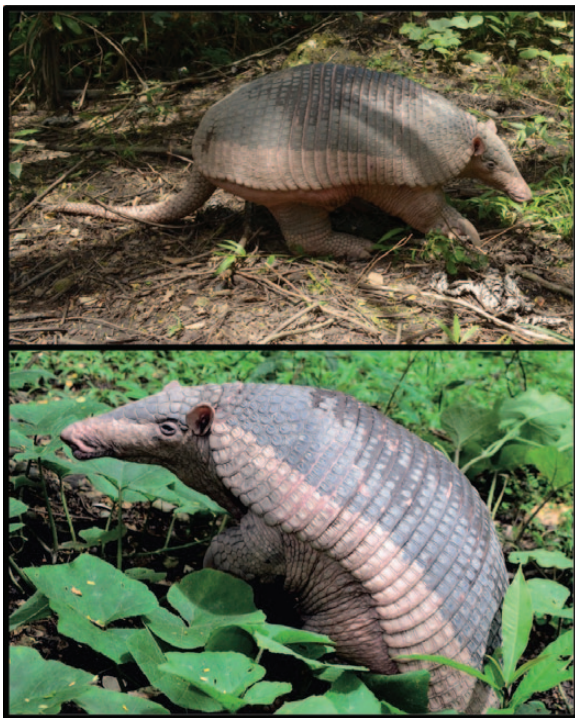
## GENERAL CHARACTERS

An adult male *Priodontes maximus* can weigh up to 60 kg (80 kg in captivity), but average adult weight is about 30 kg (Nowak 1991; Redford and Eisenberg 1992; Smith 2007; Wetzel et al. 2008). Sexual dimorphism of *P. maximus* was reported for 7 of 14 body measurements of 5 males and 2 females from Emas National Park, Brazil: males were larger than females in weight,

total length, head–body length, tail length, and circumferences of head, neck, and thorax (Silveira et al. 2009).

Carapace of *P. maximus* is divided into transverse bands of small plates; 3–4 plates on the back of the neck and the central 11–13 plates are quite flexible (Nowak 1991; Wetzel et al. 2008). Pelage of *P. maximus* is limited to a few beige hairs between the plates. Color is dark brown to black dorsally, with a broad light-colored band around the lower part of the carapace (Fig. 2). An individual *P. maximus* can be identified by the scale pattern on its carapace, particularly where dark and light scales meet, and the number of light and dark scales in each band (Noss et al. 2004; Fig. 2). Head shield of *P. maximus* is oval and does not expand between eyes. Tail is about 500 mm (Wetzel et al. 2008) and covered with small, closely set, rounded plates that are not arranged in rows (Wetzel 1985a, 1985b).

*Priodontes maximus* can balance itself on its large hind feet, with its tail forming a stable tripod while digging (Nowak 1991). Simultaneous use of forefeet permits a *P. maximus* to excavate a hole quickly to escape (Milne et al. 2009). Unlike smaller armadillos, *P. maximus* cannot enclose itself into a tight ball within its carapace, so it rarely attempts to do so. Claws on forefeet are thick and powerful; claw on the 3rd forefinger is greatly enlarged, well developed, and sickle-shaped, measuring up to 20.3 cm along the curve—the largest claw of any living mammal (Fitzinger 1871; Smith 2007).



**Fig. 2.**—The carapace of *Priodontes maximus* has a broad, light-colored band on its lower part in contrast to its dark brown to black dorsal part; the number of light and dark scales in each row is said to permit individual recognition (Noss et al. 2004). Photographs by Federico Mosquera-Guerra, Fundación Omacha (top) and Fernando Trujillo (bottom) used with permission.

## DISTRIBUTION

*Priodontes maximus* is found in Brazil, Paraguay, Guyana, Suriname, French Guiana, and east of the Andes in Colombia, Venezuela, Ecuador, Bolivia, and Peru (Meritt 1973; Emmons and Feer 1997; Vaz 2003; Anacleto et al. 2006, 2014; Zapata-Ríos et al. 2006; Smith 2007; Meritt 2008; Wetzel et al. 2008; Srbeek-Araujo et al. 2009; Porfirio et al. 2012; Zimbres et al. 2012; Fig. 3). In Argentina, *P. maximus* is probably limited to the northern provinces of Salta, Formosa, Chaco, and Santiago del Estero, as far south as 31°S (Torres and Jayat 2010); further south, temperatures are too cold (McNab 1980). Presence of *P. maximus* in the Argentinian provinces of Córdoba, Santa Fe, and Misiones is uncertain (Parera 2002; Massoia et al. 2006), in part because records from Córdoba are old; new surveys are needed in these provinces (Abba et al. 2012). Although the distribution of *P. maximus* extends over a large area of South America, it occurs in low-density, discontinuous populations in most areas (Cabrera 1957; Meritt 2006; see “Conservation” section).

## FOSSIL RECORD

Ancestral lineages within Cingulata diverged from sloths and anteaters close to the Cretaceous–Paleogene transition about 66 million years ago, and armadillos diversified thereafter in the early to middle Eocene and beyond (Kurtén 1972; Engelmann 1985; Delsuc et al. 2001, 2002; Croft et al. 2007; Vizcaíno et al. 2008; Vizcaíno and Bargo 2014; Delsuc et al. 2016). Armored species in the order Cingulata traditionally were placed in 2 extinct families, Pampatheriidae and Glyptodontidae (both were browsers and grazers), and 1 extant family, Dasypodidae (primarily insect-eaters—Fericola et al. 2008). New phylogenetic evidence concludes that there are 1 extinct family, Pampatheriidae, and 2 extant families, Dasypodidae (dasypodines) and Chlamyphoridae (traditionally including euphractines, chlamyphorines, and tolypeutines) that diverged about 42 million years ago (Gibb et al. 2015; Delsuc et al. 2016). Extinct glyptodonts and pampatheres had been thought to represent a monophyletic clade, sister to dasypodines (Engelmann 1985; Gaudin and Wible 2006); however, new evidence places glyptodonts as a subfamily within Chlamyphoridae (Euphractinae + Glyptodontinae + Chlamyphorinae + Tolypeutinae [including *Priodontes*]—Delsuc et al. 2016).

Fossil record of Cingulata is rich, with  $\geq 65$  genera of extinct glyptodonts and  $\geq 35$  genera of armadillos and pampatheres (Fericola et al. 2008). During the Pleistocene, some North American pampatheres evolved in Florida: for example, *Holmesina septentrionalis* (Simpson 1930) from *H. floridanus* (Edmund 1985). At least 2 species of giant glyptodont persisted as part of the North American megafauna through the late Pleistocene: *Glyptotherium*

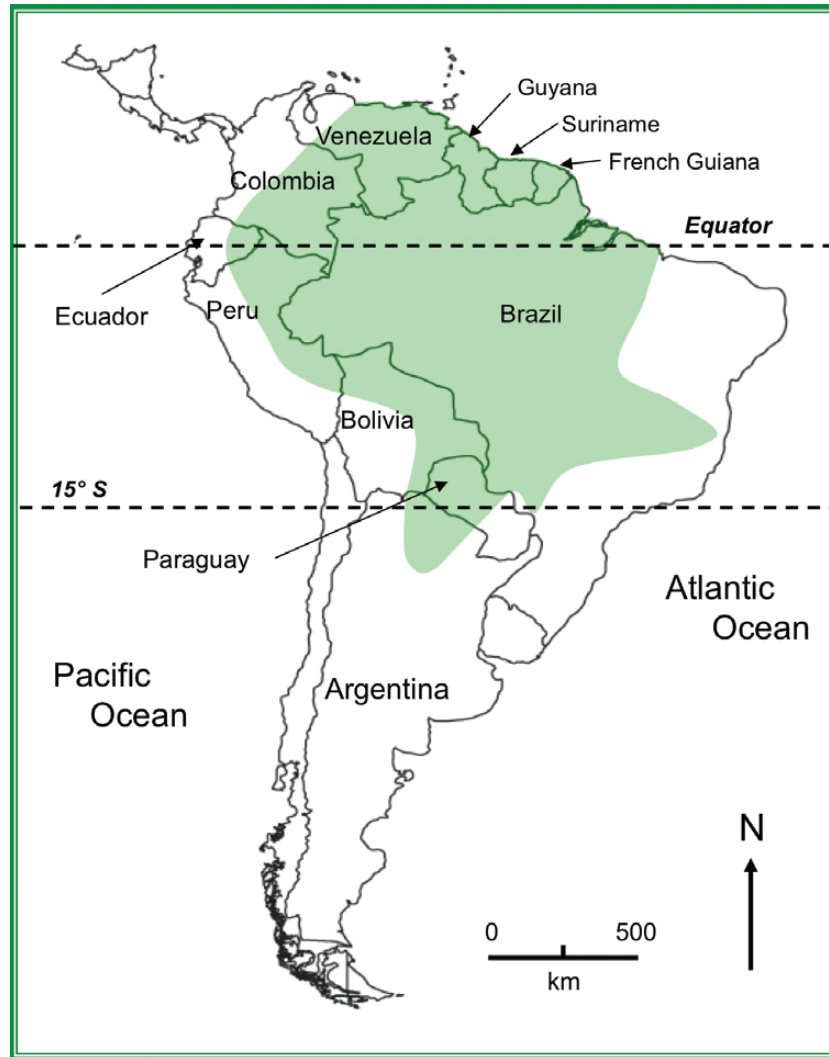


Fig. 3.—Distribution of *Priodontes maximus* in South America.

*cylindricum* as far north as Sonora, Mexico (Ramírez-Cruz and Montellano-Ballesteros 2014) and *G. floridanum* in Hunt County, Texas (Gillette and Ray 1981). They may have become extinct because of climate change or human hunting (Cione et al. 2009).

Armadillo fossils from the late Paleocene were found in Patagonia, and many species of armadillos, ranging from insect-eaters to plant-eaters, were present in South America by the early to middle Eocene (Kurtén 1972; Delsuc et al. 2016). In the Neogene, some cingulates became large, and by the Pliocene and Pleistocene, species of *Pampatherium* were the size of rhinoceroses (Kurtén 1972; Edmund 1985). Glyptodonts arose in the Eocene and diversified greatly in the Miocene and Pliocene; some glyptodonts were gigantic reaching 4 m in length, with their nearly fused plates resulting in their “inflexible structure” and common name “mammalian tortoise” (Kurtén 1972:178–179). Despite substantial differences in size, comparisons of “deep and superficial cortexes” of the osteoderm support close phylogenetic relationships among pampatheres, glyptodonts,

and tolpeutine armadillos, including *P. maximus* (Wolf et al. 2012:388).

*Priodontes* does not have a documented fossil record (de Paula-Couto 1979; McKenna and Bell 1997; Wetzel et al. 2008), but the extinct dasypodid *Eutatus* had species as large as *P. maximus* (e.g., *E. seguini*). They were less fossorial than *P. maximus* and herbivorous (Vizcaíno et al. 2003). *E. seguini* and the large glyptodont *Doedicurus clavicaudatus* were common in the late Pliocene to the early Holocene in South America and found at 7,000- to 7,500-year-old archaeological sites in Argentina, confirming early use of cingulates as food by human hunter-gatherers (Fidalgo et al. 1986; Politis and Gutiérrez 1998).

### FORM AND FUNCTION

Skull of an adult *Priodontes maximus* is  $\geq 180$  mm (Fig. 4). *P. maximus* can have as many as 100 teeth, the greatest number of teeth of any terrestrial mammal (Ungar 2010). The teeth



**Fig. 4.**—Dorsal, ventral, and lateral view of skull and lateral view of the mandible of an adult female *Priodontes maximus* (Oklahoma State University Collection of Vertebrates 10455). Greatest length of skull is 182 mm, but note that the tip of the nasals may not be intact. This female was captured in the wild on 12 December 1970 (specific location in South America unknown) and died of unknown causes after 6 years, 1 month, and 19 days in captivity at the Oklahoma City Zoo (United States).

are hypselodont (shallow-rooted, high-crowned, and ever-growing), have a thin outer layer of acellular cementum (Green and Kalthoff 2015), and lack enamel. All teeth are molariform but not easily differentiated as premolars and molars (Ungar 2010); they are small, with thin blades, twice as long anteroposteriorly as wide, numbering 15–26 per row (Fitzinger 1871; Kühlhorn 1939; Wetzel 1985b). Teeth are not replaced, and toothrows do not articulate and play little role in catching, grasping, or chewing prey (Kühlhorn 1939).

Tongue of *P. maximus* is long and vermiform, which is an adaptation to a diet of small insects; tongue of a recently dead *Priodontes* was 16 cm (Kühlhorn 1939). Salivary glands of *Priodontes* extend from under the neck to the sternum; location of submaxillary glands differs from that in other mammals because of the large size and slender head of *Priodontes* (Kühlhorn 1939). Billet et al. (2015) described the shape of the bony labyrinth of the inner ear of *P. maximus*; unlike other

morphological evidence, bony labyrinth characteristics did not support a *Priodontes*–*Cabassous* clade (Billet et al. 2015).

Limb measurements related to interspecific differences in digging abilities of armadillos have been assessed; those of *P. maximus* include (mm  $\pm$  SD): maximum humeral length, 119.8  $\pm$  4.3; ulnar length, 132  $\pm$  6.4; olecranon length, 64.9  $\pm$  8.8; and rear leg length, 85.5  $\pm$  6.5 (Vizcaíno and Milne 2002: tables 2 and 3; Milne et al. 2009)—slightly smaller lengths were provided by Vizcaíno et al. (1999). Aside from the small and highly fossorial pink fairy armadillo (*Chlamyphorus truncatus*), an index of fossorial ability (i.e., length of olecranon process divided by difference between ulnar length and olecranon length) was highest for *P. maximus* (101.17  $\pm$  34.5) and other species in the tribe Priodontini (92.86  $\pm$  6.04—Vizcaíno and Milne 2002). *P. maximus* walks on the tips of its strongly developed 3rd claws on its forefeet. Worn surfaces of claws suggest that, in contrast to *Tolypeutes*, *P. maximus* slides rather than stalks on its forehands (Krieg 1961).

Sperm shapes are unique among 4 groups of extant armadillos. *P. maximus* and the related southern naked-tailed armadillo (*Cabassous unicinctus*) group together by their sperm shapes: heads are large, long, and frontally wide, with extremely thin profiles and overall paddle shapes (Cetica et al. 1993; Cetica and Merani 2008). Other characteristics of sperm of both species include sperm head lengths of 13.2–18.0  $\mu$ m (with acrosomes occupying 74–75% of total sperm head length), sperm head widths of 11.6–16.0  $\mu$ m, and total sperm lengths of 79.9–98.0  $\mu$ m (Cetica and Merani 2008).

The pelletized feces of *P. maximus* are dry and firm, with mean widths of 14.7 mm  $\pm$  1.7 SD, mean lengths of 22.7 mm  $\pm$  3.0 SD, and mean weights of 2.8 g  $\pm$  0.9 SD (Anacleto 2007). Slow and Rapid Eye Movement (REM) sleep patterns and electrical activity of flexor muscles in the neck of *P. maximus* are typical of mammalian patterns (Affanni et al. 1972).

## ONTOGENY AND REPRODUCTION

A female *Priodontes maximus* has 2 mammae (Fitzinger 1871); extrudes a watery, bloody fluid from her vulva during estrus (T. S. Carter, in litt.); has 1 (sometimes 2) young per year (Krieg 1929); and lactates for 4–6 months (Neris et al. 2002). Other reports on basic reproductive characteristics of *P. maximus* seem to be incorrect. According to Merrett (1983), sexual maturity of male and female *P. maximus* is reached at 9–12 months, gestation is about 4 months, offspring are born with a body mass of 113 g, and weaning occurs at 4–6 weeks. Although these reproductive data have been widely cited, they are likely inaccurate for an armadillo species with the mass of *P. maximus*, and they cannot be substantiated in other scientific literature or from captive records because *P. maximus* has never reproduced in captivity (Aya-Cuero et al. 2015). Other armadillo species with similar litter size have birth weights of 6–7% of adult body mass (Superina and Loughry 2012); a neonatal *P. maximus* is therefore expected to have a body mass of 1.9–3.5 kg (Aya-Cuero

et al. 2015). Generation length has been estimated at 6–10 years (Fonseca and Aguiar 2004) and 7 years (Anacleto et al. 2014), but both are very rough estimates given the lack of life-history data for *P. maximus*.

Information on the duration of lactation provided by Neris et al. (2002) is uncertain because it seems to be based on anecdotal reports from indigenous tribes (Aya-Cuero et al. 2015). Nevertheless, it coincides with camera-trap photographs of a juvenile *P. maximus* estimated at 4–5 months of age that was repeatedly observed with its mother; several photographs taken 3 months later at an estimated age of 7–8 months showed the same individual without its mother, suggesting that weaning had occurred (Aya-Cuero et al. 2015). Parental care behavior was observed in another juvenile estimated at 7–8 months of age that shared the burrow with its mother but sometimes explored the surroundings alone (Aya-Cuero et al. 2015; Fig. 5). The female emerged from the burrow, inspected the environment by sniffing in bipedal posture, introduced its snout into the burrow entrance, and finally allowed its offspring to leave the burrow. The offspring then stood on its hind feet and supported its fore claws on its mother's back for 2–5 min, a behavior that could be observed several times per day and may be interpreted as play behavior (Aya-Cuero et al. 2015).

Adult *P. maximus* are presumably solitary most of the year, except during breeding and while a female rears her young-of-the-year. Videos of a wild female and her relatively young offspring emerging from a burrow (<http://news.mongabay.com/2013/0219-hance-giant-armadillo-baby.html>, accessed 27 August 2015) were filmed in February 2013 in Brazil. Next to nothing is known about sexual behavior of *P. maximus*, but recently a camera-trap image showed 2 adults apparently copulating, with the male mounting the female from the rear (photograph by Rachel Berzins, Office National de la Chasse et de la Faune Sauvage, Guyana; <http://www.une-saison-en-guyane.com/article/faune/piegaje-photo-de-loncfs-sur-le-centre-spatial-guyanais/>, accessed 6 November 2015). Camera-trap videos from Colombia show a female *P. maximus* digging for 30 min to open the entrance of an existing burrow and an offspring emerging (<https://www.youtube.com/watch?v=Q76K-txuWCo>, accessed 19 October 2015). Aya-Cuero et al. (2015) hypothesized that the female left its offspring inside the burrow and closed the entrance to impede predator attacks.

## ECOLOGY

**Population characteristics.**—Little is known about population characteristics of *Priodontes maximus*. It has a widespread, discontinuous distribution and has never been numerous (Cabrera 1957; Meritt 2006). There are no longevity records of marked or carefully studied *P. maximus* in the wild, but hints of life span can be gleaned from zoo animals. A wild-born male *P. maximus*, caught in Brazil in 1972, arrived at the Rotterdam Zoo (Netherlands) on 28 May 1975 and was transferred to the San Antonio Zoo (Texas, United States) in 1981; it died on 19



**Fig. 5**—Rare camera-trap images of an adult female *Priodontes maximus* and her young-of-the-year near their den in Puerto Gaitán, Meta, Colombia. Photographs by Carlos Aya-Cuero used with permission.

January 1988 at about 16 years of age, of which 12 years and 7 months were in captivity (Weigl 2005). Another wild-born male *P. maximus* lived 11 years and 7 months, arriving at the Lincoln Park Zoo (Chicago, Illinois, United States) in 1972, transferring to the San Antonio Zoo in 1981, and dying there in 1984 (Weigl 2005).

**Space use.**—Large home ranges of *Priodontes maximus* suggest that only a limited number of individuals can be sustained by an area of suitable habitat. Home ranges of males and females often overlap (Carter 1983; Noss et al. 2004). Female home ranges were about 450 ha in Serra da Canastra National Park, Brazil (Carter and Encarnação 1983) and 1,500 ha in the

Brazilian Pantanal (Desbiez and Kluwyer 2013). Maximum home-range width was 4,788 m, and average daily movement was 2,765 m in Serra da Canastra National Park (Carter 1983); mean maximum distance traveled was 3,700 m for 3 males and 1,000 m for a female in dry forests of Santa Cruz, Bolivia (Noss et al. 2004). Silveira et al. (2009) noted that *P. maximus* is somewhat nomadic in its movements, and although home ranges of individuals may overlap, sizes of these ranges result in low densities, even in favorable habitat. Density estimates of *P. maximus* range from 4.7–5.3 individuals/100 km<sup>2</sup> (Carter 1983) to 5.8–6.3 individuals/100 km<sup>2</sup> (Noss et al. 2004). Only 7 *P. maximus* were rescued in 650 km<sup>2</sup> before the completion of a dam in Suriname (Walsh and Gannon 1967).

Cerrado grassland (= savannas) of central South America comprises about 25% of the distribution of *P. maximus* (Silveira et al. 2009), but the species also lives in forests with significant undergrowth (Cabrera and Yepes 1940). Krieg (1929) mentioned that *P. maximus* avoided areas settled by humans or in which cattle were raised. It also occupies humid to dry lowland forests (Emmons and Feer 1999; Noss et al. 2004) and open savannas of the cerrado and Gran Chaco of Argentina (Ceresoli and Fernandez-Duque 2012). It occurs in the cerrado of Brazil (Marinho-Filho et al. 2002).

Not surprisingly, burrows of *P. maximus* are considerably larger than those of other armadillo species (Carter and Encarnação 1983). Thirty-two burrows of *P. maximus* in semi-arid forest in western Formosa Province, Argentina, averaged 43 cm wide and 36 cm high, and 24 of them open to the west and 8 to the east (Ceresoli and Fernandez-Duque 2012). Burrows averaged 41.3 cm wide and 30.8 cm high in Serra da Canastra National Park, Brazil (Carter 1983).

Carter (1983) found burrows most often in grassland, brushland (cerrado), and finally woodland. Although brushland made up only 5% of a study area in Serra da Canastra National Park, Brazil, it contained 28% of burrows compared to woodland, representing only 2% of the study area with 3% of the burrows (Carter 1983). Burrows located in grassland or brushland were, on average, 192 m from woodlands (often gallery forests); however, average distance of all burrows to freestanding water was 112 m (Carter 1985). *P. maximus* will sometimes escape by swimming (Civita 1970).

Depending on intensities, unintentional or prescribed fires can kill *P. maximus* (Smith 2007); 2 were found dead after a 2,000-ha fire in Emas National Park (Silveira et al. 1999). Nevertheless, *P. maximus* used burned and unburned areas equally in the cerrado of Brazil (Prada and Marinho-Filho 2004), and regular fires may reduce fuels and thus mortality risk to *P. maximus* and other species (Smith 2007).

**Diet.**—*Priodontes maximus* is in the armadillo group of ant-termites specialists that includes species of *Cabassous* and *Tolypeutes* (Redford 1985), although the diet of the 3-banded armadillo (*T. matacus*) can contain other invertebrates and even vegetation (Bolkovic et al. 1995). *P. maximus* was once thought to feed exclusively on termites (Kühlhorn 1938, 1952), but it is now considered to be somewhat opportunistic (Anacleto

and Marinho-Filho 2001). Although termites (principally species from the families Nasutitermitidae and Termitidae) and ants are primary foods, *P. maximus* eats other invertebrates (e.g., species of Aranae, Blattaria, Coleoptera, Diplopoda, and Scorpiones—Anacleto and Marinho-Filho 2001). In Mato Grosso, Brazil, 8 fecal samples of *P. maximus*, collected near burrow entrances, contained 56.8% ants (Formicidae) and 36.8% termites (Cornitermes—Anacleto 2007). It also eats spiders, worms, small snakes, and carrion.

*Priodontes maximus* has been accused of eating garden vegetables, but most were likely digging for invertebrates in the garden soil (Nowak 1991). Albeit rarely, *P. maximus* has been found to eat figs from an unknown *Ficus* species in Bolivia (Wallace and Painter 2013), and 300 seeds from an unknown plant were found in the stomach contents of 1 individual in Colombia (Barreto et al. 1985). In Peru, it has been observed eating fruit of *Annona* and *Jacaratia* trees (R. Leite-Pitman, in litt.). Taboos against eating flesh of *P. maximus* might relate to a mythical case of a *P. maximus* digging up and eating human corpses (Azara 1801).

**Diseases and parasites.**—Physiological and ecological characteristics of armadillos could make them suitable hosts for a variety of pathogens (Storrs 1974). Physiologically, armadillos have lower body temperatures than most mammals (McNab 1980, 1985) and a weak immune system; ecologically, they live mostly immersed in soil and organic matter in warm to hot regions under conditions that promote exposure to pathogens and vectors (Storrs 1974). Nevertheless, diseases and parasitic infections of *Priodontes maximus* are virtually unknown. Very little is known about potential clinical disorders of *P. maximus*, mostly because of its low survival in captivity (Diniz et al. 1997).

Barreto et al. (1985) found 1 *P. maximus* from Carimagua, Colombia, with *Trypanosoma*, and 1 individual from São Paulo, Brazil, also tested positive (Sogorb et al. 1977). A male and 4 female ixodid ticks (*Amblyomma cajennense*) were collected from 1 adult female and 1 adult male wild-caught *P. maximus* (Miranda et al. 2010). Considering the low host specificity of *A. cajennense*, which can be a disease vector, and continued encroachment of domestic livestock into the distribution of *P. maximus*, the risk of disease transmission should be evaluated (e.g., Wells et al. 1981). *A. pseudoconcolor* has also been found on *P. maximus* (Botelho et al. 1989). *P. maximus* is hunted and consumed (Meritt 1973; Leeuwenberg 1997; de Souza-Mazurek et al. 2000), so it is important to evaluate the extent of infection and probability of zoonotic disease transmission. Deem and Fiorello (2002) recommended treating injuries and injection sites from handling of *P. maximus* with a topical antibiotic to prevent infestation by screwworms (*Cochliomyia hominivorax*).

Desbiez and Kluwyer (2013) noted that microclimatic conditions in burrows of *P. maximus* could promote survival and proliferation of fungi, bacteria, ticks, fleas, other parasites, protozoa, and viruses. They propose that burrow use by other species, especially mammals, could transmit parasites and pathogens among wild and domestic species, including *P. maximus*.

**Interspecific interactions.**—There are no published accounts of behavioral interactions of *Priodontes maximus* and other species, but their burrows and mounds of soil at entrances create new habitats that are used by and influence resource availabilities of at least 24 vertebrate species (R. Leite-Pitman, in litt.; Desbiez and Kluwyber 2013). Red-footed tortoises (*Chelonoidis carbonaria*), lizards, birds, and mammals (e.g., tayra, *Eira barabara*; ocelot, *Leopardus pardalis*; and crab-eating fox, *Cerdocyon thous*) foraged, wallowed, and rested at these sites (Desbiez and Kluwyber 2013). *P. maximus* has therefore been identified as an important “habitat engineer” (R. Leite-Pitman, in litt.). Giant anteaters (*Myrmecophaga tridactyla*) took baths in mounded soil near entrances of burrows of *P. maximus*, and other species searched for prey there. Sixteen species used burrows as refuges from predators or from temperature extremes, and predators themselves used them to hunt or rest (Desbiez and Kluwyber 2013). Burrows of *P. maximus* collect seeds and organic debris, and burrow tunnels and mounds affect water infiltration, distribution of soil nutrients, and diversity of localized plants and soil biota (Desbiez and Kluwyber 2013).

### HUSBANDRY

Capturing free-ranging *Priodontes maximus* is difficult (West et al. 2014). Carter (1985) and Silveira et al. (2009) captured *P. maximus* by hand aboveground; a funnel-shaped trap placed over the burrow entrance has also been used (Carter 1985; Silveira et al. 2009; West et al. 2014:figure 28.1). Free-ranging *P. maximus* can be immobilized with a tiletamine–zolazepam combination given intramuscularly (Silveira et al. 2009). Falzone et al. (2013) immobilized 3 *P. maximus* in captivity with a combination of anesthetic drugs (butorphanol, xylazine, and midazolam) applied under physical restraint and isoflurane gas delivered by facemask for maintenance and reversal with nalbuphine and yohimbine.

Handling a wild *P. maximus* requires caution because it is strong and can inflict serious injury to handlers before being fully immobilized (Carter 1983; Fig. 6). *P. maximus* usually attempts to escape by running and if that fails, it tries to burrow; it is such a good digger that a person holding its tail could be dragged along into a burrow as it digs (Walsh and Gannon 1967). *P. maximus* can be restrained by putting it on its back away from vegetation upon which it could get purchase (Walsh and Gannon 1967; Carter 1985).

*Priodontes maximus* is extremely difficult to maintain in captivity because of its great strength, nocturnal activity patterns, and digging behavior (Diniz et al. 1997). When captured alive, it rarely survives transport to a facility and, if so, often refuses artificial diets, does not adapt to captive conditions, and dies from injury or malnutrition (Superina et al. 2008).

*Priodontes maximus* was kept in zoological institutions in many parts of the world until its inclusion in Appendix 1 of the Convention on International Trade in Endangered Species of



**Fig. 6.**—The 1st radio-marked *Priodontes maximus* (held by TSC), a fully tranquilized female from Serra da Canastra National Park, Brazil, in 1980; note the large claw on the 3rd forefinger, effective for digging and breaking open termite nests. Photograph by J. H. Shaw used with permission.

Wild Fauna and Flora (2015) in 1973. Since then, many individuals have been seized by law enforcement authorities and passed on to certified zoological institutions, often with already compromised health, resulting in low survival rates (Superina et al. 2008). The manual on the rehabilitation of armadillos by Superina et al. (2014a) includes recommendations for *P. maximus*.

A wild-caught female *P. maximus* lived 6 years, 1 month, and 19 days in the Oklahoma City Zoo (Oklahoma, United States; Fig. 4); it is 1 of only 18 *P. maximus* recorded as held in North American or European zoos in the Zoological Information Management System ([www2.isis.org](http://www2.isis.org), accessed 31 July 2015). The Lincoln Park Zoo in Chicago, Illinois, had 5 wild-caught *P. maximus* (3 males from Guyana and 2 females from Bolivia) from 1972 to 1982 but never publically exhibited them (Meritt 2006). *P. maximus* has been kept in a handful of South American



zoos, but records are difficult to confirm. In 2015, 3 individuals were held in the Bioparque Los Ocarros in Villavicencio, Colombia. *P. maximus* has never bred in captivity (Superina et al. 2008).

When standing on its hindfeet, a *P. maximus* can easily haul itself over a 1-m wall (Meritt 1976). One climbed high up in its cage and fell to its death at the Bronx Zoo, New York (Cully 1939). Enclosures need to have high, smooth walls that do not permit climbing (Superina 2000). Bare concrete flooring leads to skin abrasions on abdomens and feet (Ostenrath 1974), so soil sufficient for digging is needed to prevent foot lesions and claw damage (Superina 2000). Sawdust and peat are not appropriate substrates because they lead to constant sneezing (Ostenrath 1974). Cully (1939) successfully changed the activity period of a *P. maximus* from nocturnal to diurnal for the benefit of zoo visitors by changing its feeding time; he also noted highly stereotypic behavior, including tail slaps and constant circling.

Many artificial diets, including standard mixtures commonly used for other armadillo species, have been unsuccessful for *P. maximus* (Meritt 1976). It seems to have considerable individual preferences, and semiliquid diets seem to be accepted more easily than those that require chewing (Meritt 1976). Nevertheless, accepted diets are not necessarily well balanced and can lead to health problems, such as obesity; 1 obese captive *P. maximus* weighed 80 kg (Superina et al. 2014a).

## GENETICS

Diploid number ( $2n$ ), based on 2 male *Priodontes maximus*, is 50 chromosomes, their fundamental number (FN) is 76, the X chromosome was a medium-sized metacentric, and the Y chromosome was a small metacentric (Benirschke and Wurster 1969; Benirschke et al. 1969). Genome size of *P. maximus* is 4.47 pg (picograms)  $\pm$  0.34 SD (= 4,372 Mbp [megabase pairs]—Redi et al. 2005). Chromosomal numbers are lower in *P. maximus* than in other species of armadillos: e.g., northern naked-tailed armadillo, *Cabassous centralis*,  $2n = 62$ , FN = 78; southern long-nosed armadillo, *Dasybus hybridus*, 64, ~86; 9-banded armadillo, *D. novemcinctus*, 64, 82; 6-banded armadillo, *Euphractus sexcinctus*, 58, 104; and big hairy armadillo, *Chaetophractus villosus*, 60, 92 (Benirschke and Wurster 1969:table 1; Benirschke et al. 1969; Redi et al. 2005). Close genetic relatedness of *P. maximus* and species of *Cabassous* has been confirmed with mitochondrial genes and protein-coding nuclear genes (Delsuc et al. 2003). No genetic studies to assess the possibility of intra-specific distinction have been conducted (Moraes-Barros and Arteaga 2015).

## CONSERVATION

*Priodontes maximus* is listed as “Vulnerable” on the International Union for Conservation of Nature and Natural Resources Red List of Threatened Species due to an estimated

population decline of at least 30% in the past 3 generations (Anacleto et al. 2014). Along with being in Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (2015), *P. maximus* is on the international list of endangered species under the United States Endangered Species Act (Department of Interior 1976). *P. maximus* is affected by habitat loss and fragmentation through deforestation, land-use change, agriculture (Parera 2002), hunting for meat (Meritt 1973; Redford and Robinson 1987; Leeuwenberg 1997; de Souza-Mazurek et al. 2000; Peres and Nascimento 2006; Fig. 7), collection for museum specimens, and illegal animal trafficking (Porini 2001). These impacts are difficult to quantify (Aguar and da Fonseca 2008; Trujillo and Superina 2013; Anacleto et al. 2014).

*Priodontes maximus* has become locally extirpated in some places, especially in areas of its southern distribution (Anacleto et al. 2014). Roads into formerly undisturbed areas provide easy access for hunters, exotic species, and even pathogens (Ferretti-Gallon and Busch 2014). Subsistence hunting by native peoples occurs throughout Amazonian Brazil, some of which could result in significant conservation threats (e.g., Chiarello 2000; de Souza-Mazurek et al. 2000; Peres and Nascimento 2006). Based on direct involvement with hunters, Leeuwenberg (1997) estimated that 93 *P. maximus* were harvested in 1991, 122 in 1992, and 155 in 1993 in the 2,200-km<sup>2</sup> Xavante reservation of Brazil; sustainability of that level of harvest was of conservation concern. In many places, however, *P. maximus* is harvested at very low rates compared with more abundant and preferred vertebrates (e.g., Redford and Robinson 1987).

*Priodontes maximus* is listed as endangered in Colombia (Rodríguez-Mahecha et al. 2006), Venezuela (Rodríguez and Rojas-Suárez 2008), Argentina (Superina et al. 2012), and Paraguay, where it has been proposed to be recategorized as critically endangered (Smith 2012). It is considered vulnerable in Bolivia (Tarifa 2009), Peru (Pacheco 2002), Ecuador (Tirira



**Fig. 7.**—Illegal harvests of *Priodontes maximus* occur throughout its distribution in South America; this individual was killed in Colombia. Photograph by Tropenbos International Colombia used with permission.

2011), and Brazil (Instituto Chico Mendes de Conservação da Biodiversidade 2015). In French Guiana, it is fully protected by law, and harvest is strictly forbidden in all nature reserves (Catzefflis and de Thoisy 2012).

Local communities of the Amazon and Orinoco regions of Colombia do not usually consume meat of *P. maximus*; however, it is subjected to subsistence hunting and substantially affected by habitat loss due to land-use change in those regions (Trujillo and Superina 2013; Superina et al. 2014b). In Venezuela, *P. maximus* is hunted intensely, despite being protected by Decree 1485 that prohibits armadillo hunting (Rodríguez and Rojas-Suárez 2008). Habitat destruction is an additional threat north of the Orinoco River, where *P. maximus* is virtually extirpated (Rodríguez and Rojas-Suárez 2008).

In Argentina, populations of *P. maximus* are mainly affected by significant and sustained habitat loss and fragmentation and by hunting (G. Porini, in litt.; Superina et al. 2012). The protected areas network currently covers about 3% of the distribution of *P. maximus* in Argentina (Tognelli et al. 2011). *P. maximus* is officially protected in Paraguay, but enforcement of protective measures is difficult in remote areas. *P. maximus* is extirpated in most of eastern Paraguay, with great threats to populations in the remaining areas (Smith 2012). Even if small populations of *P. maximus* persist in Paraguay, they are probably unsustainable because of human population growth, expansion of development, deforestation causing habitat fragmentation, and increased contact with people, all seriously restricting availability of suitable habitat (Meritt 2008; Smith 2012).

In Kaa-Iya National Park, Bolivia, protected areas of dry forest provided an important stronghold for long-term conservation of *P. maximus*, but outside these areas, there is little chance of protection (Noss et al. 2004). Status of populations of *P. maximus* in Brazil varies widely (de Souza-Mazurek et al. 2000; Srbek-Araujo et al. 2009), and some populations occur in official reserves of indigenous people, where they are susceptible to extirpation by hunting (Leeuwenberg 1997; Zimmerman et al. 2001).

There are emerging technologies (including remote sensing, camera trapping, and satellite telemetry) that can aid the conservation of *P. maximus*. Innovative use of scat-detection dogs to locate feces of *P. maximus* in Brazil could become a useful tool for conservation efforts (Vynne et al. 2009). Although Zimbres et al. (2012) found that *P. maximus* would still be adequately protected under climate-change scenarios, they stressed the need for additional reserves in northeastern and central Brazil. Similarly, Tognelli et al. (2011) assessed conservation priorities for xenarthrans in Argentina; their models suggested that protection of 1 additional area in the Chaco region of Argentina would significantly increase protection of *P. maximus*.

Strong national efforts, including educating native people, and international support are needed to ensure ongoing conservation of *P. maximus*. Because it fares poorly in captivity, captive breeding and reintroductions currently are not viable, making habitat protection the key to enhancing survival prospects of

*P. maximus*. Because *P. maximus* is widespread with locally low densities and often disjunct populations, it requires large preserves and often international cooperation (Arita et al. 1990). Corridors connecting suitable habitat and protected areas could also improve the conservation status of *P. maximus*. More basic research could enhance the understanding of the behavior and ecology of *P. maximus* and better illuminate its conservation needs (Meritt 2006; Loughry and McDonough 2013; Superina et al. 2014b; Loughry et al. 2015).

## ACKNOWLEDGMENTS

We thank A. M. Abba and J. C. Fernicola for providing important historical literature; N. Smith and K. McBee for helping with the skull images; F. Trujillo, F. Mosquera-Guerra, C. Aya-Cuero, Tropenbos International Colombia, and J. H. Shaw for providing photographs of *Priodontes maximus*; and R. K. Rose and J. H. Shaw for comments on earlier drafts of this account. The Oklahoma Cooperative Fish and Wildlife Research Unit (Oklahoma State University, Oklahoma Department of Wildlife Conservation, United States Geological Survey, United States Fish and Wildlife Service, and Wildlife Management Institute cooperating) provided technical support during the preparation of this account. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the United States Government.

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- PAMELA OWEN reviewed the fossil section. Associate Editor and Editor was MEREDITH J. HAMILTON.