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Calyptophractus retusus (Cingulata: Dasypodidae)

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Abstract: Calyptophractus retusus (Burmeister, 1863), commonly called the greater fairy armadillo, is a small armadillo in a monotypic genus. It is a poorly known, fossorial species with a reduced eye and ear, fixed carapace and greatly enlarged foreclaws adapted for digging. The species is confined to the Chaco region of northern Argentina, western Paraguay, and southern Bolivia where it is apparently locally distributed in areas with soft, sandy soils. The species is considered "Data Deficient" by the International Union for Conservation of Nature and Natural Resources.

Key words: Argentina, Bolivia, Chacoan fairy armadillo, Chlamyphorinae, greater fairy armadillo, Paraguay

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Calyptophractus Fitzinger, 1871

Chlamyphorus: Burmeister, 1863:167. Not Chlamyphorus Harlan, 1825.

Burmeisteria Gray, 1865:381. Type species Burmeisteria retusa (= Chlamyphorus retusus Burmeister, 1863) by monotypy; preoccupied by Burmeisteria Salter, 1865, a trilobite.

Calyptophractus Fitzinger, 1871:388. Type species Chlamyphorus retusus Burmeister, 1863, by monotypy.

CONTEXT AND CONTENT. Order Cingulata, family Dasypodidae, subfamily Chlamyphorinae (Möller-Krull et al. 2007). Wetzel et al. (2008) included Chlamyphorinae as the tribe Chlamyphorini of the subfamily Euphractinae, but a molecular phylogeny by Delsuc et al. (2012) confirmed that the fairy armadillos were an ancient lineage worthy of subfamilial rank.

Calyptophractus retusus (Burmeister, 1863)

Greater Fairy Armadillo

Chlamyphorus retusus Burmeister, 1863:167. Type locality "Sta Cruz de la Sierra," Santa Cruz, Bolivia.

Burmeisteria retusa: Gray, 1865:381. Name combination. Calyptophractus retusus: Fitzinger, 1871:389. First use of current name combination.

Chlamydophorus retusus Macalister, 1875:224. Incorrect generic amendment.

Burmeisteria retusa clorindae Yepes, 1939:38. Type locality "Tapia, en la gobernación de Formosa," Argentina.



Fig. 1.—Adult *Calyptophractus retusus* (sex unknown) from near Colonia Neuland, Departamento Boquerón, Paraguay. Used with permission of photographers Thomas and Sabine Vinke.

CONTEXT AND CONTENT. Context as for genus. Subspecies Calyptophractus retusus clorindae (Yepes, 1939) was differentiated mainly due to perceived differences in details of the proportions of the claws and scute shapes on the dorsal bands, but with so few specimens available for analysis the recent tendency is for the species to be considered monotypic (Wetzel et al. 2008). Synonymies are modified from Wetzel et al. (2008).

NOMENCLATURAL NOTES. Calyptophractus Fitzinger, 1871 is monotypic and derived from the Greek meaning "covered or concealed" (Palmer 1904) or "cloak bearer" (Braun and Mares 1995). The species name *retusus* is from the Latin for "blunt or rounded" in reference to the carapace (Braun and Mares 1995). The Edentate Specialist Group (2004) advocates the use of Calyptophractus over Burmeisteria as the generic name for this species following Wetzel (1985a). The generic name Burmeisteria, Gray, 1865 is unavailable and preoccupied by a trilobite (Salter 1865). Previously it was commonly placed in Chlamyphorus Burmeister (1863), jointly with the pink fairy armadillo C. truncatus. Morphologically Calyptophractus differs from Chlamyphorus principally by having the carapace firmly attached to the body (attached only at dorsal midline in Chlamyphorus) and the tail tip pointed (versus spatulate *Chlamyphorus*).

Published English common names include Chaco fairy armadillo (Redford and Eisenberg 1992; Smith 2008), Chacoan fairy armadillo (Wilson and Cole 2000; Superina and Aguiar 2006), greater fairy armadillo (Redford and Eisenberg 1992; Superina and Aguiar 2006), Burmeister's armadillo (Abba and Superina 2010), greater pichi piego (Abba and Superina 2010), northern pichiciego (Anderson 1997), larger fairy armadillo (Wetzel 1985a), mouse armadillo (Warhol and Benirschke 1986).

The following Spanish language names have appeared in the literature: pichiciego grande (Redford and Eisenberg 1992; Cuéllar and Noss 2003), pichiciego mayor (Abba and Superina 2010), armadillo de Burmeister (Superina and Aguiar 2006), coseveru (Anderson 1997), pichiciego chaqueño (Superina and Aguiar 2006), islerito (Perovic et al. 2008), armadillo de manto (Peñaranda Barrios 2012), culo tapado (Cuéllar and Noss 2003) meaning roughly "butt plug," in reference to the anal shield which blocks tunnels as a form of defense. The Spanish name "pichiciego" is believed be derived from a mixture of Spanish and Mapuche: pichi meaning little in the Mapuche language and ciego blind in Spanish.

DIAGNOSIS

At least partially sympatric with the much larger Chaco naked-tailed armadillo Cabassous chacoensis Wetzel, 1980; however, Calyptophractus retusus is distinct and unmistakable within its range and unlikely to be confused with any other sympatric species because of its extremely small size, reduced eyes and ears, very short tail, distinctive carapace structure, and heavily furred body (Fig. 1).

The pink fairy armadillo *Chlamyphorus truncatus* Harlan, 1825 is superficially similar, but widely allopatric, occurring well to the south of the known range of C. retusus. The pink fairy armadillo can be easily distinguished externally by the combination of the spatulate tail tip, the presence of a nuchal constriction of the dorsal carapace, and the fact that the dorsal carapace is free at the edges, and fused to the body only along the dorsal midline. Cranially C. retusus can be distinguished from pink fairy armadillo by the following characters: (1) frontal prominences smaller and more widely separated so that no specialized enlarged scutes articulate with them; (2) pinnae not attached to the zygoma; (3) external auditory meatus not ossified or attached to the zygoma; and (4) reduced temporal musculature resulting in more pronounced lambdoidal ridge and less domed profile of the parietal-occipital (Wetzel 1985a).

GENERAL CHARACTERS

Calyptophractus retusus is an unusual, fossorial, molelike armadillo with greatly reduced eye and ear. The following description is adapted from Burmeister (1863), Slade (1891), Wetzel (1985a), and Smith (2008). The cephalic shield lacks a "step" in the dorsal surface, widens posteriorly and has a rounded posterior edge; it does not extend below the level of the eye. Cephalic shield shows even progression from larger to smaller scutes posterior to anterior, and lacks a row of distinctly larger scutes on posterior margin. Base of pinna attached to posterolateral margin of cephalic shield. The dorsal carapace is pinkish with an undulating lateral edge, and attached firmly to the skin of the dorsum. It has 20 to 23 rows of squarish scutes. The anal plate is armored with an ovoid "plug" consisting of naked, pinkish, rounded scutes. The upper part of the pelvic shield and the lateral and posterior edges of the dorsal shield have tufts of bristles. The tail is short, pinkish, lightly armored, and with a pointed tip, protruding from the lower edge of the anal carapace. The sides of the head and the fusiform body are heavily furred both ventrally and laterally, the pelage being whitish, but becoming tinged yellowish toward the ventral midline. Forelimbs are pinkish, predominately naked with large, irregular vestigial scutes. The forefeet are armed with 3 greatly enlarged claws (digits 1-3), and 1 smaller claw. The 3 largest claws are rotated and visible laterally. Hindfoot possesses 5 toes, similarly arranged but with reduced claws when compared to the forefeet.

Means and ranges of external measurements (mm) and mass (g) for 12 Bolivian specimens (6 males, 3 females and 3 unsexed, unless stated otherwise—Azurduy et al. 2005) were: total length, males 153.33 (126-199), females 136.67 (125-153), unsexed 163 (160–165); length of tail, males 35.5 (32–39), females 35 (33-37), unsexed 34 (27-38); length of ear, males 5.4 (5-6, n = 5), females 5, unsexed 5; length of hind foot, males 31.5 (28–39), females 29.66 (28–31), unsexed 32.66 (25–39); mass, males 91.3 g (71–116 g, n = 3), females 73.85 g (63.5–84.2 g, n = 2). Measurements suggest that males are consistently larger than females.

The cranium was not described during the formal description of the species as it was broken and the mandibles lost (Burmeister 1863). The description provided here is based on Wetzel (1985a, 1985b), and our own examination and cranial measurements of 1 specimen (MNHNP [Museo Nacional de Historia Natural del Paraguay] 3362, an adult of unknown sex; Fig. 2). The cranial dorsum rises steeply from the nasals to the braincase, which is slightly rounded. Frontal protuberances positioned anterior and superior to the orbits. The zygomatic arches are incomplete. The external auditory meatus is ossified. Occipital crest well developed, extending well posterior of the foramen magnum and occipital condyles. Foramen magnum triangular. Hard palate extends to level of posterior edge of posterior molar alveolus; posterior edge is U-shaped, with small medium projection. Selected cranial measurements (mm) were: greatest length of skull (nasal to occipital crest) 43.0; condylobasal length 39.5; zygomatic breadth 27.8; braincase breadth



Fig. 2.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of an adult (sex unknown) *Calyptophractus retusus* (MNHNP [Museo Nacional de Historia Natural del Paraguay] 3362) from Comunidad Indigena Campo Loro, Depto. Boquerón, Paraguay. Greatest length of skull is 43.0 mm.

20.8; height of cranium 17.1; greatest breadth across maxillary molars 10.9; length of maxillary toothrow 15.2; length of mandibular toothrow 18.4; height of coronoid process 18.7; height of condyloid process 21.1.

DISTRIBUTION

Calyptophractus retusus is endemic to the Chaco region of Bolivia, western Paraguay, and north-eastern Argentina in south-central South America (Fig. 3). The total area of the distribution is estimated at about 258,000 km² (Torres et al. 2015).

Azurduy et al. (2005) provided details of Bolivian localities. It has been most frequently recorded in the Bañados de Izozog and Parque Nacional Kaa-Iya areas of southern Santa Cruz department. The northernmost record in Bolivia is from Pampas del Urubó, west of the city of Santa Cruz de la Sierra though no specimen was collected (Azurduy et al. 2005). This undocumented record was used to suggest the possible existence of a disjunct population in the Chiquitana pampas biome. Peñaranda Barrios (2012) includes records of the species in Tarija department and it also presumably occurs in Chuquisaca department, though the species has yet to be documented there.

The presence of *C. retusus* in Paraguay was suspected (Yepes 1939), but this was not confirmed until the report of Myers and Wetzel (1979). To date, all Paraguayan records are from Boquerón department. The known range is based on few specimens, largely centered on the extreme northwestern Chaco in the areas of Parque Nacional Teniente Agripino Enciso and Parque Nacional Médanos del Chaco and the central Chaco

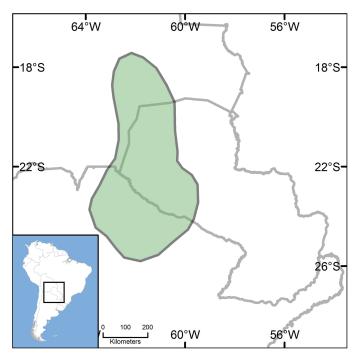


Fig. 3.—Geographic distribution of *Calyptophractus retusus*. Map redrawn from International Union for Conservation of Nature and Natural Resources (2007).

area around the Mennonite town of Filadelfia (Myers and Wetzel 1979; Smith 2012). A specimen exists from Campo Loro Indigenous Reserve in the north-central Chaco and an individual was recently captured and photographed at Neu-Halbstat close to Colonia Neuland in April 2013 (Vinke and Vinke 2014). It may be expected to occur at least marginally in western Presidente Hayes and southern Alto Paraguay departments.

In Argentina, *C. retusus* is known only from Chaco, Formosa, Santiago del Estero, and eastern Salta provinces (Mares et al. 1989; Díaz et al. 2000; Barquez et al. 2006; Quiroga and Boaglio 2006; Perovic et al. 2008; A. Abba, in litt.). Chebez (2008) considered old reports from Jujuy to be insufficiently documented and the species was omitted from the most recent review of the mastofauna of the province (Díaz and Barquez 2002), though its occurrence there is considered probable (Díaz 2000).

Despite the wide geographic range, it is locally distributed in areas of soft, sandy soil. The fossorial behavior and remoteness of much of the range means that the species is without doubt under-recorded, and it may potentially extend to sandy areas of the Paraguayan and Brazilian Pantanal (Edentate Specialist Group 2004).

FOSSIL RECORD

Divergence of *Calyptophractus retusus* from the pink fairy armadillo has been estimated at 17 ± 3 million years ago, during the Middle Miocene when significant marine incursions occurred along the Paraná river basin. These may have acted as a vicariant agent in the diversification of fairy armadillos by disrupting their ancestral range and accounting for the present-day allopatric distribution (Delsuc et al. 2012).

Divergence of the Chlamyphorinae from their tolypeutine sister group occurred approximately 32 ± 3 million years ago, shortly after the Eocene–Oligocene transition. This period was marked by the uplift of the Andes driving the development of arid habitats which may have promoted a subterranean lifestyle in the ancestral lineage (Delsuc et al. 2012).

FORM AND FUNCTION

Calyptophractus retusus shows a variety of morphological adaptations for a fossorial lifestyle including enlarged claws on the forefeet, reduced eyes and ears, a fusiform body shape, and a vertical, rounded anal carapace (Delsuc et al. 2012). Limb morphology suggests that the Chlamyphorinae are adapted for speed rather than power, essentially making them "sand swimmers," and thus explaining their absence from areas with hard soils (Vizcaíno et al. 1999; Vizcaíno and Milne 2002). The flattened anal plate acts as a plug to block tunnels, affording the animal protection as it burrows (Smith 2008).

Teeth are peg-like. *C. retusus* has no canines or incisors; there are 8 upper and 8 lower cheek teeth, 8/8, total 32. All teeth posterior to 1st maxillary and first 2 mandibular pairs are flattened

ovals in cross section, with long axes about 45° from the long axis of the toothrow (Wetzel 1985a). A specimen examined by Green (2009) did not show evidence of gouges in orthodentine and had a mean number of 8.50, predominately fine, cross-scratches and 52.50 pits, characters consistent with an insectivorous diet, though the Chlamyphorine armadillos clustered as an outgroup in the analysis.

ECOLOGY

Calyptophractus retusus is one of the most poorly known species of armadillo and has been considered a priority for research (Superina et al. 2014). It is fossorial and primarily nocturnal (Cuéllar 2001). Endemic to the Chaco biome where it is locally distributed in areas of soft, sandy soil. The typical vegetation in such areas is xeric, thorny forest or scrub, and rainfall in the known geographic range is below 400 mm (Chebez 2008). Surface habitat may be of limited importance to the species and it can occur in close proximity to humans provided soil conditions are adequate. Sandy soils are uncommon over much of the Chaco where compacted clay soils, beyond the burrowing capabilities of this species, predominate (Smith 2008).

Limited data are available on diet, but it is likely insectivorous, feeding on subterranean invertebrates and their larvae. A wild individual from near Pampas del Urubó, Bolivia, was observed feeding on larvae in palm seeds *Acrocomia totai* (R. Miserendino, pers. comm. in Azurduy et al. 2005).

A captive individual kept in a fish tank filled with soil at Brookfield Zoo was fed on cooked rice (Edentate Specialist Group 2004). Another thrived in captivity in Bolivia in a yard where it was able to burrow, but died shortly after translocation to the US National Zoo of respiratory infection where it had been fed on mealworms, raw eggs, and meat (Nowak 1991).

Calyptophractus retusus is solitary and primarily nocturnal. A Bolivian specimen was found at 22.00 h scuttling and sniffing along the ground, making occasional shallow excavations in search of food. It buried itself half way into soil when approached by observers (Cuéllar 2001). Rapid burrowing behavior was also reported by Burmeister (1863), but Chebez (2008) stated that when the species is threatened it prefers to flatten itself against the ground rather to rapidly burrow into the soil.

Slade (1891) notes that inhabitants of the Santa Cruz area where the species were 1st discovered were aware of a subterranean animal which they called "llorón," in reference to the crying noises it makes when handled which recalled a new-born infant. This call has been said to be so distinctive that Félix San Martin (who collected the first specimens) was reportedly able to locate a subterranean individual on the basis of it (Burmeister 1863).

When above ground these relatively defenseless armadillos are vulnerable to predators. Individuals are probably killed by domestic dogs and cats, and would be easy prey for other carnivorous mammals as well as owls (Smith 2008). No data are available on reproduction, though it is assumed that they give

birth to a single young (Cuéllar and Noss 2003). Guglielmone et al. (2003) reported 4 females and a nymph of the Ixodid tick *Amblyomma pseudoconcolor* Aragão, 1908 (Acari: Ixodidae) on *C. retusus*.

CONSERVATION

Calyptophractus retusus is rarely reported and considered to be "Data Deficient" by the International Union for Conservation of Nature and Natural Resources because of the lack of information available (Abba and Superina 2010). Though it is able to tolerate the close proximity of human populations, its range is restricted to areas of sandy soils which are locally distributed in the Chaco region, an ecoregion that is suffering considerable and ongoing habitat loss (Cardozo et al. 2013). It is persecuted as an animal of ill omen throughout the range (Cuéllar 2001; Chebez 2008; Meritt 2008). Neris et al. (2002) stated that the indigenous people of the Paraguayan Chaco consume the meat and carapace entirely, but Meritt (2008) suggested that this was not the case.

In Paraguay, the species occurs in at least 2 national parks (Teniente Enciso and Médanos del Chaco). However, the protection provided by these parks is nominal and the buffer zones of both have shown increased development in recent years. C. retusus is considered vulnerable nationally in Paraguay (Smith 2012). In Bolivia, the species occurs in Kaa-Iya del Gran Chaco National Park and is considered near threatened nationally (Tarifa and Miserendino Salazar 2009). The species has been highlighted as one of the small-medium habitat specialist species that is most likely to be declining in that country (Peñaranda and Simonetti 2015). In Argentina, there have been very few recent records. The species is not known to occur widely within the national park system (Fortabat and Chebez 1999) but has been reported from Parque Nacional Copo, in extreme northeastern Santiago del Estero province (Perovic et al. 2008). Supposed reports for Pilcomayo National Park, eastern Formosa province, are considered to be in error (Chebez 2008). It is considered data deficient nationally in Argentina (Superina et al. 2012), having previously been listed as vulnerable (Díaz and Ojeda 2000); however, its localized distribution and dependence on specific soil characteristics means that it is likely severely threatened by progressive habitat deforestation (Superina et al. 2012).

A continuing global decline in populations may be inferred (Abba and Superina 2010). Though the geographic range of *C. retusus* is fairly large, distribution is highly fragmented and density is low. This has been postulated to be a result of past climate variations successively expanding and retracting suitable areas of habitat, and the associated delay in the recovery of populations associated with it. Future forecasts indicate a net retraction of suitable habitat for this species which could have particularly severe consequences for its population (Torres et al. 2015). The species is included in Convention on International Trade in Endangered Species of Wild Fauna and Flora appendix 1 (Chebez 2008).

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