THE FOSSIL MAMMALS COLLECTED BY CHARLES DARWIN IN SOUTH AMERICA DURING HIS TRAVELS ON BOARD THE HMS BEAGLE

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ABSTRACT

During the first two years of his voyage aboard HMS Beagle, Charles Darwin collected a considerable number of fossil mammals from various localities in Argentina and Uruguay. Among these remains are those of large mammals that Darwin informally assigned to *Megatherium* and *Mastodon*, the only large taxa then known for South America, and of small and medium-sized mammals that Darwin recognized as representing at least two rodents and a horse. The study of Darwin's collection was entrusted to Richard Owen, who described eleven taxa between 1837 and 1845, including the six following ones: *Toxodon platensis, Macrauchenia patachonica, Equus curvidens, Scelidotherium leptocephalum, Mylodon darwini* and *Glossotherium* sp. This contribution provides a synthesis of Darwin's preliminary assignments and evaluates the reasons that led him to recognize only megatheres and mastodonts for the large fossil remains. Also, it discusses the current taxonomic status of the taxa described or erected by Owen between 1837 and 1845 and the influence that Owen's taxonomic and phylogenetic conclusions had on the development of Darwin's ideas on evolution.

Keywords: *Darwin, Taxonomy, South America, Fossil mammals.*

RESUMEN: *Los mamíferos fósiles colectados por Charles Darwin en América del Sur durante su viaje a bordo del HMS Beagle.* Durante los dos primeros años de su viaje a bordo del HMS Beagle, Charles Darwin colectó en distintas localidades de Argentina y Uruguay un considerable número de mamíferos fósiles. Entre estos se cuentan los grandes mamíferos que informalmente Darwin asignó a *Megatherium* y *Mastodon*, únicos grandes taxones conocidos hasta ese momento para América del sur y entre los pequeños y medianos mamíferos reconoció la presencia de al menos dos tipos de roedores y un caballo. El estudio posterior de todos los ejemplares colectados por Darwin fue llevado a cabo Richard Owen, quien entre 1837 y 1845 describió once taxones, entre los cuales, seis eran nuevos taxones: *Toxodon platensis, Macrauchenia patachonica, Equus curvidens, Scelidotherium leptocephalum, Mylodon darwini* y *Glossotherium* sp. En esta contribución se brinda una síntesis de las asignaciones preliminares efectuadas por Charles Darwin y se evalúan los motivos que lo habrían llevado a reconocer sólo megaterios y mastodontes entre los grandes mamíferos fósiles por él colectados. También tiempo, se discute el estatus taxonómico de los taxones descritos o fundados por Richard Owen entre 1837 y 1845 y la influencia que habrían tenido las conclusiones taxonómicas y filogenéticas de Owen en el desarrollo de las ideas evolutivas de Darwin.

Palabras clave: *Darwin, taxonomía, América del Sur, mamíferos fósiles.*

INTRODUCTION

Charles Darwin collected fossil mammals from various South American localities during his voyage aboard HMS Beagle. He recovered his first fossil at Punta Alta (Buenos Aires Province, Argentina) on September 23, 1832, and continued collecting intermittently at this locality until October 16. Three days later he collected several specimens from Monte Hermoso (Buenos Aires Province, Argentina). Darwin returned to Punta Alta between August 29 - 31, 1833. Several weeks later, around September 19, he collected in Guardia del Monte (Buenos Aires Province); the Rio Carcarañá or Tercero (Santa Fe Province, Argentina) on October 1; and the Bajada Santa Fe (Paraná, Entre Ríos Province, Argentina) on October 10. Moving to Uruguay, he collected fossils during November 25 - 26 from the Arroyo Sarandí near the city of Mercedes (Soriano Department). He returned to Argentina and collected his last specimens at Puerto San Julián (Santa Cruz Province) during the first several months of 1834 (see Fig. 1). All the specimens, sent to his mentor John Stevens Henslow and later deposited in the Royal College of Surgeons (London, England), were studied by Richard Owen beginning in 1836.

Figure 1: Map of the localities where Charles Darwin collected fossil mammals.

Regrettably, the intense bombardment suffered by this institution during April 10 and 11, 1941, destroyed a large part of its paleontological treasures. Cave's (1942) catalogue of the surviving specimens revealed that some 95% of the collection had been lost - of 5,000 specimens, only 175 remained. Among these, fortunately, are various of the specimens collected by Charles Darwin and described by Richard Owen (1837-1845) as new taxa, including *Equus curvidens, Glossotherium* sp; *Macrauchenia patachonica, Mylodon darwini, Scelidotherium leptocephalum* and *Toxodon platensis* (Cave 1942). Beginning in 1946, nearly all of Darwin's collection was transferred to the Natural History Museum (London), where it is still housed (see appendix 1). The Royal College of Surgeons retained only a single specimen, the remains of the *Megatherium americanum* specimen that apparently allowed Owen (1840) to recognize the presence of a fifth upper molariform in this taxon (see appendix 1).

The aim of this contribution is to provide an update on the taxonomic status of the various taxa recognized or established by Owen (1837-45), and to consider the influence the specimens and their assignment had on the development of Darwin's ideas.

HISTORICAL BACKGROUND

The first notices of South American "fossils" appear in the reports of early Spanish explorers to South America and in the earliest histories of America (e.g. Cieza de León 1553, Falkner 1774). These objects were interpreted as the remains of an ancient race of giant humans that inhabited this part of the world before being smitten by divine force. Cieza de León (1553, p. 183) provided the following vivid tale about huge bones found in Santa Elena, Ecuador: "*Y así, dicen que, estando todos juntos envueltos en su maldita sodomía, vino fuego del cielo temeroso y muy espantable, haciendo gran ruido, del medio del cual salió un ángel resplandeciente, con una espada tajante y muy refulgente, con la cual de un solo golpe los mató a todos y el fuego los consumió, que no quedó sino algunos huesos y calaveras, que para memoria del castigo quiso Dios que quedasen sin ser consumidas por el fuego. Esto dicen de los gigantes; lo cual creemos que pasó, porque en esta parte que dicen se han hallado y se hallan huesos grandísimos. Y yo he oído a españoles que han visto pedazo de muela que juzgaban que a estar entera pesara más de media libra carnicera, y también que habían visto otro pedazo del hueso de una canilla, que es cosa admirable contar cuán grande era, lo cual hace testigo haber pasado…*".

This sort of general belief persisted, in South America at least, until the end of the 18th century, even though some of the remains were recognized as nonhuman, as indicated in the following passages by the English Jesuit Thomas Falkner (1774, p. 54-55) "*On the banks of the River Carcarania, or Tercero, about three or four leagues before it enters into the Parana, are found great numbers of bones, of an extraordinary bigness, which seem human. There are some greater and some less, as if they were of persons of different ages. I have seen thigh-bones, ribs, breast-bones, and pieces of skulls. I have also seen teeth, and particularly some grinders which were three inches in diameter at the base. These bones (as I have been informed) are likewise found on the banks of the Rivers Parana and Paraguay, as likewise in Peru. The Indian Historian, Garcilasso de la Vega Inga, makes mention of these bones in Peru, and tells us that the Indians have a tradition, that giants formerly inhabited those countries, and were destroyed by God for the crime of sodomy.*

I myself found the shell of an animal, composed

of little hexagonal bones, each bone an inch in diameter at least; and the shell was near three yards over. It seemed in all respects, except it's [sic] *size, to be the upper part of the shell of the armadillo; which, in these times, is not above a span in breadth.*"

It was during this period that the illustrious French naturalist George Cuvier (1796) published the first scientific work on a South American fossil, which he described and named *Megatherium americanum* based on the specimen recovered by Fray Manuel Torres in 1787 from Luján in Buenos Aires Province, Argentina and sent the following year by the Marquis of Loreto, Viceroy of Río de la Plata, to the *Real Gabinete de Historia Natural* in Madrid, Spain. Mones (1986) considered the erection of this species as the first Linnean nomenclatorial act for a South American fossil species. This specimen had, however, previously been described and figured by Juan Bautista Bru de Ramón, an artist and first taxidermist of the *Real Gabinete de Historia Natural.* In this regard, Garriga (1796, as quoted in López Piñeiro and Glick 1993, p. 126) noted that "… *restaba superar la dificultad de que permitiese Bru que se diese a luz una obra que él había tenido en otro tiempo intento de publicar, y por varias circunstancias imprevistas sepultó en el olvido.*" López Piñeiro and Glick (1993, p. 66) maintained that the preparation of the monograph "… *no fue entonces editada, pero su preparación debía estar tan adelantada que un tal Roume, representante del gobierno de francés en Santo Domingo, consiguió un juego de pruebas de las planchas a su paso por Madrid en 1793.*

Roume envió las pruebas de las planchas al Institut de France, del que era miembro correspondiente, acompañadas de una "corta descripción" del esqueleto. La sección de ciencias del Institut encargó a George Cuvier un informe sobre el tema, que apareció publicado en 1796…"

Cuvier (1806) also studied fossil proboscidean remains found by Dombey in Peru and by Humboldt in various localities in Bolivia, Chile, Colombia, and Ecuador, among which he recognized three morphotypes, designated informally as "*mastodonte a dents étroites*", "*mastodonte Cordillierès*" and "*mastodonte humboldien*". Cuvier (1823) later formally named them *Mastodon angustidens, Mastodon andium* and *Mastodon humboldti*, respectively (see Cabrera 1929). In this paper, Cuvier (1823, p. 179) included a handwritten communication by "*don Dámaso Antonio Larrañaga, a priest of Montevideo, to Mr. Augusto de Saint-Hilaire*" that briefly described a group of fossil specimens, including a partial exoskeleton (or carapace), under the name "*Dasypus* (*Megatherium* Cuv)." Cuvier (1823) thus acknowledged that this carapace probably belonged to *Megatherium.* Whatever the reasons that prompted Larrañaga's subgeneric assignment (that is, in recognizing the existence of armored megatheres), the fact that his opinion appeared in a work by Cuvier ensured its credibility, so that several incomplete remains later sent to Europe were similarly recognized (e.g., as by Weiss 1830, Clift 1835). It was not until later that Owen (1839a) demonstrated that megatheres were not armored and that the remains belonged instead to the group of mammals he termed glyptodonts, a group closely related to armadillos.

Knowledge of South American fossil mammals remained at this elementary level for much of the early part of the 19th century, as is made clear from Owen's (1838, p. 13) opening paragraph on his work on the fossil mammals in Darwin's *The Zoology of the Voyage of H.M.S. Beagle: "It may be expected that the description of the osseous remains of extinct Mammalia, which rank amongst the most interesting results of Mr. Darwin's researches in South America, should be preceded by some account of the fossil mammiferous animals which have been previously discovered in that Continent. The results of such a retrospect are, however, necessarily comprised in a very brief statement; for the South American relics of extinct Mammalia, hitherto described, are limited, so far as I know, to three species of* Mastodon*, and the gigantic* Megatherium.*"*

It was against this systematic framework that Darwin began his efforts in collection and preliminary taxonomic assignments that Owen (1837-1845) later modified. Several of his assignments were considered taxonomic errors or misinterpretations (e.g., Sulloway 1982, Keynes 2001), even though his inferences were in accordance with what was then known.

DARWIN'S FOSSIL MAMMALS

The following presents a synthesis of Owen's initial taxonomic assignments (1837-45) of the remains collected by Darwin in South America, including the preliminary assignments made by Darwin. The latter's assignments were gleaned from field notes (Darwin 2002-2008), personal correspondence (Darwin 1985) and Charles Darwin's Beagle Diary (in Keynes 2001), all material written by Darwin before 1836, the year of his return to England. The suprageneric classification used here follows McKenna and Bell (1997).

SYSTEMATIC PALEONTOLOGY

Grandorder Ungulata Linnaeus, 1776
Mirorder Meridiungulata McKenna, 1975
Order Notoungulata Roth, 1903
Suborder Toxodontia Owen, 1853
Family Toxodontidae Owen, 1845
Subfamily Toxodontinae Owen, 1845
Genus ***Toxodon*** Owen, 1837

Toxodon platensis Owen, 1837
Fig. 2

The specimens assigned to this taxon by Owen (1837, 1838) were recovered by Darwin from various South American localities. On October 1 and 10, 1833, he collected at Río Carcaraña o Tercero (Santa Fe Province) and at Bajada Santa Fe (Paraná, Entre Ríos Province). His field notes (Darwin 2002-2008) describe a fossil specimen as "…*a large rotten tooth & in the layer large cutting tooth*", a description that agrees with those included in his Beagle Diary ("… *a curious & large cutting tooth*"; in Keynes 2001, p. 193) and written to John Stevens Henslow ("*In y*

R. Carcarana I got a tooth, which puzzles even my conjectures, it looks like an enormous gnawing one"; Letter 229 in Darwin 1985). Darwin's (2002-2008) field notes for November 26, 1833, state: "*Started went round by a house to see large head & bones, washed out of Barranca & found after a flood. - pieces here also of Casca - Barranca*" while his Beagle Diary (in Keynes 2001) records: "*Began my return in a direct line to M. Video; went by an Estancia where there was a part, very perfect, of the head of a* Megatherium. *I purchased it for a few shillings*". An alveolus of this specimen, recovered from Arroyo Sarandí, Departament of Soriano, Uruguay, easily accommodated a molariform tooth found by Darwin in Carcaraña (Owen 1838).

Toxodon sp.

The mandible and isolated molariforms assigned by Owen (1837, 1838) to this genus were collected between September 23 - October 16, 1832, at Punta Alta (Buenos Aires Province, Argentina). On the molariforms, Darwin (1985, Letter 192) noted that "*some large molar teeth, which in some respects would seem to belong to an enormous Rodentia*". Burmeister (1866) based the species *Toxodon darwini* on the mandible described by Owen (1838) Bond (1999) acknowledged the possible synonymy of *Toxodon darwini* with *Toxodon platensis*, although he recognized that a revision of the genus was required.
Owen (1837, 1838, p. 16) recognized *Toxodon* as "*A gigantic extinct mammiferous animal, referrible to the Order Pachydermata, but with affinities to the Rodentia, Edentata, and Herbivorous Cetacea*". Darwin (1839, p. 180) summarized the morphological basis leading to this idea of multiple affinities: "*Mr. Owen says, judging from the portion of the skeleton preserved, the* Toxodon*, as far as dental characters have weight, must be referred to the rodent order. But from that order it deviates in the relative position of its supernumerary incisors, in the number and direction of the curvature of its molars, and in some other respects. It again deviates, in several parts of its structure which Mr. Owen enumerated, both from the Rodentia, and the existing Pachydermata, and it manifests an affinity to the Dinotherium and the Cetaceous order. Mr. Owen, however, observed, that the development of the nasal cavity and the presence of frontal sinuses, renders it extremely improbable that the habits of he* Toxodon *were so exclusively aquatic as would result from the total absence of hinder extremities; and concludes, therefore, that it was a quadruped, and not a Cetacean; and that it manifested an additional step in the gradation of mammiferous forms leading from the Rodentia, through the Pachydermata to the Cetacea; a gradation of which the water-hog of South America* (Hydrochærus capybara) *already indicates the commencement amongst existing Rodentia, of which order it is interesting to observe this species is the largest, while at the same time it is peculiar to the continent in which the remains of the gigantic* Toxodon *were discovered*". The genus *Toxodon* is now considered among the more derived native notoungulates of South America. The Notoungulata, a clade of the Mirorder Meridiungulata, shares an ancestry with North American condylarths (Cifelli 1993) In other words, *Toxodon* has no close phylogenetic relationships with the groups mentioned by Owen (1838).

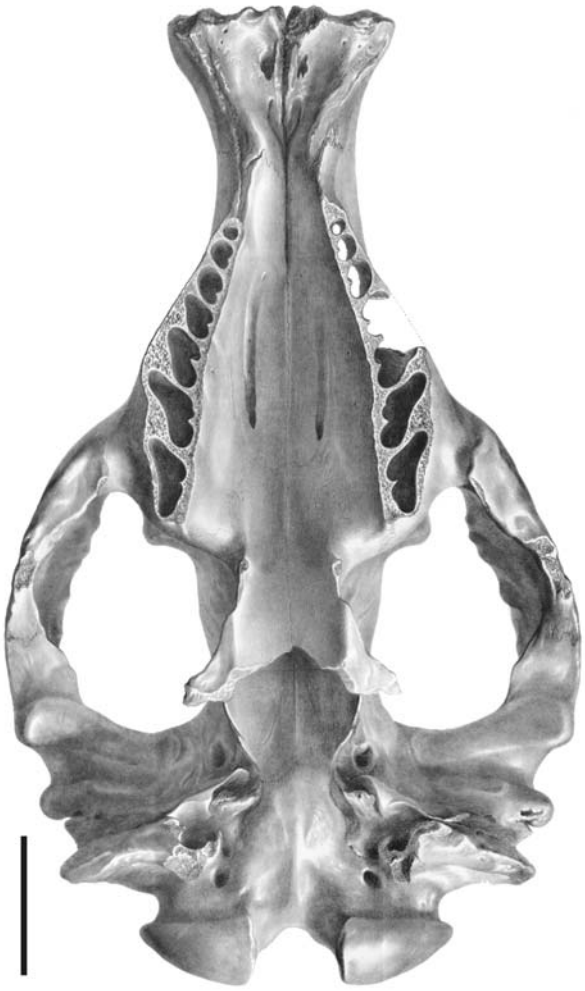

Figure 2: Skull of *Toxodon platensis* in ventral view (from Owen 1838). Scale bar = 10 cm.

Grandorder Ungulata Linnaeus, 1776
Mirorder Meridiungulata McKenna, 1975
Order Liptopterna Ameghino, 1889
Superfamily Macrauchenioidea Gervais, 1855
Family Macraucheniidae Gervais, 1855
Subfamily Macraucheniinae Gervais, 1855
Genus ***Macrauchenia*** Owen, 1838

Macrauchenia patachonica Owen, 1838
Fig. 3a

In a letter from March, 1834, to John Stevens Henslow, Darwin (1985, Letter

238) recounted that "*At Port St Julian I found some very perfect bones of some large animal, I fancy a* Mastodon". On this specimen, the only one found by Darwin in Puerto San Julián, Owen (1838, p. 35) erected *Macrauchenia patachonica*, which he considered "*A large extinct Mammiferous Animal, referrible to the Order Pachydermata; but with affinities to the Ruminantia, and especially to the Camelidae*". The evolutionary significance of this purported kinship impressed Darwin (1839, p. 210): "*The most important result of this discovery, is the confirmation of the law that existing animals have a close relation in form with extinct species. As the guanaco* [Camelidae] *is the characteristic quadruped of Patagonia, and the vicuna of the snow-clad summits of the Cordillera, so in bygone days, this gigantic species* [Macrauchenia patachonica] *of the same family must have been conspicuous on the southern plains*". The genus *Macrauchenia* is now considered as among the more derived native South American litopterns. As with the Notoungulata, the Litopterna comprises a clade of the Mirorder Meridiungulata and is closely related to North American condylarthrans, rather than camelids, as erroneously proposed by Owen (1838).

Grandorder Ungulata Linnaeus, 1776
Mirorder Altungulata Protero and Schoch, 1989
Order Perissodactyla Owen, 1848
Suborder Hippomorpha Word, 1937
Family Equidae Gray, 1821
Genus ***Equus*** Linnaeus, 1758

Equus sp.
Fig. 3b

The remains assigned to this genus represent the first fossil horses found in South America. The two molars from Argentina were recovered from Punta Alta (Buenos Aires Province) and Bajada Santa Fe (Entre Rios Province). The specimen from Bajada Santa Fe was referred to by Darwin as a horse (in Keynes 2001). We have not been able to find any mention of the other specimen in his field notes (Darwin 2002-2008), Beagle Diary (in Keynes 2001), or personal correspondence (Darwin 1985). Although Owen (1840) did not attempt specific assignation of these molars, he did note that the only difference between them and those of *Equus caballus* was the smaller size of the former. Owen (1845) erected *Equus curvidens* based on Darwin's specimens, a species which is considered synonymous with *Equus* (*Amerhippus*) *neogeus* Lund by Prado and Alberdi (1994).

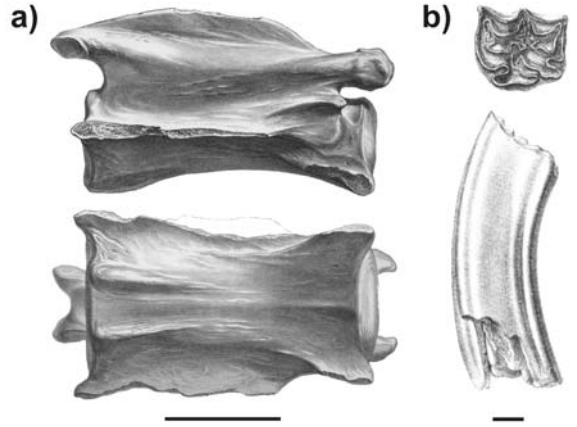

Figure 3: a) Cervical vertebra of *Macrauchenia patachonica* in lateral and ventral views (from Owen 1838). Scale bar = 5 cm; b) Tooth of *Equus* sp. in occlusal and lateral views (from Owen 1840). Scale bar = 1 cm.

Grandorder Ungulata Linnaeus, 1776
Order Uranotheria McKenna and Bell, 1987
Suborder Tethytheria McKenna, 1975
Infraorder Behemota McKenna and Bell, 1987
Parvorder Proboscidea Illiger, 1811
Superfamily Elaphantoidea Gray, 1821
Family Gomphotheriidae Hay, 1922
Subfamily Rhynchoteriinae Hay, 1922
Tribe Cuvieroniini Cabrera, 1929
Genus ***Mastodon*** Rafinesque, 1814

Mastodon sp.

The specimens assigned to this taxon, collected by Darwin at Bajada Santa Fe (Entre Ríos Province) and Río Carcarañá or Tercero (Santa Fe Province), were noted by Owen (1840, p. 180) as "…*the fragments of the teeth and portions of the skeleton which reached England, are not sufficient to lead to a determination of the species; but sufficiently prove it to have been nearly allied, if not identical, with the* Mastodon angustidens *of Cuvier, and unquestionably distinct from the* Mastodon giganteum *of the United States*". Currently *Stegomastodon platensis* is the only proboscidean species recognized from the areas yielding Darwin's specimens (Alberdi and Prado 1995).

Magnorder Xenarthra Cope, 1889
Order Pilosa Flower, 1883
Suborder Phyllophaga Owen, 1842
Infraorder Mylodonta McKenna and Bell, 1987
Superfamily Mylodontoidea Gill, 1872
Family Scelidotheriidae Ameghino, 1889
Subfamily Scelidotheriinae Ameghino, 1889
Genus ***Scelidotherium*** Owen, 1839b

Scelidotherium leptocephalum Owen, 1839b
Fig. 4

This taxon was based by Owen (1839b) on the only nearly complete skeleton found by Darwin at Punta Alta (Buenos Aires Province). We are unable to find any preliminary assignment of this specimen by Darwin, although Sulloway (1982, p. 353) noted that Darwin considered the specimen as "*allied to the Rhinoceros*". Darwin made this conjecture on September 23, 1832 (in Keynes 2001) in the following Beagle Diary entry: "… *I walked on to Punta Alta to look after fossils; & to my great joy I found the head of some large animal, imbedded in a soft rock. … It took me nearly 3 hours to get it out: As far as I am able to judge, it is allied to the* Rhinoceros. … *I did not get it on board till some hours after it was dark*". However, the specimen assigned by Owen (1839b) to *Scelidotherium* was collected by Darwin in Punta Alta in Au-

Figure 4: Partial skeleton of *Scelidotherium leptocephalum* in ventral view (from Owen, 1838b). Scale bar = 10 cm.

gust, 1833, the time during which Darwin had returned to this locality (Keynes 2001, p. 178). Further confirmation of this date appears in a letter from Darwin (1985, Letter 188), dated September 20, 1833, to Caroline S. Darwin, in which he recounts that "*I likewise at Bahia Blanca found some more bones more perfect than those I formerly found, indeed one is nearly an entire skeleton*". As indicated below, Darwin's "*allied to the* Rhinoceros" comment may more likely have been a reference to one of the cranial remains that Owen (1840) later assigned to the genus *Megatherium*, particularly as Owen's generic assignations of the sloths are for the most part still considered correct.

Magnorder Xenarthra Cope, 1889
Order Pilosa Flower, 1883
Suborder Phyllophaga Owen, 1842
Infraorder Mylodonta McKenna and Bell, 1987
Superfamily Mylodontoidea Gill, 1872
Family Mylodontidae Gill, 1872
Subfamily Mylodontinae Gill, 1872
Genus ***Mylodon*** Owen, 1839b

Mylodon darwini Owen, 1839b
Fig. 5a

The specimen assigned to this genus by Owen (1839b, p. 69) consists of "…*the lower jaw with the series of teeth entire on both sides: but the extremity of the symphysis, the coronoid and condyloid processes, and the angular process of the left ramus, are wanting*". This specimen was recovered by Darwin at Punta Alta (Buenos Aires Province), but we were unable to determine whether it was collected during his first or second sojourn to this area. In a letter sent to John Stevens Henslow in November, 1832, Darwin (1985, Letter 192) noted a completed list of fossils collected in Bahia Blanca, among which he emphasized "… *the upper jaw & head of some very large animal, with 4 square hollow molars….& the head greatly produced in front…. I at first thought it belonged either to the* Megalonyx *or* Megatherium…. *In confirmation, of this, in the same formation I found a large surface of the osseous polygonal plates, which ``late observations*" *(what are they?) show belong to the* Megatherium". A footnote on this page, presumably inserted by the editors, indicates that this specimen was "*Described in Fossil Mammalia, p. 63-73, by Richard Owen, who identified it as belonging to a distinct subgenus of Megatheroid Edentata, to which he gave the name Mylodon darwinii*". However, we believe this to be incorrect - the specimen is not the one that Owen (1839b) later assigned to *Mylodon darwini*, as Dar-win indicated that the specimen was an upper jaw and skull, rather than the mandible on which *Mylodon darwini* is based. Darwin's indication of the presence of four molariforms possibly led to the assumption (i.e., in the footnote) that the specimen belonged to *Mylodon darwini*, given that five upper molariforms are present in Megatherium. However, the earliest descriptions of *Megatherium* indicate four upper molariforms. As noted above, it was Owen (1840, p. 102) who recognized the presence of a fifth upper molariform: "*Upon clearing away the matrix from the palatal and alveolar surface of one of the cranial fragments of the* Megatherium *in Mr. Darwin's collection, I was gratified by the detection of the crown of a fifth molar".*

The taxonomic history of *Mylodon* is among the more complex for the taxa erected by Owen (1838-1840), due mainly to the ambiguity in the type species. Owen (1839b) erected *Mylodon* for two species, *Mylodon darwini* and *Mylodon harlani.* The former species was based on a left dentary from Punta Alta (Buenos Aires Province), whereas the second was based on a cast of a mandible from

North America that Harlan (1835) had assigned to *Megalonyx laqueatus*. Owen (1839b) was unclear about his choice of type species, given that in the title of his description of his new genus he referred to the fossil collected by Darwin, but in the text Owen noted that *Mylodon darwini* was the second species of the genus. This ambiguity would be trivial if the two species were congeneric, but they have been subsequently considered as belonging to different genera. Consequently, some later researchers, such as Reinhardt (1879), Lydekker (1887) and Brown (1903), considered *Mylodon harlani* as the type of the genus, whereas other, such as Leidy (1855), bestowed this status on *Mylodon darwini*. The issue was resolved by Kraglievich (1928) in favor of *Mylodon darwini* based on the following reasons:

1) the title of the generic description refers to the mandible collected by Darwin;
2) the original material available to Owen was the dentary from Punta Alta;
3) Owen (1842) recognized *Mylodon harlani* as the second species of the genus;
4) in his "*Conspectus familiarum, generum et specierum*", Owen (1842, p. 169) listed *Mylodon darwini* as the first species of the genus.

Kraglievich's (1928) logic has been accepted by the scientific community, so that *Mylodon darwini* is currently considered the type species of *Mylodon*, whereas *Mylodon harlani* is placed in the genus *Paramylodon*. The taxonomic solution provided by Kraglievich (1928) not only resolved the taxonomic problem with *Mylodon*, but also helped clarify the problematic nomenclature of the genus *Glossotherium* (see below).

Magnorder Xenarthra Cope, 1889
Order Pilosa Flower, 1883
Suborder Phyllophaga Owen, 1842
Infraorder Mylodonta McKenna and Bell, 1987
Superfamily Mylodontoidea Gill, 1872
Family Mylodontidae Gill, 1872
Subfamily Lestodontinae Ameghino, 1889

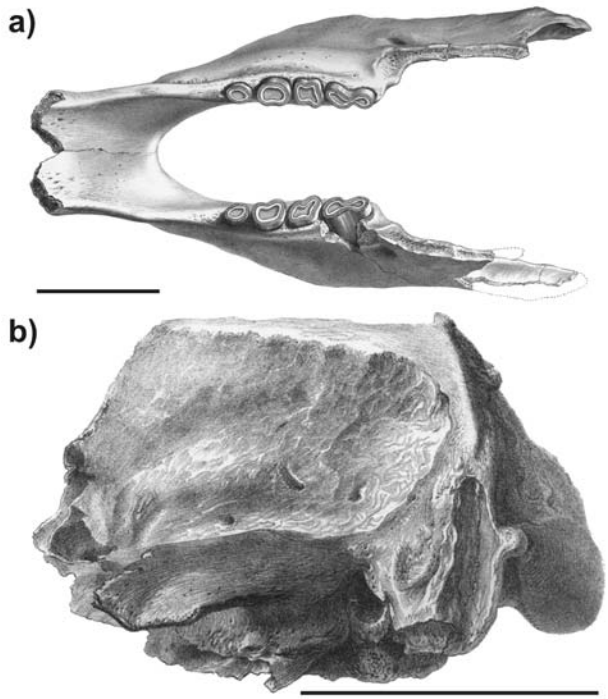

Figure 5: a) Mandible of *Mylodon darwini* in occlusal view (from Owen, 1839b). Scale bar = 10 cm; b) Cranial fragment of the skull of *Glossotherium* in lateral view (from Owen 1839b) Scale bar = 10 cm.

Tribe Glossotheriini McKenna, 1987
Genus ***Glossotherium*** Owen, 1839b

Glossotherium sp.
Fig. 5b

This genus was erected by Owen (1839b) based on the posterior half of a skull recovered from Arroyo Sarandí (Soriano Departament, Uruguay). In his Beagle Diary, Darwin (in Keynes 2001) noted that "*We heard of some giants bones, which as usual turned out to be those of the Megatherium - With much trouble extracted a few broken fragments*". As with *Mylodon darwini*, the taxonomic history of *Glossot-herium* is complex. Owen (1842) erected the new species *Mylodon robustus* on remains incluiding a nearly complete skull; and assigned to *Mylodon darwini* (based on a dentary) the cranial fragment previously described by Owen (1839b) as *Glossotherium*. Reinhardt's (1879) detailed description of a fossil sloth skull and mandible from Pergamino (Buenos Aires Province) recognized, 1) that the mandible was very similar to that described as *Mylodon darwini* by Owen (1839b), 2) that its skull features were sufficiently distinct as to suggest generic separation from *Mylodon robustus*, and 3) that the cranial fragment originally assigned by Owen (1839b) to *Glossotherium* was closely allied generically to *Mylodon robustus*. Not recognizing *Mylodon darwini* as type of the genus, Reinhardt (1879) proposed the new genus *Grypotherium*, in which he placed the dentary assigned by Owen (1839b) to *Mylodon darwini* and the specimen from Pergamino as the species *Grypotherium darwini*; and recognized *Mylodon robustus* as the type species of *Mylodon*. Ameghino (1889) accepted the generic differences noted by Reinhardt (1879), but considered, as Owen (1842) had before, that the cranial fragment of *Glossotherium* and the dentary of *Mylodon darwini* belonged to the same species, and so included these specimens - as well as the skull and mandible from Pergamino - in *Glossotherium darwini,* given that in this scenario *Glossotherium* has priority over *Grypotherium*. Smith-Woodward's (1900) revision of Darwin's South American fossil sloth collection concluded that the cranial fragment originally assigned to *Glossotherium* was congeneric with the specimen assigned to *Mylodon robustus* by Owen (1842) and that the dentary of *Mylodon darwini* and the specimen from

Pergamino, described by Reinhardt (1879), were conspecific. However, as Smith-Woodward did not recognize *Mylodon darwini* as type species of *Mylodon*, he resurrected Reinhardt's (1879) *Grypotherium*.

Kraglievich (1928) modified the taxonomy of these taxa based on a detailed revision of the group. This author held that the root of the problem was the rejection of *Mylodon darwini* as type species of *Mylodon* and the lack of agreement on the assignment of the cranial fragment assigned to *Glossotherium* by Owen (1839b). Once Kraglievich (1928) had established *Mylodon darwini* as type species of *Mylodon, Grypotherium* fell as a synonym of *Mylodon*. Kraglievich (1928) agreed with Reinhardt (1879) and Smith-Woodward (1900) that the cranial fragment of *Glossotherium* was congeneric with *Mylodon robustus* but not conspecific with it. Consequently, and with the general understanding that *Mylodon robustus* was generically distinct form *Mylodon darwini*, Kraglievich (1928) revalidated *Glossotherium*, but with two species, i.e., *Glossotherium robustus* and *Glossotherium uruguayense*, the latter including Owen's (1839b) cranial fragment. These nomenclatural conclusions were accepted by Cabrera (1936), although in this author's revision of the species of *Glossotherium*, he recognized its two valid species as *Glossotherium robustum* and *Glossotherium lettsomi* (Owen), with *Glossotherium uruguayense* a synonym of the latter (*Glossotherium lettsomi* was originally assigned to *Pleurolestodon lettsomi* by Gervais and Ameghino (1880), based on observation of a skull exhibited in the Natural History Museum, London, that had been labeled by Owen as *Mylodon lettsomi* (see Ameghino 1889).

Esteban's (1996) review of Mylodontinae considered *Glossotherium lettsomi* (sensu Cabrera 1936) a synonym of *Glossotherium robustum*, so that the cranial fragment collected by Darwin in Uruguay is currently assigned to the latter species.

Magnorder Xenarthra Cope, 1889
Order Pilosa Flower, 1883

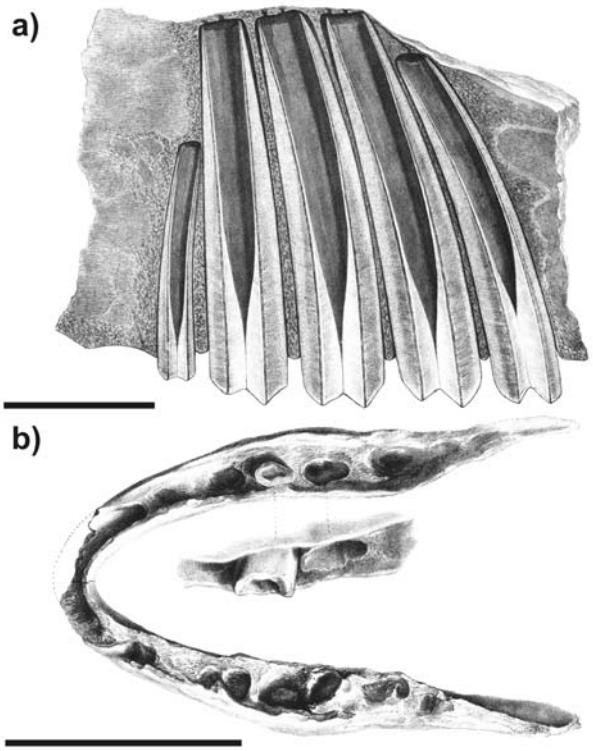

Figure 6: a) Parasagittal section through the maxilla of *Megatherium cuvieri* (= *Megatherium americanum*, see text) showing the five molariforms (from Owen 1840). Scale bar = 10 cm; b) Mandible of *Megalonyx jeffersoni* (= *Mylodon darwini*, see text) in occlusal view (from Owen 1840). Scale bar = 10 cm.

Suborder Phyllophaga Owen, 1842
Infraorder Megatheria McKenna and Bell, 1987
Superfamily Megatheroidea Gray, 1821
Family Megatheriidae Gray, 1821
Subfamily Megatheriinae Gray, 1821
Genus ***Megatherium*** Cuvier, 1796

Megatherium cuvieri Desmarest, 1822
Fig. 6a

Owen (1840) assigned to this species various cranial fragments collected by Darwin in Punta Alta (Buenos Aires Province). Although Darwin referred most of the large remains he recovered to *Megatherium*, as shown by his field notes, Beagle Diary, and personal correspondence, Owen (1840) did likewise only for the specimens collected from Punta Alta. In discussing Darwin's (in Keynes 2001, p. 107) "*allied to the* Rhinoceros" comment, we noted that it did not pertain to the *Scelidotherium* skeleton but to various skulls assigned by Owen (1840) to *Megatherium*. Indeed, Darwin's comment, dated September 23, 1832, could only refer to those skulls collected up to this time, effectively excluding *Scelidotherium* (see above) from consideration, and leaving *Megatherium* as the only taxon to which he assigned skull material from Punta Alta. Owen's (1840) assignment to the species *Megatherium cuvieri* was based on acceptance of the specific name change proposed by Desmarest (1822) for *Megatherium americanum*. However, this proposed nomenclatural alteration is unsupported and the name was considered a nomen illegitimum by Mones (1986). In this context, the specimens assigned to *Megatherium cuvieri* by Owen (1840) correspond to *Megatherium americanum*.

Magnorder Xenarthra Cope, 1889
Order Pilosa Flower, 1883
Suborder Phyllophaga Owen, 1842
Infraorder Megatheria McKenna and Bell, 1987
Superfamily Megatheroidea Gray, 1821
Family Megalonychidae Gervais, 1855
Subfamily Megalonychinae Gervais, 1855
Tribe Megalonychini Gervais, 1855
Subtribe Megalonychina Gervais, 1855
Infratribe Megalonychi Gervais, 1855
Genus ***Megalonyx*** Harlan, 1825

Megalonyx jeffersonii (Desmarest, 1822)

Fig. 6b

Owen (1840) assigned a mandible collected by Darwin at Punta Alta (Buenos Aires Province) to this species. A particular feature of this specimen, figured by Owen (1840, pl. 29), is that it preserves only one of the molariforms of the right dentary. This agrees with the description given by Darwin (in Keynes 2001, p. 109) for a mandible collected October 8, 1832: "*After breakfast I walked to Punta Alta, the same place where I have before found fossils… I obtained a jaw bone which contained a tooth: by this I found out that it belongs to the great ante-diluvial animal the* Megatherium". Leidy (1852) erected a new taxon, *Gnathopsis oweni* on this specimen, which Kraglievich (1928) assigned to *Mylodon darwini*.

Magnorder Xenarthra Cope, 1889
Order Cingulata Illiger, 1811
Superfamily Glyptodontoidea Gray, 1869
Family Glyptodontidae Gray, 1869
Subfamily Hoplophorinae Huxley, 1864
Tribe Hoplophorini Huxley, 1864
Genus ***Hoplophorus*** Lund, 1938

Hoplophorus euphractus Lund, 1938
Fig. 7a

In general, the carapace fragments and osteoderms collected by Darwin in South America were assigned preliminarily to *Megatherium*. Certainly such assignments were due to Cuvier's (1823) tacit approval of Larrañaga's (in Cuvier 1823) suggestion that megatheres were armored. Owen (1840, p. 107) recognized the close relationship, still considered correct, between glyptodonts and living armadillos and remarked the following about *Hoplophorus euphractus: "The portions of the tesselated bony dermal covering of a Dasypodoid quadruped, figured in Pl. XXXII. figs. 5 and 4, of the natural size, were discovered folded round the middle and ungueal phalanges, figs. 2 and 3, at Punta Alta, in Bahia Blanca, in an earthy bed interstratified with the conglomerate containing the remains of the fossil Edentals. In one of these fragments, measuring six inches long by five broad, the tesserae are arranged in rosettes, and so closely correspond in size and pattern with the bony armour described by M. Lund [1839], as characterizing his species,* Hoplophorus euphractus, *that I feel no hesitation in referring them to that animal*". Burmeister (1870-1874) assigned the osteoderms figured by Owen (1840, pl. 32, figs 4 and 5) to *Hoplophorus ornatus* (= *Neosclerocalyptus ornatus*) and *Hoplophorus elegans*, respectively. Ameghino (1889) synonymized the latter with *Lomaphorus elegans*.

Magnorder Xenarthra Cope, 1889
Order Cingulata Illiger, 1811
Superfamily Glyptodontoidea Gray, 1869
Family Glyptodontidae Gray, 1869
Subfamily Glyptodontinae Gray, 1869
Tribe Glyptodontini Gray, 1869
Genus ***Glyptodon*** Owen, 1839c

Glyptodon clavipes Owen, 1839c

Owen (1840) tentatively assigned to this species distinct osteoderms collected by Darwin from the Uruguayan locality of Arroyo Sarandí (Mercedes, of Soriano Departament, Uruguay); and the Argentinean localities of Bajada Santa Fe (Paraná, Entre Ríos Province) and Guardia del Monte (Buenos Aires Province).

Magnorder Epitheria McKenna, 1975
Superorder Preptotheria McKenna, 1975
Grandorder Anagalida Slazay and Mc Kenna, 1971
Mirorder Simplicidentata Weber, 1904
Order Rodentia Bowdish, 1821
Suborder Hystricognatha Woods, 1976
Infraorder Hystricognathi Tullberg, 1899
Parvorder Caviida Bryant and McKenna, 1995
Superfamily Cavioidea Fisher de Waldheim, 1817
Family Hydrochoeridae Gray, 1825
Subfamily Hydrochoerinae Gray, 1825
Genus ***Hydrochoerus*** Brisson, 1762

Hydrochoerus sp.

The fossils that Owen (1940) assigned to this genus were collected by Darwin (in Keynes 2001) in Monte Hermoso on October 19, 1832. Owen (1840, p. 10) commented that "*Mr. Darwin discovered the decomposed molar of a Rodent, equalling in size, and closely resembling in the disposition of its oblique component laminae, the hinder molar of the* Capybara (Hydrochoerus.) *The fossil differs, however, in the greater relative breadth of the component laminae.*
I have, lastly, to notice the head of a femur, and some fragments of pelvic bones from the same formation which bear the same proportion to the tooth above alluded to, as subsists between the teeth and bones of the Capybara, and which are sufficient to prove that there once has existed in South America a species of the family Caviidæ, as large as the present Capybara, but now apparently extinct".
These elements were among those that Darwin (in Keynes 2001, p. 110-111) encountered as follows: "*The Captain landed for half an hour at Monte Hermoso, (or Starvation point as we call it) to take observations. - I went with him & had the good luck to obtain some well preserved fossil bones of two or three sorts of Gnawing animals. - One of them must have much resembled the* Agouti *but it is smaller*". Even so, it is not possible to determine which of the remains Darwin thought similar to an agouti, though it is worth noting that what Darwin considered an agouti was a Patagonian hare (Darwin, in Keynes 2001, p. 103).
The following Hydrochoeridae are currently recognized from the fossiliferous horizons of Monte Hermoso: *Phugatherium cataclisticum, Anchimysops villalobosi* and *Chapalmatherium perturbidum*. Vucetich *et al.* (2005) considered the type specimens of the first two species to represent juvenile individuals and that they might be conspecific with *Chapalmatherium perturbidum*. If this is correct, then the valid name, as determined by Vucetich *et al.* (2005), for the species would be *Phugatherium cataclisticum*. In this respect, the specimen collected by Darwin might represent this latter species.

Magnorder Epitheria McKenna, 1975
Superorder Preptotheria McKenna, 1975
Grandorder Anagalida Slazay and Mc Kenna, 1971

Mirorder Simplicidentata Weber, 1904
Order Rodentia Bowdish, 1821
Suborder Hystricognatha Woods, 1976
Infraorder Hystricognathi Tullberg, 1899
Parvorder Caviida Bryant and McKenna, 1995
Superfamily Octodontoidea Waterhouse, 1839
Family Octodontidae Waterhouse, 1839
Subfamily Octodontinae Waterhouse, 1839
Genus ***Ctenomys*** Blainville, 1826

Ctenomys priscus Owen, 1840
Fig. 7b

This species was erected by Owen (1840) based on remains collected by Darwin (in Keynes 2001) on October 11, 1832. Owen (1840, p. 109) allocated to this species a "…*fragment of the upper jaw, figured in Pl. XXXII. fig. 6*" and a "...*fragment of the lower jaw of the same fossil* Rodent *. figured at fig. 10 and 11*". It should be noted that Owen's (1840) figure 6 possibly does not represent an upper jaw, but a posterior fragment of a mandible that may correspond to the posterior part of the mandible figured by Owen (1840, figs. 10, 11) (D. Verzi, pers. comm.).
Mones (1994) provided a detailed discussion of the taxonomy of *Ctenomys priscus*, concluding that it might belong to the genus *Dicoelophorus*, erected by Ameghino (1888). However, the generic name currently in use for this species is *Actenomys*, erected by Burmeister (1888). The reasons for maintaining *Actenomys* were clearly set forth by Verzi (1994, p. 183), as follows "Dicoelophorus *Ameghino, 1888 es, por prioridad, un sinónimo "senior" de* Actenomys *Burmeister… . Sin embargo, luego de que Reig (1958) adoptara el nombre genérico* Actenomys *para todos los materiales referibles a las formaciones Monte Hermoso y Chapadmalal, este nombre ha sido ampliamente usado hasta el presente por lo cual nosotros nos inclinamos a mantenerlo*".

Rodentia

A third rodent was briefly described by Owen (1840) but not assigned to a genus. Owen (1840, p. 110) described "*The portion of the right hind-foot of the Rodent figured at fig. 12, includes the calcaneum, astragalus, cuboides, external and middle cuneiform bones, and the metatarsals and proximal phalanges of the toes corresponding with the three middle toes of five-toed quadrupeds. The metatarsals are chiefly remarkable for the well-developed double-trochlear articular surface, and intermediate ridge. These remains, as well as the jaws and teeth of the* Ctenomys*, were discovered at Monte Hermoso in Bahia Blanca*". These pedal remains are possibly those that Darwin (1985, Letter 192) described in a letter, dated November 12, 1832, to John Stevens Henslow as "*the Tarsi & Metatarsi very perfect of a* Cavia" although it is not possible to determine this with certainty.

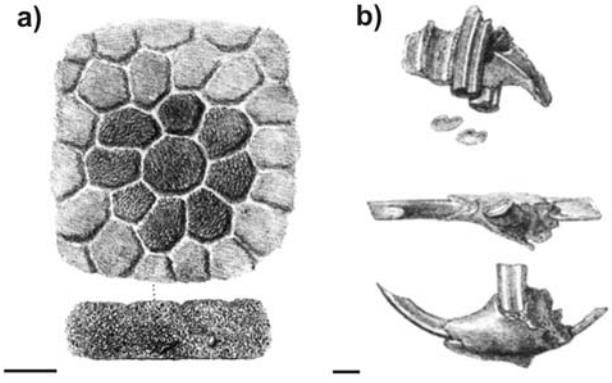

Figure 7: a) Osteoderms assigned by Owen (1840) to *Hoplophorus euphractus* (= *Neosclerocalyptus ornatus*, see text) in dorsal and lateral views (from Owen 1840). Scale bar = 1 cm; b) Maxilla and mandible assigned by Owen (1840) to *Ctenomys priscus* (= *Actenomys priscus*, see text) (from Owen 1840). Scale bar = 5 mm.

Mastodonts and armored megatheres

As noted in the preceding historical summaries, the large South American fossil mammals recognized by Cuvier (1823) amounted to an armored megathere and three mastodonts. A detailed consideration of Darwin's preliminary assignments demonstrates that he was strongly influenced by Cuvier's taxonomic scheme. In essence, the fossil specimens recognized by Darwin may be grouped as large vs. medium and small mammals. Among the latter is the first fossil of a South American horse, obviously identified as such by Darwin, and three rodents, two of which were assigned by Darwin to *Cavia* and the Patagonian hare (*Dolichotis patachonica*), whereas the third was later considered by Owen (1840) as representing the genus *Hydrochoerus*.
Among the large mammals, Darwin recognized an enormous rodent and four genera: *Rhinoceros, Megalonyx, Megatherium* and *Mastodon.* The first two listed do not appear in Cuvier's (1823) taxonomic list of fossil South American mammals. The assignment to *Rhinoceros* was the first such attempt by Darwin (in Keynes 2001, p. 107) for a South American fossil skull, collected during his first visit to Punta Alta (September, 1832). However, this assignment does not appear in the taxonomic list of specimens collected from Punta Alta and Monte Hermoso sent to John Stevens Henslow (Darwin 1985, Letter 192). Darwin may possibly have changed his first impression, but it is not easily ascertainable with the available evidence.
The only mention of *Megalonyx* appears in the previously noted list as "*2nd the upper jaw & head of some very large animal, with 4 square hollow molars.-& the head greatly produced in front.- I at first thought it belonged either to the Megalonyx or Megatherium.- In confirmation, of this, in the same formation I found a large surface of the osseous polygonal plates, which* "*ate observations*" *(what are they?) show belong to the Megatherium.- Immediately I saw them I thought they must belong to an enormous Armadillo, living species of which genus are so abundant here*…". In this as in many other cases (see below) Darwin decided in favor of *Megatherium* based on the presence of osteoderms collected in the same formation.
Owen (1838-1840) recognized the specimens assigned by Darwin to *Megatherium* as glyptodonts, toxodonts, and large

ground sloths. In our estimation, the only factor that led Darwin to assign remains of such a heterogeneous group of forms to *Megatherium* was the presence of osteoderms or carapace fragments in the same horizon. In effect, all the specimens that Darwin assigned to *Megatherium* were recovered from the Arroyo Sarandí (Uruguay) and Punta Alta (Argentina), and Darwin also reported carapace elements. Further evidence supporting our contention appears in Darwin's (1985, Letter 215) letter of September 20, 1833 sent to Caroline S. Darwin, in which he wrote "*At the Guardia del Monte, I found some more of the armour of the giant* Megatherium, *which was to me very interesting, as connecting the Geology of the different parts of the Pampas*". Indeed, Darwin used the presence of osteoderms as a diagnostic feature of *Megatherium*.

In this context, one might hypothesize that it was the absence of osteoderms in the layers yielding the only Santa Cruz specimen, which led Darwin to regard this specimen as follows: "*At Port St Julian I found some very perfect bones of some large animal, I fancy a* Mastodon" (Darwin 1985, Letter 238) and Darwin (1839) later admitted that "*I had no idea at the time, to what kind of animal these remains belonged*". Certainly, this is the only mention of *Mastodon* that was not later corroborated by Owen (1838-1840).

Lastly, *Toxodon* was the only species the remains of which Darwin (1985, Letter 192, 2002-2008) assigned to different species. Darwin assigned a molar collected in Punta Alta to an enormous rodent and a skull from Arroyo Sarandí to *Megatherium*. The latter assignment makes sense in that the horizon yielding the skull also preserved osteoderms, whereas Darwin's inference on the molar is understandable given that the teeth of *Toxodon*, as noted by Owen (1838), bear a certain resemblance to those of rodents.

Implications of the "erroneous" assignments of the youthful Darwin

Twenty years before the publication of the *Origin of Species* and only two years after he had begun recording his thoughts on transmutation, Darwin (1839, p. 209-210) had this to say about the South American paleofauna: "*The most important result of this discovery, is the confirmation of the law that existing animals have a close relation in form with extinct species. As the guanaco is the characteristic quadruped of Patagonia, and the vicuna of the snow-clad summits of the Cordillera, so in bygone days, this gigantic species of the same family must have been conspicuous on the southern plains. We see this same relation of type between the existing and fossil* Ctenomys*, between the* Capybara *(but less plainly, as shown by Mr. Owen) and the gigantic* Toxodon; *and lastly, between the living and extinct Edentata. At the present day, in South America, there exist probably nineteen species of this order, distributed into several genera; while throughout the rest of the world there are but five. If, then, there is a relation between the living and the dead, we should expect that the Edentata would be numerous in the fossil state. I need only reply by enumerating the* Megatherium*, and the three or four other great species, discovered at Bahia Blanca; the remains of some of which are also abundant over the whole immense territory of La Plata. I have already pointed out the singular relation between the armadilloes and their great prototypes, even in a point apparently of so little importance as their external covering*". Similarly, Darwin (1845, 1859, p. 339) noted that "*In South America, a similar relationship is manifest, even to an uneducated eye, in the gigantic pieces of armour like those of the armadillo, found in several parts of La Plata; and Professor Owen has shown in the most striking manner that most of the fossil mammals, buried there in such numbers, are related to South American types… … I was so much impressed with these facts that I strongly insisted, in 1839 and 1845, on this 'law of the succession of types,'-on 'this wonderful relationship in the same continent between the dead and the living*".

As noted by Sulloway (1982), the role of the naturalists who studied the South American fauna was critical to the development of Darwin's transformationist ideas in that they provided a systematic framework. In reference to Darwin's erroneous taxonomic assignments, Sulloway (1982, p. 353) recognized that "*The general effect of these confusions during the Beagle voyage was to minimize the evolutionary implications of the diverse fossil forms*".

Paradoxically, many of Owen's (1838-1840) proposed relationships that so influenced Darwin (1839, 1845, 1859) in the development of his transformationist theory were later rejected. Indeed, toxodonts and macrauchenids are highly derived native South American ungulates distantly related phylogenetically to rodents and guanacos, whereas the large glyptodonts are not the ancestors of armadillos, but to the contrary, the latter are antecedent to the former. In this respect, we may suppose that the affinities proposed by Owen (1838-1840) maximized the evolutionary implications of the South American paleofauna.

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APPENDIX 1

List of fossil mammal specimens collected by Charles Darwin and housed in the Natural History Museum, London, England (provided by Andrew Currant, Curator of Fossil Mammals), and in the Royal College of Surgeons of England (provided by Simon Chaplin, Director of Museums and Special Collections). Abbeviations. **RCSHM**/CO: Royal College of Surgeons of England Hunterian / College Museum. RCS: Royal College of Surgeons of London. **NHM:** Natural History Museum, London.

***Equus* sp. NMH M16557:** left upper molar (ex RCS2012). **NMH M16558:** left upper molar (ex RCS2013).

***Glossotherium* sp. NMH M16586** part of cranium (ex RCS3491).

Machrauchenia patachonica. Holotype **NMH M43402**: vertebral fragments (ex NMH M16556 and ex RCS2209); detached proximal and distal ends of right tibia and fibula (ex NMH M16559 and ex RCS 2215); right femur (ex NMH M16561 and ex RCS2214); right astragalus (ex M16569 and ex RCS2216); middle cervical vertebrae (ex NMH M16570 and ex RCS2208); fragments of pelvis (ex NMH M16571 and ex RCS2210); proximal end of fused radius and ulna (ex NMH M16572 and ex RCS2212); metacarpals and phalanges of the right manus (ex NMH M16573 and ex RCS2213); incomplete left scapula (ex NMH M16574 and ex RCS2211); metatarsal (ex M16575 and ex RCS2216).

Megatherium americanum. **NMH M16585**, posterior part of cranium (ex RCS3445); **NMH M16588**, fragment of left maxilla with M2 and M3 in horizontal section (ex RCS3446); **NMH M16589**, part of left temporal (ex RCS3457). **RCSHM/CO** 3443 fragment of cranium with teeth.

Mylodon darwini. Holotype **NMH M16563:** mandible (ex RCS3490).

Mylodon darwini. **NMH M16587:** fragment of left dentary with transverse section of teeth (ex RCS3491).

Scelidotherium leptocephalum. Holotype: **NMH M16579**, deformed skull with horizontal section taken from right dentary (ex RCS3506); Holotype: **NMH M16580**, upper molariform (ex RCS 3507); Holotype: **NMH M16581**, cervical vertebrae (ex RCS3510); Holotype: **NMH M16582**, parts of ribs (ex RCS 3511); Holotype: **NMH M16583**, left astragalus (ex RCS3520); Holotype: M16584, right astragalus with distal end of right tibia (ex RCS3519).

Toxodon platensis. Holotype **NMH M16560**: incomplete cranium lacking teeth (ex RCS2223).

Toxodon platensis. **NMH M16562** right M2 (ex RCS2224); **NMH M16564** part of left dentary with fragments of four molars (ex RCS2226); **NMH M16565** right lower molar (ex RCS2227); **NMH M16566** fragment of right dentary with incisor roots and most of the molars (ex RCS2225); **NMH M16567** left lower incisor (ex RCS2228); **M16568** fragmentary teeth (ex RCS 2229).

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