

ARTICLE

WHAT IS *Lutra paranensis* RENGGER, 1830?

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Abstract: Described from Paraguay, *Lutra paranensis* Rengger, 1830 has long been associated by international authors with the Giant Otter *Pteronura brasiliensis*. However regional South American authors in the early 20th Century applied the name to the Neotropical River Otter *Lontra longicaudis*. The validity of each of these positions is evaluated by comparing the description with both species and the name is found to have been proposed for, and therefore correctly to apply to *L. longicaudis*.

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INTRODUCTION

Johann Rudolph Rengger (1795-1832) was a Swiss doctor, explorer and naturalist who travelled around Argentina, Brazil and Paraguay between the years 1818 and 1826 (Ramella and Perret, 2011). Though he amassed a large collection of flora and fauna (much of which was later confiscated by the Paraguayan government), his principal contribution to the zoological literature was a tome describing the mammals that he encountered, some of these being new for science (Rengger, 1830). A description of his travels was published posthumously (Rengger, 1835), but none of his mammal specimens survived.

Lutra paranensis Rengger, 1830 was coined for Paraguayan specimens of a species of otter which inhabits the Paraguay and Paraná Rivers. Rengger (1830) considered his species to be the same as the “Nutria“ of Azara (1801) which was also based on Paraguayan specimens. Rengger’s name was treated as valid by regional authors working in the late 19th and early 20th Century (von Ihering, 1893, 1910; Bertoni, 1914, 1939; Werneck, 1937). From the description provided by von Ihering (1893, 1910) these regional authors applied the name to the species now known as the Neotropical River Otter *Lontra longicaudis* (Olfers, 1818).

Usage by European authors of the same period differed however. Nehring (1900) was the first to associate the description of *L. paranensis* with the Giant Otter *Pteronura brasiliensis* (Gmelin, 1788), this being repeated by Pohle (1919) and then, perhaps more significantly, by Cabrera (1957) in his influential catalogue of South American mammals and subsequently by Harris (1968) in his monograph of the otters. The latter three authors applied the name for a southern subspecies: *P. b. paranensis*. From then to the present day the name has been consistently treated as referring to *P. brasiliensis* (Larivière, 1999; Noonan et al. 2017). Indeed some recent authors have continued to recognise *P. b. paranensis* as a valid subspecies for the southernmost population (Chebez, 2008), albeit sometimes with an expression of doubt (Duplaix, 1980).

A thorough review of Rengger's (1830) text (which includes no illustrations) and comparison with a specimen of *Lontra longicaudis* leaves no doubt that his name refers to that species. My English translations of the original German texts are provided, along with a discussion of the conclusions of Nehring (1900) and the repercussions of the misapplication of this name. I have numbered Rengger's paragraphs for convenient reference in the discussion.

METHODS

The text of Rengger (1830) was compared with modern literature descriptions and anatomical illustrations of *Lontra longicaudis* and *Pteronura brasiliensis*, and a large female specimen of the former from Paraguay housed in the Colección Zoológica de Pilar La Tierra, based at Centro IDEAL, Pilar, Ñeembucú department, Paraguay (CZPLT-M-515; 18 July 2018; 72km E of Pilar, Paraguay; skin and skeleton). No Paraguayan specimens of *Pteronura brasiliensis* were available for examination, although the species is confirmed to occur in the country (Cartes et al., 2013). The results were then compared against the text of Nehring (1900) to examine the validity of the claims therein.

Rengger's text (1830)

Lutrinae

Introduction: Paraguay has only one genus of otter, the first and only description of which we owe to Azara. In his work on mammals of Paraguay, he gives them the systematic name of Mustela lutra brasiliensis, considering them to be identical to the otters found in Brazil. In fact, there is so much resemblance between the two in form and colour that, without comparing the teeth with each other, one could regard one as only a modification of the other. The Brazilian otter has, according to all descriptions, the same number of teeth as the European; in the case of the Paraguayan, on the other hand, this is not the case, which is why I consider it to be a separate genus and describe it with the name Lutra paranensis, swimming in both the Parana and the Paraguay Rivers. Lutra paraguaensis, mentioned in some systematic works, does not occur in Paraguay, and must not be confused.

1) *I was as unsuccessful as Azara in finding out the Guaraní name of this species of otter. In Paraguay, as well as along the Paraná, it is called "Lobo" by the Indians and the Creoles, incorrectly being regarded as a kind of seal, from the Spanish "lobo marino".*

2) *The coat is covered with two types of hair, which are very dense and almost vertical to the skin. The woolly hairs are about six lines long, straight and extremely soft to the touch. The bristle-hairs differ from them only in that they are about one line longer, somewhat stiff, and not quite so soft, and are more shiny in their upper half. Around the mouth and over the eyes are a few, one-and-a-half- to five-inch-long, shiny bristles, and a tuft of similar hair is found behind each corner of the mouth on a kind of wart. The septum of the nostrils, the eyelids and the lower side of the toes and the webs are naked.*

3) *The colour of the whole fur, except the throat, is dark brown and shiny. At the throat there is a large, almost square, bright spot, the color of which differs according to the age of the animal. In very young individuals, which still possessed the deciduous teeth, I found them brownish-red in the case of those which had just changed them, and yellowish-white in the case of very mature individuals several*

years old. It should be noted that in the infants the upper lip is set forward with brownish-red hair, which is replaced by brown at the first moult.

4) I found no difference in colour between the male and the female. Azara, on the other hand, mentions a white tip to the tail of the latter, a statement that I cannot dismiss, as I have seen only two very young female individuals, which, as is often the case with young animals, could differ from mature females in their colour.

5) A large male of this species of otter had the following dimensions:
5" 6 lines length of head; 1' 8" 8 lines length from the occiput to the root of the tail; 1' 7" length of the tail; 11" around the midsection.

6) Azara stated that the female has a slightly shorter tail than the male, but this is not the case with very young individuals.

7) The difference in the proportions of the body parts to each other between a young and fully grown animal, especially that of the head to the body, may be shown by the following dimensions, which are taken from the skeleton of a specimen of *Lutra paranensis* of approximately four months of age:

1' 8" 3 lines total length; 3" 9 lines length of the head; 2" 2 lines greatest width of the cranium; 1" 8 lines cranial height; 9" length of the spine to the first caudal vertebra; 7" 6 lines length of the tail; 1" 9 lines length of the upper arm; 1" 11 lines length of forearm; 1" 9 lines length of the front foot; 1" 8 lines length of the thigh; 1" 10 lines length of the leg; 3" length of hindfoot.

8) Although these otters are similar in their outward forms to the European ones, if one compares them carefully, there is a significant difference between them. The head of the former, is large in proportion to the rest of the body, vertically compressed and wide. The face occupies only a quarter of its length. The rounded muzzle protrudes slightly above the lower jaw. The nostrils are almost completely covered by crescent-shaped valves, the convex margin of which looks down below; Azara compares them to a C with horns pointing upwards. These flaps close the nostrils just as the animal submerges. The eye is small, round, black and shiny, the eye socket is forward-facing. The pinnae are also small, about seven lines wide and high, and with a rounded edge. The muscular neck is of about the same width as the head. The trunk is almost cylindrical, and the broad tail is compressed dorsally and rounded at the end. The four legs are short, but very muscular. The toes are connected by a thick web which leaves the last phalanx free, and even reaches to the nail on the outermost toe. The nails are small but strong, laterally compressed, and hardly bent.

9) As for the teeth, the adult has six tightly packed incisors in the upper jaw. The four central incisors are almost of equal size, laterally compressed, wedge-shaped and with a convex cutting edge. The two outer incisors are thicker and slightly longer than the inner ones. They are conical, and curved outwards and backwards, so that, in the direction of the edge of the jaw, they appear bent backward and resemble canine teeth. Separated from them on each side by a small space is a six-line long canine, angled slightly backwards, conical, and curved slightly to the inside, and then four molars. Of these, the first has only a blunt, conical spike, which is slightly curved on the inner and the posterior side. The second is very similar to the first one in its form, but it is half as large again. The third, or carnassial tooth (*grande carnassière*), has on its outer margin three spikes, of which the foremost is small, the two rear ones are strong, and there is a large depression, with a notched margin on the inner edge. On

the fourth, which is one-third broader than it is long, two bumped cusps are noted on the outer side, and two inward, both pairs separated by a wide depression. There are also six incisors in the lower jaw, which increase in size from the inside outwards, and, at least when they have just emerged, show a slight elevation in the middle of the cutting edge. The canine teeth are like those of the upper jaw. They are followed by five molars on each side. The first two have the same shape as the two first upper molars; the third likewise has only one cusp, which is compressed at the sides, but ridged at the front and back from the tip to the base; in the middle of the back ridge a very small spike rises vertically. The crown of the fourth molar consists in the front of three spikes, which have the shape of three-sided pyramids and form a triangle, and behind a large depression, which shows some sharp elevations on its outer edge. You also notice a depression on the circular crown of the fifth molar.

10) *The deciduous teeth in each jaw consist of six incisors, two canines and six molars, all of which are very small by comparison with the adult teeth. The incisors and canines deviate only slightly in shape from those that replace them, unlike the molars. The first molar in the upper jaw is small and pointed; the second has the form of a four-sided pyramid, with a strong, curved edge, on the inner side a small step, with a ridge running along the back; the third possesses two lumps and is step-like on the inner side. In the lower jaw, the first molar has the same shape as the first upper molar, the second has a curved rear edge, and the third two triangular edges, which are behind one another, in addition to a small cusp on the inner side of the second edge and a depression on the rear side.*

11) *Both the permanent and the deciduous teeth have larger interior cavities than are found in other predatory animals.*

12) *Taking into account what I have said so far about the otter of Paraguay, it can be said to differ from the Brazilian in the absence of the long white or yellowish stripes on the lower part of the neck, in the absence of the reddish-yellow spot on the breast, and, at least according to Azara, by the white tail tip of the adult female; furthermore, there are only four molars on each side of the upper jaw, while the latter has five. Finally, it never seems to me to reach the size of the Brazilian species, as I have not seen any individual that has a total length of four feet.*

13) *This otter is common in Paraguay along the two great rivers, the Paraná and Paraguay, but is found more rarely on the tributaries which flow from the interior of the country into those waterways. How far to the south of this it occurs I do not know; however, it is said to have been found on the Paraná as far as 29°S latitude.*

14) *The otter lives partly on land and partly in the water. It spends the night on land and a few hours during the day to sleep, or when it needs a rest. It also goes ashore to eat. Sometimes it will take overland excursions and visits marshes and small lakes close to the place of residence. The rest of the time it stays in the water and hunts for its food, which consists of fish alone. It swims faster and lighter than our European otter, which may well be due to the broad tail, and is able to spend longer under water; the head is usually submerged and rarely rises above the water when it floats over large distances.*

15) *Incidentally, the way of life is not the same all year round. After the mating season, which is in the months of July and August, that is to say in the Paraguayan winter, it lives in pairs, and remains in a territory until the litter is grown. Afterwards*

the female seeks a steep bank on the river or lake she inhabits, and there digs a four to five foot deep den, the mouth of which is one and a half to two feet in diameter. Here, the pair regularly spend the night and in cool weather, they sun themselves by day in front of the entrance. In spring the female gives birth to two or three young, and together with the male, they raise the brood with fish. Sometimes, at this time of the year, the rising waters may threaten the young litter, so the adults dig a new den higher up the shore, and bring their young to safety. As soon as they are able to crawl on land, the juveniles follow the mother into the water and pursue fish. The whole family returns to the den each night, and from time to time throughout the day. This behaviour continues until mid- summer, at which time the otters unite into groups of eight to ten, or twenty individuals. At this time they never spend long in the same area, and will swim for whole days upstream, penetrating well into the smaller streams and into lakes. This happens especially in autumn, when the waters are high and most fish leave the Paraná and the Paraguay rivers and enter flooded areas, where they find abundant food. Also on these migrations, the otters ascend to the land during the day, whether to consume their prey or to rest, and at night, to sleep. It is not uncommon for them to fight, giving a scream that is not unlike that of cats but much louder.

16) *During the hunt on the Paraguay River, I had several opportunities to observe closely such common groups of otters nearby. Soon these animals, either with their snouts or with their whole heads, appeared on the surface of the water, snarling and snorting, and expelling the water which had penetrated into the nostrils. Immediately however, they submerged again and rose again far away, where I lost sight of them. From the water surface, they submerged in two ways, either sinking straight down or, diving with their backs raised above the water. Not infrequently, they held a wriggling fish in the mouth when they reappeared, and they immediately swam ashore to consume it, including the head and the bones. These predatory animals take not only small fishes, but also larger ones, two or more feet long.*

17) *As these otters are seldom pursued by humans, they are curious and not shy, and even closely approach boats, often rising out of the water with half of their bodies.*

18) *Azara's information on the wild behaviour of the species is based on the testimony of the Payaguas. That several females rear their cubs in the same den, and that males and females spend the night there throughout the year is quite incorrect. I do not understand how he could attach such faith to the testimony of these people, since he, like everyone else in Paraguay, must know them as the most lewd and mischievous of all the Indians. However, I can confirm Azara's own observations, that he made on a tame otter. Mine was a male, and when I received it, it was about two months old. During the first two weeks of its captivity it was stubborn and bit when I tried to touch it; however, it did not hesitate to consume its food in the presence of a human being. I raised it with fish, raw meat, milk and water. Gradually it became so tame, that after two months it ran free without trying to escape. It played with its guard, as well as with cats and dogs, obeyed his call and followed him in the house. It harmed neither the poultry nor the other domestic animals. When it was freed it usually first visited the water tank located in a corner of the courtyard and bathed there for some time. If a live fish was thrown into the container, it caught it at once and immediately left the water to consume its prey on land. Several times I took the caught fish from its mouth without bother, and threw it into the container; but no sooner did I do this then it had taken the fish out again. Unfortunately, this tame animal would later be trampled on by a horse, otherwise I would have made an attempt to train it to fish in the River*

Paraguay, which as a result of the cooperative character that it had hitherto shown, I have no doubt would have been successful.

19) This otter slept curled up at night, and at midday; the rest of the time it was awake, but, unlike other predatory animals, without moving much on the leash to which it was tethered. Even when untied; it walked only briefly around the yard, and soon sought out a man or a pet, beside whom it would lie down. The usual gait was a slow step; sometimes jumping in series. In general the movements on land were neither agile nor swift. It was only vocal when angered by mistreatment. It was a unique shriek, comparable to the wail of a cat. Like most predators, it loved cleanliness, and usually deposited its excrement in the same place. In the water it abstained from defecating and always got out of the container first. It did not have an unpleasant odour, unlike the European species.

20) In Paraguay the meat of the otter is considered unpalatable by both the Indians and the Creoles. Freshly fried or boiled, it has no pleasant taste; but if it is first pickled and then prepared, then it can be eaten. Neither is the coat used, though the quality of it would be appreciated in Europe. As this species of animal is of no use to the inhabitants and does no harm to them, it lives undisturbed by man in the waterways of Paraguay.

21) If one seeks to hunt the species, it is best to do so during the mating period, waiting in the vicinity of the den. At this time it is not difficult to kill the animal as it comes ashore, but if one follows the otters in the water, though it may be easy to fire a deadly shot, the body is extremely difficult to retrieve as wounded animals remain submerged and no longer come into view. Only once did I catch an otter away from the water; the dog which I brought with me immediately attacked it, but was met with obstinate resistance, the animal bravely defending itself with its teeth, whilst at the same time making screeching noises; it would probably have reached the safe refuge of the water again if I had not had my dog for help.

22) Among the mammals the otter has only the jaguar as an enemy, which takes it at night when it is resting on the shore. In the water, however, there is another, equally terrible, enemy a great water-snake, which belongs to the genus *Erix* (author note - probably in reference to a species of *Eunectes*). I found a near adult otter in the stomach of an eighteen foot long snake of this type.

DISCUSSION

The opening line of Rengger's (1830) introduction and descriptive text indicates that he considered his otter to be the same species as Azara's (1801) "Nutria" (the only species of otter cited in that work). Rengger clearly was under the impression that Azara was discussing a Paraguayan form of *Pteronura brasiliensis* (surmised from his reference to it as "The Brazilian"), and this was not an unreasonable assumption given that Cuvier had attached the name *Mustela lutra brasiliensis* to the description in the French translation of the work (the first version of Azara's tome to appear in print). Azara's original Spanish text was printed later (Azara, 1802) but the author himself did not employ any Linnean names. The description of Azara's (1801) "Nutria" is, however, conclusively a Neotropical River Otter *Lontra longicaudis* based on the measurements provided (Table 1), the description of the pelage, the extremities of the toes free from webbing, the naked nose and the broad-based, pointed tail. However the ecological data he provides, information derived in part

from the Payagua indigenous peoples of the Paraguay River, certainly refer in part to *Pteronura brasiliensis*.

Table 1. External measurements for male specimens and female specimen CZPLT-M-515.

	Large male <i>Lutra paranensis</i> of Rennger (1830)	Azara's "Nutria" (1801)	<i>Lontra longicaudis</i>	<i>Lontra longicaudis</i> CZPLT-M-515	<i>Pteronura brasiliensis</i>
Length of head	140.26 mm	N/A	Skull 94-120 mm	148 mm	Skull 155.5-175 mm
Length of ear	"Approximately" 15.47 mm	12.70 mm	18-22 mm (Larivière, 1999)	15 x 19 mm	22 mm (Noonan et al., 2017)
Length of head and body	661.14 mm	617.22 mm	500-790 mm	570 mm	960-1230 mm
Length of tail	477.80 mm	457.20 mm	375-570 mm	460 mm	450-650 mm
Guard hair length	15.46 mm	15.47 mm	14 mm	13-15 mm	8 mm
Length of upper canine	13.26 mm	15.47 mm	NA	14 mm	21 mm (de Oliveira et al., 2007)
Total length	1138.94 mm	1074.42 mm	900-1360 mm	1030 mm	1450-1800 mm

An inch is interpreted as 25.4 mm, a line is interpreted as 2.21 mm as per the conventions of the early 19th Century (Azara, 1801; Smith et al., 2018). Measurements for *L. longicaudis* and *P. brasiliensis* taken from Foster-Turley et al. (1990) unless otherwise stated.

Rengger (1830) distinguishes *Lutra paranensis* from "the Brazilian" (i.e. *Pteronura brasiliensis*) in his text by the "the absence of the long white or yellowish stripes on the lower part of the neck" (Paragraph 12). It should be noted that whilst the neck markings on the throat of *P. brasiliensis* are individually variable, and very occasionally even absent (Groenendijk et al., 2014), Rengger's statement that the species is common along the Paraguay and Paraná Rivers makes it questionable whether such variation could credibly account for the absence of mention of the classic throat markings in the description. Furthermore, the statement that he has "not seen any individual that has a total length of four feet", realistically excludes *Pteronura brasiliensis*, in which even the smallest adults habitually exceed that length. Indeed Rengger's measurements of his "large male" are remarkably consistent with those of Azara's (who also measured his "largest" specimen), and both are of standard length for adult *Lontra longicaudis* (Table 1).

Nehring (1900) first proposed that *Lutra paranensis* was *Pteronura brasiliensis*, providing a rather selective case based largely on his own comparison of the description with a captive specimen of that species in the Berlin Zoological Gardens. He justifies the selectivity by invoking the idea that Rengger lost many of his specimens and thus his description (written later in Switzerland) may be considered only partly reliable (a thought process later echoed by Pohle (1919)). This is somewhat true, and there are elements of his description that suggest it is partly composite, but it is possible to mitigate this effect by examining the level of detail provided in the different parts of the description. It would seem reasonable for example that a high level of detail or the provision of measurements in the description of characters would be reflective of greater accuracy and not memory, whilst limited or vague description might theoretically be of questionable reliability, or even inaccurate; however, such an approach is subjective and open to dispute. As if to

demonstrate this, Nehring (1900) cherry-picks the characters consistent with the specimen of *Pteronura* he had at hand, and contrives rejection of anything that is inconsistent with it as an artefact of Rennger's allegedly faulty memory. Notably the author makes no direct comparison of the description with specimens of *Lontra longicaudis*.

For the most part Rennger's (1830) description of the animal is extremely detailed and, if taken to apply to *L. longicaudis*, accurate; Nehring (1900) does the author a disservice by implying that such significant portions of the description are embellished or erroneous. Below I discuss the strength of Nehring's arguments.

Size (Paragraphs 5 and 12): Nehring (1900) notes the significant difference in size between *L. paranensis* and *P. brasiliensis*, but adds that that the measurements for Rennger's (1830) "large male" are comparable to the size of his female *P. brasiliensis*, an inconsistency that he explains away as potentially a product of immaturity of the male. However, Rennger specifically referred to this specimen as a large male, there being no obvious need to do so unless this was in fact true. Rennger's (1830) measurements are also, importantly, perfectly consistent with a large male *Lontra longicaudis* (Table 1).

Face (Paragraph 8): Nehring's (1900) claim that Rennger's statement that "the face occupies only a quarter" of the head is consistent with *Pteronura* is not borne out by skulls (assuming for the sake of argument that measurement of the "face" is from the tip of the snout to the zygomatic process). In fact the face of *Pteronura* occupies a significantly greater portion of the head than it does in *Lontra*, representing approximately a third of the skull in the former, and much closer to a quarter in the latter. In a skin specimen of *Lontra longicaudis* (CZPLT-M-515) the "face" (measured externally from the tip of the snout to the posterior border of the eye) was 38 mm, whilst the head length (tip of the snout to the occiput) was 148 mm: this gives a ratio extremely close to a quarter.

Feet (Paragraph 8): Nehring (1900) simply states that the description of the webbing is consistent with *Pteronura*, but offers no further discussion. In fact this is untrue. Rennger states: "The toes are connected by a thick web which leaves the last phalanx free, and even reaches to the nail on the outermost toe". In *Pteronura* the webbing is complete and reaches the base of the nail between all toes, whilst the webbing in the three Paraguayan specimens of *Lontra longicaudis* examined is consistent with Rennger's description. Nor is there any reference in Rennger to the conspicuously "oversized" feet of *Pteronura*. Although the claws are described as "hardly bent", this does not mean that the claws are not bent at all and the extent of bending can only be guessed at because Rennger does not clarify with what kind of bent claw he is comparing his otter. Certainly, compared with the claws of certain felines with which the present author is familiar, the claws of *L. longicaudis* may be understood to be "hardly bent".

Pelage (Paragraph 2): Nehring (1900) claims that Rennger's description of the texture of the coat is consistent with *Pteronura* but provides no supporting data. However *Pteronura* is described in the modern literature as having the fur composed mainly of short, velvety guard hairs of approximately 8 mm length and virtually no underfur (Ihering, 1893; Foster-Turley et al., 1990; Carter and Rosas, 1997). Rennger makes specific reference to a woolly underfur of 6 lines (13.25 mm) in length, with bristled guard hairs one line longer (15.46 mm). The pelage of *Lontra longicaudis* has guard

fur length of approximately 14 mm and abundant underfur, this being consistent with that of the description of Rengger (Table 1).

Nose (Paragraph 8): Images of the rhinarium of *Lontra longicaudis* and *Pteronura brasiliensis* are provided by Foster-Turley et al. (1990) on pages 101 and 112 respectively. The description of the shape of the nostrils and valves is clearly consistent with that of *L. longicaudis*. Furthermore a naked septum is present in Paraguayan *Lontra longicaudis* (Figure 1), with *Pteronura* notable for its fully-furred nose (Ihering, 1893; Noonan et al., 2017). In order to explain away this inconsistency with *Pteronura* Nehring (1900) suggested that Rengger's captive animal may have rubbed its own nose bare whilst living in his apartment (Nehring, 1900), whereas Pohle (1919) arbitrarily elected to put this down to Rengger's by now infamous failing memory. The same supposition was repeated by Harris (1968). All authors ignored the fact that Azara (1801) also described the same bare nose for his "Nutria".



Figure 1. Muzzle of Paraguayan specimen CZPLT-M-515 showing naked septum.

Ear (Paragraph 8): Rengger described the ear pinna of his specimen as having a rounded edge. Though the ears of *Pteronura* are more rounded than those of *L. longicaudis* (which are commonly referred to as "pointed"), both species have a rounded edge to the pinna (Figure 2).

Molars (Paragraph 9): Nehring (1900) was of the opinion that more data were required in order to evaluate the importance of the number of molars reported by Rengger, adding that his female *Pteronura* possessed four upper molars. In fact the first premolar is extremely small in both species, being situated on the internal side of the canine where it is not visible externally, and indeed is sometimes even absent (Ihering, 1910; Husson, 1978). There is no diagnostic value in the number of molars. Both *Pteronura* and *Lontra longicaudis* share the same dental formula of $i3/3, c1/1, p4/3, m1/2 = 36$ (Larivière, 1999, Noonan et al., 2017).



Figure 2. Ear of Paraguayan specimen CZPLT-M-515 showing rounded edge.

Tail (Paragraphs 8 and 14): The crux of Nehring's argument rests on the description of the flattened tail and rounded shape to its tail tip, to which he affords great weight. It is true that the description of a compressed, broad tail with rounded end is more consistent with *Pteronura* than *Lontra*. The tail of *Lontra* is more cylindrical (though somewhat flattened), broad at the base and tapers to a point. What is notable about the reference to the tail however is the lack of detail Rengger provides on what might be considered to be an important diagnostic character. Notable too is the omission of mention of the ridged edges of the tail present in *Pteronura* (Gray, 1868). If one were to look for circumstantial indications of text that may have been added from memory as Nehring infers, then this would arguably be a case where the level of precision is inconsistent with that of the rest of the text.

*Comparison with *Lutra lutra** (Paragraph 8): Rengger (1830) notes the similarity of his animals to the Eurasian Otter *Lutra lutra* (Linnaeus, 1758). The much larger and quite differently-shaped *P. brasiliensis* cannot be said to invoke any such similarity.

Omissions: There is no mention in the texts of Azara or Rengger of the conspicuous tufts of hair on the ankles of *Pteronura brasiliensis*, a character that is absent in *Lontra longicaudis* (Gray, 1868; Noonan et al., 2017).

Ecology (Paragraphs 14-22): The description of the ecology of the species is consistent in some key characters with *Pteronura brasiliensis*, most notably the description of sociality, reproduction and the den. It seems likely that this section of the description is composite, but as the type series of *L. paranensis* includes all the specimens referred to by the author, including those of Azara (Art. 72.4.1; ICZN International Code of Zoological Nomenclature), and all of the described specimens are identifiable as *L. longicaudis*, there is little to be gained in nomenclatural terms by

speculating on the possible composite nature of observed behaviours, especially when these originated in most cases from unknown sources. The possible composite nature of this part of the description is of little consequence.

CONCLUSION

L. paranensis Rengger, 1830 was considered the valid name for the smaller otter species inhabiting the Paraguay and Paraná river basins at the turn of the 19th to 20th centuries by Bertoni (1914, 1939) and Ihering (1893, 1910). It was employed because of its priority over *Lutra platensis* Waterhouse, 1838: 21, another name which had been applied earlier to the same taxon in the most influential works of the 19th Century (Hensel, 1872: 87; Burmeister, 1879: 166; Cope, 1889: 141; Thomas, 1889: 199; Forsyth Major, 1897: 137; Trouessart, 1897: 286). There was in fact much debate over the specific limits within the genus at this time, complicated by an abundance of available names, a scarcity of specimens, and general morphological conservatism amongst otters coupled with great individual variation. Scientific names published in Olfers (1818) (including *Lutra longicaudis*) had until that point been overlooked, but were later listed and validated by Hershkovitz (1959). By the time this work was published however *L. paranensis* was already being widely misapplied to *Pteronura brasiliensis*.

The decision by Cabrera (1957) to follow Pohle (1919) in attaching the name *paranensis* to a supposed southern subspecies of *Pteronura brasiliensis* (with a restricted type locality of “Rio Paraná”) was perhaps most influential in cementing the incorrect usage. This is unfortunate given that no type specimen(s) survived for the taxon. Nor did Harris (1968), in a key work on the Lutrinae, question the conclusions of Nehring (1900) and Pohle (1919).

Today *Pteronura brasiliensis* is generally considered monotypic (Noonan et al. 2017), though the name *paranensis* has still been occasionally employed for southern populations (Duplaix, 1980; Chebez, 2008). Genetics do not however support any such subspecific separation (García et al., 2007). Furthermore, even if Rengger’s description could be fitted to a species of *Pteronura*, the degree of difference described by Rengger (1830) would be at the specific, and not the subspecific level. There is no doubt however that *Lutra paranensis* Rengger, 1830 when correctly applied, is a junior synonym of *Lontra longicaudis longicaudis* Olfers, 1818 and is available for application to that taxon. Given the clarity of this case I consider it would be not valid to declare a neotype (under Articles 75.1 and 75.3 of the ICZN (1999) International Code of Zoological Nomenclature): there is no ambiguity to be dispelled, merely a longstanding mistake in application to be corrected.

As an additional observation *Lutra paraguaensis* Schinz, 1821: 213, which was described as “Otter aus Paraguai” has also been placed in the synonymy of *Pteronura brasiliensis* since Thomas (1889) and Pohle (1919). Schinz (1831) includes *Lutra brasiliensis* in his work, and lists *L. paraguaensis* separately with the following brief description:

“Kleiner als der vorige, Pelz dunkel weich und glänzend. En Paraguai und am Plata Flusse”. (Smaller than the previous species. Fur dark, soft and shiny. In the Rivers Paraguai and Plate).

The previous species with which the “Otter aus Paraguai” is compared, and said to be smaller than, is “Wolfsotter” *Lutra lupina*. That species is described confusingly as “as large as a pointer (Hühnerhund)” and was also placed in the synonymy of *P. brasiliensis* by Thomas (1889) and Pohle (1919). Regardless of the vagaries of the description, an animal that is smaller than a Pointer dog is also smaller than an adult *Pteronura brasiliensis*. Furthermore the only otter species that shows the distribution provided of the Rivers Plate and Paraguai is *Lontra longicaudis* (Hunter and Barrett,

2011). No type of *L. paraguaensis* exists to my knowledge, and the description is obviously deficient. However whilst the description is inconsistent with *P. brasiliensis* it is broadly consistent with *L. longicaudis*, and it thus probably belongs in the synonymy of the latter.

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RÉSUMÉ

QUI EST *Lutra paranensis* RENGGER, 1830?

Décrit au Paraguay, *Lutra paranensis* Rengger, 1830 a longtemps été associée par des auteurs internationaux à la loutre géante *Pteronura brasiliensis*. Cependant, au début du XXe siècle, des auteurs régionaux sud-américains appliquèrent ce nom à la loutre à longue queue, *Lontra longicaudis*. La validité de chacune de ces positions a été évaluée en comparant la description des deux espèces et il s'avère en conséquence que le nom proposé, à savoir *L. longicaudis*, est correctement utilisé.

RESUMEN

¿QUÉ ES *Lutra paranensis* RENGGER, 1830?

Descrito de Paraguay, *Lutra paranensis* Rengger, 1830 ha sido por mucho tiempo asociado por autores internacionales con la Nutria Gigante *Pteronura brasiliensis*. No obstante, autores Sudamericanos trabajando en los primeros años del Siglo 20 aplicaban el nombre al Lobito del Rio *Lontra longicaudis*. Se examina la validez de ambas posiciones comparando la descripción con ambas especies, con la conclusión que la aplicacion correcta se refiere a *L. longicaudis*. Se declara un neotipo Paraguayo para *L. paranensis*, para fijar su utilización.